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BINOCULAR RIVALRY: A GATEWAY TO CONSCIOUSNESS

Hosted by
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BINOCULAR RIVALRY: A GATEWAY TO CONSCIOUSNESS

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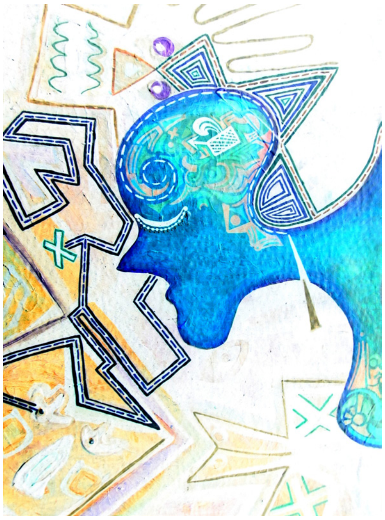

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Brain-mind problems like consciousness have been stimulating the interest of philosophers and scientists since the ancient times. In the last decades, the dramatic development of neuroscience has allowed studying such phenomena at several different levels – from single neurons to behavior. Binocular rivalry, a paradigm dissociating the sensory input from the conscious perception during dichoptic viewing of incongruent images, has been a celebrated example of such a tool. During the last century, empirical research on binocular rivalry contributed the first important insights into the neuronal mechanisms of subjective visual perception. Recent advances in brain imaging and electrophysiological recording/stimulating techniques as well as novel theoretical concepts and analytical methods could be exploited to expand our knowledge on this fascinating phenomenon of visual perception and elucidate the neural processes underlying visual consciousness. This Research Topic aims to bring together contributions that could expand the current frontiers of knowledge in binocular rivalry. In particular we would like to focus on reviews, hypothesis & theory or original research articles that specifically combine novel concepts, analytical tools and neurophysiological techniques with binocular rivalry. We expect that these contributions will a) integrate the vast knowledge already existing in the field b) formulate and, when possible, address questions under the light of recent methodological advances in neuroscience and c) provide a benchmark that will stimulate future cutting edge research.

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EDITORIAL
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Introduction to research topic – binocular rivalry: a gateway to studying consciousness

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In 1593, Neapolitan polymath Giambattista della Porta publicly lamented that he was unable to improve his impressive productivity (he had published in areas as diverse as cryptography, hydraulics, pharmacology, optics, and classic fiction). Della Porta was trying to read two books simultaneously by placing both volumes side-by-side, and using each eye independently. To his great surprise, his setup allowed him to only read one book at a time. This discovery arguably marks the first written account of binocular rivalry (Wade, 2000) – a perceptual phenomenon that more than 400 years later still both serves to intrigue as well as to illuminate the limits of scientific knowledge. At first glance, binocular rivalry is an oddball. In every day vision, our eyes receive largely matching views of the world. The brain combines the two images into a cohesive scene, and concurrently, perception is stable. However, when showing two very different images (such as two different books) to each eye, the brain resolves the conflict by adopting a "diplomatic" strategy. Rather than mixing the views of the two eyes into an insensible visual percept, observers perceive a dynamically changing series of perceptual snapshots, with one eye's view dominating for a few seconds before being replaced by its rival from the other eye. With prolonged viewing of a rivalrous stimulus, one inevitably experiences a sequence of subjective perceptual reversals, separated by random time intervals, and this process continues for as long as the sensory conflict is present.

This Frontiers Research Topic focuses on contemporary research on binocular rivalry and related visually multistable phenomena, covering a large variety of topics and techniques. It contains several reviews by leading experts in the field that provide perspectives on important insights that were gained during the past decades of research on rivalry, as well as a focus on outstanding conceptual, methodological, and empirical questions. Additionally, this collection includes research articles using psychophysical, computational, developmental, and imaging techniques that address fundamental questions related to the nature, origins, and neural implications of binocular rivalry. A short overview of the work is outlined in the following paragraphs (please refer to the original articles for further details).

Introducing a novel computational model based on a non-linear algorithm, Lehky (2011) suggests that – at least theoretically – each eye's view can be extracted following binocular integration at later processing stages of the visual system, which could explain some apparent conflicts between previous psychophysical and neurophysiological results. An alternative model that employs an attractor-based neural network architecture previously used to understand working memory, attention, and decision making is presented by Theodoni et al. (2011). One of the hallmarks of binocular rivalry is its unpredictable switching between each eye's views. Kang and Blake (2011) review our current understanding of these dynamic processes, and provide a new framework that integrates the empirical data. Single neuron recordings show perceptual modulation to binocular rivalry as early as V1 (Leopold and Logothetis, 1996; Keliris et al., 2010), ranging all the way to the frontal lobe (Panagiotaropoulos et al., 2012). The long-ranging effects of the neuronal processes that give rise to binocular rivalry can also be measured on the scalp electroencephalogram (EEG). Recent developments in this field, using a combination of new experimental and analytical approaches are reviewed by both Pitts and Britz (2011) as well as Kornmeier and Bach (2012), linking binocular rivalry to other multistable visual phenomena such as the famous "Necker Cube." Wolf and Hochstein (2011) present evidence that binocular rivalry alternations can be modulated by high-level, semantic influences that might originate beyond the visual system. Paffen and Alais (2011) add to the discussion of high-level influences during binocular rivalry by reviewing the most recent literature on attentional influences on perceptual alternations, concluding that high-level selection processes can influence, but are not required to explain the temporal dynamics of binocular rivalry. Dieter and Tadin (2011) provide a complementary review of the interaction between selective attention and binocular rivalry, and place the results in a unifying framework that is based on the classic biased competition model (Desimone and Duncan, 1995). Focusing on low-level influences, on the other hand, Roumani and Moutoussis (2012) review literature on the role of visual adaptation for binocular rivalry alternations. While binocular rivalry is typically studied using artificial stimuli under laboratory conditions, Arnold (2011a,b) and O'Shea (2011) engage in a debate on how often binocular rivalry occurs under natural viewing conditions that ends in mutual agreement about the special nature of perceptual alternations. Alais and Parker (2012), on the other hand, demonstrate that even spatially matched images in each eye can rival for perceptual dominance, as long as their temporal modulation is sufficiently different. Andrews and Holmes (2011) revisit the question whether binocular rivalry is mutually exclusive with visual fusion between the two eyes, and present evidence that it is possible to extract stereoscopic depth from stimuli that are perceptually suppressed. Hudak et al. (2011) examine developmental differences of binocular rivalry by measuring its perceptual dynamics in pre-adolescent children. Fahle et al. (2011) combine tactile perceptual responses of subjects with measurements of pupil dilation to demonstrate that rather than constituting an all-or-none event; the internal decision about a perceptual transition seems to build slowly over time. Stuit et al. (2011) present data that suggests additive Gestalt-like grouping effects between binocular rivalry stimuli within and between hemispheres. In the same vein of testing visual interactions between binocular rivalry and other visual phenomena, Masuda et al. (2011) demonstrate that binocular rivalry suppression of key stimulus parts diminishes other visual illusions such as the Craik-O'Brien-Cornsweet effect. Rather than focusing on what is perceptually dominant during binocular rivalry, Zadbood et al. (2011) study what it takes to notice the physical removal of a stimulus that is perceptually suppressed. They find that the result depends on the specific visual feature under scrutiny (Zadbood et al., 2011), suggesting that two equivalent perceptual states can be accompanied by distinct neural events (see also Maier et al., 2007). Denison et al. (2011) tests the influence of perceptual history on binocular rivalry, and find that the visual system favors patterns for perceptual dominance if they are predicted by prior stimulation. Pelekanos et al. (2011) also find an effect of stimulus history that they liken to high-level modulation of perceptual selection. Stanley et al. (2011) review data on the initial ("onset") stage of binocular rivalry that follows immediately after the presentation of binocular conflict. Their overview demonstrates that the initiation of binocular rivalry exhibits a variety of idiosyncratic properties that are absent during the ongoing perceptual fluctuations that follow (Stanley et al., 2011). Stienen and De Gelder (2011) present data that suggests that social cues such as fear expression can influence perceptual dominance during rivalry. Stein et al. (2011) investigate in the time it takes for visual stimuli to reach perceptual dominance under continuous flash suppression (Tsuchiya and Koch, 2005), a class of phenomena related to binocular rivalry. They caution against potential over-interpretation of the resulting data for inferences on the brain's processing of unconscious stimuli (Stein et al., 2011). Genç et al. (2011) use diffusion tensor imaging (DTI) to demonstrate a direct relationship between anatomy of transcallosal connections and the perceptual dynamics of rivalry transitions. A refreshing new perspective gets provided by Miller et al. (2011), who suggest that some behavioral characteristics of the fruit fly resemble rivalry-like state changes in humans.

The reviews and empirical articles collected in this research topic demonstrate the many methodological and conceptual advances that have been made by the ever-growing field. The profound insights presented here do not only reflect on our understanding of binocular rivalry and its implications for visual awareness, perceptual organization, and binocular vision, but also have profound implications for our understanding of visual function in general.

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Binocular rivalry produced by temporal frequency differences

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When the eyes view images that are sufficiently different to prevent binocular fusion, binocular rivalry occurs and the images are seen sequentially in a stochastic alternation. Here we examine whether temporal frequency differences will trigger binocular rivalry by presenting two dynamic random-pixel arrays that are spatially matched but which modulate temporally at two different rates. We found that binocular rivalry between the two temporal frequencies did indeed occur, provided the frequencies were sufficiently different. Differences greater than two octaves (i.e., a factor of four) produced robust rivalry with clear-cut alternations similar to those experienced with spatial rivalry and with similar alternation rates. This finding indicates that temporal information can produce binocular rivalry in the absence of spatial conflict and is discussed in terms of rivalry requiring conflict between temporal channels.

Keywords: binocular rivalry, temporal channels, temporal frequency, form, motion

INTRODUCTION

Binocular rivalry occurs when two sufficiently different images are presented to each eye. This prevents binocular fusion of the two images and triggers a stochastic alternation between the monocular images (Blake and Logothetis, 2002; Alais and Blake, 2005; Alais, 2011). This perceptual alternation is of considerable interest to visual neuroscientists because despite two distinct images entering the visual system, only one of them reaches conscious perception. Generally, binocular rivalry is induced by presenting pairs of images that differ in terms of a spatial property, typically orientation, but rivalry can also be triggered by interocular differences in spatial frequency, form and color (Yang et al., 1992; Kovacs et al., 1996; Tong et al., 1998; Alais and Melcher, 2007). In this paper, we will focus on the temporal dimension and examine whether binocular rivalry can be elicited by interocular differences temporal frequency differences.

The easiest way to introduce temporal modulations is to use motion and it has long been known that motion can greatly influence rivalry. For example, if one stimulus is set in motion, it will strongly predominate over a static pattern (Breese, 1899; Walker and Powell, 1979; Blake et al., 1985). Flickering a rival target too will enhance its predominance over the other target (Blake and Fox, 1974). Rivalry will also occur when both rival targets are motion stimuli, provided they drift in different directions or at different speeds (Fox et al., 1975; Wade et al., 1984; Blake et al., 1985; Wiesenfelder and Blake, 1990; Alais and Blake, 1998; Blake et al., 1998; Nguyen et al., 2003; Alais and Parker, 2006). A general limitation of this literature is that form and motion are often confounded because the motion stimuli also differ in spatial form (e.g., drifting orthogonal gratings). A further problem is that motion is a step removed from the basic mechanisms of temporal processing, since visual temporal filters logically precede the computation of speed and direction (Reisbeck and Gegenfurtner, 1999; Priebe et al., 2006).

Orthogonally oriented drifting gratings are commonly used to elicit motion rivalry (Alais and Blake, 1998; Andrews and Blakemore, 2002). With such stimuli, it could well be the orientation conflict that is responsible for initiating rivalry, rather than the motion. Similarly, form differences between opposite-throw spirals (Nguyen et al., 2003) and radial versus concentric patterns (Wade et al., 1984) could provide the image conflict that provokes rivalry rather motion conflict. The same can be said of orthogonally drifting random-dot patterns (Blake et al., 1998; van de Grind et al., 2001) because translating random-dot patterns create motion streaks (Geisler, 1999) when drifting fast, effectively transforming them into a type of grating. Recent studies have confirmed that “motion streaks” created by translating random-dot patterns do activate orientation-selective mechanisms (Apthorp et al., 2010, 2011) and do produce an orientation-specific suppression in binocular rivalry (Apthorp et al., 2009).

The seeming inevitability of the form/motion confound has led some researchers to conclude that it is form conflict that triggers rivalry and that rivalry between motion signals does not occur at all (Ramachandran, 1991; He et al., 2005). It is worthwhile resolving this question because if rivalry can occur between temporal modulations, then the temporal dimension must have an input into the binocular matching process. To verify this would require rival stimuli that differ only in the temporal dimension and which still elicit rivalry alternations. One attempt to do this tested whether rivalry would occur between motion aftereffects produced by adaptation to orthogonal translating gratings (Blake et al., 1998). Testing the aftereffects with a binocularly-viewed dynamic test pattern did elicit rivalry alternations. Against this, however, another study using full-field flicker found that different temporal modulation rates in each eye failed to elicit any rivalry at all (O'shea and Blake, 1986).

Complicating the debate further are findings showing that motion and form can rival independently (Andrews and Blakemore, 1999; Alais and Parker, 2006). In Andrews and Blakemore's study, orthogonally drifting gratings were presented dichoptically and it was found that the two orientations rivaled reliably but the motions did not. On about 50% of trials, the single grating that happened to predominate at a given moment did not drift orthogonally to its orientation but obliquely—in the direction expected if both motions were integrated (inconsistent with one motion being suppressed). Similar results have been reported by another group (Cobo-Lewis et al., 2000). It has also been found that overlaying two orthogonally drifting gratings of low spatial frequency and viewing them through a binocular grid (allowing a fine-scale binocular match) will completely prevent rivalry from occurring (Carlson and He, 2004). In such a case, a dichoptic plaid is perceived through the apertures of the grid which moves in the global motion direction defined by the "intersection of constraints" rule (Adelson and Movshon, 1982; Alais et al., 1994).

Overall, it is not clear from the literature whether interocular temporal frequency differences elicit rivalry. The presence of form conflict clearly represents a confound in many rivalry studies using motion stimuli, and using motion to assess the role of temporal frequency is not the most direct approach. An ideal stimulus would contain temporal modulations and no form conflict. The full-field flicker stimulus of O'shea and Blake (1986) comes close to this, but it contains no contrast—the primary attribute driving the response level of early visual neurons. In the present study, we will examine whether interocular temporal differences elicit rivalry using a novel stimulus: a random dynamic-noise sequence that is temporally filtered into narrow temporal pass-bands. Being spatially random, the stimulus contains no coherent form to confound the results and it modulates temporally without translating in any direction, removing the motion direction confound. It also contains visual contrast to effectively drive visual neurons and allows precise control over temporal frequency, with the advantage that spatial frequency can be filtered independently.

To preview the results, we find that interocular temporal frequency differences do elicit rivalry alternations—very reliably for differences greater than two octaves (Experiment 1)—and rivalry alternations experienced for large temporal frequency differences have a similar character to those elicited in spatial rivalry (e.g., orthogonal gratings), with perceptual alternations occurring crisply every two seconds or so. When the modulation rates are too close to engage in rivalry, observers perceive the average temporal frequency and do not perceive temporal beating at the difference frequency (Experiment 2). When the modulation rates do differ enough to produce robust rivalry, observers can accurately select the perceptually alternating frequencies from a range of non-rivaling comparison frequencies (Experiment 3). Finally, we show that measures of alternation dynamics for robust temporal frequency rivalry are comparable to those of spatial rivalry (Experiment 4).

GENERAL METHODS

SUBJECTS

The first two authors served as subjects in all experiments, together with two or three naïve observers. All had normal stereo acuity and normal or corrected visual acuity.

STIMULI

To make the temporally filtered random dynamic dot sequences (see **Figure 1**), 100 random-dot noise patterns were generated. Each noise pattern was 128 by 128 pixels with a 2-pixel check size and subtended 2.5° of visual angle at the viewing distance of 57 cm. Playing these images as an animation would produce standard dynamic random noise with a very broad (white) frequency spectrum. Our approach in this paper was to filter these image sequences in the temporal frequency domain to produce narrow bands of temporal frequencies. Before temporal filtering, the stack of 100 noise images was duplicated so that the left and right eyes received spatially identical noise sequences. The image stack was then Fourier transformed and filtered in frequency space using a three-dimensional mask (x, y, t) in which the height of the image stack (100 images, in this case) represents the time dimension. The video monitor had a vertical scan rate of 85 Hz and noise images were updated every second refresh to produce an image update rate of 42.5 Hz and therefore a maximum achievable temporal frequency of 21.25 Hz.

The available temporal frequency range of 0 to 21.25 Hz was filtered into six narrow temporal pass-bands, each with a full-width of 0.33 octaves. The pass-bands were octave multiples of each other and had center frequencies of: 0.59, 1.18, 2.37, 4.73, 9.47 and 18.93 Hz. Since the time dimension is orthogonal to the (x, y) plane, spatial, and temporal dimensions could be filtered independently. The spatial filtering for all conditions in these experiments was band-pass with a full-width of 1 octave and a center frequency of 1.13 cyc/deg so that the only difference between left- and right-eye stimuli was temporal frequency. After spatiotemporal filtering the images were back transformed from the frequency domain and normalized to the full luminance range of the monitor to maximize stimulus contrast.

All stimuli were generated using the psychophysics toolbox (Brainard, 1997; Pelli, 1997) for Matlab on a G4 Macintosh computer and were presented on a 22″ Phillips CRT monitor (1024 × 768 resolution) with a refresh rate of 85 Hz. Stimuli were viewed through a mirror stereoscope, with a black square frame surrounding the circular stimulus apertures to aid binocular fusion. A small fixation cross was positioned in the center of the stimuli to help minimize eye movements. The average luminance of the stimulus arrays was 34.7 cd/m2 and the background region of the monitor was set to this value.

EXPERIMENT 1

The aim of the first experiment was twofold: to determine whether dichoptic, spatially matched stimuli modulating at different temporal rates elicit rivalry alternations, and to find which frequency pairs rival most vigorously. Subjects therefore observed all pairings of the six temporal frequencies for 15 s and indicated whether at least one rivalry alternation was perceived.

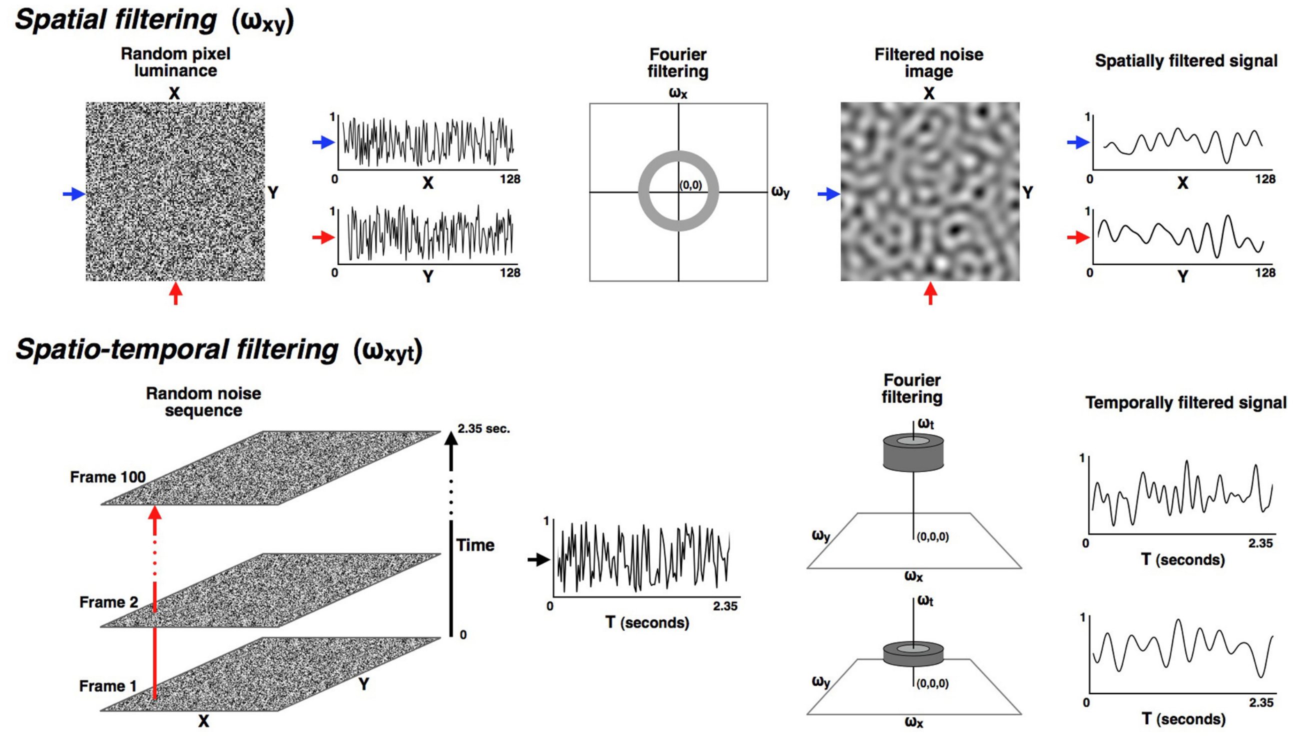

FIGURE 1 | All stimuli were made from a random dynamic noise sequence that was filtered in both the spatial and temporal dimensions into narrowly defined pass-bands. The upper part of the figure illustrates the spatial filtering. All stimuli in these experiments were isotropically filtered into a fixed spatial pass-band ranging from 0.8 to 1.6 cyc/deg. The lower row illustrates how the noise sequences were filtered in the temporal dimension so that the modulation rate over time could be carefully controlled. Six narrow temporal pass-bands were used in these experiments, with each band having a full-width of 0.33 octaves (where octaves are calculated as the base-two logarithm of the ratio of the upper and lower cut-off frequencies). The pass-bands were all separated by one octave and had center frequencies of: 0.59, 1.18, 2.37, 4.73, 9.47, and 18.93 Hz. Since the time dimension is orthogonal to the (x, y) plane it could be manipulated without altering the spatial frequency range, which remained constant at 0.8 to 1.6 cyc/deg for all conditions.

Before the experiment we ran a pilot to determine whether the various temporal frequency pairings needed to be equated for stimulus strength (Levelt, 1965). An earlier rivalry study using uniform fields of flicker showed that high temporal frequencies tend to predominate over lower ones (O'shea and Blake, 1986). We therefore measured predominance ratios of various temporal frequency combinations at four different contrast levels. If a strong tendency for high-frequency stimuli to predominate is observed, reducing its contrast will be an effective means to weaken it and equate the two stimuli.

METHODS

The pilot experiment used the fastest modulation (18.93 Hz) paired with four slower modulations (4.73, 2.37, 1.18, and 0.59 Hz). Four observers viewed the four stimulus pairs for 2 min while tracking perceptual alternations between fast and slow modulations. Observers did three repetitions of each pair and predominance ratios (total time the fast image was visible divided by the total time the slow image was visible) were averaged. Group means are shown in **Figure 2**. Observers repeated this procedure four times with the high temporal frequency stimulus (18.93 Hz) taking one of 4 contrast levels (0.4, 0.6, 0.8, and 1.0)

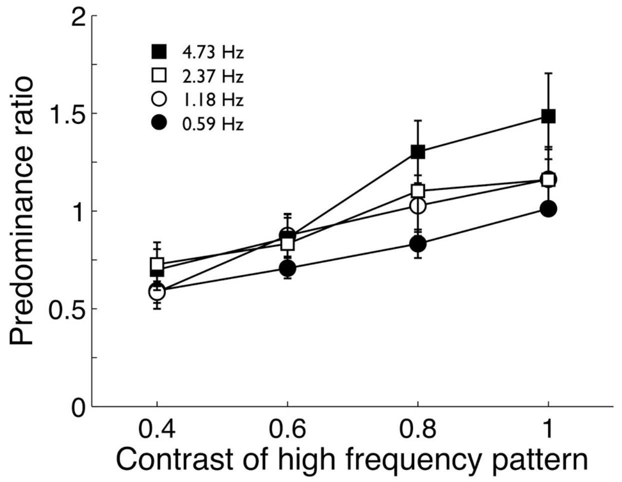

FIGURE 2 | Pilot data (group mean; $n = 4$) from Experiment 1 showing the predominance ratio of a high temporal frequency pattern (18.93 Hz) to various lower temporal frequency patterns. The tendency of the high frequency pattern to predominate over lower frequencies declined as its contrast was reduced. Error bars show ±1 standard error of the mean.

in a randomized order. The lower frequency stimuli were fixed at maximum contrast.

The stimuli in Experiment 1 are described in General Methods and **Figure 1**. Participants did four sessions of 105 trials each. In each session, the full set of 15 frequency combinations was presented, plus six kinds of catch trial (one for each of the 6 temporal frequencies) in which identical temporal frequencies were paired to verify that participants were responding correctly to perceived alternations. These 21 stimulus combinations were repeated five times in a session, with each session repeated four times. Trials were self-paced and the order within a session was completely randomized. Participants were instructed to press a key if they saw a perceptual alternation in modulation rate (from fast to slow, or vice versa). If a key was pressed to indicate rivalry, participants were taken straight to the next trial, otherwise the trial continued for the full 15 s.

We also ran a control condition to see whether the static frames would elicit rivalry. The reason is that although the left- and right-eye patterns are made from matched noise patterns, once temporally filtered they modulate at different rates and the relative phase between them varies periodically. Using the same method just described, five subjects made 16 judgments of rivalry incidence for static images selected to have a phase difference of either 90°, where the modulations are orthogonal (i.e., independent), or 180°, where the patterns are maximally different (i.e., anti-phase). On each trial, one eye viewed a frame selected at random from the modulation sequence and the other viewed a subsequent frame corresponding to either 90° or 180° phase offset.

RESULTS: PILOT DATA

Pilot data showed the high-frequency stimulus did tend to predominate over the lower frequency patterns when both had maximum contrast (**Figure 2**). As expected, reducing the contrast of the high-frequency stimulus reduced it predominance, confirming O'Shea and Blake's (1986) finding. At maximum contrast, none of the stimulus pairs produced extremely biased predominance ratios and none were greater than 2:1 and it was decided to maintain all stimuli at maximum contrast.

RESULTS: EXPERIMENT 1

The data from Experiment 1 are shown in **Table 1** which shows the incidence of rivalry for each temporal frequency pair. The dark oblique shows cells with a temporal frequency difference of one octave, and the light oblique shows a three-octave difference. Temporal frequency pairs on or above the light shaded oblique (i.e., three-, four-, and five-octave differences) all produced reliable rivalry alternations. The average rivalry incidence for a three-octave difference was 0.87, and ~1.0 for four- and five-octave differences. Overall, rivalry incidence increased strongly with temporal frequency difference $F_{(4,\ 12)} = 89.325$, $p < 0.001$. As the data on the major oblique show, subjects never falsely reported rivalry alternations on the catch trials.

The main effect of temporal frequency difference on rivalry incidence (average of each oblique in **Table 1**) is shown in **Figure 3A**. Contrasts testing for trends revealed a significant linear trend, [$F_{(1,\ 3)} = 209.69$, $p = 0.001$], and quadratic trend, [$F_{(1,\ 3)} = 62.108, p = 0.004$]. **Figures 3B,C,D** plot the one-, two-, and three-octave obliques from **Table 1**, showing that the effectiveness of a given temporal frequency difference in eliciting rivalry varies along the temporal frequency dimension. The effect of temporal frequency difference was significant for two octaves, [$F_{(3,\ 12)} = 33.732$, $p < 0.001$] (**Figure 3C**) and three octaves, [$F_{(2,\ 8)} = 5.580, p < 0.05$] (**Figure 3D**). Significance in this case indicates rivalry incidence for a given difference depends on the frequencies making up the pair. **Figures 3C,D** show that a given frequency difference is more effective when located at the higher end of the frequency spectrum. There were no significant effects for the one-octave difference, [$F_{(4,\ 16)} = 2.530$, $p = 0.081$], or four-octave difference, [$F_{(1,\ 4)} = 2.667, p = 0.178$].

Table 1 | Proportion of trials yielding a perception of binocular rivalry for various temporal frequency combinations.

		Temporal frequency 1 (Hz)					
		0.59	**1.18**	**2.37**	**4.73**	**9.47**	**18.93**
Temporal frequency 2 (Hz)	**0.59**	0	0.01	0.13	0.69	0.98	1.00
	1.18		0	0.05	0.43	0.95	1.00
	2.37			0	0.15	0.89	0.98
	4.73				0	0.23	0.87
	9.47					0	0.11
	18.93						0

Data are group means averaged across five observers. Along each diagonal, the cells are equally separated in temporal frequency when expressed in terms of octave differences (i.e., the ratio of the two frequencies expressed as a base-two logarithm). The dark gray shading shows frequency combinations differing by one octave, and the light gray shading represents frequency combinations differing by three octaves.

Although each eye's temporal modulation were made from identical noise images, they modulate at different rates and so their relative phases vary over time. The horizontal lines in **Figure 3** plot group mean results from the control conditions in which we measured rivalry incidence for two static images taken from different points of the modulation sequence to determine if phase differences contribute to temporal frequency rivalry. We chose two phase offsets, 90° (where the motion sequences are independent, in cosine and sine phase) and 180° (where the sequences are in anti-phase and are maximally different). Sustained viewing for 15 s of the static phase differences did produce alternations, although much less than the two- and three-octave conditions that rivaled vigorously (**Figures 3C,D**).

DISCUSSION

These data establish that differences in temporal modulation rates between spatially matched patterns do indeed engage in binocular rivalry. Overall, the most straightforward summary of the data is that a temporal frequency difference of at least two octaves is needed to generate temporal frequency rivalry (**Figure 3A**). This is surprisingly large, especially when compared to rivalry between spatial frequency or orientation differences. This probably reflects the fact that there are only two (or three) temporal frequency channels in the visual system (Mandler and Makous, 1984; Anderson and Burr, 1985;

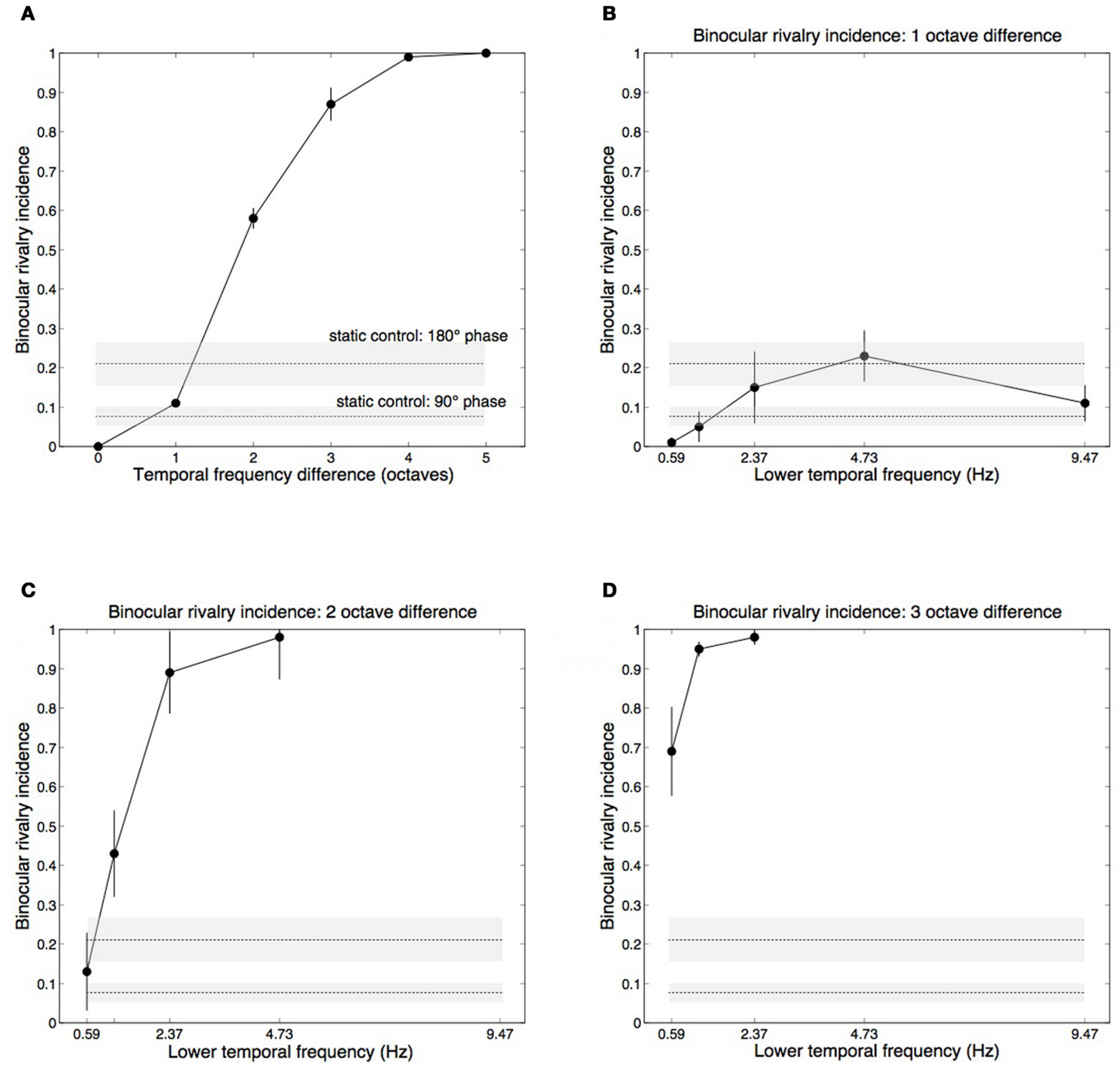

FIGURE 3 | Group mean data with ±1 standard errors from Experiment 1 showing rivalry incidence for various temporal frequency combinations. Horizontal dashed lines show results from a static control condition (see Methods), with ±1 standard error shading. **(A)** Rivalry incidence increases with temporal frequency difference. The data here are means of the diagonals in **Table 1**. **(B)** Rivalry incidence for one-octave temporal frequency differences. The x-axis shows the lower frequency of the two rivaling frequencies. One-octave differences are generally not sufficient to trigger rivalry. **(C)** Two-octave frequency differences produce robust rivalry except at the low end of the temporal dimension. **(D)** Three-octave frequency differences produce robust rivalry at any point of the temporal dimension.

Hammett and Smith, 1992; Hess and Snowden, 1992; Cass and Alais, 2006), whereas spatial frequency and orientation channels are more numerous, perhaps numbering six to eight (Graham, 1972; Stromeyer and Julesz, 1972; Braddick et al., 1978; Graham, 1989), and are therefore more tightly tuned than temporal frequency channels. This is taken up in the "General Discussion," but the clear implication is that rivalry occurs when the stimuli are sufficiently different to activate separate channels. In the temporal domain, this requires a rather large difference of about two octaves, whereas the narrower orientation and spatial frequency channels require only a one-octave difference to produce rivalry (Blakemore, 1970; Braddick et al., 1978; Yang et al., 1992).

Although a two-octave temporal frequency difference will generally elicit binocular rivalry, sheer frequency difference does not entirely explain the data in **Table 1**. There is a dependence on where a given frequency difference is located along the temporal frequency dimension. Looking at **Figure 3C**, the higher frequency pairings were more likely to produce rivalry alternations. This tendency is also present in the three-octave data

(**Figure 3D**) where rivalry was less likely for 4.73 vs. 0.59 Hz than for the same frequency difference located higher on the temporal frequency dimension. This interaction most likely arises from the location and intersection point of the underlying temporal channels.

Most investigations of temporal channels have revealed a broad, low-pass channel at the low end of the frequency spectrum with a band-pass channel at the high end (Anderson and Burr, 1985; Hess and Snowden, 1992; Snowden et al., 1995; Cass et al., 2009b). There is also some evidence for a second, higher band-pass filter in a three-channel model (Mandler and Makous, 1984; Hess and Snowden, 1992; Johnston and Clifford, 1995). In either case, the low-pass channel crosses over the high bandpass channel at about 6–8 Hz. **Table 1** shows that rivalry incidence is highest when the two frequencies span this crossover point. This is true for the four- and five-octave differences (which average 0.99 incidence), and for the two highest pairs on the three-octave oblique (which average 0.97). Rivalry incidence drops for the lowest pair of three-octave differences because 4.73 and 0.59 Hz both lie on the low side of the crossover point. Finally, in the two-octave conditions (**Figure 3C**), the two upper frequency pairs span the 6 Hz crossover point and elicit high rivalry incidence (averaging 0.88) while the two lower frequency pairs do not. In sum, rivalry occurs when the stimuli are sufficiently different to activate separate temporal channels.

Finally, using relative dominance as an index of stimulus strength (Levelt, 1965), the pilot experiment showed that effective stimulus strength tended to increase with temporal frequency (**Figure 2**). Yet, even when the high-frequency stimulus had maximum contrast, its tendency to predominate was not particularly strong, peaking at about 1.5:1 against the 4.73 Hz stimulus and was not large enough to need correction through contrast adjustment. The reason why the high-frequency modulation predominated more over the 4.73 Hz modulation than the lower rates is not clear. One possibility is that mechanisms signaling static form may also be able to track slow modulations, adding strength to the low temporal channel's response. Overall, however, the lack of strongly skewed predominances confirms that any failures to report rivalry alternations in the 15 s observation period were not due to a strongly dominant pattern assuming dominance for the entire observation period. We therefore presented all stimuli in the following experiments at maximum contrast.

The dynamics of temporal frequency rivalry were not formally measured in this experiment (see Experiment 4 for alternation dynamics), however, observers' subjective experiences were that differences of three or four octaves produced robust rivalry alternations that were typical of those elicited by large (static) orientation differences, with perceptual alternations occurring crisply every one to two seconds. Two octave differences rivaled well if the frequencies were both high, but if both were low rivalry was slow in the manner of rivalry between low contrast stimuli. Frequency differences of one octave seldom produced perceptual alternations, and did not exceed the level of alternations produced by the static control conditions. The control condition, however, probably overestimated the contribution of phase-related rivalry because the phase differences were presented for the entire 15 s observation period, whereas in the temporal frequency rivalry conditions the phase relationship was cyclic, moving in and out of phase periodically.

In sum, temporal frequency rivalry does occur when frequencies differ by two octaves or more, and the control data show that this cannot be attributed solely to periodic phase differences.

EXPERIMENT 2

Experiment 1 established that interocular differences in temporal frequency do elicit reliable rivalry alternations, provided the frequencies differ by at least two octaves. Experiment 2A will measure increment thresholds for the temporal frequencies used in Experiment 1 to verify that perceptual alternations between temporal frequencies with a one-octave difference would have been perceptible. Experiment 2B is a temporal frequency matching experiment that quantifies what frequency is perceived when the temporal frequency difference is too small to produce rivalry. One possibility is that the two frequencies merge into an average and are perceived as an intermediate frequency. One possibility is that a difference frequency or "beat" will be perceived. O'shea and Blake (1986) reported that interocular differences in full-field flicker rates produced a phenomenon similar to a temporal beat pattern at the difference frequency. Carlson and He (2000) also reported a temporal beat of about 2 Hz when LEDs modulating at 28 and 30 Hz were dichoptically presented.

METHODS: EXPERIMENT 2A

Spatially, the stimuli were as described in the "General Methods" but the temporal filtering was more narrowly spaced to produce enough resolution for a psychometric function of temporal frequency increment perception. Increment thresholds were measured for all but the highest frequency used in Experiment 1 (0.59, 1.18, 2.37, 4.73, and 9.47 Hz) with the stimuli binocularly presented through a mirror stereoscope. Five observers participated in a two-interval forced-choice temporal frequency discrimination task. Each interval lasted for 2 s separated by a 0.8 s break. In a completely randomized order, each standard frequency was paired with all of its comparison frequencies (see **Table 2**) a total of 20 times, with the interval order also randomized. Observers indicated which interval appeared to modulate at a higher rate. Psychometric functions were fitted to the data and the frequency increment producing 75% correct performance was taken as the increment threshold (see **Figure 4A**).

METHODS: EXPERIMENT 2B

Experiment 2B is a temporal frequency matching experiment. The one-octave rivalry stimuli used in Experiment 1 (**Table 1**, dark oblique) were presented for a random period of between 4 and 8 s followed by an array of nine comparison stimuli modulating a various frequencies. Observers made an unspeeded selection of the comparison closest to the perceived modulation rate when the rivalry period terminated. **Table 2** shows the temporal frequencies of each pair of rival stimuli, together with their nine comparison frequencies spaced in quarter-octave steps (half-octave steps for the two slowest modulation pairs). Five observers made 50 matches each to the rivalry pairs shown in **Table 2** to

Table 2 | A summary of the temporal frequencies of the rivalry stimuli used in Experiment 2B (left-hand side: all are one-octave pairs) and the corresponding nine comparison stimuli for each rivalry pair.

Rivalry frequencies (Hz)	Comparison frequencies (Hz)								
0.59 vs. 1.18	0.42	**0.59**	0.84	**1.18**	1.67	2.37	3.35	4.73	6.69
1.18 vs. 2.37	0.42	0.59	0.84	**1.18**	1.67	**2.37**	3.35	4.73	6.69
2.37 vs. 4.73	1.67	1.99	**2.37**	2.81	3.35	3.98	**4.73**	5.63	6.69
4.73 vs. 9.47	3.35	3.98	**4.73**	5.63	6.69	7.96	**9.47**	11.26	13.39
9.47 vs. 18.93	6.69	7.96	**9.47**	11.26	13.39	15.92	**18.93**	22.51	26.77

The rival frequencies within the comparison series are shown in bold.

produce distributions of frequency matching responses for each pair of one-octave frequency differences.

RESULTS AND DISCUSSION: EXPERIMENT 2A

Figure 4A shows data from one observer discriminating temporal frequency increments against a 9.47 Hz standard, producing an increment threshold of 11.7 Hz in this case. Thresholds were obtained for five fixed frequencies (**Figure 4B**) from five observers and were combined into a group mean (**Figure 4C**). Weber fractions were computed by calculating the differences between the fixed frequencies and the increment threshold frequencies and plotting these differences against the fixed frequencies (**Figure 4D**). The Weber fractions were well fit by a straight line passing through the origin with a slope of 0.26, confirming that Weber's law holds for temporal frequency discrimination. A Weber fraction of 26% is relatively high relative to other perceptual dimensions. The Weber fraction for spatial frequency discrimination is between 0.08 and 0.13 for a frequency of 1 cpd (Hirsch and Hylton, 1982; Regan et al., 1982), similar to the mean frequency of 1.1 cpd used here, and is 0.15 for speed (Mandriota et al., 1962). Discrimination thresholds for orientation are also very fine, ~1° (Bradley and Skottun, 1984; Bowne, 1990). The magnitude of the Weber fraction may reflect the resolution of the underlying channels. Temporal frequency channels are fewer and broader than orientation and spatial frequency channels (Graham, 1972; Stromeyer and Julesz, 1972; Braddick et al., 1978; Graham, 1989). In any case, a Weber fraction of 26% for discriminating temporal frequencies means that rivalry between two temporal frequencies one octave apart (i.e., 100% as a proportionate difference) should have produced easily discriminable alternations in Experiment 1 if they did elicit perceptual alternations. The fact that alternations were rarely reported for a one-octave frequency difference (**Figure 3B**) confirms the difference was too small to elicit binocular rivalry.

RESULTS AND DISCUSSION: EXPERIMENT 2B

Figure 5A shows distributions of temporal frequency matches for the five one-octave rivalry conditions. In each case the distributions are unimodal, as expected if the two eyes were not engaging in binocular rivalry. (Rivalry would produce a bimodal distribution with peaks at the rival frequencies.) The five distributions are separated by about one octave, agreeing with the spacing of the five conditions. Notably, each peak sits approximately halfway between the frequencies presented to each eye, consistent with fusion rather than rivalry. **Figure 5B** compares the geometric mean (or logarithmic midpoint) of the rivalry frequencies with the distribution peak and shows very little discrepancy: none of the differences exceed the ±0.26 Weber fraction or "just-noticeable difference" (dashed lines). Distribution peaks at the mean of the rival stimuli is consistent with both frequencies activating the same temporal channel, producing an average frequency percept. There was a tendency for the low frequency pair to be perceived slightly higher than their mean, and for higher frequency pairs to be perceived slightly below their mean. This may be due to temporal frequency adaptation, as Johnston et al. (2006) have shown that adaptation to high temporal frequencies lowers perceived frequency, and adaptation to low frequencies raises perceived frequency.

The fact that the distributions of temporal frequency matches were centered tightly around the mean of the dichoptic frequencies shows that observers did not perceive temporal beats, even though the frequencies were too close to elicit rivalry. If temporal beating had occurred, it would have been at the difference frequency. In all five conditions, the modulation rate in one eye was simply twice the rate in the other so the difference would always be equal to the lower of the two frequencies. In none of the conditions were the distributions centered on the lower frequency. Instead, the data point to a perceptual fusion produced by two slightly different frequencies activating the same temporal channel.

Figure 5C plots the standard deviations of the Gaussian distributions. These were all narrow, fullwidths less than one octave, and therefore contained within the one-octave interval between the rivalry stimuli. Lower frequencies produced broader distributions, which might reflect the shape of the low frequency channel, which is broad and low-pass.

EXPERIMENT 3

Experiment 3 uses a temporal frequency matching approach to reveal what frequencies observers perceive when presented with dichoptic frequencies differing by three octaves (1.18 vs. 9.47 Hz), a difference which produced robust perceptual alternations in Experiment 1. The present experiment will confirm which frequencies are perceived and whether there is any bias, perhaps to the higher frequency (O'shea and Blake, 1986). Unlike Experiment 2, frequency matching distributions in Experiment 3 should be bimodal with peaks corresponding to the frequencies of the rival stimuli.

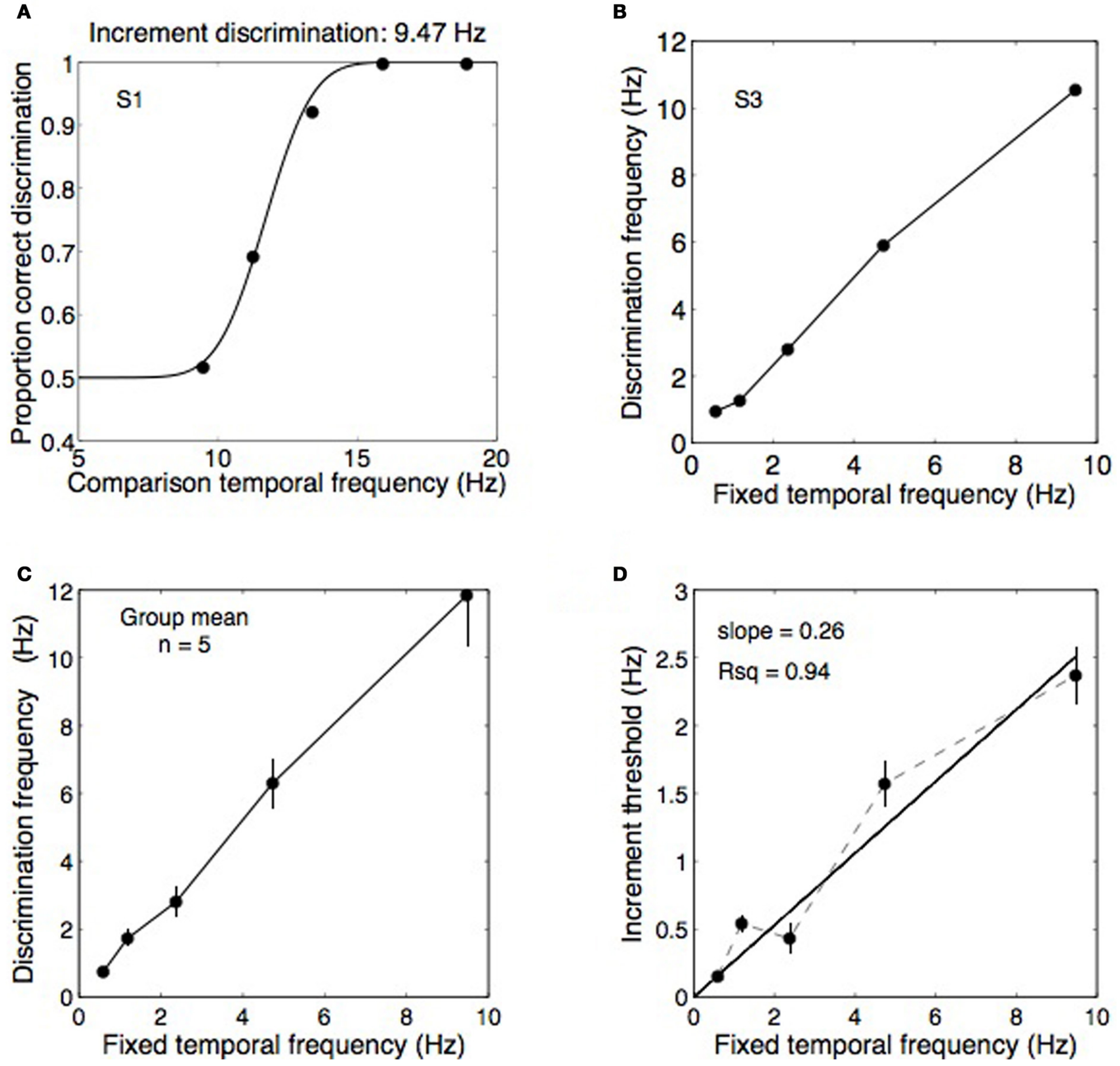

FIGURE 4 | Data from Experiment 2A showing temporal frequency discrimination performance for a range of base frequencies. (A) An example psychometric function from one observer discriminating temporal frequency increments on a 9.47 Hz standard. In this example, threshold performance was obtained at a frequency of 11.7 Hz. **(B,C)** Thresholds obtained as in panel **(A)** were measured for five standard frequencies: 0.59, 1.18, 2.37, 4.73, and 9.47 Hz and the data from five observers was pooled into a group mean. **(D)** From the group mean data, the discrimination frequencies were converted to Weber fractions (i.e., $\Delta f/f$) were computed by plotting the difference between the fixed frequencies and the increment threshold frequencies against the fixed frequencies. The slope of the best-fitting straight line (constrained to pass through the origin) provides an estimate of the Weber fraction, in this case relatively high at 0.26. Error bars show ±1 standard error of the mean.

METHODS

Four observers participated in a frequency matching experiment similar to Experiment 2B. The dichoptic temporal frequencies were 1.18 vs. 9.47 Hz and produced strong rivalry. Because of the three octave frequency range, we provided 13 comparison stimuli spaced in half-octave intervals: 0.42, 0.59, 0.84, 1.18, 1.67, 2.37, 3.35, 4.73, 6.69, 9.47, 13.39, 18.93, and 26.78 Hz. Subjects viewed the rival stimuli for brief period (random within 4–8 s) and then chose the comparison frequency most closely matching their percept when the rivalry period ended. Each subject did 75 trials.

RESULTS AND DISCUSSION

Figure 6A shows raw data for one observer. The data are very clearly bimodal, forming two clear distributions with no overlap between them. This confirms the subjective impression when viewing these stimuli that they produced vigorous binocular rivalry with clearly defined alternations between the high- and

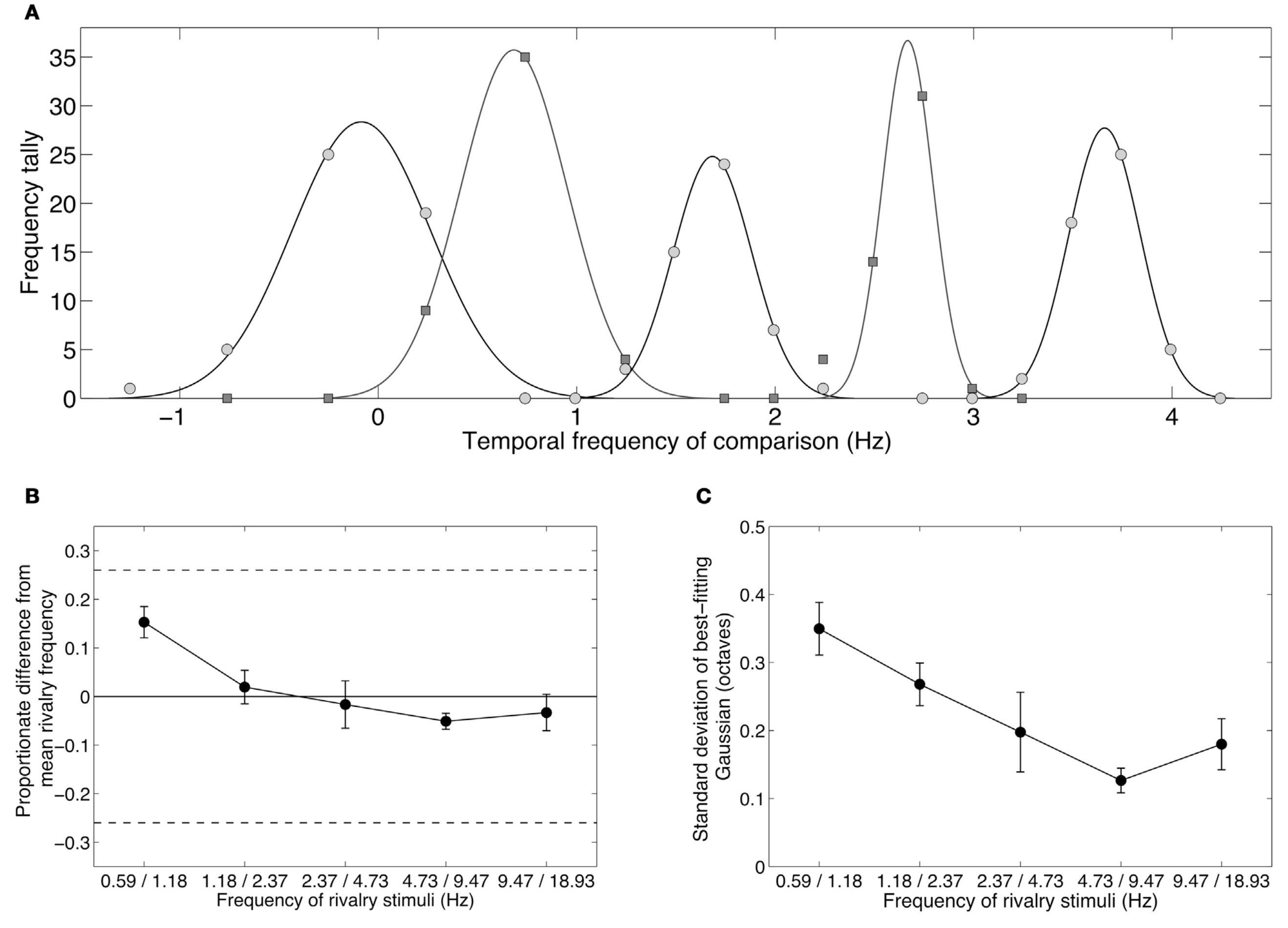

FIGURE 5 | Results from Experiment 2B showing the temporal frequency perceived during binocular rivalry between stimuli differing by one octave. Observers chose their matches from a range of nine temporally modulating stimuli (see **Table 2**). **(A)** Data from one observer showing distributions of temporal frequency matches for each of the one-octave pairs shown in **Table 1**. The data were well described by Gaussian distributions. Note that the frequencies were converted to a $\log_2$ scale (i.e., an octave scale) before fitting the Gaussian. **(B)** Group mean data plotting the means of the Gaussian distributions with respect to the geometric means of the rivalry stimuli. A value of zero would indicate a Gaussian distribution centered exactly on the geometric average of the rivalry stimuli. All distributions are very close to this zero point, and all lie within the dashed lines indicating the just-noticeable difference for temporal frequency discrimination. **(C)** Group mean data plotting the standard deviations of the Gaussian distributions. All standard deviations are well less than 0.5, which would correspond to a distribution with a one-octave full-width at half height. All error bars show ±1 standard error of the mean.

low-frequency patterns. The two peaks align very closely with the true modulation rates of 1.18 and 9.47 Hz. This was consistent across the group, as shown in **Figure 6B** which plots perceived frequency (the mean of the Gaussian distribution) against true frequency. The dashed line at 45° is the identity line and the four observers' data clusters closely around it. The peak frequencies across the group averaged 1.25 and 9.89 Hz, very close to the true frequencies of 1.18 and 9.47 Hz, which conforms that subjects did experience rivalry alternations between the competing stimuli. Notably, unlike in Experiment 2B, no matches were made to intermediate frequencies or to the average frequency and the distributions were narrowly distributed around the true peaks. This is shown by the standard deviations in **Figure 6C** which are much less than 0.5 (corresponding to a one octave fullwidth) and are similar to those in **Figure 5C**.

Given that rivalry dominance periods are stochastic in terms of duration, (Fox and Herrmann, 1967; Levelt, 1967; Hupe and Rubin, 2003; Brascamp et al., 2005), rivalry between two temporal modulations of equal stimulus strength would mean the final percept in each 4–8 s trial would be unpredictable. This would result in roughly equal numbers of matches to each stimulus, yet the numbers of observations in each distribution were not equal, indicating a bias for one stimulus to predominate more than the other. The low-frequency distribution, when summed across observers, totalled 136 observations, whereas the the high-frequency distribution totalled 164 observations. The biased 40–60% split between low and high frequencies points to slightly greater stimulus strength for the high frequency modulation. This confirms an earlier report of a high-frequency bias with orthogonal counterphasing gratings (O'shea and Blake, 1986),

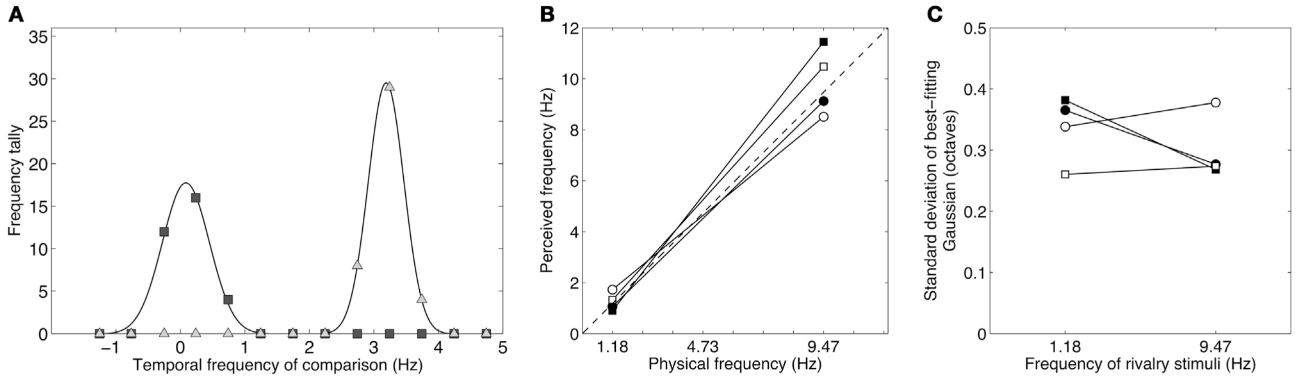

FIGURE 6 | Results from Experiment 3 showing the distributions of perceived temporal frequency during binocular rivalry between stimuli differing by three octaves (1.18 and 9.47 Hz). (A) Data from one observer showing a bimodal distribution of temporal frequency matches. The peaks of the best-fitting Gaussians lie very close to the true values of the rivalry stimuli and the data are clearly dichotomous, with no intermediate or "average" frequencies reported. **(B)** Taking the peaks of the Gaussian distributions as estimates of perceived frequency, it is clear that the perceived frequencies correlate very well with the actual frequencies. The group mean peak frequencies were 1.25 and 9.89 Hz. **(C)** The standard deviations of the Gaussian distributions were similar across the group. All standard deviations were well less than 0.5 (i.e., well less than one-octave full-width at half height), indicating that subjects experienced clear rivalry alternations between the competing temporal frequencies and did not experience intermediate frequencies.

although our bias is somewhat weaker than this earlier report. The high frequency bias is consistent with the recent finding that low temporal frequencies are attenuated by the presence of high frequencies (Cass and Alais, 2006; Cass et al., 2009a) and with the high frequency bias seen in the pilot experiment.

EXPERIMENT 4

The results of Experiments 2B and 3 demonstrate that interocular differences in temporal frequency between spatially matched patterns do elicit rivalry alternations. Temporal frequency rivalry should therefore exhibit the well-known signature of binocular rivalry dynamics with distributions of dominance durations showing a positive skew such as a Gamma distribution (Fox and Herrmann, 1967; Levelt, 1967) or the log-normal distribution (Murata et al., 2003; Brascamp et al., 2005). Also, autocorrelations of rivalry time series should reveal little or no correlation between the durations of successive rivalry periods (Fox and Herrmann, 1967; Levelt, 1967). Experiment 4 aims to verify these two features for temporal frequency rivalry.

METHODS

Five subjects monitored their rivalry alternations while viewing a four–octave temporal frequency difference (1.18 vs. 18.93 Hz) in 10 one-minute trials. Each observer's data were binned into 150 ms epochs and the frequency tallies were normalized to the maximum tally and fitted with a log normal distribution. The resulting frequency histogram was fitted with a log-normal distribution. Autocorrelations were calculated for each observer on the unbinned time-series data.

RESULTS AND DISCUSSION

Figures 7A and **B** show dominance duration distributions from two experienced observers. Gamma distributions traditionally have been fitted to dominance distributions for binocular rivalry (Fox and Herrmann, 1967; Levelt, 1967) and other bistable stimuli (Borsellino et al., 1972; Hupe and Rubin, 2003; Long and Toppino, 2004; Zhou et al., 2004; van Ee, 2005), although the log-normal provides a slightly better description of the distribution (Hupe and Rubin, 2003; Brascamp et al., 2005). Apart from this, the log normal's parameters are more intuitive as they correspond to the distribution's peak dominance duration and its width (i.e., standard deviation) rather than the shape and scale parameter of the Gamma distribution (Brascamp et al., 2005). Overall, the dominance durations from all observers were similar, with a group mean peak duration of 1.29 s and standard deviation of 0.40 s. Overall, the distribution data for temporal frequency rivalry resemble very closely those for spatial rivalry.

Figures 7C–F shows the autocorrelation coefficients for each observer and shows whether the duration of a given dominance period is correlated with subsequent periods. Such analyses often show non-significant correlations for all non-zero lags (Fox and Herrmann, 1967; Levelt, 1967), meaning the durations of dominance percepts are sequentially independent. This is often considered one of the hallmarks of binocular rivalry and these data show that it holds for temporal frequency rivalry as it does for spatially induced rivalry. One notable point is that two of four observers showed significant correlations at lag one, meaning the duration of a given rivalry period was related to the previous one, and other reports too have noted significant lag one correlations (Lehky, 1988; van Ee, 2009). This could arise from neural adaptation operating within a mutual inhibition model of rivalry (Sugie, 1982; Lehky, 1988; Klink et al., 2008; Alais et al., 2010) simply because a long dominance period of one stimulus would lead to more adaptation than would a short period, with a consequently longer recovery period during which the other stimulus would be stronger. This could lead to significant correlations at lag one, as is sometimes observed. Other possible contributions to significant correlations at lag one have been suggested, including attention, eye movements and blinks (van Ee, 2009).

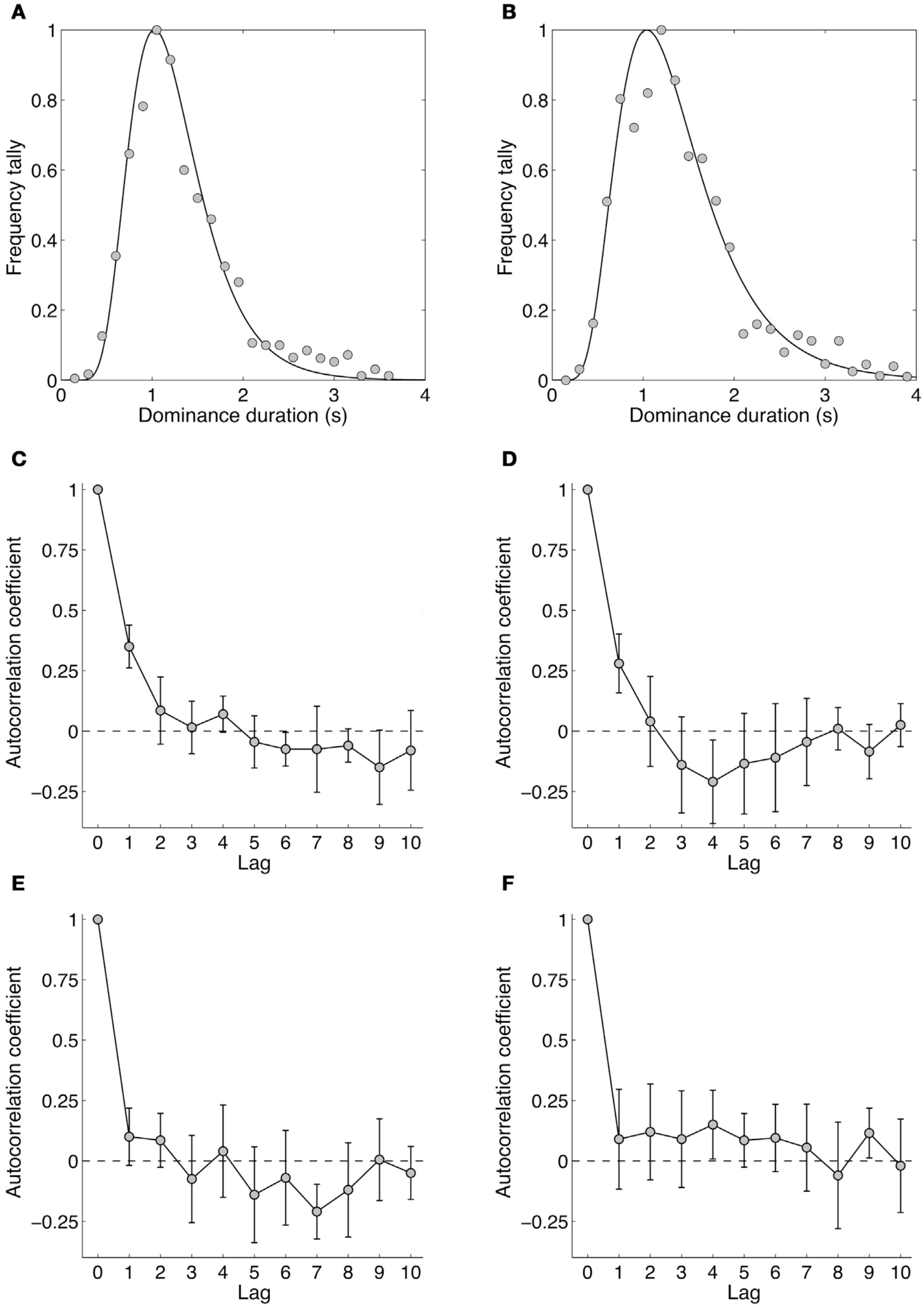

FIGURE 7 | Data from Experiment 4 showing the dynamics of binocular rivalry between stimuli differing by four octaves (1.18 and 18.93 Hz). (A,B) Data from two individual observers (authors David Alais and Amanda Parker) showing distributions of dominance times obtained from 10 one-minute rivalry trials. Data were binned into 150 ms epochs and the frequencies normalized to the maximum. The curve shows the best fitting log-normal distribution. **(C–F)** Autocorrelation functions for four observers. Autocorrelations were computed for each of the 10 rivalry periods and averaged. The data in panels **(C–F)** are plotted with 95% confidence intervals, meaning that there are significant lag-one correlations in panels (**C,D**).

GENERAL DISCUSSION

The present study found that interocular temporal frequency differences do produce binocular rivalry, provided the frequency difference is two or more octaves, and that temporal frequency rivalry dynamics show the same characteristics as rivalry induced by spatial differences. Because binocular rivalry is the default outcome when binocular matching fails (Blake and Boothroyd, 1985), these results indicate that temporal frequency is one of the stimulus attributes the visual system uses to decide whether images from corresponding retinal locations are from the same object or not.

The results also indicate that binocular rivalry takes place between temporal channels rather than within them. The observation that a two-octave frequency difference (i.e., a four-fold difference, such as 3 Hz vs. 12 Hz) is required to produce robust rivalry supports this because temporal channels are much more broadly tuned and fewer in number than spatial frequency or orientation channels (see **Figure 8**). Psychophysical studies show the entire temporal dimension is encoded by just two (Anderson and Burr, 1985; Hess and Snowden, 1992; Snowden et al., 1995; Cass and Alais, 2006), or perhaps three temporal frequency channels (Mandler and Makous, 1984; Hess and Snowden, 1992; Johnston and Clifford, 1995). If rivalry is indeed a between channels process it would require rather large temporal frequency differences so that each eye's signal could drive separate channels. Otherwise, frequencies close enough to activate the same channel would merge into an average and binocular fusion would result. This can be seen in **Figure 5A** where a one-octave temporal frequency difference produced a unimodal distribution of perceived frequencies centered on the average frequency, whereas

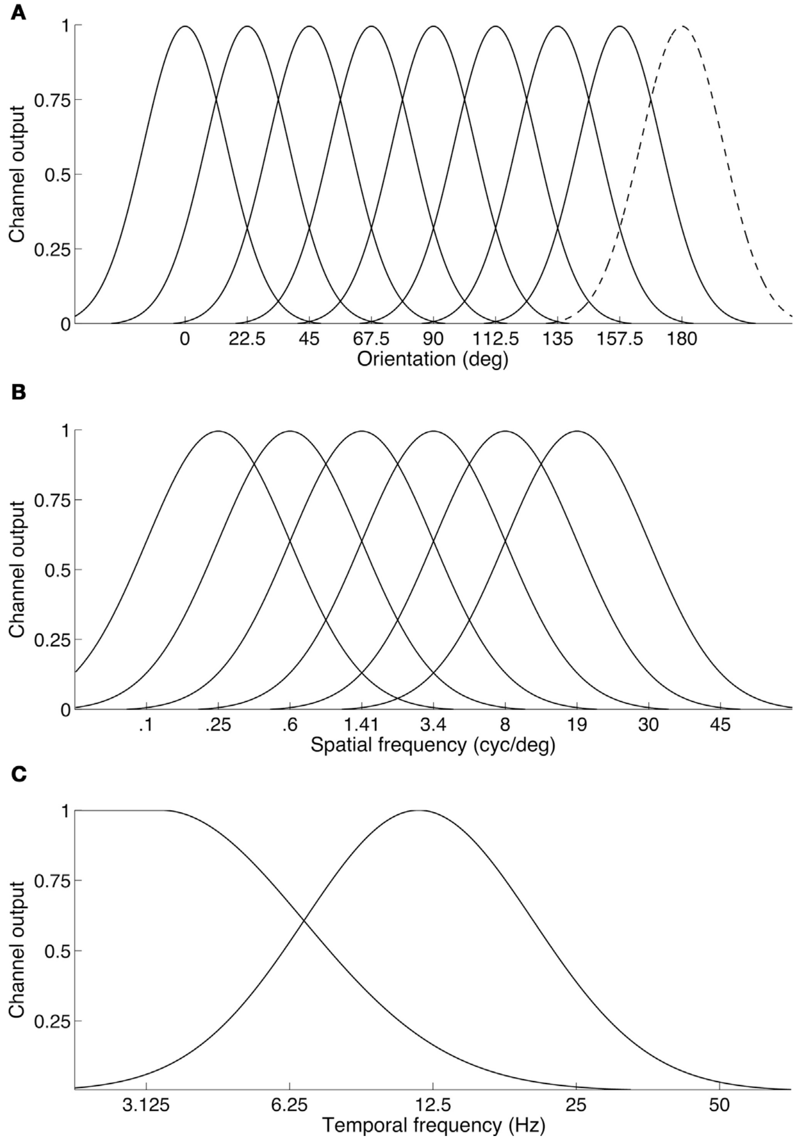

FIGURE 8 | Illustration of the differing organization of channels across basic visual feature dimensions. (A) Orientation channels are thought to be narrow and finely sample the orientation dimension. Here eight channels are shown. Because a full cycle of orientation is 180°, the dashed curve centered at 180° is simply a duplicate of the channel located at 0°. **(B)** Spatial frequency channels: six channels are sufficient to span the spatial frequency dimension. The channels shown here have a standard deviation of 1.25 octaves. On a log frequency axis, the channels are modeled as Gaussian normal curves. **(C)** Temporal frequency channels: consistent with many studies, two channels are shown on a log temporal frequency axis, a broad low-pass channel and a high bandpass channel. Some studies suggest a third, very high bandpass channel may also exist.

as larger frequency differences produced bimodal distributions (**Figure 6A**).

The principle of "rivalry between channels" appears to operate in other stimulus dimensions, even though they are encoded by a finer array of channels. About six narrowly tuned band-pass filters with a full bandwidth of about 1.25 octaves account for our fine spatial frequency sensitivity (Graham, 1972; Stromeyer and Julesz, 1972). About eight tightly tuned band-pass filters with a full bandwidth of 15° underlie orientation perception (Movshon and Blakemore, 1973; Phillips and Wilson, 1984). Because of this finer grain, binocular rivalry can be produced with small spatial differences. For example, compared to the two-octave difference required to trigger temporal frequency rivalry, a one-octave spatial frequency difference will trigger rivalry between two vertical gratings (Blakemore, 1970; Yang et al., 1992). A spatial channel-based approach was also used successfully by Mayhew and Frisby (1976) to account for their study of rivalry and stereopsis. Regarding orientation, orthogonally oriented gratings are a standard rival stimulus yet rivalry can be evoked by orientation differences down to ±15° or less (Braddick et al., 1978). Thus, the interocular differences required to trigger rivalry varies consistently with the grain of the underlying sensory channels.

Another observation indicating that rivalry occurs between channels is that the temporal, spatial and orientation dimensions produce fused percepts when the interocular difference is less than a channel width. Near-vertical lines differing in orientation by a small amount do not rival and instead fuse into a single vertical grating perceived to slant in depth around the horizontal axis, as originally observed by Wheatstone (1838). Similarly, vertical gratings differing slightly in spatial frequency do not rival but fuse into a single grating tilted in depth around the vertical axis (Blakemore, 1970). These percepts are thought to occur when the two stimuli activate a single spatial or orientation channel (Blakemore, 1970; Schor, 1977; Yang et al., 1992) and the perceived depth is an ecologically valid resolution of the small interocular differences. Thus, a consistent principle holds: rivalry occurs when dichoptic signals drive different channels, and fusion occurs when they drive the same channel.

The data in **Table 1** reveal a close correspondence between rivalry incidence at various frequencies and the shape of temporal channels. The data on the two-octave diagonal show that it is not the magnitude of the frequency difference *per se* that produces rivalry but where on the temporal frequency dimension the stimuli are located. The two lowest pairs (0.59 vs. 2.37 Hz; and 1.18 vs. 4.73 Hz) produce modest levels of rivalry, whereas the two highest pairs (2.37 vs. 9.47 Hz; and 4.73 vs. 18.93 Hz) produce robust rivalry. This fits with "rivalry between channels" because the cross-over point between the broad low-pass temporal channel and the high bandpass channel is about 6–8 Hz (Anderson and Burr, 1985; Hammett and Smith, 1992; Hess and Snowden, 1992; Snowden et al., 1995; Cass and Alais, 2006). Therefore, the two highest pairs had one frequency on each side of the cross-over, activating separate temporal channels and rivaling strongly. The two lowest pairs had a lower incidence of rivalry because both frequencies strongly activated the low-pass channel, with a modest response from the overlapping portion of the high frequency channel (**Figure 8**). The absence of rivalry when both stimuli drive the same channel also explains Carlson and He's (2000) report that dichoptic flicker at 28 and 30 Hz produces a temporal beat at 2 Hz, rather than rivalry alternations. Another study examining small dichoptic temporal frequency differences (Baitch and Levi, 1989) compared several frequency pairs (12 and 14 Hz; 18 and 20 Hz; 30 and 32 Hz) and also found reliable 2 Hz beat patterns.

One study arguing against "rivalry between channels" examined dichoptically overlaid translating motion patterns (random pixel arrays) that moved either orthogonally or in opposite directions at various speeds (van de Grind et al., 2001). When slow moving patterns (0, 1.05 and 4.2 deg/s) were paired with patterns moving at speeds of up to 12 deg/s, binocular rivalry was frequently reported, but pairing a slow moving pattern with a very fast moving pattern produced motion transparency. The authors' interpretation was that two speed channels exist—one slow and one fast—and that rivalry occurs when both stimuli activate the same channel (otherwise, transparency results). Two factors might explain this discrepancy. First, they manipulated speed and did not consider the temporal and spatial frequency components of speed (speed = TF/SF) (Smith, 1987; Smith and Edgar, 1991; Alais et al., 2005). Understanding how their stimulus would activate spatial and temporal channels leads to a critical point: their random-pixel stimulus was spatially very broadband, meaning it had a correspondingly large range of temporal frequencies (TF = speed × SF). Consequently, with so much interocular conflict across all spatial and temporal channels, their data could also be interpreted as rivalry between spatial and temporal channels.

There has been a broader debate about whether motion rivalry *per se* exists. Some have argued that rivalry is fundamentally a spatial process resulting from pattern conflict and must therefore occur within the parvo (or form) stream (Ramachandran, 1991; Carlson and He, 2004; He et al., 2005). One study suggesting rivalry does not occur between motion (Ramachandran, 1991) adapted different motion aftereffect directions in each eye but did not observe rivalry between the aftereffects on a static test pattern. Instead they fused into a single direction (Riggs and Day, 1980; Alais et al., 1994). Subsequently, Blake et al. (1998) repeated the experiment and found that conflicting motion aftereffects do produce rivalry alternations, provided a dynamic test stimulus is used. A static pattern, unlike a dynamic pattern, would not effectively tap the adapted state of the MT neurons thought to underlie the MAE (Huk et al., 2001) as these motion-specialized neurons have no sustained response to static patterns.

Another argument against motion rivalry is that motion stimuli invariably contain form and the form conflict triggers rivalry (He et al., 2005). Motion stimuli usually do contain form, whether complex objects or simple gratings, but even stimuli with no coherent form such as translating dots, if moving fast, can leave a pattern of elongated motion streaks due to temporal integration in neurons (Geisler, 1999; Burr and Ross, 2002). Although motion streaks are not usually perceived, they do activate orientation-tuned neurons to induce tilt illusions and aftereffects (Apthorp and Alais, 2009; Apthorp et al., 2010).

In a binocular rivalry study, it was shown that “streaks” from fast moving dot patterns produce orientation-tuned rivalry suppression (Apthorp et al., 2009; Stuit et al., 2009), even though no orientation is present in the static stimulus. In some cases, then, apparent examples of motion rivalry may indeed be cases of spatially-triggered rivalry.

It is worth considering whether motion streaks are present in the stimuli we have used here, potentially triggering rivalry from spatial conflict. Geisler (1999) established that dots begin to leave motion streaks once they translate further than their spatial period in a time period of 100 ms (that is, 10 periods per second). Could our temporally filtered stimuli leave motion streaks, creating a source of spatial conflict? Although our stimuli are not translating smoothly in a fixed direction, they do contain specific spatial and temporal frequencies and so speeds can be calculated from the ratio of temporal to spatial frequency: [0.59, 1.18, 2.37, 4.73, 9.47, and 18.93] Hz/1.13 cyc/deg = [0.5, 1.0, 2.1, 4.2, 8.4, and 16.8] deg/s. Given that our stimuli have a spatial period of 0.89°, and the streak threshold is 10 periods per second, the highest temporal frequency used here (18.9 Hz) clearly contains a speed above the threshold to produce motion streaks. This analysis indicates that motion streaks are not likely to have played a role in most conditions in this study, although they may have contributed a spatial component in conditions involving the highest temporal frequency.

Taken together, our results demonstrate that rivalry can occur between temporal frequencies, despite carefully controlled spatial parameters. As temporal frequency channels encode dynamic stimuli, they are part of the magno pathway and our findings show that rivalry is not limited to processes encoding static form. Indeed, our rival stimuli contained very little that would drive cells in the parvo stream because they were unoriented and filtered into a low spatial pass-band (0.8–1.6 cpd). In addition, most temporal modulations in this study were well above the temporal preference of the parvo stream. Our stimuli therefore would strongly activate the magno stream (Lennie, 1980; Gegenfurtner and Hawken, 1996) and yet still elicited robust binocular rivalry, suggesting it is not limited to form conflict.

A related recent paper by Denison and Silver (2012) used flicker-and-swap rivalry (Logothetis et al., 1996) to study magno and parvo processing in binocular rivalry. Flicker-and-swap rivalry can produce slow, irregular alternations (interocularly grouped percepts) and percepts of fast orientation alternations (eye-based percepts). Conditions favoring the magno processing (fast flicker, low spatial frequency) produced more percepts of fast orientation alternation than conditions favoring the parvo processing (slow flicker, high spatial frequency, isoluminance). This implies the motion and form pathways can each engage in rivalry, and each uses a different kind of rivalry process to resolve ambiguous inputs. Carney et al. (1987) also examined form and motion in rivalry using counterphasing gratings with a 90° interocular phase lag. Interocularly grouping these gratings produces smooth motion, whereas a single eye sees ambiguous motion. To induce rivalry, one grating was red/green, the other was black/yellow. They observed color rivalry with unimpaired translational motion, demonstrating color/motion independence in rivalry: suppression of one eye’s color does not entail suppression of its motion signal.

CONCLUSION

Overall, these experiments demonstrate that interocular temporal frequency differences do produce rivalry in spatially matched patterns. The data can be explained in terms of “rivalry between channels,” with interocularly conflicting inputs to different temporal channels triggering rivalry in the same way that rivalry between orientations and spatial frequencies can be explained. The temporal frequency differences required to trigger rivalry are rather large (about 2 octaves), but are entirely consistent with the broader width of temporal channels relative to the width of orientation and spatial frequency channels. Once triggered, temporal frequency rivalry exhibits the same pattern of temporal dynamics as spatially triggered rivalry. Our results, like those of Blake et al. (1998), provide no support for the claim that binocular rivalry is exclusively a parvo-pathway function, and are consistent with earlier work showing that motion and form rivalry are independent (Andrews and Blakemore, 1999; Alais and Parker, 2006).

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Stereoscopic depth perception during binocular rivalry

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When we view nearby objects, we generate appreciably different retinal images in each eye. Despite this, the visual system can combine these different images to generate a unified view that is distinct from the perception generated from either eye alone (stereopsis). However, there are occasions when the images in the two eyes are too disparate to fuse. Instead, they alternate in perceptual dominance, with the image from one eye being completely excluded from awareness (binocular rivalry). It has been thought that binocular rivalry is the default outcome when binocular fusion is not possible. However, other studies have reported that stereopsis and binocular rivalry can coexist. The aim of this study was to address whether a monocular stimulus that is reported to be suppressed from awareness can continue to contribute to the perception of stereoscopic depth. Our results showed that stereoscopic depth perception was still evident when incompatible monocular images differing in spatial frequency, orientation, spatial phase, or direction of motion engage in binocular rivalry. These results demonstrate a range of conditions in which binocular rivalry and stereopsis can coexist.

Keywords: stereopsis, binocular rivalry

INTRODUCTION

Theories of binocular integration are usually based around the phenomenon of stereopsis, which necessitates that the two monocular images are combined to form a single cyclopean image (Wheatstone, 1838; Julesz, 1971). The success of this conception is best exemplified by our current understanding of stereopsis, which depends on the convergence of monocular information onto disparity-sensitive binocular neurons that generate (or at least initiate) a sensation of depth (Cumming, 1997; Parker, 2007). However, the idea that binocular vision always involves integration of the two eye views is not easily reconciled with the experience of binocular rivalry (Alais and Blake, 2005). For example, if vertical stripes are presented to one eye and horizontal stripes are presented to a corresponding location in the other eye, the same region of visual space is perceived as being occupied by vertical stripes or horizontal stripes, but not by both. If the two monocular streams were simply united, one would presumably see a grid.

So, how can the visual system deal with monocular signals in such different ways? One possible explanation is that binocular rivalry is the default outcome when binocular correspondence cannot be solved (Blake, 1989; Lehky and Blake, 1991). In this model, rivalry results from reciprocal inhibition between monocular signals prior to binocular convergence. In the presence of well-matched monocular signals, the reciprocal inhibition responsible for rivalry is reduced by binocular neurons that generate the sensation of stereoscopic depth. However, if the modulating effect of the binocular circuitry is weakened by poorly matched stimuli, then the two monocular signals can engage in rivalry. Evidence in support of this model, comes from studies that show stereoscopic depth is disrupted during binocular rivalry (Blake et al., 1991; Harrad et al., 1994; Cogan et al., 1995).

The idea that binocular suppression only occurs when fusion is not possible is challenged by other studies that report that rivalry and stereopsis can coexist in the same location of the visual field (see Wolfe, 1986, for review). For example, it has been reported that stereoscopic depth is still evident when stereo targets are presented on a background undergoing rivalry (Treisman, 1962; Ogle and Wakefield, 1967; Harrad et al., 1994). Other studies have shown that random dot stereograms can still elicit a perception of depth in the presence of rivalrous noise (Julesz and Miller, 1975; Mayhew and Frisby, 1976). However, in all these studies judgments of stereoscopic depth could result from only partial dominance during binocular rivalry (Blake et al., 1991). So, it is possible that stereoscopic depth and rivalry are occurring at different spatial locations, giving the impression of coexistence.

Our aim was to determine whether a monocular stimulus whose appearance was reported as being completely suppressed from awareness could contribute to the perception of stereoscopic depth. Our stimulus involved judging the relative depth of grating patches that were presented at different binocular disparities. The grating patches in the two eyes differed in spatial frequency, orientation, spatial phase, and motion, so that they engaged in binocular rivalry on the majority of trials. Participants were asked to make stereoscopic depth judgments and then immediately report the perceptual appearance of the stimuli. Only trials in which the form from one eye dominated perception were used to generate stereoacuity thresholds.

MATERIALS AND METHODS

STIMULI

Stimuli were programmed using a VSG2/5 graphics card (CRS, Rochester, England) and presented on a monochrome monitor with a fast phosphor decay (Clinton Monoray) and a frame-rate of 120 Hz. Gamma correction was used to ensure that the monitor was linear over the entire luminance range used in the experiments. Participants viewed the display in a darkened room at a distance of 2.28 m through ferro-electric shutter-goggles (CRS, Rochester, England), which alternately occluded the two eyes at the same frequency as the frame-rate of the monitor. Thus, successive frames were seen by only one eye with no perceptible flicker at this high alternation rate. Participants fixated on a dark spot that remained visible throughout the experiments. In all of the experiments reported here, stimuli were circular patches of sinusoidally modulated grating (contrast, 40%) with a 0.8° hard edge envelope on a background of average luminance. Responses were recorded via a CB3 response box (CRS, Rochester, England). Participants were experienced psychophysical observers and had normal or corrected-to-normal vision and good stereopsis.

PSYCHOMETRIC PROCEDURE

Stereoacuity thresholds were first determined for monocular stimuli that differed in spatial frequency. To increase the number of trials in which full dominance was reported, we used a technique known as flash suppression (Wolfe, 1984; Holmes et al., 2006; see http://www.scholarpedia.org/article/Flash_suppression for a demonstration). First, an identical adapting stimulus was presented to both eyes. The adapting stimulus was a vertical grating patch in the center of the display with a spatial frequency between 1.5 and 6.0 cycles/deg. Participants adapted to the form/appearance of this grating patch for 1 s. This was followed by a 1.5-s binocular presentation of three vertically arranged patches of grating. **Figure 1** shows the spatial layout of the stimuli. On each trial, the spatial frequency of the gratings in one eye was 3 cycles/deg, while the spatial frequency of the gratings in the other eye varied between 1.5 and 6.0 cycles/deg. The spatial frequency of the gratings presented to one eye was identical to the adaptor. The top and bottom of the three grating patches in each monocular image were given opposite horizontal disparities such that one or other was in front of fixation during the stereo presentation. The central patch was always at zero disparity. Horizontal jitter ±5 arc min was applied independently to the spatial position of the top and bottom patches. This prevented the use of monocular cues to determine depth. The task of the observers was to press a button to indicate which grating patch (top or bottom) was closest. Immediately after their stereo judgment, observers were asked to indicate which grating patches were perceptually dominant. Trials in which full dominance was not reported for all grating patches in one eye and for the duration of the presentation were discarded from further analysis. Participants were easily able to detect differences between 3 cycles/deg patch and all spatial frequencies that were used.

Next, observers judged stereoscopic depth for monocular stimuli that differed in orientation, spatial phase, and direction of motion. In orientation blocks, participants viewed an identical adapting grating patch in the center of the screen that was either vertical, or tilted to the left or right of vertical (5° or 7.5°). This was followed by a stereo presentation of three vertically aligned grating patches with the same stimulus parameters to one eye and gratings with an opposite tilt to the other. Participants determined the relative depth of the grating patches and then reported whether the patch was tilted to the right or left. In the spatial phase blocks, the adapting stimulus was composed of a patch of vertical grating in the center of the display (spatial freq: 3 cycles/deg) with a spatial (cosine) phase of 0°. This was followed by a stereo presentation of three grating patches with the same spatial phase (0°) as the adaptor in one eye and grating patches with a spatial phase of either 0° or 180° to the other eye. Participants indicated depth and then indicated whether all grating patches had a spatial phase of 0° (bright in the center) or 180° (dark in the center). Finally, stereoacuity thresholds were determined for stimuli that differed in their direction of motion. In this experiment, observers viewed an identical adapting stimulus in the center of the display that was presented to both eyes for 1 s. The adapting stimulus was composed of a patch of vertical gratings (spatial freq: 3 cycles/deg) with a temporal frequency of 0.5 cycle/s to the left or to the right. This was followed by a 1.5-s stereo presentation of three grating patches with the same direction of motion as the adaptor in both eyes or with opposite directions-of-motion in each eye. Participants indicated depth and then indicated the perceived direction of movement of the gratings in the patches.

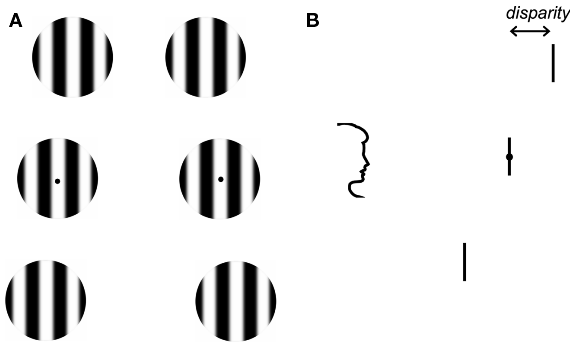

FIGURE 1 | Front and side views of the stimulus. (A) Stimuli were three vertically arranged grating patches. Each patch was 0.8° in diameter and they were separated by 1°. The gratings presented to each eye could vary in either: spatial frequency, orientation, spatial phase, or direction of motion. **(B)** The top and bottom of the three grating patches in each monocular image were given equal and opposite horizontal disparities such that one or other was in front of fixation during the stereo presentation. The task of the participant was to press a button to indicate which grating patch was closest and then to report the appearance of the gratings.

Stereoacuity functions in each experiment were based on five repetitions of a test block for each observer. Each test block contained 10 disparity steps for each stimulus combination and each stereo judgment was repeated five times. Within each test block, stimulus combinations were varied in a counterbalanced design, so that each stimulus was presented an equal number of times to the right and left eyes. For threshold discrimination, cumulative-Gaussian curves were fitted to the data. The difference between performance at 0.25 and 0.75 was taken as the threshold.

RESULTS

SPATIAL FREQUENCY

Observers reported the complete dominance of all grating patches in one eye for the duration of the stimulus in over 90% of trials (S1: 96.1 + 3.1%; S2: 93.7 + 3.1%; S3: 95 + 1.7%). Trials in which the gratings from one eye or the other did not dominate

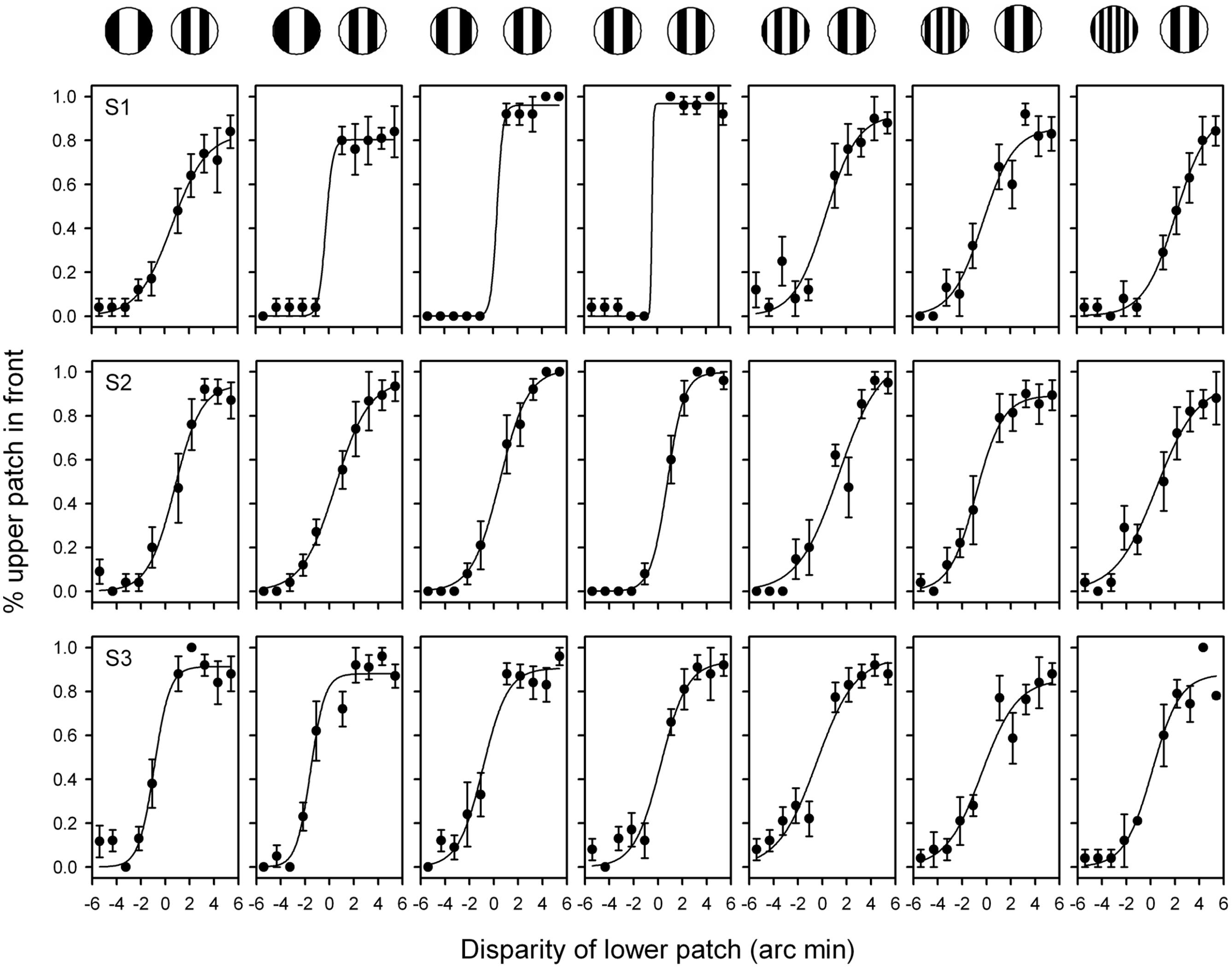

FIGURE 2 | Stereoacuity functions for grating stimuli patches with different spatial frequencies in the two eyes. The combination of spatial frequencies used from (left to right) were: 1.5:3.0, 1.9:3.0, 2.4:3.0; 3.0:3.0; 3.8:3.0; 4.9:3.0; 6.0:3.0 cycles/deg. Participants were asked to indicate whether the upper or lower grating patch was closest. A negative value on the x axis represents an uncrossed disparity. Bars represent SEM.

exclusively were not analyzed. Therefore, with the exception of when both gratings had the same spatial frequency, stereoscopic judgments were made when the form from only one eye was visible. **Figure 2** shows the stereoscopic depth functions from three observers. Thresholds were lowest when the gratings had the same spatial frequency (3.0: 3.0 cycles/deg: mean + SEM = 1.47 + 0.59) and increased as the spatial frequency of the gratings were made more different from each other (1.5: 3.0 = 2.83 + 0.64; 1.9: 3.0 = 1.93 + 0.54; 2.4: 3.0 = 1.90 + 0.53; 3.8: 3.0 = 3.13 + 0.28; 4.9: 3.0 = 3.00 + 0.31; 6.0: 3.0 = 3.43 + 0.23). An ANOVA showed that there was an effect of spatial frequency for S1 [$F(1,6) = 4.3$, $p < 0.005$], but not for S2 ($F = 0.71$, $p = 0.64$) or S3 ($F = 0.92$, $p = 0.49$). Nevertheless, the key point is that clear psychometric functions are apparent for each observer when the spatial frequency of the two monocular images differed by as much as a factor of two.

ORIENTATION

Next, stereoacuity thresholds were determined for grating patches that varied in orientation from 0° to 15° (**Figure 3A**). When the orientations of the two gratings were different, participants indicated complete suppression of the form of the gratings presented to one eye or the other in about 90% of trials (S1: 88.6 + 1.6%; S2: 89.0 + 2.2%). Stereoscopic depth judgments were only assessed in these trials. The results, shown in **Figure 3**, show that thresholds were lowest when the grating patches had the same orientation (i.e., vertical) and increased as they were made more different from each other. An ANOVA revealed that there was a significant effect of orientation for S1 ($F = 5.9$, $p < 0.05$), but not for S2 ($F = 2.8$, $p = 0.1$). However, again both observers were still able to generate good stereoscopic depth functions when the content of the grating patches in one eye was suppressed from perception.

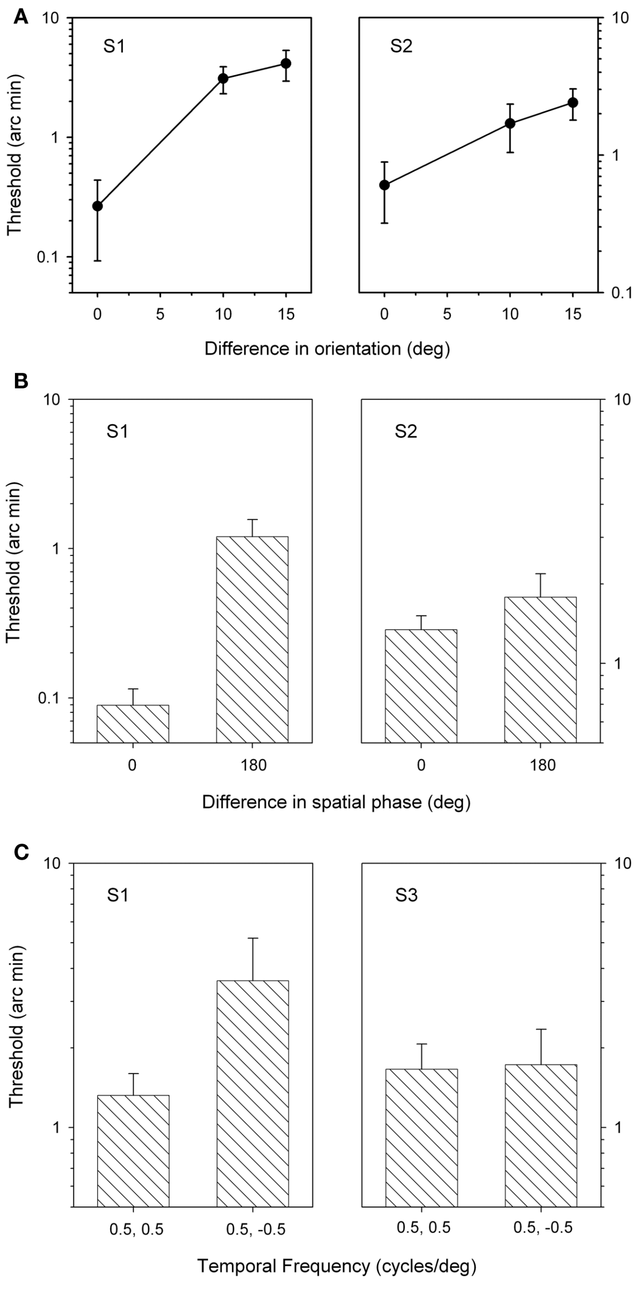

FIGURE 3 | Stereoacuity thresholds for grating patches that varied in orientation (A), spatial phase (B), or direction of motion (C). Bars represent SEM.

SPATIAL PHASE

Stereoscopic depth judgments were then made when grating stimuli differed in their spatial phase. Clear dominance of one or other stimulus was apparent in over 90% of the 180° phase different trials (S1: 92.0 + 5.0%; S2: 97.2 + 1.2%). **Figure 3B** shows that thresholds were lower when both sets of gratings had the same spatial phase (0°) compared to when the gratings were 180° out of phase (0° and 180°). This difference was significant for S1 ($t = 9.4$, $p < 0.05$), but not for S2 ($t = 1.9$, $p = 0.20$). Nonetheless, reliable stereoscopic depth functions were still obtained when the form of one image was suppressed from awareness.

DIRECTION OF MOTION

Finally, stereoacuity thresholds were determined for stimuli that differed in their direction of motion. Participants reported complete dominance of one spatial frequency or the other across all three grating patches for the duration of the presentation on over 40% of trials (S1: 97 ± 0.9%; S3: 48 ± 6.6%). **Figure 3C** shows the stereoacuity thresholds from two participants. For one participant, thresholds were significantly lower when the gratings had the same direction of motion and increased when the direction of motion of the gratings was in the opposite directions. However, this difference was not statistically significant S1 ($t = 2.5$, $p = 0.16$). There was not difference in the stereo-thresholds for S3 ($t = 0.01$, $p = 0.93$). Again, stereo judgments were still possible even when the direction of motion of one stimulus was completely suppressed from perception.

DISCUSSION

The aim of this study was to determine whether depth judgments based on binocular disparity can occur for two monocular objects that differ in spatial structure or local motion. Our results show that stereopsis is still possible when the appearance of an object from one eye is completely suppressed from awareness during binocular rivalry.

A number of previous studies have reported that stereoscopic depth perception can coexist with binocular rivalry (Treisman, 1962; Ogle and Wakefield, 1967; Julesz and Miller, 1975; Harrad et al., 1994). However, in all of these studies participants were not asked to report whether the image in the "suppressed" eye was perceptually dominant during judgments of depth. So, it is possible that, in these studies, partial dominance could result in stereoscopic depth and rivalry occurring at different spatial locations, giving the impression of coexistence. These problems were circumvented in the present study by having participants report the depth and appearance of the stimulus on each trial. Only those trials in which the form from one eye dominated perception for the duration of the trial were used to generate stereoacuity thresholds.

The coexistence of stereopsis and binocular rivalry in this study demonstrates that binocular disparity information can be processed even when the appearance of one monocular image has been suppressed from awareness. These findings fit with a recent study that showed binocular integration and suppression are possible when vertical gratings were presented to each eye (Su et al., 2009). In this study, the stimuli in the two eyes were identical gratings except that a circular patch in the center of the vertical grating of one eye was phase-shifted relative to the surrounding grating. This generated both local rivalry and disparity signals. Although participants used the disparity information to generate a perception of stereoscopic depth, thresholds for the detection of a probe stimulus at the location of the circular patch in corresponding regions of the other eye were increased. This clearly demonstrates the coexistence of binocular integration and suppression. Interestingly, the stimulus used by Su et al. (2009) is similar to the phase-shifted stimulus used in this experiment

(**Figure 3B**). However, in this experiment, we used the participant's reports of awareness to indicate interocular suppression.

The illusory conjunction of form and depth reported in this study fits with other reports that have shown that independent competition between different features of a stimulus can occur during binocular rivalry. For example, a suppressed stimulus can influence the appearance of the dominant stimulus by changing the perception of its orientation (Pearson and Clifford, 2005), direction of motion (Andrews and Blakemore, 2002), luminance (Carlson and He, 2000), and color (Carney et al., 1987; Holmes et al., 2006; Hong and Shevell, 2009). The implication from these studies is that the neural mechanisms underlying suppression during binocular rivalry can operate independently on the features that make up the stimulus. These findings suggest that a stimulus that is suppressed during binocular rivalry is not equivalent to physical removal of the stimulus. Rather, the stimulus can continue to influence perception. These findings are consistent with the idea that the suppression of information during rivalry is not an all or nothing process, but one that occurs at multiple sites throughout the visual system (Blake and Logothetis, 2002; Tong et al., 2006; Blake and Wilson, 2011).

Circumstances in which rivalry and stereopsis coexist are common in natural viewing. For example, when we view a 3D scene, occluding objects typically generate images in corresponding regions of the two eyes that are different (Anderson and Nakayama, 1994). However, if these rivalrous zones are consistent with viewing an occluding object, they are perceived at an appropriate depth (Shimojo and Nakayama, 1990). In this study, when a disparity was applied to the images, the rival stimuli in the two eyes did not occupy corresponding retinal points throughout. Nevertheless, when one grating patch dominated perception, it always appeared as a single circular patch. It would appear, therefore, that it is possible for binocular rivalry to take place even when some aspects of the rival stimuli occupy non-corresponding regions of visual space. Presumably, information from stereoscopic processing can influence which regions of the retina interact during rivalry.

Although our results show that stereo-depth is possible when the monocular input differs on a variety of stimulus dimensions. A number of other reports have shown that reducing the correspondence in spatial structure between the two monocular images affects stereopsis. For example, adding masking noise at one spatial frequency impairs stereoscopic depth at similar, but not at different spatial frequencies (Julesz and Miller, 1975; Mayhew and Frisby, 1976; Yang and Blake, 1991). Neurophysiological studies have shown that there are two possible mechanisms that the visual system could use to process binocular disparity information (Cumming, 1997; Blake and Wilson, 2011). One model is based on binocular detectors, with identical receptive field structures, located at different locations for the left and right eyes (Anzai et al., 1997). An opposing model proposes that the envelope enclosing the receptive fields in the right and left eye are in corresponding retinal positions, but have a different spatial structure (DeAngelis et al., 1991). These mechanisms are based on first-order mechanisms that involve detecting corresponding luminance profiles in the two eyes. In our paradigm, the first-order or luminance pattern of the rivalrous stereograms did not match in the two eyes. This suggests that a second-order mechanism is involved. Behavioral evidence for second-order stereo-depth mechanism has been shown in a number of studies (Zeigler and Hess, 1999; Hess and Wilcox, 2008). Stereoscopic depth perception can even be obtained with dichoptically mixed first- and second-order stimuli (Edwards et al., 2000). Physiological support for second-order depth perception is evident in a subset of neurons in extrastriate regions of cat visual cortex (Tanaka and Ohzawa, 2006). Our findings suggest that the second-order stereo mechanisms can still operate during binocular rivalry.

In conclusion, our results show that a stimulus that is completely suppressed from awareness during binocular rivalry can nonetheless contribute to the processing of disparity. This gives rise to an illusory conjunction in which form information from one eye is combined with depth information from both eyes. These results demonstrate a range of stimulus conditions in which rivalry and stereopsis can coexist.

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Why is binocular rivalry uncommon? Discrepant monocular images in the real world

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When different images project to corresponding points in the two eyes they *can* instigate a phenomenon called binocular rivalry (BR), wherein each image seems to intermittently disappear such that only one of the two images is seen at a time. Cautious readers may have noted an important caveat in the opening sentence – this situation can instigate BR, but usually it doesn't. Unmatched monocular images are frequently encountered in daily life due to either differential occlusions of the two eyes or because of selective obstructions of just one eye, but this does not tend to induce BR. Here I will explore the reasons for this and discuss implications for BR in general. It will be argued that BR is resolved in favor of the instantaneously stronger neural signal, and that this process is driven by an adaptation that enhances the visibility of distant fixated objects over that of more proximate obstructions of an eye. Accordingly, BR would reflect the dynamics of an inherently visual operation that usually deals with real-world constraints.

Keywords: binocular rivalry, binocular suppression, occlusion

Binocular rivalry (BR) papers usually begin with a fib. The near ubiquitous phrase is something like "*when different images are shown to the two eyes they rival for perceptual dominance, such that only one image is seen at a time while the other is suppressed from awareness.*" Statements like this are greatly misleading, and the reasons for this misconception speak both to the function of binocular suppression, and consequently to processes that are fundamental to BR.

DISCREPANT MONOCULAR IMAGES IN THE REAL WORLD

There are at least two reasons why humans frequently encounter completely different monocular images at corresponding points on the two retinas, differential occlusions of the two eyes and selective obstructions of just one eye. Neither situation typically results in BR.

As depicted in **Figures 1A,B**, when an object can be seen in both eyes it will occlude more distant parts of the visual scene. Importantly, different sections of the distant scene can be selectively visible to either eye. **Figure 1A** depicts an example where a disembodied head is floating in space behind a pillar. Obviously this graphic is not going to win any artistic accolades, and there is more than a touch of irony in trying to depict a real-world constraint using a disembodied head, but hopefully this will serve to illustrate a point. The disembodied head is peering down at a point beyond the pillar. The bold lines depict the nearest points visible to either eye just to the left of the pillar. As can be seen, a region beyond the pillar is selectively visible to the left eye (as images of the pillar will reside at corresponding points on the right retina). This zone, shaded gray, is called a monocular occlusion zone (Gillam and Borsting, 1988; Nakayama and Shimojo, 1990; Ono et al., 2003; see also Harris and Wilcox, 2009 for a recent review).

Figure 1B attempts to depict the same type of scenario viewed from above. Here the right eye is colored black and the left eye gray. Both eyes are converged to fixate a distant point (the dash) beyond the pillar (which is now depicted as a gray circle). Black dotted lines depict the limits of the monocular occlusion zone caused by the image of the pillar in the right eye, and dotted gray lines depict the limits of the monocular occlusion zone for the left eye. Note that both of these zones are visible to the other eye. The important point to take from these illustrations is that we frequently encounter monocular occlusion zones, but these very rarely, if ever, induce BR in daily life.

A selective obstruction of just one eye is depicted in **Figure 1C**. Here someone has crept up to a doorway and is peeking around the doorframe. This attempt to see without being seen results in the exposed eye having an unobstructed view of the distant scene, whereas the occluded eye can only see the back of the doorframe. This type of scenario does not just occur when people are sneaky. An analogous situation can occur if you try to look down past your nose at an acute angle, or if you lie down with the side of your face in a pillow while looking across a room, or if you stick a finger directly in front of one eye while reading this text. As the reader can demonstrate for themselves, none of these situations typically result in BR despite the presence of completely different images at corresponding points in the two eyes. Why?

WHY DIFFERENTIAL OCCLUSIONS DON'T CAUSE BR

There is a geometric cue available to the brain when unmatched monocular images result from differential occlusion. As can be inferred from **Figures 1A,B**, a monocular occlusion zone will project to the temporal side of the retina (the side closest to the ear) relative to the image of the occluder (in this case the pillar). Stimuli that obey this constraint are resistant to suppression during BR. In contrast, unmatched monocular images that project to the nasal side of the retina, relative to an image seen in both eyes, are susceptible to BR (Shimojo and Nakayama, 1990, 1994). Thus at

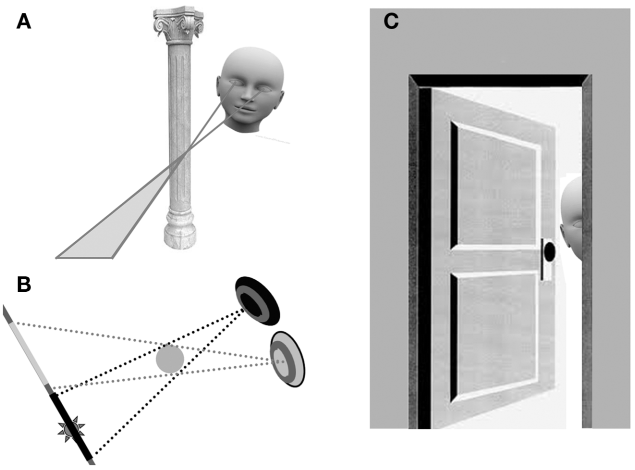

FIGURE 1 | Graphic depictions of a differential occlusion of two eyes (A,B) and a selective obstruction of just one eye (C).

least one reason BR is uncommon is that the processes responsible are sensitive to differential occlusion cues. So BR is not instigated by the unmatched monocular retinal images that are encountered in daily life as a consequence of differential occlusion.

WHY SELECTIVE OBSTRUCTIONS DON'T CAUSE BR

When an occluder is so close that it only obstructs one eye there is no geometric cue to signal which of the unmatched retinal images is of an occlusion, and which is of a more distant point of regard. Evidently the visual system does, however, differentiate between these images as perception tends to be dominated by images relating to more distant objects. We are usually only faintly aware of images of selective obstructions because they are persistently suppressed from awareness. Hence you can still read this text if you place a finger directly in front of one eye. One can also easily demonstrate that this involves an active suppression, as the image of the selective obstruction jumps into awareness if one shuts the unobstructed eye. So what cues, or properties, of an image of a selective obstruction does the visual system tap to ensure it is suppressed from awareness?

SIGNAL STRENGTH

The concept of signal strength (Levelt, 1968) will be familiar to most readers with a passing interest in BR. Historically signal strength seems to have been a somewhat circular concept. Whenever a stimulus property was found to influence the probability of perceptual dominance during BR it was added to a grab bag of characteristics collectively termed signal strength. However, close inspection of this grab bag reveals that many features within it could be used to differentiate images of selective obstructions from images of more distant objects (see Fahle, 1982a,b; Arnold et al., 2007; Changizi and Shimojo, 2008).

The reader should bear in mind that young adults can only accommodate to focus on an object at a viewing distance of ~10 cm, so images of selective obstructions are necessarily blurred, as they have to be very close to an eye in order to obstruct it selectively. Tellingly, image blur was one of the first characteristics placed under the term "signal strength" (Levelt, 1968). When an image is blurred it selectively reduces higher spatial frequency content, and this too contributes to signal strength (Fahle, 1982a,b; Wolfe, 1983). Similarly, blurring an image reduces image contrast (Fahle, 1982a,b), and both luminance and chromatic contrasts contribute to signal strength (Levelt, 1968; Mueller and Blake, 1989; Kovacs et al., 1996; Pearson and Clifford, 2004). Clearly signal strength, or at least a number of characteristics grouped under this term, would be useful for a process that strives to suppress awareness of selective obstructions in order to enhance the visibility of more distant objects (Fahle, 1982a,b; Arnold et al., 2007; Changizi and Shimojo, 2008). So another reason BR is uncommon is that the images of selective obstructions have a very low signal strength.

SIGNAL STRENGTH AND NATURAL IMAGES

Natural images are complicated, so historically vision scientists have focused on simplified stimuli that are more easily controlled. However, some brave souls have investigated the properties of natural images and how the visual system responds to them (Maloney, 1986; Field, 1987; Zetzsche et al., 1993; Geisler et al., 2001; Simoncelli and Olshausen, 2001; Mante et al., 2005; Geisler, 2008). Pertinently, it has been established that the mechanisms responsible for BR are sensitive to the characteristics of a natural image (Baker and Graf, 2009).

Natural images contain luminance changes that can be detected at different spatial scales. Imagine you have taken a picture, and you want to know how luminance changes are distributed in terms of spatial scale. Figuratively, you could move a very small circle around each part of the image and work out how often that circle contains a difference in luminance, and how large that variance is. You now have an estimate of how much variance in luminance occurs within the image at a fine spatial scale. You can then repeat the exercise with progressively larger circles to determine estimates for progressively coarser scales. When this type of analysis was applied to images of natural scenes most of the variance was found at coarse spatial scales and progressively less variance was found at finer spatial scales. Importantly the drop off was linear if plotted on a log scale, so it is said to obey a $1/f$ amplitude spectrum, where f reflects spatial scale (Maloney, 1986; Field, 1987; Geisler et al., 2001; Simoncelli and Olshausen, 2001; Mante et al., 2005; Geisler, 2008). The relevance of this for BR is that you can generate random patterns that obey this constraint and compare them to patterns that don't, and the former tend to dominate perception during BR (Baker and Graf, 2009).

We could add a $1/f$ amplitude spectrum to the grab bag of properties that contribute to image signal strength, or we could perhaps simplify things further. The images analyzed to determine the properties of natural scenes tend to be taken by proficient photographers. Omitted are the numerous defocused images taken by less gifted practitioners. If blurry photos were analyzed one would find that their amplitude spectrum does not conform to a $1/f$ spectrum, as there would be no content at a fine spatial scale and so the drop off in content with increasingly fine spatial scale would be too rapid. So we can take this type of finding as yet further evidence that focused images tend to dominate perception during BR, contributing to BR being uncommon as distant focused images tend to suppress awareness of the blurred images of selective obstructions.

SOME LAWS ARE MADE TO BE BROKEN

Ultimately BR is uncommon as unmatched monocular images in real life are often persistently suppressed. So you can place a finger immediately in front of one eye while reading this text, and wait, and wait, and wait, and for the vast majority it will never dominate perception by suppressing awareness of the text. This might prompt the question, are these situations relevant to BR, which after all is characterized by changes in perceptual dominance?

One of the oft quoted characteristics of BR is that increasing the relative signal strength of an unmatched monocular image will increase the frequency at which it becomes dominant, but will not extend its individual periods of dominance (Levelt, 1968). There is a great deal of evidence consistent with this premise (Levelt, 1968; Fox and Rasche, 1969; Mueller and Blake, 1989; Bossink et al., 1993), but clearly this second law of BR (Levelt, 1968) must be broken if the inherently weak signal strength of images relating to selective obstructions contributes to BR being absent in daily life.

More recently it has been established that the second law of BR breaks down if you further increment the signal strength of an image that already has a greater relative signal strength (Brascamp et al., 2006). This, and similar findings (Mueller and Blake, 1989; Bossink et al., 1993), has prompted a more nuanced guideline – that changes to relative signal strength will predominantly impact the dominance durations for the stimulus with a higher signal strength (Brascamp et al., 2006). Critically the impact is to lengthen its dominance durations. So, if we take this to a logical extreme the inherently weak signal strength of the blurred images of selective obstructions could result in their being reliably and persistently suppressed via the focused images of more distant objects.

SIGNAL STRENGTH, EYES, AND PATTERNS – EVERYONE'S WRONG

One of the longest running debates concerning BR regarded whether suppression targets the input from a given eye (Blake and Fox, 1974; Blake et al., 1979, 1992; Dutour, 1760 translated by O'Shea, 1999; Tong and Engel, 2001), or if it targets one of the two conflicting images (Dorrenhaus, 1975; Logothetis et al., 1996). There is good evidence that supports both propositions (Dorrenhaus, 1975; Blake et al., 1979; Logothetis et al., 1996), so contemporary consensus holds that both views were right all along, which is a popular sort of resolution, but not one that is necessarily correct. In the interests of being deliberately provocative one could suggest an alternative – that both camps were fundamentally wrong.

One possibility, that has perhaps not attracted the attention it deserves, is that during BR perception simply tracks the unmatched monocular signal with the instantaneously higher signal strength. Sometimes this might be tied to a particular monocular channel whereas at others it might switch rapidly between monocular channels. Why would an adaptation that has evolved to deal with a real-world constraint allow for a signal to switch rapidly between monocular channels?

For illustrative purposes, refer to the picture of a cute kitten that is **Figure 2**. As happens so often, this kitten has found itself in a tree. As a consequence one of its two eyes could easily become obstructed by a leaf while it looks into the distance, searching for a kind hearted soul with a ladder. If the wind were to start moving the branches a leaf could rapidly switch between selectively obstructing one or another eye, both eyes or neither eye. To maximize the kitten's chances of spotting a distant rescuer it would be optimal if the image of the proximate obstruction could instantaneously be suppressed no matter which eye it projects to, even if it rapidly switches between being encoded in different monocular channels.

Adult humans perhaps spend less time in trees than they should, and presumably much less time than our monkey-like forebears, but a conceptually similar scenario with which the reader might be better acquainted can happen when walking past a picket fence. If one looks through a proximate picket fence while walking, distant points of interest can rapidly switch between projecting to either eye, to both eyes, or to neither eye. Thus again, in order to maximize the visibility of interesting distant objects, it would beneficial to instantaneously suppress signals relating to proximate obstructions regardless of which eye they project to.

In a conceptual emulation of these real-world scenarios, recent studies have shown that if conflicting images that differ in signal strength alternate between the eyes, the stronger signal can reliably and persistently suppress awareness of the weaker signal (Arnold et al., 2007, 2008). Crucially the participants in these studies were very bored. While this is common in psychophysical tasks, in this context their boredom had scientific merit. In a majority of trials participants felt they were simply watching a static picture of a girl or a house (Arnold et al., 2007) or of even more tedious static white noise (Arnold et al., 2008). They were unaware that these images were switching between projecting to either eye in counterphase with a weaker signal. Note that there was no flicker to mask these alternations, as is necessary for persistent perceptual dominance

FIGURE 2 | Picture of a cute kitten stuck in a tree.

when conflicting images have approximately equal signal strength (Logothetis et al., 1996; Lee and Blake, 1999). Thus these studies were akin to our kitten being able to persistently see fixated objects in the distance as a swaying leaf rapidly switches between obstructing either eye.

While it is pleasing this could be demonstrated in BR experiments (Arnold et al., 2007, 2008), to continue the real-world emphasis of this discourse an uninhibited reader can demonstrate this principle by wiggling fingers in front of their eyes, such that each eye is alternately obstructed. You should find that you have no difficulty reading, that this text is persistently visible despite switching between being encoded in different monocular channels. If you are not secluded you may also find that people are looking at you.

The fact that perceptual dominance can seamlessly track an image as it is switched between the eyes (Arnold et al., 2007, 2008) implies that during BR perceptual dominance is resolved in favor of the instantaneously higher strength signal, as is required of a process that enhances the visibility of distant fixated objects over that of selective obstructions of an eye (see also Changizi and Shimojo, 2008). Consequently, from a functional perspective, BR is not resolved in favor of a signal from a specific eye (Blake and Fox, 1974; Blake et al., 1979, 1992; Dutour, 1760 translated by O'Shea, 1999; Tong and Engel, 2001), or in favor of a particular perceptual interpretation (Dorrenhaus, 1975; Logothetis et al., 1996), it is simply resolved in favor of the instantaneously higher strength signal.

WHY DOES PERCEPTUAL DOMINANCE CHANGE IN BR EXPERIMENTS?

Because relative signal strength changes.

A common assumption is that an image associated with a higher signal strength will begin to dominate perception, but its signal strength disproportionately wanes over time, resulting in a relative neural signal strength change, and a consequent switch in perceptual dominance (Lehky, 1988; Blake, 1989). The fine details of this standard account are a matter of debate, but the waning of the dominant signal seems to be at least partially driven by neural adaptation (Blake et al., 1990, 2003; Carter and Cavanagh, 2007; Alais et al., 2010). An additional common assumption is that some source of noise is necessary to explain the stochastic dynamics of BR (Brascamp et al., 2006; Kim et al., 2006). Note that a commonly overlooked source of noise would involve an interaction between involuntary stochastic eye movements (Yarbus, 1967; Murakami and Cavanagh, 1998; van Dam and van Ee, 2005; Martinez-Conde et al., 2006) and neural adaptation (see Sabrin and Kertesz, 1983; Georgeson, 1984). While the fine details of the standard account will doubtless continue to be debated, many are comfortable with the basic assumption that a dominance change is driven by a change in relative signal strength. Surprisingly behavioral evidence for this standard account was lacking until recently. But it has now been established that there is a gradual switch in the depth of suppression for content in either eye leading up to a dominance change. Crucially, content in the suppressed eye becomes relatively less suppressed in the moments leading up to a dominance change (Alais et al., 2010). These observations are perfectly consistent with BR being resolved in favor of the instantaneously stronger signal.

IS BR RELATED TO OTHER MULTI-STABLE PHENOMENA?

If perceptual suppressions during BR are driven by an adaptation that enhances the visibility of focused retinal images, instead of the blurred images of selective obstructions, BR would be unlikely to be *directly* related to a range of other multi-stable phenomena.

A popular assumption is that BR and other multi-stable phenomena are driven by a common process that deals with situations wherein perceptual input is ambiguous (Andrew and Purves, 1997; Leopold and Logothetis, 1999; Sterzer et al., 2009). For instance, an impression of a rotating cylinder or globe can be created by using a field of dots that translate back and forth. Crucially the direction of rotation is ambiguous, and seems to intermittently reverse (Miles, 1931; Howard, 1961; Blake et al., 2003). Motion-induced blindness is another example, wherein static dots can seem to intermittently disappear when surrounded by movement (Bonneh et al., 2001; Graf et al., 2002; Hsu et al., 2006; Wallis and Arnold, 2009) or flicker (Kawabe and Miura, 2007; Wallis and Arnold, 2008). Another classic example, depicted in **Figure 3**, is the Necker cube (Necker, 1832). Here lines mark the edges of a three dimensional cube. One of the sides of the cube is gray, whereas others are white. At times the gray side may seem to be located in front and at others behind, and as one watches this relationship will seem to intermittently reverse.

Other than their subjective similarity, with perception flipping between different states in the presence of unchanging input, is there any evidence that links various instances of multi-stable perception? In short, yes there is, but the evidence is inconclusive and it does not dictate that the diverse phenomena are driven by a common process.

One piece of evidence linking diverse multi-stable phenomena is that distributions of periods for which percepts seem to persist tend to conform to a gamma distribution (Kovacs et al., 1996; Logothetis et al., 1996; Andrew and Purves, 1997; Carter and Pettigrew, 2003; Murata et al., 2003). This is a complicated way of saying that a few percepts will persist for a very brief period and a few will persist for variable longer periods, but most will persist for a medium duration, in sum producing a distribution with a marked right skew. This constitutes weak

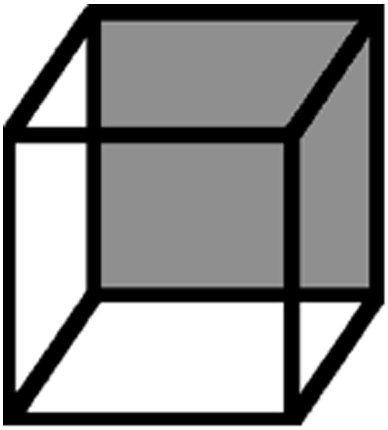

FIGURE 3 | The Necker cube.

evidence for a link for at least two reasons. First, distributions of obviously unrelated phenomena also conform to a gamma distribution, such as the distribution of rainfall over time (Barger and Thorn, 1949). Second, if one asks a person to press a button randomly, the distribution of times for which they depress the button might also conform to a gamma distribution (see Edwards and Li, 2002).

Stronger evidence for a link can be found in the fact that people who report slow perceptual switches during one type of multi-stable perception also tend to report slow switching in other forms (Carter and Pettigrew, 2003). This evidence is inconclusive, however, as perceptual dominance changes are seldom sharply defined. During BR, for instance, a switch in perceptual dominance can begin, with the dominant image seeming to fade or blur, then pause, reverse, then begin all over again. Consequently the criterion adopted for reporting a change in perceptual dominance can have a profound impact on the dynamics of the phenomenon as recorded by the experimenter. The correlation between the dynamics of diverse multi-stable phenomena might therefore speak to a tendency to adopt tight or relaxed criteria when reporting changes, rather than to the diverse phenomena being driven by a common process.

NEURAL SUBSTRATE – SOME OUTRAGEOUS SPECULATION

One of the reasons BR research has enjoyed a resurgence in prominence is the tantalizing prospect that it might shed light on the neural substrates of consciousness. Thus far this discussion has focused on the plausible function of binocular suppression – the proposal being that it is to facilitate the visibility of distant focused objects over that of more proximate obstructions. If this is the goal of perceptual suppressions during BR what, if anything, does this say about the neural substrates of BR?

At the risk of stating the obvious, this goal would necessitate that the substrate has access to each of the conflicting signals, so that it can determine which of the two signals most likely relates to an obstruction. Seemingly this would place the critical substrate in cortex, the first site in the human visual system where there is robust evidence of cross talk between inputs from the two eyes (Barlow et al., 1967; Poggio and Fischer, 1977). This goal also implies that the substrate is unlikely to be found at sites where activity maximally correlates with perception during BR. At such sites there is little evidence of a signal relating to suppressed input (Tong et al., 1998; Moutoussis et al., 2005; Jiang and He, 2006). If there is no activity relating to a suppressed input there would be no need to suppress that signal, and no prospect of that signal subsequently overcoming its counterpart. Such sites likely reflect the consequence of a process at an earlier critical substrate.

To have any hope of identifying a critical neural substrate for BR one probably needs a targeted measure of brain activity, not a gross measure. Targeted measures can simultaneously track signals relating to different inputs from within a single brain structure, and can therefore track slight fluctuations in relative signal intensity (see Brown and Norcia, 1997; Haynes and Rees, 2005). A gross measure of activity, on the other hand, can only provide information about the aggregate response of a neural substrate, and so one should probably not expect these to be sensitive to the critical signal strength fluctuations that seem to drive dominance changes during BR (see Alais et al., 2010). Gross measures of brain activity can, however, provide very pretty pictures of the brain, although the images are very expensive, and at least on occasion they are more colorful than computationally informative.

At this point popular consensus holds that there is no single critical site at which one or another signal is selected for suppression. This contention is encouraged by behavioral data showing that dominance can sometimes track the content of an eye (Blake et al., 1979), whereas at others it can track a particular image (Dorrenhaus, 1975; Logothetis et al., 1996). It is also encouraged by neuroimaging showing that signals at multiple sites can correlate with perception during BR (Tong et al., 1998; Lee and Blake, 1999; Polonsky et al., 2000; Tong and Engel, 2001; Haynes et al., 2005; Moutoussis et al., 2005; Wunderlich et al., 2005; Jiang and He, 2006). However, the interconnectivity of different brain regions dictates that neither observation rules out the possibility of there being a single critical substrate where activity is modulated via interactions with other brain regions (Watson et al., 2004; van Boxtel et al., 2008a,b; Arnold et al., 2009; Kang et al., 2009; Quinn and Arnold, 2010). For instance, recent behavioral data (Arnold et al., 2009) has strongly implicated monocular mechanisms within the spread of perceptual dominance across complex images (human faces) that are usually linked to coding in higher-level brain structures. The implication is that, due to feedback, activity in higher-level brain structures could shape analyzes at a single critical monocular substrate. Thus at this point there is no convincing evidence to discount the possibility that there is a single critical neural substrate for BR.

SO WHY IS BR UNCOMMON?

Discrepant monocular images are frequently encountered in daily life, but BR is seldom, if ever, experienced. So why do unmatched monocular images in the laboratory induce BR while those encountered outside it don't?

Binocular rivalry does not occur in daily life as the images of either differential occlusions of the two eyes or of selective obstructions of one eye are persistently suppressed. If one accepts that the mechanisms responsible for this are responsible for binocular suppressions during BR, it follows that BR is uncommon as images of obstructions almost never rival their counterpart, presumably largely because of signal strength differences. By implication, perceptual dominance during BR would simply track the instantaneously stronger signal, and is therefore unlikely to reflect the dynamics of a more abstract process that deals with ambiguity.

Alternatively, one could presume that the mechanisms responsible for the perceptual suppression of obstructions are unrelated to BR – that unmatched monocular images excite completely different processes in and outside of the laboratory. One could adopt this position, but it doesn't seem sensible.

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Binocular rivalry stimuli are common but rivalry is not

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A commentary on

Why is binocular rivalry uncommon? Discrepant monocular images in the real world

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Recently Arnold (2011) asked "Why is binocular rivalry uncommon?". He answered in an entertainingly written, provocative article, for which I thank and congratulate him. However, I will argue that Arnold's answer falls short in two respects and his assumption that rivalry is uncommon is correct for two reasons other than the one he discusses.

Binocular rivalry is a phenomenon of human visual perception that is easy to demonstrate in the laboratory by using a stereoscope to present one image to one eye and a different image to the other: one perceives one image rather than both, and the image one perceives alternates between the two at random (Wheatstone, 1838).

In answering the question, Arnold (2011) identified two situations outside the laboratory in which the view of one eye differs from that of the other for which he claimed there is no rivalry. The first is when an object, such as the trunk of a small tree, is near both eyes as we fixate on distant objects. The trunk projects a blurry, low-contrast, low-spatial-frequency (for which Arnold adopted Levelt's, 1968, umbrella term "stimulus strength") image onto the temporal region of the right-eye retina and onto the nasal region of the left-eye retina. In the corresponding regions of the other eye's retina, the distant objects project different, sharp images. The second is when a similar object, the tree trunk again, is closer to one eye, blocking its view. The trunk projects a blurry image onto the fovea of that eye, and the distant objects project different, sharp images onto the fovea of the other eye. In both these situations, Arnold said the sharp images dominate perception forever, preventing rivalry.

There are two problems for Arnold with these sorts of examples:

1. Although it is true that one will not immediately experience alternations between the blurry and sharp images, it is not true that there is no rivalry. Rather, the sharp images' dominating perception *is* a form of rivalry, well-known from laboratory studies as permanent suppression (Ooi and Loop, 1994).
2. If one waits for long enough, the blurry image *will* alternate with the sharp images (cf. Blake, 1977). Indeed, George (1936) reported that the extremely low-stimulus-strength image of the back of one's closed eyelid will eventually dominate the extremely high-stimulus-strength images viewed by the open eye.

There are at least two reasons other than that Arnold offered for why rivalry is not noticed outside the laboratory:

First, although Arnold is correct that images of equal stimulus strength rarely fall on the foveae of the two eyes, it is common that images of equal stimulus strength fall on corresponding peripheral areas of the retinae. For example, as I type this on my laptop, images of the rest of the room, several meters further from my eyes than the laptop screen, fall on the retinae below the fovea. When I attend to these areas, I can see that there are burry, diplopic images there, for example the vertical edge of a fireplace appears superimposed on the horizontal edges of the bricks of the fireplace. Similarly, when I look up at the fireplace, I can see the blurry vertical edge of my laptop screen crossing the blurry horizontal edge of a nearby table. If I pay attention to these diplopic areas, I see slow alternations of binocular rivalry. Laboratory studies show that rivalry rate in peripheral vision is much slower than in central vision (e.g., Blake et al., 1992).

The ubiquity of diplopic images away from fixation was discovered by al-Haytham in the eleventh century (Alhazen, 1989). These arise for regions off the location in space where images would be identical in the two eyes, the *horopter* (Aguilonius, 1613; Panum, 1858; Ogle, 1953). Binocular rivalry could be common off the horopter – it is simply not noticed.

In both situations Arnold describes, the tendency is for one to look at the nearby object (Mandelbaum, 1960), bringing identical sharp images onto the foveae. What is needed to resolve the issue of the ecological optics of binocular vision, rather than examples, is for them to be quantified by sampling the images the real world presents (cf. Howe and Purves, 2002; Howe and Purves, 2005).

Second, the eyes move about three times a second (e.g., Otero-Millan et al., 2008). This potentially places fresh images on each retinal region at the same rate. In the laboratory, these are likely to be similar to the previous images (because rival stimuli tend to be two-dimensional stimuli that display rivalry information wherever we look at them). But outside the laboratory, these images could be quite different during each fixation, and may be identical for some corresponding retinal regions. That is, any pair of corresponding retinal regions might have rival images for one fixation and similar, fusible images for the next. We know from laboratory research that turning on rival images briefly and turning them off for longer prevents rivalry from occurring by creating fusion of the two eyes' views (Dawson, 1915–1917; Kaufman, 1963; Wolfe, 1983; O'Shea and Crassini, 1984). Moreover, interspersing periods of fusion with periods of rivalry tends to prevent rivalry by promoting fusion (Julesz and Tyler, 1976; Buckthought et al., 2008).

In conclusion, Arnold (2011) posed an interesting question of why we do not notice rivalry when we look at the visual world outside the laboratory. In answering it, he identified two situations in which different strength images are projected into the two eyes, and claimed that rivalry does not occur. I have argued, to the contrary, that:

- Perception in the situations Arnold identified is consistent with what we know about rivalry and offers no challenge to theory;
- Different images in the two eyes are much more common in peripheral regions of the retinae than in central vision;
- We do not notice potential rivalry in peripheral vision because it is slower than in central vision and anyway we do not attend to it; and
- Movement of the eyes prevents rivalry from developing.

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I agree: binocular rivalry stimuli are common but rivalry is not

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I have recently argued that binocular rivalry (BR) is uncommon, despite discrepant monocular images being frequently encountered in daily life, because the images of proximate obstructions tend to be persistently suppressed from awareness by the better-focused images of objects near fixation (Arnold, 2011). This has the functionally adaptive consequence of enhancing the visibility of fixated objects. O'Shea has tapped his' encyclopedic knowledge of BR and come up with two facts on which, he suggests, this proposal falls short (O'Shea, 2011). I think this reflects a misapprehension, and it comes down to a perennial question, how long is a piece of string?

Readers should note the language above and in the original paper. I have argued that BR is uncommon, that exposure to unmatched monocular images in daily life does not typically result in BR, that images of proximate obstructions tend to be persistently suppressed from awareness. I would not, however, like to suggest that BR can never happen in daily life, nor that the images of proximate obstructions will invariably be eternally suppressed. This prudence was motivated by the very facts that O'Shea has now helpfully emphasized. But I should stress that these facts are entirely consistent with my conclusions.

So how long is persistent? A universal estimate is impossible assuming individual variability in the rate and extent of adaptation, so I will adopt a boredom threshold. Pick a word on this page and stare at it fixedly while placing a finger a couple of centimeters (perhaps an inch to the metrically challenged) in front of one eye. Wait. Wait some more. Keep waiting. I suspect the vast majority of readers will give into boredom before the word fades from view to be replaced by a blurry image of a finger. BR, as characterized by alternating perceptions, will not have begun because one of the two images (your blurry finger) was persistently suppressed. It is possible that this status is not eternal, but if it exceeds your boredom threshold I would regard it as persistent. In real life suppression would usually only need exceed 333 ms (the typical interval between gaze shifts, see Otero-Millan et al., 2008). I suspect suppression of your finger in the above circumstances would persist for at least two orders of magnitude longer than that, sufficient for you to gaze into a loved one's eyes, with just one of your own, for a period that becomes awkward. Such suppression may well be eternal for many, but the requisite experiment to test this seems impractical.

What of the points raised by O'Shea? First he reminds us that I am far from the first to point out that images with much greater signal strength can persistently suppress awareness of weaker images. This has been referred to as "permanent suppression" (see Ridder et al., 1992; Ooi and Loop, 1994). Well no conflict there. He then points out that if one waits long enough a very blurry image can suppress awareness of a focused image (Levelt, 1968; Fahle, 1982, 1983; Arnold et al., 2007), and that some people can even experience BR by simply closing an eye (eventually the visible scene apparently rivals with an impression of darkness from the closed eye, see George, 1936). So how long is that piece of string? Suffice to say that in daily life the suppression of proximate obstructions is of sufficient duration to enhance the visibility of fixated objects over selective obstructions and to ensure that BR is seldom, if ever, experienced.

Readers should also consider that a simple demonstration with your own finger might better indicate how persistent suppressions of selective obstructions can be than published papers on blur and BR. The physical characteristics of a defocused retinal image are difficult to emulate, and studies that have simply added Gaussian blur to rival images fail to do so (Arnold et al., 2007). Better attempts to mimic optical blur may not have approached the magnitude of blur characteristic of selective obstructions of one eye (Fahle, 1982, 1983). When studying visual phenomena one should not ignore the evidence of one's own eyes.

So why should BR ever happen in daily life? In answer I am going to launch into a discourse on the effects of Troxler (1804) fading and sensory adaptation, and how these interact with eye movements. This should be very familiar to most BR researchers, so if you want to skip ahead four paragraphs, feel free.

Occasional reports of BR in daily life are related to an apparent fading of visual input that can be apparent when one maintains steady fixation, a phenomenon known as Troxler (1804) fading (see http://en.wikipedia.org/wiki/File:Lilac-Chaser.gif for a demonstration). In the extreme, if retinal images are completely stabilized the entire scene can seem to fade to gray. Troxler fading is disrupted by either large voluntary (Otero-Millan et al., 2008) or slight involuntary (Martinez-Conde et al., 2006) eye movements. Both dictate that images are almost never entirely stable on the retina for any appreciable time and thereby disrupt adaptation, the oft-cited cause of both Troxler fading (Martinez-Conde et al., 2006) and dominance changes during BR (Blake et al., 1990, 2003; Carter and Cavanagh, 2007; Alais et al., 2010).

It is interesting to note that Troxler fading is more apparent in peripheral vision. It is believed this happens because involuntary eye movements are less effective at disrupting adaptation by changing the receptive fields used to encode input in peripheral vision (where receptive fields are relatively large) than at fixation (where receptive fields are small). Shifting input from an adapted into an unadapted cell's receptive field can bring about a sudden change in relative signal strength (Georgeson, 1984). As this would happen less frequently in peripheral vision, it may contribute to the slower rate of BR there than at fixation (Blake et al., 1992).

Because of Troxler fading and adaptation, an initially strong signal can become weak and thus begin to rival with other weak signals. This is entirely consistent with my proposal. Not only did I discuss the effects of adaptation at some length in the original article, and mention the importance of involuntary eye movements, but elsewhere colleagues and I have argued that the two most successful protocols for using binocular masking to persistently suppress awareness (Tsuchiya and Koch, 2005; Arnold et al., 2008) owe their efficacy to disrupting adaptation, thereby ensuring that masks retain a higher relative signal strength (see Arnold et al., 2008).

O'Shea has also pointed out that approximately equally blurred images are often encountered in the visual periphery, and that these might be subject to slow BR that is unnoticed due to inattention. At this juncture I would like to note that attention has been described to me as the Psychologist's weapon of mass explanation (D. Burr, personal communication), not because I think this point is particularly pertinent, but I do think it is amusing. On a more serious note, this suggestion poses no problem for my functional account. Inattention to peripheral stimuli might further contribute to BR being uncommon, but this would be irrelevant to my arguments concerning how suppressing awareness of proximate obstructions serves to facilitate visibility near fixation.

In a concluding statement O'Shea suggests that perceptual suppressions of proximate obstructions are consistent with what we know of BR and therefore pose no challenge to theory. To some extent I agree. I regard my contribution as being along the lines of pointing out that we all have a rather large appendage in front of our faces, but it is difficult to see the side of one's nose as it usually appears as a transparent thing, suppressed from awareness by the images of more distant better-focused objects. This, of course, is entirely consistent with a huge amount of BR research and with models of BR for which the concepts of signal strength and adaptation are central. My suggestion is simply that perception during BR is resolved in favor of the instantaneously higher strength signal, and that in daily life this has the functionally adaptive consequence of enhancing the visibility of distant fixated objects. I regard this as a very conservative proposal, but one which strongly implies that BR is driven by an inherently visual operation, and thus not by a more abstract process designed to deal with perceptual ambiguity (Andrew and Purves, 1997; Leopold and Logothetis, 1999; Sterzer et al., 2009).

In conclusion, O'Shea has argued that:

- The tendency for images of proximate obstructions to be persistently suppressed by the focused images of objects near fixation is consistent with what we know about BR.
- Different images, approximately matched in terms of signal strength, are common in the periphery of vision, and this may result in slow unnoticed BR. Unmatched images corresponding with fixation, however, are almost invariably unequal in terms of signal strength, and this has predictable consequences for BR.
- Movement of the eyes is also an important factor in preventing BR in daily life.

All of these points are in perfect harmony with my proposal that BR is driven by an adaptation that enhances the visibility of distant fixated objects over that of more proximate obstructions.

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Predictive context influences perceptual selection during binocular rivalry

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Prediction may be a fundamental principle of sensory processing: it has been proposed that the brain continuously generates predictions about forthcoming sensory information. However, little is known about how prediction contributes to the selection of a conscious percept from among competing alternatives. Here, we used binocular rivalry to investigate the effects of prediction on perceptual selection. In binocular rivalry, incompatible images presented to the two eyes result in a perceptual alternation between the images, even though the visual stimuli remain constant. If predictive signals influence the competition between neural representations of rivalrous images, this influence should generate a bias in perceptual selection that depends on predictive context. To manipulate predictive context, we developed a novel binocular rivalry paradigm in which rivalrous test images were immediately preceded by a sequence of context images presented identically to the two eyes. One of the test images was consistent with the preceding image sequence (it was the expected next image in the series), and the other was inconsistent (non-predicted). We found that human observers were more likely to perceive the consistent image at the onset of rivalry, suggesting that predictive context biased selection in favor of the predicted percept. This prediction effect was distinct from the effects of adaptation to stimuli presented before the binocular rivalry test. In addition, perceptual reports were speeded for predicted percepts relative to non-predicted percepts. These results suggest that predictive signals related to visual stimulus history exist at neural sites that can bias conscious perception during binocular rivalry. Our paradigm provides a new way to study how prior information and incoming sensory information combine to generate visual percepts.

Keywords: prediction, expectation, visual perception, ambiguous stimuli, multistable perception

INTRODUCTION

The visual system often receives ambiguous patterns of stimulation that are compatible with multiple interpretations of the visual environment. It therefore must use additional information to construct a single perceptual interpretation of the world. What is the nature of this additional information, and how does the visual system combine this information with incoming sensory signals to determine the contents of perceptual experience at any given moment? One possibility, based on Bayesian accounts of perception, is that prior knowledge about the likely contents of a visual scene influences the interpretation of sensory signals (von Helmholtz, 1866; Gregory, 1997; Weiss et al., 2002; Kersten et al., 2004; Knill and Pouget, 2004; Kveraga et al., 2007; Hohwy et al., 2008). Indeed, expectations arising from repeated presentations of visual stimuli or explicit instructions have been shown to facilitate processing of expected stimuli, resulting in improved visibility (Sekuler and Ball, 1977; Eger et al., 2007; Esterman and Yantis, 2010; Melloni et al., 2011) and both speeded (James et al., 2000; Eger et al., 2007; Esterman and Yantis, 2010) and enhanced (Dolan et al., 1997) recognition of visual stimuli.

Since natural environments are structured in time, one potentially rich source of prior information is patterns of visual stimulation in the recent past. Predictive coding frameworks describe how such a prior might be represented by neural activity, proposing that the brain continuously generates predictions of forthcoming sensory signals (Rao and Ballard, 1999; Friston, 2005). Comparisons of brain activity during expected and unexpected sensory stimulation have provided physiological evidence consistent with these frameworks (Summerfield and Koechlin, 2008; Alink et al., 2010). However, the effects of predictive neural signals on conscious perception have not been well explored. In particular, little is known about how prediction may influence the selection of a specific percept from competing alternatives.

A few studies have used ambiguous stimuli to provide initial insights into this question. For example, it has been shown that pairing secondary cues with rotating stimuli whose direction of rotation is defined by binocular disparity allows these cues to influence perception of rotation direction when disparity information is removed, making the physical rotation direction ambiguous (Haijiang et al., 2006; Sterzer et al., 2008). Specifically, the secondary cues increase the probability that the ambiguous stimuli will be perceived to rotate in the same direction as in the preceding conditioning period, showing that cue-induced expectations can influence perceptual selection. In addition, priming one perceptual interpretation of a binocular rivalry stimulus using either unambiguous low-contrast stimuli (Brascamp et al., 2007; Pearson et al., 2008) or mental imagery (Pearson et al., 2008) has been shown to bias perception during subsequent rivalry in favor of the primed percept.

Closer to the question of prediction, Maloney et al. (2005) found that recent visual experience influences the perception of an ambiguous apparent motion quartet. In this study, subjects viewed sequences of quartets with unambiguous rotation directions followed by an ambiguous quartet that could be perceived as rotating either clockwise or counterclockwise. Subjects' perceptual reports were influenced by the pattern of the preceding sequence, with an increased probability of interpreting ambiguous motion in a manner that was consistent with the expectation generated by the sequence.

Binocular rivalry provides a powerful and well-studied paradigm for investigating the effects of predictive context on visual perceptual selection. Binocular rivalry occurs when incompatible images are presented to the two eyes, leading to a perceptual alternation between the images, even though the visual stimuli remain constant. Unlike many other types of multistable percepts (Liebert and Burk, 1985; Peterson, 1986; Toppino, 2003; Shimono et al., 2011), binocular rivalry is often only weakly susceptible to cognitive control (Meng and Tong, 2004). In addition, there is evidence that binocular rivalry can be resolved at stages of visual processing as early as monocular regions of V1 (Polonsky et al., 2000; Tong and Engel, 2001) and the LGN (Haynes et al., 2005; Wunderlich et al., 2005), although this point continues to be debated (Logothetis et al., 1996; Lee and Blake, 1999; Blake and Logothetis, 2002; Tong et al., 2006). Therefore, studying the effects of predictive context on perceptual selection in binocular rivalry may improve understanding of the role of expectation in early visual processing. In one theoretical proposal, perceptual alternations during binocular rivalry are a product of predictive coding mechanisms (Hohwy et al., 2008), but specific hypotheses arising from this framework have not yet been experimentally tested.

In order to investigate the effects of predictive visual information on perceptual selection, we developed a novel binocular rivalry paradigm. On each trial, we first presented a sequence of identical images to the two eyes that generated an expectation about the next image in the series. We followed this predictive sequence with a rivalry display in which the predicted image was presented to one eye and a non-predicted image was presented to the other eye. We found that subjects were initially more likely to select the predicted image than the non-predicted image. In three additional experiments, we showed that only patterns of visual stimulation in the recent time period before the onset of rivalry contributed to the prediction effect and that prediction of the upcoming stimulus and adaptation to preceding stimuli had separate influences on perceptual selection. We also observed speeded perceptual selection of predicted relative to non-predicted stimuli. Our results suggest that predictive signals exist at neural sites that contribute to perceptual selection during binocular rivalry, and they emphasize the importance of prior information in determining the contents of conscious visual experience.

GENERAL METHODS

SUBJECTS

Forty-five subjects participated in one or more of the experiments. Five data sets were excluded from analysis (see Subject Exclusion), resulting in a total of 41 subjects (aged 18–41 years, 27 female), 15 of whom participated in Experiment 1, 8 in Experiment 2, 16 in Experiment 3, and 13 in Experiment 4. Two of the authors participated in two experiments, and one author participated in all four experiments. All subjects provided informed consent, and all experimental protocols were approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley.

VISUAL STIMULI

Stimuli were generated on a Macintosh PowerPC computer using Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were displayed on two halves of a gamma-corrected NEC MultiSync FE992 CRT monitor with a refresh rate of 60 Hz at a viewing distance of 100 cm. Subjects viewed all stimuli through a mirror stereoscope with their heads stabilized by a chin rest. Visual stimuli were circular patches, 1.8° in diameter, and were surrounded by a black annulus with a diameter of 2.6° and a thickness of 0.2°. Binocular presentation of this annulus allowed it to serve as a vergence cue to stabilize eye position and to ensure that the rivaling stimuli were presented to corresponding retinal locations in the two eyes. All stimuli were presented at 10% contrast on a neutral gray background (luminance of 59 cd/m^2), except in Experiment 4, in which the contrast of the stimuli was varied. All stimuli had the same mean luminance as the background.

On each trial, subjects viewed a stream of items presented identically to both eyes (the "pre-rivalry stream"), followed by a pair of rivalrous stimuli. A brief auditory cue signaled the start of each trial. Each stream item was presented for 300 ms and was followed by a 100 ms blank period. The rivalrous test stimuli were always two monochromatic, sinusoidal grating patches with a spatial frequency of 3 cpd and orthogonal (±45°) orientations. Rivalrous stimuli were presented for 4, 5, or 10 s in Experiment 1 (fixed stimulus duration for a given subject, with $N = 4, 5,$ and 6, respectively), 5 s in Experiments 2 and 4, and 10 s in Experiment 3.

One of the rivalrous test gratings always had an orientation that was consistent with the preceding predictive context; that is, it was the expected next image following the pre-rivalry stream. We call this the "matching" stimulus, since it matches the predictive context. The orientation of the other rivalrous test grating (the "non-matching" stimulus) was orthogonal to that of the matching stimulus and was inconsistent with the predictive context.

RIVALRY TASK

After passively viewing each pre-rivalry stream, subjects continuously reported their percept during presentation of the rivalrous test stimuli by holding down one of two keys: (1) grating tilted to the left, and (2) grating tilted to the right. Subjects were instructed to begin responding whenever the stimuli stopped moving or changing orientation in a regular fashion, to press a key continuously for as long as the corresponding percept persisted, and not to press any key for ambiguous percepts. Trials in which there was no response during the rivalry period were excluded from the analysis.

MEASURES OF PERCEPTUAL SELECTION

We expected that predictive context effects would be strongest at the beginning of the rivalry period, so analysis was focused on the initial response to the rivalry stimuli. In particular, we measured the proportion of trials in which the initial percept was the matching vs. the non-matching grating. We also measured the latency and duration of the initial response for both matching and non-matching percepts. The experiments were designed to investigate the effects of predictive context on initial rivalry percepts, and the relatively short rivalry presentation durations did not allow these effects to be assessed for subsequent percepts.

CATCH TRIALS

To ensure that subjects were following task instructions, approximately 10% of the trials in each experiment were catch trials, in which both eyes viewed identical left- or right-tilted gratings in the "rivalry test" portion of the trial. Catch trials were counterbalanced for grating orientation predicted by the stream (left or right tilt) and direction of tilt of the test stimuli (left or right). Catch trial latencies were used to assess the possibility of response bias, since response bias would be expected to lead to shorter response latencies for catch trial stimuli matching perceptual expectations than for non-matching catch trial stimuli.

EYE DOMINANCE SCREENING

Before participating in the study, each subject's eye dominance was measured in a brief pre-test. On each of 24 trials, subjects viewed static orthogonal rivalrous gratings with ±45° orientations for 10 s and continuously reported their percept as described above. Pre-rivalry streams were not presented in these screening trials. Eye dominance was defined as the relative number of trials in which the initial perceptual report corresponded to the grating presented to the left eye vs. the right eye.

SUBJECT EXCLUSION

Subjects with strong eye dominance were excluded because a substantial bias in favor of the left or right eye during binocular rivalry limits assessment of the effects of experimental manipulations in this study. Subjects whose initial eye dominance in either eye was greater than 85% during the eye dominance screening session were excluded and did not participate in any portion of the study. We also measured eye dominance throughout each experiment by analyzing initial rivalry responses and excluded subjects who had >85% eye dominance for at least half of the experimental session.

In addition to subjects who did not pass the initial eye dominance screen, five data sets from individual subjects were excluded from specific experiments (one from Experiment 1, three from Experiment 3, and one from Experiment 4). In each of Experiments 1 and 3, one subject was excluded for exhibiting excessive eye dominance during the experiment. In Experiment 3, one subject was excluded as an outlier (proportion first response matching was more than 2.5 SD away from the sample mean for one condition comparison). Finally, one subject was excluded in each of Experiments 3 and 4 for using incorrect response keys.

EXPERIMENT 1

Subjects viewed a predictive stimulus stream consisting of a series of oriented gratings presented identically to the two eyes. This stream generated a percept of rotating apparent motion, thereby establishing an expectation regarding the orientation of the next image in the series (**Figure 1A**). We measured the effect of this predictive context on subsequent perceptual selection during rivalry between orthogonal gratings. We hypothesized that predictive and sensory information would be integrated, increasing the likelihood of selecting the predicted percept. In this framework, predictive context functions as a prior that influences perceptual interpretation of the ambiguous visual stimuli.

METHODS

The pre-rivalry stream consisted of a sequence of monochromatic sinusoidal grating patches with a spatial frequency of 3 cpd. Orientations of successive stream items either increased or decreased by 45°, generating an apparent motion percept of rotation in either the clockwise or counterclockwise direction (**Figure 1A**). In the subsequent rivalry test, one of the two static gratings (the "matching" grating) had the orientation that came next in the apparent-motion series, and the other grating (the "non-matching" grating) had an orientation orthogonal to that predicted by the stream. The orientation of the first pre-rivalry stream stimulus was selected

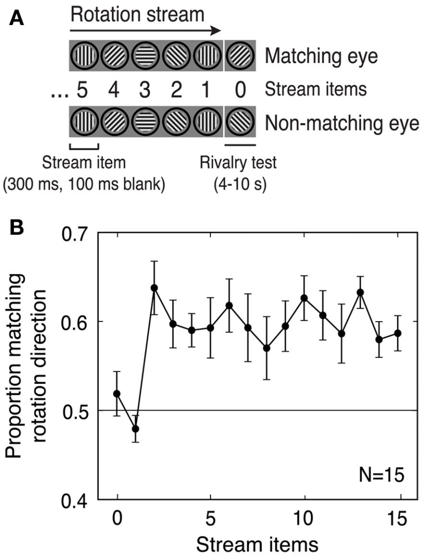

FIGURE 1 | Experiment 1: Predictive context in a pre-rivalry rotation stream influences initial perceptual selection in binocular rivalry. **(A)** Schematic of the stimuli (pre-rivalry stream and rivalry test). This example stream has clockwise rotation and five stream items shown. Stream items were always presented identically to both eyes, and rivalry items were always a pair of gratings with orthogonal ±45° orientations, with one of the two gratings matching the rotation direction (i.e., it was the expected next item in the rotation stream). **(B)** Subjects initially perceived the rivalrous grating that matched the rotation direction more often than they initially perceived the non-matching grating whenever the number of stream items was sufficient to define a rotation direction (two or more stream items). The size of this effect was similar for all stream durations from 2 to 15 items. Error bars are SEM.

so that the rivalrous gratings would always have oblique (±45°) orientations.

There were four pre-rivalry stream conditions: number of stream items (between 0 and 15), the grating orientation predicted by the stream (left or right tilt), the eye to which the "matching" rivalrous grating was presented (left or right eye), and stream rotation direction (clockwise or counterclockwise). The four stream conditions were fully counterbalanced across trials, resulting in a $16 \times 2 \times 2 \times 2$ design. Subjects completed either 24 or 32 trials for each stream length, and all conditions were randomly intermixed.

RESULTS

Perceptual selection is biased in favor of the predicted percept

A rotation stream of variable length (0–15 stream items; **Figure 1A**) was followed by presentation of a rivalrous pair of test gratings. The rotation stream generated a consistent percept of rotating apparent motion in either a clockwise or counterclockwise direction, and one of the rivalrous stimuli was consistent with this apparent motion percept (the "matching" stimulus), while the other (the "non-matching" stimulus) was not.

The results provide clear support for our hypothesis that prediction would influence perceptual selection: for rotation streams with two or more items (the minimum number needed to establish an apparent motion percept), perceptual selection in binocular rivalry was consistently biased in favor of the matching grating. Specifically, the matching grating was initially selected on about 60% of trials, regardless of the number of items in the stream (**Figure 1B**).

EXPERIMENT 2

In Experiment 1, the predictive context provided by rotation streams with 2–15 items enhanced selection of the matching grating, but the size of this effect did not depend on the length of the stream. We therefore asked in Experiment 2 whether very recent stimulus history (only the two items immediately preceding the rivalry test) was sufficient to bias perceptual selection, even for longer stream conditions.

METHODS

Half of the streams were composed of gratings that rotated either clockwise or counterclockwise (as in Experiment 1), and the other half were scrambled such that each orientation in the rotation stream was presented in a random position in the scrambled stream sequence (**Figure 2A**). However, for both rotation and scrambled trials, the final two stream items preceding the rivalrous test stimulus were always consistent with a particular rotation direction. This rotation direction defined the "matching" and "non-matching" rivalrous test grating. For scrambled streams, we ensured that there were no complete rotations in the stream by requiring at least two items in the first part of the stream to be different from the original rotation sequence. There were five stream conditions which were fully counterbalanced across trials: stream type (scramble or rotation), number of stream items (between 4 and 7), and the same final three conditions as in Experiment 1 (grating orientation predicted by the stream, the eye to which that matching grating was presented, and stream rotation direction). Subjects completed 24 trials for every combination of stream type and number of stream items, and all conditions were randomly intermixed.

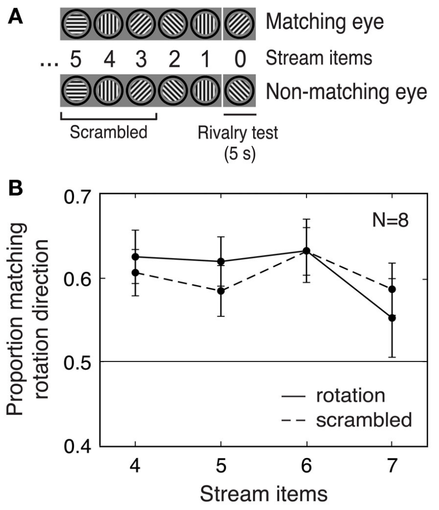

FIGURE 2 | Experiment 2: Effects of predictive context depend only on recent stimulus history. (A) Schematic of the stimuli. For the scrambled condition, the order of the gratings in the first part of the rotation stream (preceding the final two items) was randomized so that the first part of the stream did not contain a consistent rotation. However, the two stream items immediately before the rivalry test were always consistent with a particular rotation direction (in this example, clockwise) for both rotation and scrambled trials. **(B)** Scrambling the sequence of orientations in the stream prior to the final two stream items did not diminish the rotation matching effect. Error bars are SEM.

RESULTS

Recent stimulus history drives predictive effects on perceptual selection

We compared initial perceptual selection for rivalrous test stimuli presented after streams with either a scrambled sequence of orientations in the initial part of the stream or with fully coherent rotation throughout (**Figure 2A**). If consistent predictive stimulus history over an extended viewing period is required for the rotation matching effect, then disruption of predictive context in the early part of the stream in the scrambled condition should reduce the size of this effect, compared to the full rotation condition. However, if only recent stimulus history is responsible for the rotation matching effect, then the size of the effect should be identical in the rotation and scrambled conditions, and this is the result that was obtained.

For rotation streams, we found increased selection of the predicted percept (combining all stream lengths), replicating the results of Experiment 1 [$t(7) = 21.28$, $p < 0.001$; **Figure 2B**]. Scrambled streams also generated a significant rotation matching effect [$t(7) = 29.77$, $p < 0.001$; **Figure 2B**], suggesting that consistent rotation throughout the stream was not required for the effect. Moreover, there was no significant difference between the rotation and scrambled conditions in the size of the mean matching effect across all stream lengths [paired t-test, $t(7) = 0.19$, n.s.; **Figure 2B**]. Together, these results show that the predictive context provided by only the two items immediately preceding the rivalry test was sufficient to maximally bias perceptual selection in this paradigm.

EXPERIMENT 3

Orientation-specific adaptation to stream gratings might have contributed to the rotation matching effects observed in Experiments 1 and 2. The stimuli in these experiments controlled for adaptation to the final stream item, because the angular difference between the final stream grating and each of the rivalrous gratings (both matching and non-matching) was always 45°. However, it was still possible that the rotation matching effect was influenced by orientation-specific adaptation to the second-to-last stream item (**Figure 3A**). This grating always had the same orientation as the non-matching rivalry grating, so it was possible that adaptation to this grating biased perceptual selection against the non-matching grating orientation (e.g., Blake and Overton, 1979, but also see Brascamp et al., 2007), perhaps contributing to the rotation matching effect. We conducted Experiment 3 to compare the effects of prediction and adaptation on perceptual selection in this paradigm.

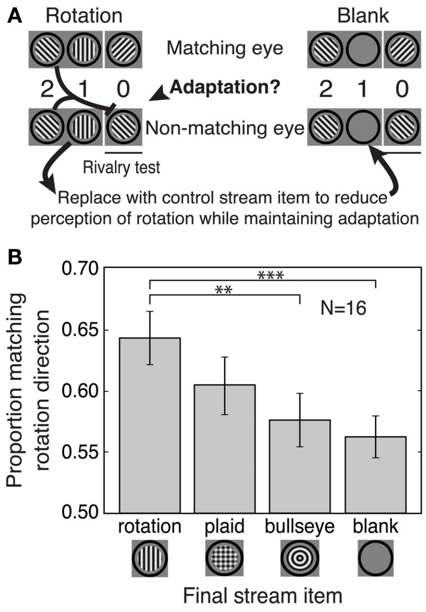

FIGURE 3 | Experiment 3: Separate contributions of prediction and adaptation to the matching effect. (A) Schematic of the stimuli. Left: An example rotation stream showing how adaptation to the second-to-last stream item could bias selection toward the matching stimulus. Right: To control for adaptation, the final stream item was replaced with one of three other stimuli (plaid, bullseye, or blank; the blank condition is shown here). These alternative final stream items reduced the perception of rotation while maintaining any orientation-specific adaptation to the second-to-last stream item. **(B)** The size of the rotation matching effect decreased with increasing disruption of rotation perception. The bullseye and blank conditions quantify the effects of adaptation alone, as no perception of rotation was possible for these conditions. The matching effect for the rotation condition was significantly larger than that for the bullseye or blank condition, indicating an effect of predictive context that cannot be accounted for by adaptation. Error bars are SEM. $^{**}p < 0.01$; $^{***}p < 0.005$.

METHODS

Subjects viewed two pre-rivalry stream items on all trials, based on our finding from Experiments 1 and 2 that two stream items were sufficient to produce the rotation matching effect. The first stream item was always a sinusoidal grating with an orientation of either +45° or −45°, presented to both eyes. The second stream item, also presented binocularly, was one of the following: a vertical or horizontal grating (generating, together with the first stream item, apparent clockwise or counterclockwise rotation, as in Experiment 1), a blank (mean luminance), a bullseye pattern of 3-cpd sinusoidal concentric circles, or a plaid pattern formed by superimposing vertical and horizontal 3-cpd gratings.

The blank, bullseye, and plaid stimuli were designed to disrupt rotational apparent motion perception for the pre-rivalry stream, compared to the rotation stimulus. In all trials, the orientation of the first stream item determined the orientation of the test grating that would be consistent with perceived rotational motion and therefore defined which rivalrous test grating was "matching" and which was "non-matching." Each trial had four fully counterbalanced conditions: stream type (the four types described above) and the same final three conditions as in the earlier experiments (grating orientation predicted by the stream, the eye to which that matching grating was presented, and stream rotation direction). Each subject completed 48 trials for each stream type, and all conditions were randomly intermixed.

RESULTS

Separate effects of prediction and adaptation on perceptual selection

To determine the contribution of adaptation to the matching effect, we created streams that preserved the second-to-last stream item, thereby maintaining orientation-specific adaptation, but that altered the final item in the stream, thereby reducing or eliminating the perception of stream rotation (**Figure 3A**). Perceptual selection for these reduced predictive context streams was compared to that for a full rotation condition.

This experiment included a total of four stream conditions (**Figure 3B**). Matching effects in the *rotation* condition could be due to prediction, adaptation, or some combination of these factors. In the *blank* and *bullseye* conditions, there was no apparent-motion percept (and therefore no predictive information available), so any bias in perceptual selection for this condition could only be due to adaptation. Finally, the *plaid* condition was an intermediate condition in which the presence of both vertical and horizontal grating components in the plaid may have interfered with the perception of apparent motion in the stream without abolishing it altogether. This is because both vertical and horizontal components were consistent with the same "matching" rivalry grating. For example, a left-tilted grating followed by a plaid could be seen as clockwise apparent motion if the vertical plaid component were emphasized or as counterclockwise apparent motion if the horizontal plaid component were emphasized, but both of these apparent rotation percepts predict a right-tilted matching grating during the rivalry test. The plaid condition therefore contains some predictive context but presumably generates a weaker apparent motion percept than the rotation condition.

The results of Experiment 3 revealed separate effects of adaptation and prediction on perceptual selection (**Figure 3B**). There were reliable matching effects in the adaptation-only conditions (blank and bullseye), indicating that orientation-specific adaptation to the second-to-last stream item biased selection against the non-matching (adapted) grating. However, the matching effect for the rotation condition (resulting from both adaptation and prediction effects) was significantly larger than the adaptation-only effects [rotation vs. blank, $t(15) = 3.36$, $p < 0.005$; rotation vs. bullseye, $t(15) = 2.96$, $p < 0.01$], indicating that prediction enhances the rotation matching effect beyond what is found for adaptation alone. The size of the matching effect for the plaid was in between that of the rotation condition and the adaptation-only conditions, as expected if this stimulus produced intermediate levels of apparent motion perception. Thus, the effects of pre-rivalry stream rotation on perceptual selection of binocular rivalry stimuli reflect a combination of adaptation and prediction effects that can be experimentally dissociated.

EXPERIMENT 4

The strength of orientation-selective adaptation depends on stimulus contrast (Blakemore and Nachmias, 1971), while predictive context is provided for any contrast for which the stream items are visible. We therefore conducted Experiment 4 to measure the contrast dependence of the adaptation and prediction effects described above.

METHODS

The rotation and blank stream conditions from Experiment 3 were used, and the items in the streams had 5, 25, or 100% contrast. The contrast of the rivalrous gratings was also 5, 25, or 100%, independent of the stream contrast. Thus, each trial had six fully counterbalanced conditions: stream type (rotation or blank), stream item contrast, rivalrous stimuli contrast, and the final three conditions as in the earlier experiments. "Matching" and "non-matching" rivalrous test gratings were defined as in Experiment 3. Each subject completed 32 trials for every combination of stream type, stream item contrast, and rivalrous stimuli contrast, and all conditions were randomly intermixed.

RESULTS

Effects of stimulus contrast dissociate prediction and adaptation

We independently varied the contrast of the stream items and of the rivalrous stimuli for both the rotation and blank conditions from Experiment 3 and observed a main effect of stream contrast [ANOVA, $F(2,48) = 11.95$, $p < 0.001$; **Figure 4**], with increasing stream contrast causing a dramatic increase in the magnitude of the matching effect in the blank (adaptation-only) condition. However, increasing stream contrast led to a smaller increase in the matching effect in the rotation condition [stream contrast × stream type interaction, $F(2,48) = 10.74$, $p < 0.001$], mainly due to the significantly larger matching effect for the rotation compared to the blank condition at the lowest stream contrast [ANOVA for 5% stream contrast condition, main effect of stream type, $F(1,24) = 7.31$, $p < 0.05$]. At this low contrast, adaptation is weak, and prediction effects dominate.

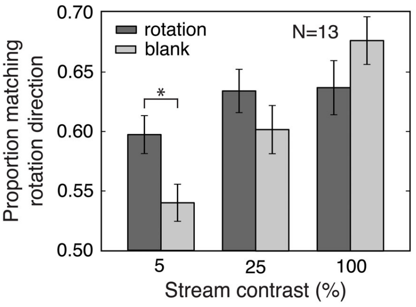

FIGURE 4 | Experiment 4: Effects of stream contrast on prediction and adaptation. Increasing the contrast of the stream items increased the size of the matching effect for the blank condition more than for the rotation condition. The prediction effect corresponds to the difference between the rotation and blank values and was greatest at the lowest stream contrast. The blank condition quantifies the effects of adaptation alone, and these effects were larger for higher stream contrasts. Error bars are SEM. $^*p < 0.05$.

We also observed a main effect of contrast of the rivalrous test gratings [$F(2,48) = 8.65$, $p < 0.005$], with the size of the matching effect decreasing as rivalry stimulus contrast increased, for both rotation and blank conditions [no interaction between rivalry stimulus contrast and stream type: $F(2,48) = 0.01$, n.s.]. This effect of rivalry stimulus contrast could be because competition between higher contrast rivalry stimuli is less affected by either prediction or adaptation. Because the blank condition represents only adaptation effects, while the rotation condition includes effects of both adaptation and prediction, the lack of a significant interaction indicates that adaptation was the more important factor in the effect of rivalry stimulus contrast. **Figure 4** displays data for each stream contrast condition, collapsed across rivalry stimulus contrast.

The different effects of stream contrast in the rotation and blank conditions provide an additional dissociation of prediction and adaptation effects. This experiment showed a robust prediction effect even for a very low (but still above the visibility threshold) stream contrast of 5%, while adaptation effects were minimized at this contrast. These results suggest that low-contrast stimuli can be used to reduce adaptation effects, providing a strategy for emphasizing prediction effects that could be employed in future studies of predictive context. Experiments 1–3 used 10% contrast for both pre-rivalry stream and rivalry stimulus items, and this relatively low contrast may have helped to reveal prediction effects in these experiments.

ADDITIONAL RESULTS

PREDICTION SPEEDS PERCEPTUAL SELECTION AS MEASURED BY LATENCY TO REPORT INITIAL PERCEPT

So far we have demonstrated that predictive context affects which percept is initially selected during binocular rivalry. We also analyzed the effects of predictive context on the latency and duration of the initial response to the rivalrous test stimuli. We present latency data for Experiment 3 because it contains the most effective experimental control of adaptation effects. For the conditions that contain predictive context (rotation and plaid), response latencies were shorter for matching than for non-matching initial percepts, while no differences between matching and non-matching initial percepts were observed for the bullseye and blank conditions, which lack predictive context [**Figure 5**; rotation, $t(15) = 4.26$, $p < 0.001$; plaid, $t(15) = 3.06$, $p < 0.01$; bullseye, $t(15) = 1.73$, n.s.; blank, $t(15) = 1.63$, n.s.]. Therefore, adaptation effects alone do not reliably speed perceptual report, while prediction does. Similar results were also obtained in Experiments 1, 2, and 4: we found shorter response latencies for matching than for non-matching initial percepts, indicating that predictive context speeded perceptual report for predicted stimuli.

We observed less consistent effects of prediction on the duration of the initial response across the experiments. Our ability to accurately estimate the initial response duration may have been affected by the duration of the rivalry test period, which was 10 s or shorter, depending on the experiment. Because of this limited response window, some initial responses were maintained until the end of the trial and terminated at that point. When we excluded those truncated responses, we found a longer mean duration of initial responses for matching than for non-matching stimuli in the rotation condition for all four experiments. In Experiment 3, the difference in mean first response duration between matching and non-matching trials with non-truncated initial responses was significant only in the rotation condition [rotation, $t(15) = 2.82$, $p < 0.05$; plaid, $t(15) = 0.19$, n.s.; bullseye, $t(15) = 0.19$, n.s.; blank, $t(15) = 1.11$, n.s.]. This suggests that prediction prolongs the predicted initial percept compared to the non-predicted percept.

POSSIBLE CONTRIBUTION OF RESPONSE BIAS TO PREDICTIVE CONTEXT EFFECTS

In principle, the effects of predictive context we report could be due to perceptual selection of matching stimuli and/or a response bias in favor of these stimuli. However, data from catch trials argue against a simple response bias as the source of our predictive context effects. Every experiment contained catch trials, in which the pre-rivalry stream sequences were the same as in the experimental trials, but instead of a rivalrous pair of gratings, the same grating was presented to both eyes. For these unambiguous test stimuli, there were no significant effects of predictive context in any experiment, either on the initially selected percept (proportion of responses matching the rotation direction) or on the initial response latency (matching vs. non-matching responses). These findings suggest that predictive context did not result in errors in perceptual report that led subjects to report the matching percept when they did not actually see it and did not result in subjects responding to a matching stimulus more quickly, given identical perceptual latencies for matching and non-matching stimuli.

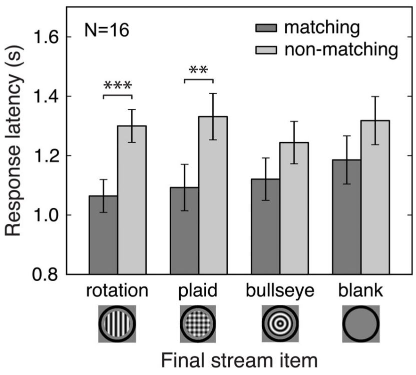

FIGURE 5 | Effects of prediction and adaptation on latency of initial response. Results from Experiment 3 are shown. Response latencies were shorter for initially reported matching compared to non-matching rivalry stimuli. This effect was observed only in the rotation and plaid conditions, suggesting that prediction but not adaptation speeded perceptual report. Error bars are between-subject standard errors of the difference between matching and non-matching percept response latencies. $^{**}p < 0.01$; $^{***}p < 0.001$.

DISCUSSION

Our experiments provide the first evidence that predictive information influences perceptual selection during binocular rivalry: stimuli that were consistent with the established predictive context tended to dominate over inconsistent stimuli in initial perceptual selection. We further characterized three key aspects of the effects of predictive information on perceptual selection in our paradigm. First, we showed that only recent visual stimulus history contributed to the prediction effect. As few as two stream items (the minimal number required to establish a rotation direction) produced the maximal rotation matching effect (Experiment 1), and introducing random sequences of grating orientation prior to these two stream items did not change the size of the matching effect (Experiment 2). Second, prediction and orientation-specific adaptation separately contributed to the matching effect (Experiment 3), and the results of Experiment 4 suggest a strategy for minimizing the influence of adaptation, namely using a low stream contrast. Adaptation effects were reduced for low stream contrasts, while prediction effects were robust for all tested contrasts. Third, subjects were faster to report initial percepts that matched the predictive context compared to those that did not. In Experiment 3, this effect was specific to the prediction conditions and was not found in the adaptation-only conditions.

PREDICTIVE CONTEXT AND RESPONSE LATENCY

We found that the latency of the first response was shorter for percepts that matched the expectations established by predictive context. Physiological studies also suggest that prediction may reduce the latency of neural responses to expected stimuli. Melloni et al. (2011) found that EEG activity differentiating seen and unseen stimuli occurred about 100 ms earlier when the visual stimulus was expected compared to when it was unexpected. In addition, James et al. (2000) showed that BOLD responses peaked earlier for primed than for unprimed visual stimuli in a manner that correlated with behavioral report. Finally, latencies of single cell responses to images embedded in natural sequences are shorter than response latencies for the same images presented in isolation (Perrett et al., 2009).

EFFECTS OF PRIMING ON PERCEPTUAL SELECTION

Perceptual history has previously been shown to contribute to perceptual selection during binocular rivalry in various priming paradigms. Intermittent presentations of rivalry stimuli tend to stabilize the perceptual interpretation, such that the perceptual alternations characteristic of continuous rivalrous viewing are markedly slowed (Leopold et al., 2002; Pearson and Brascamp, 2008). In this case, priming arises from a neural signal associated with the previous perceptual decision and not with the stimulus *per se*, since the stimulus is always ambiguous. Unambiguous primes can also increase the likelihood that the primed stimulus will be selected during subsequent rivalry. This effect depends strongly on contrast, with lower contrast primes facilitating subsequent selection of the prime, and higher contrast primes suppressing it as a result of adaptation (Brascamp et al., 2007; Pearson et al., 2008). Mental imagery can also bias subsequent selection during rivalry toward the previously imagined percept (Pearson et al., 2008).

In the present study, the rotating pre-rivalry stream could be considered a prime for the predicted rivalry stimulus. However, our experiments are importantly different from previous binocular rivalry priming studies in that the predicted ("primed") orientation never appeared immediately before the rivalry period and indeed was often not presented at any time during the pre-rivalry stream. Therefore, the effects of predictive context in our study could not be due to a residual memory trace from a previously presented stimulus but instead were due to a predictive signal specific to the expected grating orientation. Likewise, our predictive effects were likely not due to subjects imagining the expected next stimulus, since imagery effects are negligible for brief imagery durations (Pearson et al., 2008), and the rivalry stimuli were always presented immediately after the pre-rivalry stream in our experiments. Nonetheless, it is possible that selection biases due to stimulus priming, imagery, and prediction share common neural and/or psychological substrates, a question which will be of interest in future research.

ATTENTION AND PREDICTIVE CONTEXT

It is possible that increased allocation of attention to the features of the expected stimulus may have played a role in the prediction effects we observed. Exogenously cueing attention to one of two superimposed stimuli has been shown to increase the likelihood that the cued stimulus will initially dominate when the two stimuli are made rivalrous (Ooi and He, 1999; Mitchell et al., 2004; Chong and Blake, 2006; Hancock and Andrews, 2007). Similar effects on initial dominance have been found when endogenous attention is directed toward one of the stimuli during a difficult task prior to binocular rivalry (Chong and Blake, 2006).

It should be noted, however, that in these studies, a cue draws attention to a currently visible stimulus, thereby increasing the likelihood that the cued stimulus perceptually dominates in a subsequent rivalry period. This is different from our study, in which the grating presented immediately before the rivalry display (the final stream item) has equal angular distance from the two rivalrous gratings. If attention were simply cued to the features of the final grating in the pre-rivalry stream, it would not favor either of the rivalrous gratings.

In creating predictive context that generates an expectation about the appearance of a future stimulus, our study should also be distinguished from previous studies of expectation that have used instructions to generate an attentional set for a particular kind of stimulus (Summerfield et al., 2006; Summerfield and Koechlin, 2008; Summerfield and Egner, 2009). In these studies, many types of stimuli appear with equal likelihood, but only one type (the "expected" stimulus) is relevant for performing the task. We might call expectations of this type "attentional expectations." In our study, on the other hand, subjects presumably expect that a stimulus rotating in a particular direction will continue to rotate in that direction, but the predicted and non-predicted stimuli (matching and non-matching orientations) are equally task relevant. Such expectations about the likely future state of the stimulus are "perceptual expectations." An important task for future research will be to understand how these two types of expectations are represented in the brain and how they influence the processing of sensory signals (Summerfield and Egner, 2009).

Finally, attention and predictive coding mechanisms are thought to have different effects on sensory responses in the brain, with attention facilitating (Carrasco, 2011) and predictive coding mechanisms suppressing responses at early stages of visual processing (Summerfield and Koechlin, 2008; Garrido et al., 2009; Alink et al., 2010; Melloni et al., 2011; but see Spratling, 2008, 2010 for an attempt to reconcile effects of attention and predictive coding in a single model). An attention-based account of our predictive context effects would postulate enhanced responses in neurons representing the predicted stimulus at lower hierarchical levels of the visual system, while reduced responses in these areas would be consistent with predictive coding models.

RELATIONSHIPS WITH OTHER EFFECTS OF PREDICTIVE VISUAL MOTION CONTEXT ON PERCEPTION

The prediction effects we describe may share mechanisms with recently reported effects of predictive motion extrapolation on a visual detection task (Roach et al., 2011). In this study, detection performance for patterned targets at the leading edge of a moving grating was measured, and the results suggest that the visual system generates a predictive signal resembling a low-contrast extrapolation of the grating in the direction of motion. The effects depended on the spatial phase of the gratings and extended over only about 1° of visual angle, leading the authors to speculate that they could be mediated by cortical area V1. A similar weak but pattern-specific representation generated by extrapolation of rotational motion could also account for the predictive rivalry effects we observed. Our results suggest that this type of motion signal extrapolation could influence not only visual sensitivity but also perceptual selection during ambiguous visual stimulation.

Our findings may also be related to the phenomenon of representational momentum – the observation that memory for the final position of a moving target is mislocalized in the direction of motion (Freyd and Finke, 1984; Hubbard, 2005). Representational momentum can be observed following presentation of a series of discrete views of a rotating target, in which motion was implied (as in our study; Freyd and Finke, 1984; Freyd and Johnson, 1987). The spatiotemporal continuity of motion may be a particularly strong prior that could play a role in a range of perceptual and neural effects (Watamaniuk and Mckee, 1995; Doherty et al., 2005).

PRIORS AND PERCEPTION

An important question for future research is the extent to which the predictive effects we report generalize to other types of priors. Although they are not always discussed in a Bayesian framework, other rivalry studies have also documented what may be the effects of priors on perceptual selection. For example, images with natural image statistics tend to dominate over more artificial images (Baker and Graf, 2009), upright faces tend to dominate over inverted faces (Engel, 1956; Zhou et al., 2010), and images of floors tend to dominate over images of ceilings (Ozkan and Braunstein, 2009). These findings, including our own, can be interpreted as empirical evidence for a long-standing notion, that perception is an inference process (von Helmholtz, 1866; Gregory, 1997; Kersten et al., 2004; Kveraga et al., 2007). Bayesian modeling of perception of ambiguous visual displays has been a particular focus of theoretical work in this vein (Dayan, 1998; Schrater and Sundareswara, 2007; Hohwy et al., 2008; Sundareswara and Schrater, 2008; Gershman et al., 2009), and recent empirical work shows that Bayesian cue combination can explain perception of a bistable depth stimulus (Moreno-Bote et al., 2011).

PREDICTIVE CODING AND NEURAL MECHANISMS OF BINOCULAR RIVALRY

In predictive coding models of the visual system (Mumford, 1992; Rao and Ballard, 1999; Friston, 2005; Friston and Kiebel, 2009), higher levels of the visual hierarchy predict upcoming responses in lower levels, and these predictions are compared with actual responses in the lower levels via an inhibitory mechanism. Residual signal in the lower levels therefore serves as an error signal that is then transmitted to higher levels in order to improve future predictions. According to this model, posterior information about the percept is represented at higher hierarchical levels, and the dominant percept corresponds to the perceptual hypothesis with the highest posterior probability. Top-down predictions therefore explain away predicted bottom-up signals, and so the representation of a stimulus at the lower levels should have reduced error-related activity while that stimulus is perceived (Murray et al., 2002; Friston, 2005; Hohwy et al., 2008; Summerfield and Koechlin, 2008; Alink et al., 2010).

Neurophysiological studies during binocular rivalry have yielded mixed results regarding correlations between perception and activity in different visual areas. Few (if any) neurons in early visual areas such as the LGN (Lehky and Maunsell, 1996; Wilke et al., 2009) and V1 (Leopold and Logothetis, 1996) have spiking responses that vary as a function of perception during binocular rivalry. In contrast, later visual cortical areas such as V4, MT, and IT have more neurons with perceptually correlated responses (Logothetis and Schall, 1989; Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997). This increase in the proportion of neurons whose activity reflects the perceptual interpretation of a rivalry stimulus at increasingly higher levels of the visual processing hierarchy is consistent with predictive coding frameworks, in that the highest levels of predictive coding hierarchies should most closely reflect the final perceptual interpretation. That being said, these neurophysiological studies all employed stimuli that were matched to the response preferences of the recorded neurons in each visual area, raising the possibility that perception-related neural modulation depends on stimulus complexity, as neurons in higher-order areas respond preferentially to more complex stimuli than those in lower-order areas. However, even for similar rivalrous grating stimuli, the proportion of neurons with perceptually modulated responses is higher in V4 than in V1/V2, making it unlikely that stimulus complexity is the only factor accounting for differences between visual areas in percept-related modulations (Leopold and Logothetis, 1996).

In predictive coding frameworks, lower hierarchical levels should carry an error signal for suppressed percepts, and the existence of neurons in V4 (Leopold and Logothetis, 1996) and MT (Logothetis and Schall, 1989) that show enhanced responses during rivalry suppression of their preferred stimulus may be consistent with this. On the other hand, Leopold and Logothetis (1996) did not find V1/V2 neurons that showed enhanced responses when their preferred stimulus was perceptually suppressed, which is at odds with predictive coding models and may be an interesting avenue for further investigation.

In contrast to single cell activity, fMRI and low frequency (<30 Hz) LFP signals have been shown to correlate strongly with perception during binocular rivalry in visual areas as early as V1 (fMRI: Polonsky et al., 2000; Tong and Engel, 2001; Lee and Blake, 2002; Lee et al., 2005; LFP: Wilke et al., 2006) and the LGN (fMRI: Haynes et al., 2005; Wunderlich et al., 2005; LFP: Wilke et al., 2009). In the context of predictive coding, these responses could be interpreted as reflecting top-down predictive feedback from higher cortical regions (Hohwy et al., 2008), particularly if BOLD and LFP signals primarily reflect synaptic inputs to a given population of neurons (Logothetis et al., 2001; Logothetis, 2008).

CONCLUSION

The extent to which the resolution of binocular rivalry is driven by competition between representations at lower levels, higher levels, or multiple hierarchical levels in the visual system has been the subject of much debate (Logothetis et al., 1996; Lee and Blake, 1999; Blake and Logothetis, 2002; Tong et al., 2006). Our approach of experimentally manipulating top-down priors on perceptual selection could help to clarify this question by providing experimentally distinguishable hypotheses about how prior information and sensory information combine within neural circuits. Such studies could be especially informative when psychophysical manipulations of prior information are combined with physiological measures of neural activity at different hierarchical levels in the visual system.

Here, we have demonstrated predictive effects on perceptual selection during binocular rivalry. Therefore, predictive context influences what is often thought to be a low-level competitive process in a manner consistent with theories of predictive coding. Our findings suggest that the visual system uses recently encountered visual information to help construct a single perceptual interpretation of a scene. Thus, predictive information may play an important role in natural vision by helping to constrain perceptual interpretations of the visual world to those that are most consistent with the recent past.

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Understanding attentional modulation of binocular rivalry: a framework based on biased competition

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Starting from early scientific explorations of binocular rivalry, researchers have wondered about the degree to which an observer can exert voluntary attentional control over rivalry dynamics. The answer to this question would not only reveal the extent to which we may determine our own conscious visual experience, but also advance our understanding of the neural mechanisms underlying binocular rivalry. Classic studies, intriguingly, reached contradictory conclusions, ranging from an absence of attentional control, as advocated by Breese, to nearly complete control of rivalry dynamics, as reported by Helmholtz. Recent investigations have revisited this question, but the results have continued to echo the conflicting findings of earlier studies, seemingly precluding a comprehensive understanding of attentional effects on rivalry. Here, we review both classic and modern studies, and propose a unifying framework derived from the biased competition theory of attention. The key assumption of this theory is that the nature of stimulus conflict determines the limits of attentional modulation. For example, a condition in which unresolved stimulus conflict transpires through many levels of visual processing should be very susceptible to attentional control. When applied to binocular rivalry, this framework predicts strong attentional modulations under conditions of unresolved stimulus conflict (e.g., initial selection) and conditions where conflict is resolved at higher levels of visual processing (e.g., stimulus rivalry). Additionally, the efficacy of attentional control over rivalry can be increased by utilization of demanding, behaviorally relevant tasks, and likely through perceptual training paradigms. We show that this framework can help facilitate the understanding and synthesis of a diverse set of results on attentional control over rivalry, and we propose several directions for future research on this interesting topic.

Keywords: visual attention, binocular rivalry, bistable perception, biased competition

INTRODUCTION

Binocular rivalry has long been of fascination to researchers largely because it is a captivating phenomenon that dissociates sensory stimulation from conscious perceptual experience. During binocular rivalry, incompatible images are presented one to each eye, but instead of perceiving a blend of the two images, observers typically report slow, irregular perceptual alternations of the two stimuli (**Figure 1**). The neural processes underlying the resolution and temporal dynamics of this visual conflict have been the subject of numerous studies and debates over the past century (Blake and Logothetis, 2002; Tong et al., 2006). One issue of particular interest is the influence of selective attention over the dynamics of binocular rivalry. Because binocular rivalry involves an inherent dissociation between sensory input and visual experience, the study of attentional influences over the ebb and flow of perceptual dominances during rivalry holds the allure of shedding light on the extent to which we may determine our own conscious visual experience. Moreover, an understanding of attentional control over binocular rivalry may reveal important insights about the neural mechanisms involved in resolving the conflict that arises during rivalry and, more generally, during other forms of visual competition.

Throughout the history of binocular rivalry research, prominent scientists have reached vastly different conclusions as to the extent to which an observer can voluntarily control perception while viewing incompatible dichoptic patterns. Some concluded that there was a strong degree of voluntary control over binocular rivalry. Notably, Helmholtz (1925) reported that he could completely determine his perception during binocular rivalry while performing a demanding task, such as counting the lines in one of the rival patterns. On the contrary, others believed that no voluntary control over alternations in binocular rivalry was possible (Hering, 1879/1942; Levelt, 1968; Moray, 1970). Breese (1899) reported controlling rivalry in a task similar to that used by Helmholtz, but concluded that the effects were simply the result of eye movements – when he carefully fixated, attentional control diminished. However, Washburn and Gillette (1933) did find a degree of voluntary control over rivalry between afterimages, thereby supporting Helmholtz's assertion that attention can influence rivalry. One of the earliest systematic explorations of this

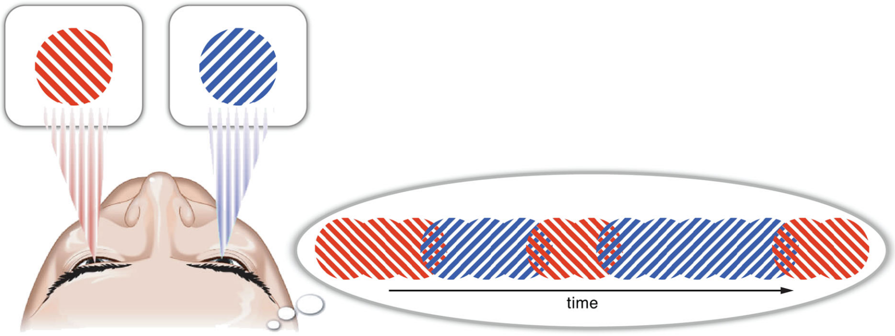

FIGURE 1 | Binocular rivalry occurs when different images are presented, one to each eye. In this situation, observers do not perceive a blend of the two stimuli, but instead experience irregular perceptual alternations between the two images such that only one image is typically perceived at a time. Head image courtesy of Jamie Simon.

research question was by Lack (1978), who found a very strong modulatory effect of voluntary attention over rivalry alternation rates. In Lack's study, participants were asked either to speed the rivalry alternations, or to slow them. This turned out to be an easy task: Lack's subjects were able to increase or decrease the rate of rivalry switches in accordance with their instructions, suggesting a degree of voluntary control over alternations in binocular rivalry.

However, from the onset, a distinction must be made between voluntary control of alternation rates and attentional modulations that are *selective* to one of the two competing images. The ability to modulate alternation rates during rivalry (Lack, 1978; van Ee et al., 2005) does not necessarily imply selective control over rivalry (Meng and Tong, 2004). In other words, a change in alternation rate can occur without a change in the predominance of one of the two inputs with respect to the other. Furthermore, simple physiological factors can cause changes in the rivalry switch rate. For example, the number of eye blinks is correlated with switch rate (Peckham, 1936), while paralyzing one eye can reduce its dominance during binocular rivalry (McDougall, 1903). These results reveal a simple, and arguably less interesting, link between eye blinks/eye movements and switch rates, and consequently, an easy way to willfully affect the rivalry alternation rate. For these reasons, the present review will mostly focus on studies that have investigated the role of selective attention over rivalry, defined here as cases in which attention boosts predominance of the attended item and/or decreases predominance of the unattended item. However, even in selective control studies, non-attentional factors may influence rivalry dynamics (see **Box 1**).

The general aim of this review is to propose a unifying attentional framework that can provide an explanation for the wide range of results from studies that investigated the effects of selective attention on rivalry. Although binocular rivalry is a rare perceptual experience, it is fair to assume that rival stimuli are at least in part processed by mechanisms that participate in everyday perception (see Arnold, 2011 for an insightful discussion of this issue). Therefore, we sought an attentional framework developed for visual competition *in general* that was also able to explain the results obtained during rivalrous viewing. Our general hypothesis, then, is that attentional modulations over binocular rivalry should adhere to the same principles that have been established for visual competition in other, more typical forms. As detailed below, we argue that the biased competition theory of attention (Desimone and Duncan, 1995) can provide an adequate understanding of a seemingly disparate set of findings from studies of rivalry and attention.

A GENERAL FRAMEWORK FOR UNDERSTANDING THE EFFECTS OF SELECTIVE ATTENTION ON RIVALRY

A fundamental property of binocular rivalry is that it involves sustained visual competition whose outcome fluctuates over time (**Figure 1**). The processes leading to the dynamic resolution of this conflict and, consequently, to the determination of an observer's visual percept, are thought to reside at multiple levels of the visual hierarchy, with contributions from both low- and high-level mechanisms (Ooi and He, 1999, 2003; Blake and Logothetis, 2002; Tong et al., 2006). Similarly, a key characteristic of attention is that it involves selection among multiple competing alternatives – a process whose outcome results in preferential processing of the "winning" alternative(s) (James, 1890; Broadbent, 1958; Desimone and Duncan, 1995; Egeth and Yantis, 1997; Kastner and Ungerleider, 2000; Reynolds and Chelazzi, 2004; Lavie, 2005). Furthermore, like binocular rivalry, effects of attention occur throughout the visual system (Kastner and Ungerleider, 2000; Treue, 2001; Hochstein and Ahissar, 2002; Serences and Yantis, 2006). These parallels between key properties of rivalry and attention suggest the likely existence of mutual interactions (Leopold and Logothetis, 1999; Stoner et al., 2005). Indeed, as this review shows, a wide variety of attentional effects on rivalry have been documented. However, there is currently no general framework that integrates these empirical results. Here, our aim is to discuss these findings within the theoretical context of a set of rules that have been proposed to govern attentional modulations during typical visual experience; specifically, we apply the principles established by the biased competition theory of attention (Desimone and Duncan, 1995; Desimone, 1998). We find that this framework provides a satisfactory explanation of a range of results. For reasons of simplicity and readability, we do not present a critical evaluation of other theories of attention, but largely take a more focused approach.

Box 1 | Does attention influence rivalry dynamics by changing effective stimulus contrast?

Before changes in rivalry dynamics are attributed to attentional mechanisms *per se*, other factors should be considered. For instance, even a simple increase in the frequency of eye blinks can speed up rivalry (Peckham, 1936). Faster rivalry switching has also been linked to increasing instability of eye fixation (van Dam and van Ee, 2006) and increases in arousal (George, 1936). Experimental control of such factors is particularly important in studies that investigate the effects of attention on the alternation rates in rivalry as they constitute easy ways to either consciously or subconsciously affect rivalry dynamics.

Another important issue is the relationship between attention and changes in effective stimulus contrast (see Paffen and Alais, 2011 for review). Both exogenous and endogenous attention to a stimulus increase its effective contrast (Carrasco, 2006). This is an important issue because changes in stimulus contrast affect rivalry dynamics. For example, increasing the contrast of both rival images will cause them to switch more rapidly, while increasing the contrast of one rival stimulus will decrease dominance durations of the other stimulus (Levelt, 1968). Thus, when one finds an effect of attention on rivalry, that effect may be a direct effect of attention or an indirect effect that is due to attention-dependent changes in stimulus contrast. Indeed, slowing of alternation rates under conditions of diverted attention may be explained by a corresponding decrease in effective stimulus contrast (Paffen et al., 2006; Paffen and Hooge, 2011). Interestingly, the magnitude of the slowing seems to depend on the nature of the stimuli, with higher-level stimuli such as faces and houses showing more slowing with diverted attention than orthogonal gratings (van Ee et al., 2005; Alais et al., 2010a; also see section Effects of Attention on Binocular Rivalry Dynamics). On the other hand, attention-dependent increases in effective stimulus contrast may explain triggering of rivalry alternations caused by exogenous attentional cuing (Paffen and van der Stigchel, 2010). Changes in effective contrast, however, do not explain all effects of diverting attention away from rival stimuli (Pastukhov and Braun, 2007). Indeed, there are several instances where rivalry slowing occurs when attention is directed *toward* rival stimuli (Chong et al., 2005; van Ee et al., 2009), and additional examples of more complex patterns of results that cannot be easily explained by attention-dependent changes in stimulus contrast (Alais et al., 2010a).

Changes in effective stimulus contrast should also be considered in studies that investigated selective attentional control of rivalry, that is, studies where attention was directed to only one of the rival targets (Chong et al., 2005; Hancock and Andrews, 2007; see section Behavioral Relevance Promotes Attentional Control). While both of these studies found an increase in the predominance of the attended item, each was caused by different factors. Chong et al. (2005) found that selective attention boosted the average dominance durations of the attended item, with no change to the unattended item. On the other hand, Hancock and Andrews reported a decrease in the average dominance duration of the unattended item, with no change to the attended item. If attention simply increased the effective stimulus contrast of the attended item *throughout* the experiment then, in accordance with Levelt's (1968) second proposition, one would expect to see results similar to those reported by Hancock and Andrews. However, in these studies observers attended to the target stimulus only when it was dominant, making it unlikely that its effective contrast was affected while it was suppressed from awareness. Indeed, when a stimulus' contrast is physically increased only during its dominance periods, its dominance durations increase with no changes to the dynamics of the other rival stimulus (Mueller and Blake, 1989; Chong et al., 2005).

In summary, there are a number of indications that attention-dependent changes in effective stimulus contrast may explain some effects of attention on rivalry. This simple explanation, however, does not fully account for all of the results, indicating that attention *per se* likely has additional effects on rivalry. It will be important for future research to isolate both indirect and direct effects of attention. Importantly, simply demonstrating that attentional modulation effects can be *mimicked* by changes in physical stimulus contrast is insufficient to conclude that the observed effects of attention are indirect. Such a conclusion will require actual measurement of attention-induced changes in stimulus contrast during rivalry and subsequent testing of whether measured contrast changes are sufficient to replicate the effects of attention on rivalry dynamics.

The fundamental role of attention is to modulate neural processes in order to prioritize attended items. In nearly all visual scenes, there are multiple items that are in competition for neural resources. The biased competition theory of attention (Desimone and Duncan, 1995; Desimone, 1998) argues that the very existence of this competition is central to the understanding of attention. Accordingly, the effects of attention can only be understood in so far as they lead to the resolution of conflict between stimuli – without competition there is no need for attention. For example, attention can easily modulate neural responses to spatially overlapping stimuli (Serences et al., 2004; Liu et al., 2007; Ciaramitaro et al., 2011) as they are in clear competition. Similarly, when two stimuli fall within the same neural receptive field, attention can boost the processing of the attended item relative to the other unattended items (Moran and Desimone, 1985; Reynolds et al., 1999). Importantly this attentional boost is the strongest when the competing stimuli fall inside the neuron's receptive field, as compared to the case when the unattended stimuli are outside the receptive field (Motter, 1993; Luck et al., 1997). Similar results are found in human fMRI studies. When multiple items are presented in a visual scene, attentional modulations of BOLD responses are seen only in visual areas in which the items fall within the same neural receptive fields (i.e., compete within a receptive field), but not in earlier visual areas where receptive fields are too small to "see" more than one item (i.e., competition is across multiple receptive fields; Kastner et al., 1998; Beck and Kastner, 2009). Overall, these results highlight the importance of competitive interactions between stimuli in enabling attentional modulations, and suggest that only unresolved conflict should be subject to attentional modulation. This hypothesis was recently tested by McMains and Kastner (2011), who manipulated perceptual grouping in order to modulate stimulus conflict. Spatially distributed stimuli will compete when they are placed such that multiple stimuli fall within the receptive field of a single neuron; however, perceptual grouping can reduce the magnitude of competitive interactions by integrating multiple stimuli into a single unified whole (Wertheimer, 1938; Tadin et al., 2002). Indeed, when perceptual grouping was strong, attentional modulations of the BOLD signal were much smaller than when the same stimuli formed weak perceptual groups (McMains and Kastner, 2011, see **Figure 2**). This simple study shows that the degree of stimulus conflict determines the magnitude of attentional effects. Taken together, these findings show that unresolved competition in the visual system is important, and likely necessary, to observe selective attentional modulation of neural processing.

These principles have direct implications for understanding attentional modulations of binocular rivalry. By definition, binocular rivalry involves conflict between two spatially corresponding stimuli. According to the biased competition theory of attention, attentional control over rivalry dynamics should depend first on the presence of stimulus conflict, and also on how and when this conflict is resolved. For example, conflict in binocular rivalry remains unresolved for a brief period after the stimuli are initially presented (Wolfe, 1983), which predicts a large degree of attentional control over early rivalry dynamics (see section Effects of Attention on Initial Selection). In contrast, ongoing rivalry contains periods of clear conflict resolution (when perceptual dominance of one stimulus occurs), and, consequently, should be less susceptible to attentional control (see section Effects of Attention on Binocular Rivalry Dynamics). The second assumption of the biased competition theory is that attentional modulations occur within the same neural substrate where stimulus competition takes place. This again has clear implications for binocular rivalry. For example, if the resolution of conflict during rivalry is limited to low-level, bottom-up mechanisms, then there are few opportunities for attentional modulation. Moreover, any attentional modulation should be biased toward the location in the visual system at which the rival stimuli compete (Beck and Kastner, 2009), which in this case should be early visual mechanisms. On the other hand, if conflict resolution (i.e., determination of perceptual dominance) is a high-level process, that suggests the presence of unresolved conflict throughout the visual hierarchy, and consequently more opportunities for attentional modulation. Finally, as an added benefit, applying the framework outlined in this paragraph should help explain not only the effects of attention on rivalry, but also give insight into the mechanisms of binocular rivalry *per se*. Specifically, determining the degree of attentional control over a certain aspect of binocular rivalry, might give insights into the nature of underlying visual competition (cf., Mitchell et al., 2004).

The straightforward application of this framework, however, is complicated by two important factors. First, as discussed below, rivalry almost certainly does not involve exclusively low- or high-level processes (Blake and Logothetis, 2002). Second, treating rivalry as a process carried out by a single mechanism is overly simplistic. Instead, binocular rivalry seems to be mediated by an aggregate of related processes that determine different aspects and stages of its dynamics, including the instigation of rivalry, the initial perceptual selection, and subsequent alternations of dominance and suppression (Alais and Blake, 2005). Each of these processes may be differentially susceptible to attentional modulation, precluding a simple conclusion about effects of attention on rivalry. In this review, we will consider these complications as we apply the proposed attentional framework.

EFFECTS OF ATTENTION ON INITIAL SELECTION

When two stereoscopically compatible images are presented, the visual system almost instantly fuses the two images into a 3D percept (Cumming and DeAngelis, 2001; Blake and Wilson, 2011). However, when two incompatible images are presented, it takes some time for binocular rivalry to begin. Perhaps because of the overwhelming amount of binocularly compatible information that we receive throughout our lives, the visual system first attempts to fuse the inputs from the two eyes by default. For example, orthogonal dichoptic gratings that are presented very briefly will "abnormally fuse," giving rise to a percept of a plaid (Wolfe, 1983; de Belsunce and Sireteanu, 1991). With typical stimuli, exclusive dominance of one of the stimuli occurs only after about

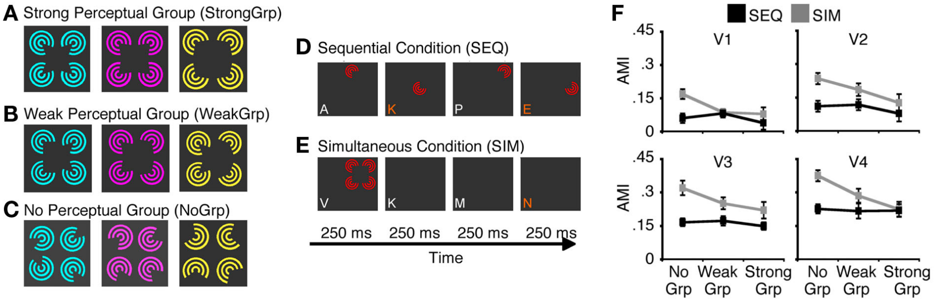

FIGURE 2 | A study by McMains and Kastner (2011) demonstrates that susceptibility to attentional modulation is dependent on the degree of unresolved stimulus conflict. (A–C) Inducer stimuli used in the experiment, which varied in the strength of perceptual grouping, ranging from strong grouping **(A)** to no perceptual grouping **(C)**. In these displays, stimulus conflict decreases as the strength of perceptual grouping increases. **(D,E)** Illustrations of experimental conditions and tasks. In the sequential condition **(D)**, inducers are presented in sequence, which precludes competitive interactions among stimuli. In the simultaneous condition **(E)**, all inducers are presented at the same time. This typically results in suppressive interactions among stimuli – a result thought to indicate their competition for neural resources (Kastner et al., 1998; Reynolds et al., 1999). To estimate susceptibility to attentional modulation, observers were asked to perform either a demanding RSVP task at fixation (attention diverted task) or luminance detection task on one of the inducers (attention deployed task). This allowed computation of attentional modulation indices (AMI), which quantified how much responses increased when attention was directed toward the inducer stimuli. **(F)** The results showed that attentional modulation was strongest in the simultaneous condition and when inducer stimuli did not from a perceptual group. This key finding indicates that the unresolved competition between stimuli is linked with strong susceptibility to attentional modulation. Adopted from McMains and Kastner (2011) with permission from the Society for Neuroscience.

150 ms (the fusion period can be shorter for pairs of stimuli where one is perceptually much stronger, Su et al., 2011). This fusion period indicates the presence of unresolved conflict throughout the visual system, and a possible role for higher-level factors to influence rivalry initiation. For example, imagine a real-world circumstance in which an object is occluded, but the observer stands such that his left eye is able to see the occluded object, while the right eye cannot. In such cases, binocular rivalry does not occur, even though each eye's input is incompatible with the other (Shimojo and Nakayama, 1990; Arnold, 2011). On the other hand, even identical inputs can be made to rival or fuse depending on how they are interpreted in context (Andrews and Lotto, 2004). These results indicate that there is some flexibility in how compatible and incompatible binocular inputs are initially processed, which may result from low-level (i.e., Shimojo and Nakayama, 1990) or higher-level (i.e., Andrews and Lotto, 2004) factors. Importantly, in relation to the framework proposed in this review, this suggests a possible role for attentional modulation during initial selection. Indeed, numerous investigations have shown strong attentional modulations over initial selection in binocular rivalry (Ooi and He, 1999; Mitchell et al., 2004; Chong and Blake, 2006; Hancock and Andrews, 2007; Kamphuisen et al., 2007).

In one such study by Mitchell et al. (2004), object-based exogenous (i.e., involuntary) attention was shown to bias initial dominance in binocular rivalry. The experimental paradigm started with the presentation of two superimposed transparent surfaces to both eyes (**Figure 3A**). On each trial, one surface was cued by a brief translation – a manipulation designed to exogenously draw attention to the cued surface. After 150 ms, one of the surfaces was removed from each eye, leaving two incompatible surfaces in the two eyes and resulting in the initiation of binocular rivalry. The key result was that the cued grating was about three times more likely to be perceived as dominant during the initial period of binocular rivalry (**Figure 3B**). This effect of attention was specific to initial dominance, disappearing 2 s after the presentation of the exogenous cue. Subsequent study by Chong and Blake (2006) reported similar results for endogenous (i.e., voluntary) attention. Their paradigm involved the binocular presentation of two superimposed gratings, with subjects instructed to track either rotation or spatial frequency changes of one of the two gratings. After 5 s, one grating was removed from each eye to initiate binocular rivalry (again, by leaving two incompatible surfaces in two eyes). Results revealed a twofold bias of the initial dominance in favor of the cued stimulus. This effect was only observed on trials where subjects correctly tracked stimulus changes, indicating an important role of sustained endogenous attention.

These studies convincingly demonstrate that both exogenous and endogenous attention can bias initial selection during binocular rivalry. This susceptibility to attentional modulation may be explained by the temporal dynamics that characterize the initial presentation of incompatible binocular stimuli. Here, the delayed onset of exclusive dominance of one of the rival targets provides a period of unresolved conflict between two rival stimuli. As outlined above, such unresolved competition should allow for strong attentional modulations. Moreover, because neither stimulus is perceptually dominant in the first 150 ms, there is unresolved competition throughout the visual hierarchy. Thus, there are a range of levels at which attentional modulations may occur (Beck and Kastner, 2009). Interestingly, with some stimuli it is possible to resolve interocular competition in as little as 30 ms (Su et al., 2011). Our proposal is that for such stimuli, the magnitude of attentional control over initial dominance would be much smaller. Additionally, recent EEG results (Zhang et al., 2011) suggest that, in fact, attention may be necessary for the abnormal fusion of two rival stimuli to transition into rivalry alternations (but see Roeber et al., 2011 for a different result; also see **Box 2**). However, even though this argument may explain why attentional modulation of initial dominance is strong, it also makes it harder to pinpoint the exact neural mechanisms that are involved (see **Box 3** for future directions that may resolve this issue).

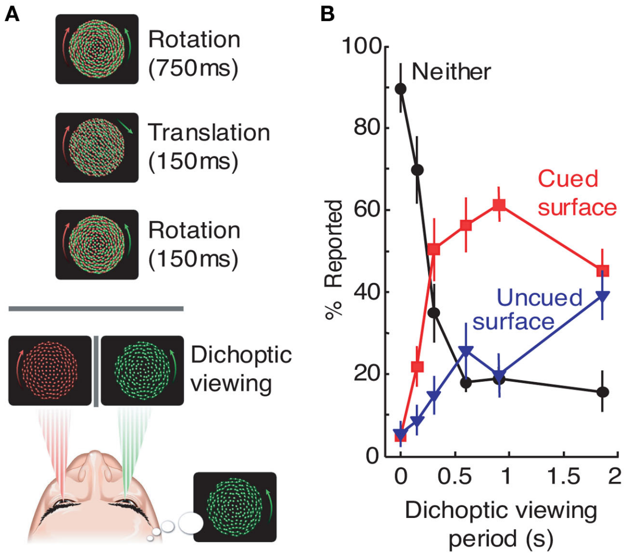

FIGURE 3 | Exogenous attention biases initial dominance in binocular rivalry. In a study by Mitchell et al. (2004), rivalry was initiated between conflicting rotating surfaces, one of which was cued during preceding binocular presentation by a brief translation period **(A)**. After rivalry was initiated, observers reported which of the two surfaces was dominant at the end of variable dichoptic viewing periods **(B)**. After 150 ms of dichoptic viewing, in most cases observers did not perceive exclusive dominance of either surface, consistent with previous reports (Wolfe, 1983). However, for viewing periods between 300 and ∼1500 ms, the cued surface was the predominant percept, indicating a strong effect of attention on the initial dominance during rivalry. Adopted from Mitchell et al. (2004). Adapted by permission from Macmillan Publishers Ltd.: Nature, copyright 2004.

EFFECTS OF ATTENTION ON BINOCULAR RIVALRY DYNAMICS

Following a brief period of abnormal fusion and subsequent determination of initial dominance in binocular rivalry, rivalry enters its characteristic dynamic of perceptual alternations between the two incompatible stimuli. Because there is considerable evidence that the mechanisms underlying the dynamics of sustained binocular rivalry are at least partially distinct from those underlying initial selection (Wolfe, 1983; de Belsunce and Sireteanu, 1991; Carter and Cavanagh, 2007; Bartels and Logothetis, 2010; Stanley et al., 2011), it is important to determine whether the nature of selective

Box 2 | Does binocular rivalry require attention?

The resolution of binocular rivalry requires selection of one rival image for dominance, and another for suppression. Since selection is a fundamental feature of the attentional system, this fact raises the question of whether the processes giving rise to perceptual fluctuations during binocular rivalry actually *require* that attention be deployed to the rival stimuli. However, getting a clear answer to this question is precluded by a fundamental problem in all behavioral investigations of attention and rivalry. If one wants to investigate how two processes interact, one should first understand each process in isolation, and then examine what happens when the two are combined. However, such a clean design cannot be applied to the behavioral study of attentional effects on binocular rivalry due to the simple fact that reporting a subjective perceptual state during rivalry requires directing attention toward rival stimuli. Therefore, it is impossible to behaviorally measure rivalry dynamics in the absence of attention. Some studies have tried to circumvent this limitation by asking observers to attend to rival stimuli only sporadically, and then using the observers' reports during these brief periods of attending to infer rivalry dynamics during preceding periods of diverted attention (Cavanagh and Holcombe, 2006; He et al., 2007; Pastukhov and Braun, 2007). The results suggest that rivalry either considerably slows down or possibly stops alternating outside of the scope of attention. However, because attention must be periodically directed to the rival stimuli (in order for observers to make responses), these studies do more to highlight the impossible task of behaviorally measuring rivalry dynamics without attention than to actually circumvent this limitation. This fundamental problem, fortunately, can be avoided by using non-behavioral methods of assessing rivalry dynamics. Specifically, neuroimaging methods can be used to characterize neural signature(s) of rivalry alternations, which then can be examined with and without attention. This was done in a recent EEG study by Zhang et al. (2011), who found that when attention was directed away from the rival stimuli, rivalry stopped. These intriguing findings suggest that attention may be necessary for the resolution of conflict in binocular rivalry. However, an opposite finding was reported in an event-related potential (ERP) study by Roeber et al. (2011). Evidently, a simple answer to this important question remains elusive.

attentional modulation might also differ. The first modern study to address this question was by Meng and Tong, who instructed subjects to hold one of the two rival stimuli dominant for as long as possible. Consistent with the older hypothesis by Moray (1970), the results showed essentially no effect of attention (**Figure 4**). There were no changes in the average dominance durations or total predominance in favor of the held item or against the ignored stimulus. Evidently, simply directing endogenous attention toward one of the rival stimuli has little effect over the dynamics of binocular rivalry (as discussed in the following section, different results are found if attended stimuli are behaviorally relevant). In contrast, when the same subjects were asked to perform an analogous task with the bistable Necker cube, strong attentional modulation was observed (**Figure 4**; Meng and Tong, 2004; also see Toppino, 2003). Similar results are found for other types of ambiguous visual stimuli, including apparent motion (Suzuki and Peterson, 2000) and 3D structure-from-motion (Hol et al., 2003). In fact, voluntary attention to the alternate perceptual explanation is often required see ambiguous figure reversals (personal in-class observation with E. G. Boring's Young girl/Mother-in-law image). One explanation of these results is that the nature of competition in ambiguous stimuli is high-level, and therefore it is easily affected by attentional control. Overall, this contrast between rivalry and ambiguous figures supports the hypothesis that conflict during binocular rivalry is resolved at early stages of visual processing in a bottom-up fashion (Blake, 1989), thereby limiting the degree of attentional modulation (McMains and Kastner, 2011).

Competition during binocular rivalry, however, is not exclusively confined to early, monocular mechanisms, but may involve different levels of the visual system depending on the nature of the competition (Blake and Logothetis, 2002; Lee, 2004). One notable case that reveals an important role of higher-level processes is stimulus rivalry (Logothetis et al., 1996). In this paradigm, each eye receives conflicting input, but the ocular configuration is rapidly swapped between the eyes (∼3 Hz). Under these specific conditions rivalry dynamics remain largely unchanged (Logothetis et al., 1996; Lee and Blake, 1999), precluding an eye-based explanation. Importantly, visual competition leading to these dynamics by definition involves a conflict between two stimuli rather than a conflict

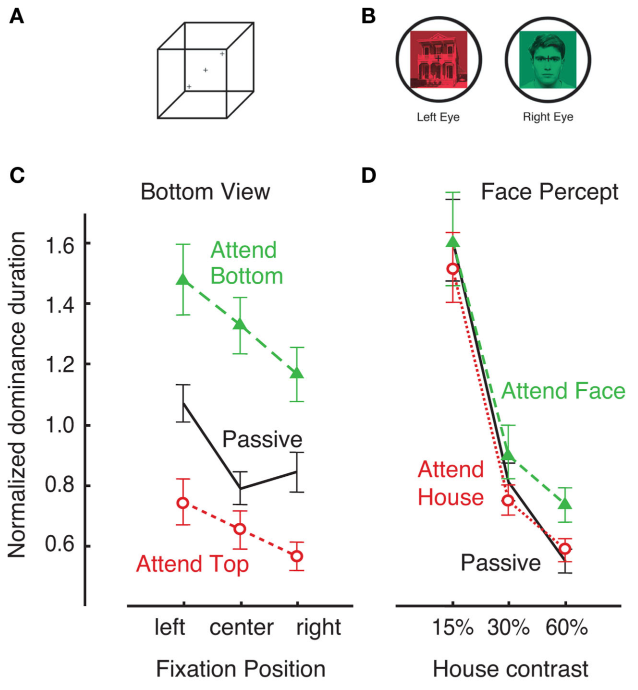

FIGURE 4 | In a study by Meng and Tong (2004), observers were asked to willfully affect dynamics of Necker cube reversals (A) and binocular rivalry (B) by trying to hold one of two possible perceptual interpretations. This was an easy task for the Necker cube stimulus **(C)**. When asked to "attempt to perceive the cube from the bottom view for as long as possible," observers were able to do that regardless of the fixation position [denoted by crosses in **(A)**]. However, the degree of attentional control over binocular rivalry was considerably smaller **(D)**. When asked to "try to maintain the percept of the face for as long as possible," observers exhibited only weak ability hold the face dominant over a range of stimulus contrasts. Adopted with permission from Meng and Tong, 2004; ARVO©).

between two eyes and likely involves higher visual areas (Pearson et al., 2007). Modeling studies indicate that stimulus rivalry occurs for stimuli that bypass the low-level competition that normally occurs at early, monocular stages (Wilson, 2003; Freeman, 2005; Tong et al., 2006). Another example involves composite stimuli created by fragmenting two larger images and pseudorandomly assigning the corresponding fragments to two eyes (i.e., each eye would see a mosaic containing complementing components of two source images). For such stimuli, rather than perceiving rivalry between two mosaic images, subjects often perceive the unfragmented source images (Diaz-Caneja, 1928, translated by Alais et al., 2000; Kovács et al., 1996). In addition, globally grouped motion (Alais and Blake, 1998), surface contours (Ooi and He, 2003; van Bogaert et al., 2008), textures with common luminance or color (Silver and Logothetis, 2004), as well as other grouped stimuli (Logothetis, 1998) can influence locally competing rival stimuli. These effects indicate involvement of object-based processes operating at multiple stages throughout the visual hierarchy. Because of the higher-level nature of visual competition in these examples, the framework introduced in this review predicts a greater degree of attentional control. While this specific hypothesis remains to be tested, there are some indications that these forms of visual rivalry are more susceptible to top-down factors. For example, unlike eye rivalry, stimulus rivalry requires high levels of pattern coherence, indicating a key role of object-based mechanisms (Bonneh et al., 2001). An analogous dissociation is evident in the perceptual stabilization that occurs when rival stimuli are presented intermittently (Leopold et al., 2002). Object features, such as color, are the primary factor determining perceptual stabilization during intermittent stimulus rivalry (Pearson and Clifford, 2004). On the other hand, low-level eye of origin is almost the sole determinant of perception during intermittent binocular rivalry (Chen and He, 2004; Pearson and Clifford, 2004). Additional evidence that the level where stimuli compete affects their susceptibility to attentional modulation comes from studies that investigated the slowing of rivalry that occurs when attention is diverted (see **Box 1**). Observed effects are larger for rivalrous face/house stimuli than for orthogonal gratings (van Ee et al., 2005; Alais et al., 2010a). This is likely due to the fact that conflict between faces and houses arises later in the visual hierarchy than does conflict between gratings (cf., Beck and Kastner, 2009).

Arguably the strongest indication that stimulus rivalry may be more susceptible to attentional modulation comes from a recent study by Silver and Logothetis (2007). Here, one of two dichoptically presented orthogonal gratings was embedded with a conspicuous visual tag. Throughout the course of a trial, this tag either remained with the same stimulus (and switched eye at every eye swap) or remained in the same eye (and switched stimulus on each eye swap). When the tag remained in one eye, subjects were biased toward perceiving fast stimulus switches, indicating sustained periods of eye dominance. Importantly, when one of the two *stimuli* was tagged, subjects tended to experience slow, irregular stimulus alternations (i.e., they perceived stimulus rivalry). In this study, participants likely used attentional tracking strategies to follow the cue. During conditions where the tag remained with one stimulus, this effectively deployed selective attention to that tagged stimulus. Although the goal of this study was not to study attentional modulations, it does suggest stronger attentional control over stimulus rivalry than binocular rivalry. Evidently, as the visual competition is biased toward higher-level mechanisms, the susceptibility to attentional modulation increases.

BEHAVIORAL RELEVANCE PROMOTES ATTENTIONAL CONTROL

The predominantly low-level nature of conflict during binocular rivalry, however, should not by itself preclude attentional modulations. Although attentional modulations are more closely associated with higher visual processes, attentional effects in early visual areas, including V1 and LGN, are well documented (Treue, 2001; O'Connor et al., 2002; Roberts et al., 2007; Fischer and Whitney, 2009). So, what then may be a reason for weak attentional modulation of conventional binocular rivalry? One reason binocular rivalry continues to fascinate is that it is not a common perceptual experience. This also indicates that we are rarely in situations where we have to select between conflicting inputs arising from two eyes. On the other hand, we frequently select between higher-level stimulus features, such as objects. This ecological difference might explain the resistance of binocular rivalry to attentional control. But, what if one eye's stimulus is behaviorally relevant, for instance through an eye-specific, attentionally demanding task? Would that promote attentional control? Evidence supporting the load theory of attention indicates that the efficacy of attentional deployment critically depends on the effort involved in processing of the attended target, with high loads yielding stronger attentional modulations (Lavie, 2005). Another key question is whether continuing behavioral relevance of one eye's stimulus gradually strengthens any modulatory effects of attention. While we do not normally select between two eyes, the visual system does have the capability to do so. A striking example is amblyopia, a condition where the brain essentially ignores poor visual input from one eye in favor of behaviorally relevant input from the other eye (Campos, 1995; Simons, 2005; Levi and Li, 2009). In a way, amblyopia can be thought of as a limiting case of binocular rivalry, where both eyes are sending differing inputs to the brain, but the visual system learns to ignore the information from the weak eye, thereby resulting in a profound and possibly complete dominance of the stronger eye.

Although amblyopia is clearly a special case and may not involve attentional mechanisms, it demonstrates that an effort to maintain the most relevant visual information may alter the relative dominance of two monocular images. Indeed, recent studies with typical observers have shown that relative dominance can be biased in favor of an attended stimulus if an appropriate attentionally demanding task is used. In one study that addressed this question, participants were instructed to identify small aspect ratio changes in a bullseye pattern presented to one eye, while completing no task when the other eye's stimulus was dominant (**Figure 5A**; Chong et al., 2005). The results revealed an approximately 50% increase in the dominance durations of the attended stimulus (**Figure 5B**). Importantly, for this attentional effect to occur, attention needed to be directed toward the *features* of one of two rival stimuli – simply performing a demanding task at the same spatial location during dominance periods of the target stimulus was insufficient to bias rivalry dynamics. In a related study, one of two

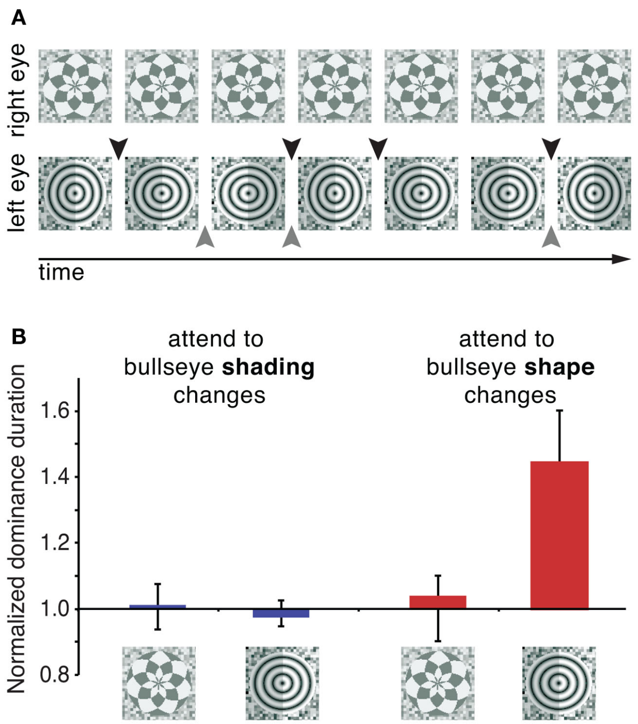

FIGURE 5 | Performing a demanding attentional task promotes selective attentional control over rivalry dynamics. (A) Stimuli used by Chong et al. (2005). One eye views a control stimulus (a radial checkerboard), while the other eye is shown a bullseye pattern. In two separate attentional tasks, observers were instructed to track either shape changes (black arrows) or shading changes (gray arrows) of the bullseye pattern. These tasks were demanding and required sustained attention. For illustration purposes, the magnitudes of the shape and shading changes are greatly exaggerated. Results **(B)** indicate that completing a demanding task that directs attention toward a rival stimulus lengthens its average dominance duration. On the other hand, an equally demanding task where attention was directed to the same location in space but not to rival stimulus *per se* did not affect rivalry dynamics. Adopted with permission from Chong et al., 2005; ARVO©).

orthogonal dichoptic gratings was cued, and participants were instructed to identify small rotations of the cued grating (Hancock and Andrews, 2007). This task also resulted in an increase in the predominance of the attended stimulus. (Interestingly, these two studies measured opposite factors giving rise to this outcome. See **Box 1** for more details). These findings indicate that behavioral relevance of a rival stimulus facilitates its attentional susceptibility, a process that likely involves attentional modulation of early visual processes. This argument is supported by recent ERP results indicating that neural changes associated with a demanding attentional task occur at earlier stages when the attended stimulus is engaged in binocular rivalry (Khoe et al., 2008; Mishra and Hillyard, 2009). Specifically, the P1 component, an early ERP component that is believed to reflect extrastriate neural activity, was modulated by attention only when the attended stimulus was presented under dichoptic conditions and rivaled with the unattended stimulus, and not during monocular presentation of the same stimuli. However, even with the utilization of demanding attentional tasks, the magnitude of attentional modulation in these studies (Chong et al., 2005; Hancock and Andrews, 2007) was considerably smaller than attentional effects on initial dominance (see above), indicating that initial selection is more susceptible to attentional control than sustained binocular rivalry.

The use of demanding attentional tasks, however, is not the only way to increase behavioral relevance of a rival target. Other paradigms that increase the relative importance of a rival stimulus also increase its predominance. For example, faces with emotional content dominate over neutral faces during binocular rivalry (Alpers and Pauli, 2006; Bannerman et al., 2008) and emerge faster from perceptual suppression (Yang et al., 2007). Neutral faces that are paired with negative gossip predominate over faces paired with neutral statements (Anderson et al., 2011). In addition, observers' ability to control the alternation rate during rivalry is greatly enhanced if a rival stimulus is paired with a congruent auditory stimulus (van Ee et al., 2009). Even implicitly learned stimulus usefulness biases initial selection in binocular rivalry (Chopin and Mamassian, 2010). In summary, different ways of introducing behavioral relevance (i.e., without using explicit attentional tasks) are very effective at modulating rivalry dynamics. One hypothesis is that at least some of these manipulations work because they enable more effective direction of attention to a rival stimulus – a conclusion consistent with the load theory of attention (Lavie, 2005).

PLASTICITY OF ATTENTIONAL EFFECTS

Evidence that an eye-specific behavioral task can boost the predominance of the task-relevant stimulus raises two interesting questions. First, increased predominance of the attended stimulus could be as a result of either an attentional boost to the high-level stimulus representation and/or an attentional modulation of low-level monocular processes. Second, the link between behavioral relevance and attentional control raises the question of whether the magnitude of the observed effects could be increased. Perceptual training studies might answer both of these questions. Recent research has revealed that plasticity indeed occurs during prolonged viewing of binocular rivalry (Suzuki and Grabowecky, 2007; Klink et al., 2010), in turn opening a possibility that prolonged attentional control over rivalry may alter its own effectiveness. Moreover, any permanent change in the effectiveness of attentional control allows subsequent determination of whether observed changes are specific to the trained eye and/or the trained stimulus.

An early series of studies by Lack indicated that voluntary control over rivalry alternation rate may be subject to training. Lack's observers were asked to view rival stimuli and to either speed up or slow down their alteration rates – a task that is relatively easy to accomplish (Lack, 1978; van Ee et al., 2005). Interestingly, over the course of 10 days, observers became considerably better at controlling their own switch rates (Lack, 1978). As discussed above (also see **Box 1**), non-attentional factors may explain such changes in alternation rates. Still, Lack's results warrant a more controlled investigation into the plasticity of attentional control during rivalry. More recent work (Suzuki and Grabowecky, 2007) revealed that long-term observation of binocular rivalry indeed modulates alternation rates. However, observers in this study

Box 3 | Questions for future research.

- The attentional framework outlined in this review can help synthesize results from a number of behavioral studies that examined the effects of attention on binocular rivalry. However, in most cases, it does not specify where these attentional effects are occurring in the brain (one exception would be eye-specific effects of attentional training). The key complication is that binocular rivalry is a complex mechanism that involves processes spreading out throughout the visual hierarchy (Blake and Logothetis, 2002; Tong et al., 2006). The uncertainties of where exactly rivalry competition takes place carry over to the uncertainty in where behaviorally measured attentional effects occur. Brain imaging, however, holds promise to provide some specificity as to where attentional modulation of rivalry occurs, and, in turn, to help us understand the brain mechanisms involved in rivalry competition. The simple hypothesis motivated by attentional studies (Luck et al., 1997; Beck and Kastner, 2009; McMains and Kastner, 2011) is that the biggest effects of attention should be seen at the stages where rival stimuli are first in competition and not before. It is also possible that some brain areas may play a special role in attentional modulation of rivalry. One such region is the parietal cortex, which is involved in both top-down attention (Behrmann et al., 2004) and has been linked with binocular rivalry (Lumer et al., 1998; Britz et al., 2010; Kanai et al., 2010; Zaretskaya et al., 2010; but see Knapen et al., 2011).
- While biased competition can provide a *post hoc* explanation of published results on attentional modulation of binocular rivalry, direct empirical tests of this framework are needed. The general hypothesis is that the degree of attentional modulation of rivalry will depend on the unresolved competition between rival stimuli. One specific prediction is that attentional modulation over rivalry dynamics will vary over the course of a single dominance epoch, being weaker at the beginning and stronger near the end. This prediction derives from recent results (Alais et al., 2010b) that show that suppression depth decreases over the course of a dominance period. As strong suppression indicates relatively resolved visual competition, the effects of attentional deployment should vary accordingly.
- However, even after localization of brain area(s) where attentional modulation of rivalry occurs, the exact mechanisms of attentional control over rivalry might still remain a mystery. While physiological changes such as increased alertness and attention-dependent changes in effective stimulus contrast almost certainly play a role (see **Box 1**), these effects likely do not fully account for attentional modulations of binocular rivalry, particularly under conditions of behavioral relevance of one of the two stimuli.
- An important goal for future research will be to determine the limits of attentional control over rivalry. Was Helmholtz actually correct, after all, about the possibility of complete control over rivalry? Currently, demonstration of complete voluntary control seems elusive, except perhaps after 25 years of intensive meditation training (Carter et al., 2005). Understanding of this limitation will shed light on the conditions under which we may determine our own conscious visual experience.
- If the degree of unresolved stimulus conflict indeed determines susceptibility to attentional modulation, then does an observer's ability to exert attentional control over rivalry fluctuate during different periods of rivalry dynamics? For example, are mixed periods – rivalry periods where an observer perceives a mixture of two stimuli – more susceptible to attentional modulation? If so, could targeted deployment of attention during mixed periods be an effective strategy to significantly prolong predominance of a rival stimulus?
- Although this review focused on *modulatory* effects of attention on rivalry, a recent study (Zhang et al., 2011) indicates that attention may also have a fundamental *enabling* role in the initiation of rivalry alternations. However, Roeber et al. (2011) found signatures of rivalry even when attention was diverted. These recent findings open an exciting new line of binocular rivalry research.
- Finally, it will be important to explore possible practical benefits of attentional control over rivalry, particularly its plasticity. Xu et al. (2010) recently demonstrated that perceptual training that combines binocular rivalry and an attentional task can result in improvements of stereopsis. It remains to be determined whether similar paradigms may be used as a behavioral treatment for amblyopia.

passively viewed rival stimuli, so it remains unclear how these changes might be altered by the addition of attentional influences.

Additional suggestions that attentional modulation of rivalry is subject to plasticity come from two recent studies. In a study by Paffen et al. (2008), observers were trained on a direction-specific speed discrimination task over the course of 5 days. After training, the task-relevant (trained) direction and task-irrelevant (ignored) motion direction were pitted against one another in binocular rivalry. Perceptual learning resulted in a decrease in the predominance of the task-irrelevant motion. Furthermore, initial dominance was biased in favor of the task-relevant motion direction. Evidently, prolonged training with a specific stimulus changes its predominance during binocular rivalry. Another study examined whether the pairing of exogenous attention and binocular rivalry could alter sensory eye dominance (Xu et al., 2010; also see Xu et al., 2011a,b). Sensory eye dominance describes a condition, akin to handedness, in which the input from one eye is stronger than that from the other eye, resulting in increased dominance of the stronger eye. In this study, an exogenous attentional cue to the weak eye was followed by a brief presentation of rival gratings. This "push–pull" training led to a significant decrease in the magnitude of sensory eye dominance. The training effects only minimally transferred to other retinal locations and other stimuli, indicating high specificity. Importantly, no changes were found in push only training where no rival stimulus was shown to the stronger eye, suggesting that the involvement of inhibitory interactions during rivalry was key to obtain this low-level plasticity. Preliminary results from our lab (Dieter et al., 2010) show that prolonged training in which observers perform an attentionally demanding task on one rival stimulus (same task as in Chong et al., 2005; see **Figure 5A**) can lead to increasing voluntary control of rivalry dynamics. The changes giving rise to this additional control were partially eye-specific, as indicated by transfer to untrained stimuli presented to the trained eye.

While more research is needed to understand the plasticity of attentional control over rivalry, it is becoming clear that the limits of attentional effects can be changed through appropriate perceptual training. One striking example is that Tibetan Buddhist monks with over 25 years of practice at "one-point" meditation were able to almost completely control their perception during rivalry (Carter et al., 2005), even though they had no prior experience with binocular rivalry. This unique observation indicates a possibility that complete control over binocular rivalry may be possible with extensive training.

SUMMARY

The influence of selective attention over the dynamics of binocular rivalry has been of interest to researchers for over a century. Early investigations came to vastly different conclusions foreshadowing the seemingly diverse set of findings seen in modern studies. The aim of this review is to introduce an attentional framework that can help facilitate the understanding and synthesis of these results. Perhaps reassuringly, the effects of attentional control over binocular rivalry seem to mimic those seen in other paradigms of attentional modulation. Namely, the degree of attentional modulation over rivalry dynamics seems to depend on the presence of stimulus conflict, and the level of the visual system at which conflicting stimuli first compete. This framework predicts strong attentional control under conditions of unresolved stimulus conflict (e.g., initial selection) and conditions where conflict is resolved at higher levels of processing (e.g., stimulus rivalry). In addition, limits on attentional control can be alleviated by the utilization of demanding, behaviorally relevant tasks, and likely through perceptual training paradigms. Future research on this topic (**Box 3**) will likely reveal not only the extent to which an observer may voluntarily control his or her own perceptual experience, but also new insights into the mechanisms that resolve conflict during binocular rivalry.

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How much of the "unconscious" is just pre – threshold?

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Visual awareness is a specific form of consciousness. Binocular rivalry, the alternation of visual consciousness resulting when the two eyes view differing stimuli, allows one to experimentally investigate visual awareness. Observers usually indicate the gradual changes of conscious perception in binocular rivalry by a binary measure: pressing a button. However, in our experiments we used gradual measures such as pupil and joystick movements and found reactions to start around 590 ms before observers press a button, apparently accessing even pre-conscious processes. Our gradual measures permit monitoring the somewhat gradual built-up of decision processes. Therefore these decision processes should not be considered as abrupt events. This is best illustrated by the fact that the process to take a decision may start but then stop before an action has been taken – which we will call an abandoned decision process here. Changes in analog measures occurring before button presses by which observers have to communicate that a decision process has taken place do not prove that these decisions are taken by a force other than the observer – hence eliminating "free will" – but just that they are prepared "pre-thresholdly," before the observer considers the decision as taken.

Keywords: binocular rivalry, decision making, pupil, conscious visual perception

INTRODUCTION

Visual awareness, a specific form of consciousness, is challenging to approach experimentally (Myerson et al., 1981; Crick and Koch, 1995; Bhardwaj et al., 2008). One of the few suitable paradigms is binocular rivalry, the alternation of visual consciousness resulting when the two eyes view differing stimuli (Blake and Logothetis, 2002; Alais and Blake, 2005; Kim and Blake, 2005). If a grating presented to the left eye is oriented perpendicularly to that shown to the right eye as in the present study conscious experience alternates between the two orientations (O'Shea and Crassini, 1981; Fahle, 1982) though the stimulus stays constant (**Figure 1A**). Observers usually have to indicate these gradual changes of conscious perception by a binary measure: pressing one of two buttons, one for the emergence of each grating. Here we argue that analog, or gradual measures better reflect the gradual changes in awareness (and decision processes) than button presses (Naber et al., 2011). We used three measures of visual awareness – button presses, pupil size, and joystick movements. In our experiment, the grating to one eye differed in orientation (provoking rivalry) and luminance (eliciting pupil responses) from that in the other eye (**Figure 1A**). Differences in stimulus luminance cause differences in pupil size. Because pupil size is similar in both eyes (Ettinger et al., 1991; Miller et al., 2005), we expected pupil size to change depending on which of the stimuli was consciously perceived (Barany and Hallden, 1948). That is to say that both pupils should constrict when observers perceive the brighter grating and enlarge when observers perceive the dimmer grating (Harms, 1937; Lowe and Ogle, 1966; Fahle et al., 2010; Naber and Einhäuser, 2010). This change could serve as an objective correlate of the internal choice between two stimuli both represented in (early) visual cortices (Kovacs et al., 1996; Fang and He, 2005; Tong et al., 2006). And indeed, pupils not only reacted to the transitions between perceived orientations (Fahle et al., 2010; Naber and Einhäuser, 2010), but pupil sizes predicted which stimulus was perceived (**Figure 1B**). These earlier studies, however, did not discuss the temporal lead of the pupil response and neither did they relate it to decision processes in general.

The pupil starts to change around 590 ms before observers signal changes in conscious perception by pressing a button, not just in our data, but also to be found – at least for dilations – for other types of bi-stable stimuli (Einhauser et al., 2008). That is, the pupil seems to access even sub-threshold, or pre-conscious processes. However, the lag of the behavioral response relative to the pupil response disappears if observers move a joystick rather than press a button. Hence decision processes seem to require some processing time, building up over time rather than being all-or-none events and hence require gradual measurements rather than binary ones such as button presses (Soon et al., 2008). Averaging analog measures such as pupil diameter or the EEG identifies even pre-threshold portions during the built-up of decision processes. This insight may prevent the misinterpretation of data demonstrating changes in analog measures such as the EEG occurring before binary decisions are consciously taken (Libet, 1985). These data were interpreted by some as indicating that humans do not have a "free will" since the changes in (analog) EEG potentials preceding (binary) button presses were interpreted as produced by a force independent from the observer proper, while the observer seemed to be "informed" about the decision only after a decision had been taken by this independent force (whatever this force may be; e.g., Libet et al., 1999).

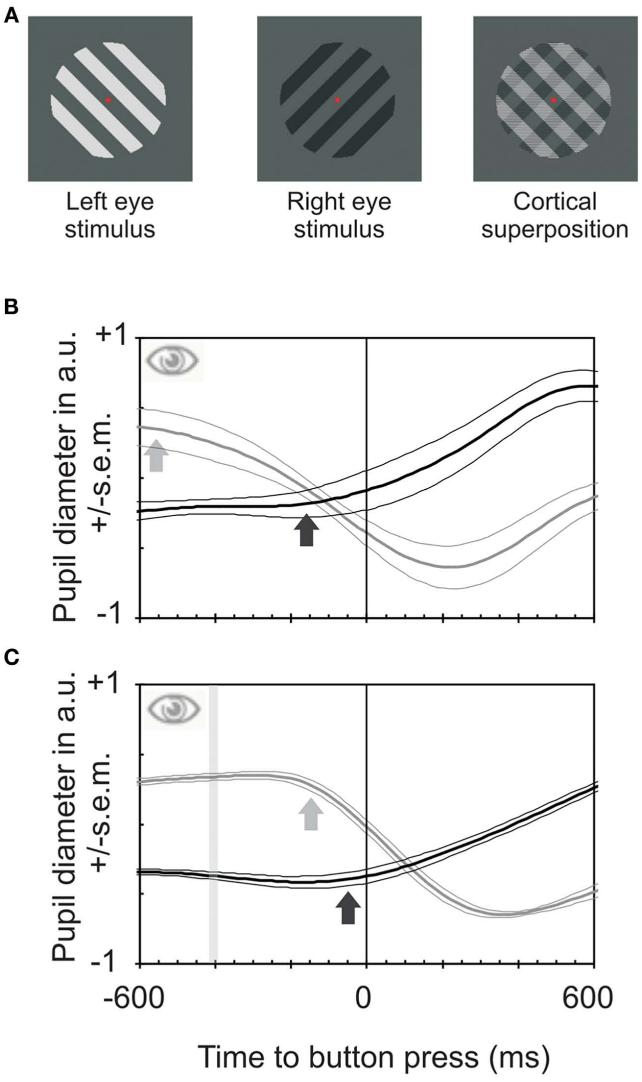

FIGURE 1 | Stimuli used and pupil reactions obtained during binocular rivalry and between stimuli of differing luminances. (A) Stimuli used to elicit binocular rivalry. An oblique darker grating was projected to one eye, a perpendicular brighter one to the other eye, resulting in alternation of perception between the two stimuli. **(B)** Pupil reactions (means and SEM for four observers) to a change in subjective perception between the two gratings relative to time of button presses during binocular rivalry. The black line shows the relative pupil response for transitions from bright to dark and the gray line transitions from dark to bright. Pupil constrictions start on average about 590 ms before the button presses (gray arrow); pupil dilations start about 120 ms before the button presses (for movement onset estimates see Bergamin and Kardon, 2003). Hence the pupil reacts to internally triggered transitions between percepts much earlier than button presses do. **(C)** Pupil responses to a change in *physical* stimulus properties in both eyes from dark to bright or vice versa. The bar indicates the time of change of physical stimulus properties. It is an interval rather than a fixed point in time because data were averaged relative to button presses and reaction times vary slightly (both intra-individually and between observers). The constriction starts about 120 ms before the button is pressed (gray arrow); dilation starts only marginally before the button press. Hence reaction times for pupil responses and button presses are quite similar for externally caused changes of perception. The lead of pupil responses in **(B)** is not mainly due to a faster reaction time of the pupil.

RESULTS

The pupil response for a subjective switch to a brighter target started around 590 ms (±30 ms SEM) before the button presses by which observers indicated this change in subjective percept – even though observers were instructed to react as fast as possible (**Figure 1B**; Einhauser et al., 2008; Hupe et al., 2009; Alais et al., 2010). To rule out the possibility that the pupil responses are faster than button presses, we performed a first control experiment. Both eyes viewed the same grating that changed orientation and luminance simultaneously in both eyes at pseudo-random intervals (**Figure 1C**). Then, pupil constrictions and dilations occurred with latencies around 265 and 305 ms, respectively, after the change in stimulus orientation and luminance – only marginally before the button presses. Hence, the "lead" of pupil response in the first experiment is not primarily due to a faster response-time of the pupil as compared to the finger. Since the pupil reactions during binocular rivalry are about one fourth of the ones elicited by switching physically between the same stimuli. Therefore, as with the visually evoked potentials (VEP), averaging is required to obtain clear results. A prediction of which eye dominates during binocular rivalry, based on online pupil size, yields only between around 60% (Crouzet et al., 2011) and 70% correct responses (Naber et al., 2011 and our own data), depending on exact experimental conditions as well as on subjects (cf. also Kreiman et al., 2002; Fried et al., 2011).

We were tempted to conclude that the pupil knows something about the unconscious planning of cognitive events – in this case the internally generated decision to switch conscious perception between stimuli – that the owner of the brain does not know yet (Fahle et al., 2010). However, the apparent temporal lead of analog measures such as brain potentials and pupil size relative to button presses may rather be an artifact caused by the comparison between averaged continuous versus discontinuous signals (button presses or precise clock position; Libet, 1985). Such a comparison is in a way unfair. To press a button, a discontinuous (yes/no) decision is made on the basis of quite noisy (internal) processes which require that the signal has to pass a threshold. If the internal process fails to reach threshold, it fails to leave any trace. Pupil responses and brain potentials, on the other hand, are retained even if they fail to reach a threshold and can be averaged over time. For a fairer comparison between pupil and behavioral responses, we asked subjects in a second control experiment to move a joystick between left (one orientation dominates completely) and right (the other orientation dominates completely) with all possible in-betweens. This measure captures early parts of transitions as well as incomplete transitions. The results show a gradual transition in visual awareness that requires, on average, almost 1000 ms (shaded area in **Figure 2A$_1$**). In this second control experiment the pupil constricts with a time course very similar to the joystick response (while the dilation is somewhat slower; **Figure 2A$_2$**), and very similar to the main experiment (**Figure 1B**). This similarity in time courses of pupil responses under different experimental conditions allows one to compare reaction times between these conditions, and especially between button versus joystick responses. Button presses occurred, on average, at about the middle of the joystick transition time. In other words, observers pressed the buttons in the main experiment at about

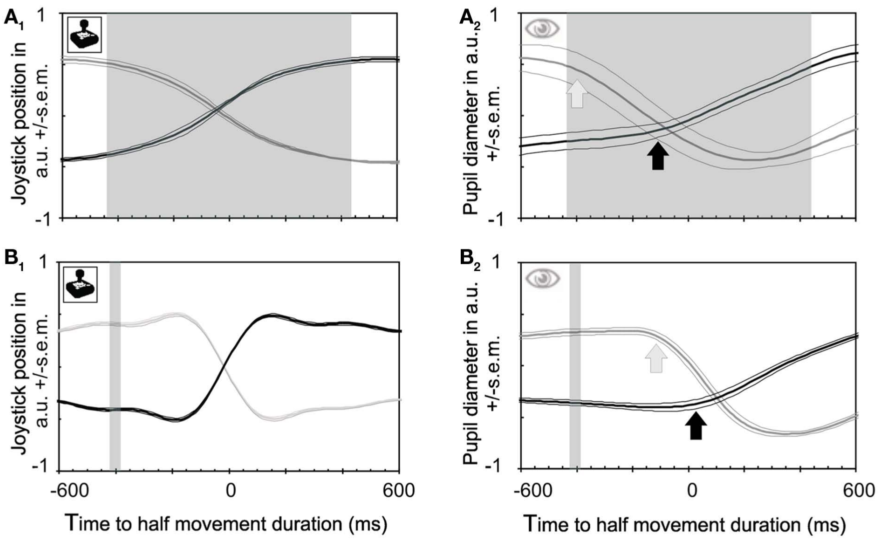

FIGURE 2 | Joystick and pupil responses obtained during binocular rivalry and between stimuli of differing luminances. (A) Joystick position and pupil responses to subjective changes in perceived grating orientation relative to joystick responses. Time zero is defined as half of the movement duration (not the mid position of the joystick which occurs earlier). This midpoint corresponds rather well with the time of button presses. **(A$_1$)** Joystick position. The transition between the two percepts requires on average 928 ms in both directions (shaded area), and joystick responses start about 460 ms (left side of shaded area) before the joystick reaches its midpoint, mirroring the relative slowness of the perceptual transition. **(A$_2$)** Pupil constrictions (which are known to be faster than dilations, Miller et al., 2005) start at about the same time as joystick responses [see **(A$_1$)**]. Hence the apparent lead of pupil responses over behavioral responses disappears if a continuous measure is taken rather than a discontinuous one (button presses). **(B)** Joystick and pupil responses to physical changes of stimuli. **(B$_1$)** Joystick responses relative to physical stimulus changes which took place within the shaded area. Latencies when expressed as midpoints of the joystick movement are very similar to those for button presses. Joystick movements are much faster here than for rivalrous transitions, reflecting the fact that the transition here is instantaneous (external) rather than gradual (internal; rivalrous). **(B$_2$)** Pupil constrictions caused by physical stimulus transitions start at the same time as joystick movements [see also **(B$_1$)**].

the time when they had used half of the transition time between the outer joystick positions in the control experiment (compare **Figure 1B** with **Figure 2A$_2$**). This interpretation receives further support from the comparison between button presses and joystick responses to physical stimulus changes (compare **Figure 2B$_1$** with **Figure 2B$_2$**). The joystick transitions for these physical changes of both stimuli had latencies comparable to those of button presses and pupil responses [compare **Figure 2B$_1$** (time to mid-interval) with **Figure 1C** (time to button press)].

To push the button or to move the joystick several internal thresholds must be passed. First a change in stimulus must be detected. Secondly, an internal decision criterion must be reached and third the motor threshold must be passed to initiate the movement. To cross these three thresholds and to move the hand requires about 200 ms (initial Joystick movement) or 400 ms (Button) for physical stimulus changes. We assume that reaching the third, the motor threshold; will follow the same time course also during rivalry. Comparison between the data for button presses versus joystick movements shows that the delay of responses in the initial button press experiment is not due to the fact that the stimulus change stays undetected. Quite to the contrary, the change is detected and indicated by a joystick movement, i.e., the first threshold is crossed fast. It is the second threshold, a cognitive one, which produces the delay: participants push the button not before the perceived stimulus change crosses an internal decision criterion, or threshold, which corresponds to a relative dominance (50 or more percent) of the new stimulus.

DISCUSSION

We infer from these results that the internal decision process during binocular rivalry – switching between the input of one eye to the input of the partner eye, clearly is not an abrupt one, occurring within a few milliseconds, but one that gradually builds up over a time course of about a second – possibly due to the piecemeal nature of the rivalry process and due to the incomplete inhibition between the two eyes or stimuli during the gradual transition time. The completely endogenously generated switching process during binocular rivalry may be an example of decision processes in general, with the advantage of being relatively slow and directly observable, since it relates to the decision between two different stimuli. The time difference between the start of the pupil response and the pressing of the button is not due to pupils having access to signals predating the conscious switch from one percept to its alternative. Rather, averaged analog signals allow one to detect imminent internal decisions earlier than a binary decision that has to be taken on the basis of a noisy trial-by-trial signal (Soon et al., 2008). This interpretation relates to the results of Libet (1985) who investigated a different type of internally generated decision processes. In his experiments, subjects were asked to press a button at irregular intervals, performing what Libet calls "freely voluntary, fully endogenous motor acts." During the experiments, subjects watched a revolving spot and were asked to recall the spatial "clock position" of this spot at the time when they became first aware of their decision or intention to move their finger. Libet found cortical potentials starting around 300–500 ms *before* the time at which subjects had consciously made the decision to press the button – i.e., these potentials were pre-conscious. Libet and others hypothesized that the brain makes a decision *before* the owner of the brain actually becomes aware of this decision (van de Grind, 2002; Wegner, 2003; Haggard, 2005). This interpretation would have significant consequences for theories of decision making including, as some argue, the concept of free will. But based on our own results, we would not jump to such conclusions, as outlined above. We would rather argue that also in the case of Libet's experiments likewise a certain proportion of decision processing are started ("Maybe I should press the button now?"), but are abandoned before the button is actually pressed ("I'd rather wait a little longer"). Under these circumstances, subjects would wait, in a way analogous to the situation during binocular rivalry, until they were sufficiently sure that the decision process just started would, indeed, lead to a button-press and, hence, press the button clearly after the decision process started. Some indicators of actions to be taken can be detected at much longer lead times than the ones found in Libet's as well as our experiments (Soon et al., 2008), up to 10 s. These indicators presumably reflect activity in high level control areas of the cortex that prepare actions in a way even more basic (and possibly completely unaware for the subject), and are (therefore?) far less reliable than the ones we measured here.

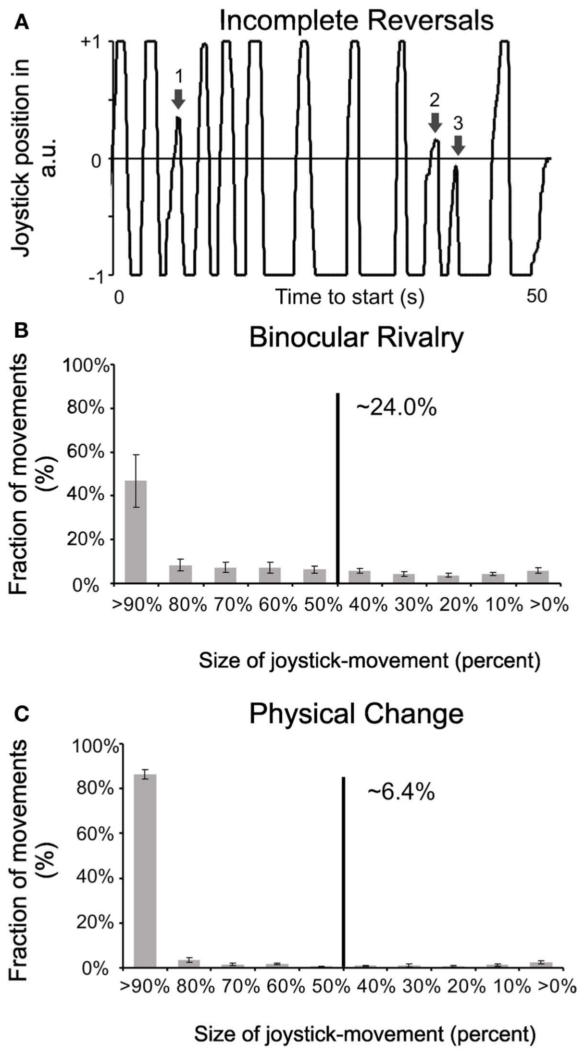

FIGURE 3 | Complete versus incomplete reversals. (A) Example for interrupted joystick movements, for an arbitrary 50 s period (*x*-axis). Joystick position "1" signals a complete percept of a dark grating and position "−1" that of a bright grating (*y*-axis). Movement "1" is considered as a sufficient transition (>60%), "2" is still considered as a sufficient reversal (>50%) but not included in pupil analysis while "3" is considered as an incomplete reversal (<50%), i.e., it does not qualify as a transition. **(B)** Percentages of complete versus incomplete joystick movements for changes during rivalry. Movements of less than half amplitude are considered as "incomplete" here since they indicate that percepts did not switch sufficiently to the competing stimulus or else the dominance of the competing stimulus was too short lived. **(C)** Percentages of complete versus incomplete joystick movements for physical stimulus changes. Note that the Poisson distribution determining physical changes contained dominance times down to 20 ms, leading observers to change joystick-direction before the reached the endpoint.

For a quantitative comparison between the binary versus analog response times, we measured the mean transition times of the joystick response of all observers to be 928 ms (± 51 ms SEM), and the rate of incomplete or interrupted joystick moves (i.e., those not even reaching the mid position, see movement "3" in **Figure 3A** to be 24% (± 3% SEM). The earlier the subjective percept moves back to the initial orientation or the shorter the interval between subsequent physical stimulus changes, the smaller becomes the joystick movement. As can be seen in **Figure 3**, the relative probability of all these partial movements does not differ much between all possible intervals. This is time both for purely perceptual changes (**Figure 3B**) as well as for physical changes (**Figure 3C**). However, in the latter case, the overall probability is much reduced since intervals below 1 s were relatively rare. From the results above, one can conclude that it takes on average 464 ms to complete half of the transition between percepts, and to perceive as dominant the competing stimulus. This interval corresponds nicely to the time difference between the beginning of pupil and joystick response on one hand and the button press on the other hand. Around 24% of incomplete transitions obviously prevent the subjects from signaling, by button press, the very start of the transition, since they cannot be sure whether this beginning transition will indeed lead to a dominance of the competing stimulus. This uncertainty results in very similar latencies for button presses and the middle of joystick transition time: observers press the button when the competing stimulus becomes dominant, not when the "previous" one starts to fade. Incidentally the speed of change in incomplete decision processes does not differ from those of complete ones and is not related to the frequency of switches in individual observers. Our results are in good agreement with single cell and field potential studies in monkeys that found neurons in cortical areas on several levels of the visual pathway reflecting the perceptual switches of binocular rivalry (Logothetis and Schall, 1989; Leopold and Logothetis, 1996) which in turn may influence the subcortical centers regulating pupil size (Barbur, 2004).

We conclude that (a) the pupil is a valid objective correlate of subjective perceptual changes in binocular rivalry (Naber and Einhäuser, 2010; Crouzet et al., 2011), (b) the start of pupil reactions predates the button presses of subjects by about 590 ms, and

(c) this time difference is not due to different motor response times, but (d) is due to averaged analog responses starting before all – or none (binary decisions) are taken – the latter requiring a certain threshold to be reached. Therefore, perceptual decisions during binocular rivalry require almost 1000 ms to develop fully (Wilson et al., 2001; van Ee et al., 2005). These results bear consequences for the interpretation of a number of similar experiments that compare analog responses (such as averaged brain responses; Morgan, 2005) with binary ones such as button presses or memorizing the exact position of a clock's hand. We conclude that extreme care should be taken not to over-interpret such comparisons between continuous and discontinuous indicators. In addition, we conjecture that the pupil seems to be a promising candidate for an objective measure of subjective phenomena such as binocular rivalry.

MATERIALS AND METHODS

GENERAL METHODS

All observers had normal or corrected-to-normal vision and gave written informed consent to participate. All procedures conformed with national and institutional guidelines and the Declaration of Helsinki. Observers saw stimuli at a distance of 0.6 m on a LED monitor (Zalman Trimon 2D/3D 22″) with polarizing filters of opposite circular polarization for odd and even pixel lines and matched filters in front of both eyes. Heads were stabilized with a headrest, the room was darkened and special care was taken to prevent scattered light. Stimuli had a diameter of 4°, a spatial frequency of 2 cycle/° and a Weber-contrast of eight relative to the background (luminances of 2.8 versus 108 cd/m^2). Observers ($n = 4$) looked at a central fixation point and indicated the change of the prevailing orientation of their percept as fast as possible by pressing the corresponding button in the first experiment and by moving a joystick between left and right in the control experiments. Transitions between grating orientations and the correlated luminance differences were caused either by internal decision processes (binocular rivalry) or by changing the stimulus orientation and luminance of the stimulus at random intervals (Poisson distribution) between one frame and the next. The start of pupil reactions and joystick movements was determined by the positive peak of the second derivative, the end of joystick movement by the negative peak of this derivative (Bergamin and Kardon, 2003). Observers were tested for 10 min twice for each experiment. Each data point in the graphs relies on a least 200 reports from each observer. Details regarding the recording and analysis of the data as well single subject results are to be found under Sections "Recording" and "Analysis." A separate pilot experiment with six additional observers reproduced the main results, i.e., reaction of pupils before button presses and simultaneous pupil and joystick reaction during rivalry. (Results not shown, since not all observers participated in all conditions). Data analysis was implemented in Matlab (MathWorks, Natick, MA, USA).

RECORDING

Joystick

We used the standard joystick for the pilot experiments but preferred the "throttle" for the experiment proper since it has a linear mechanical characteristic without favoring the middle position. Resolution of the joystick movement was 8 bit (256 levels).

Pupil

The right eye was illuminated by means of two infrared LEDs and recorded through a CCD camera (Watec 902 H3 supreme) at a rate of 50 Hz and a spatial resolution of 752 × 582. A computer program developed in house fitted the pupil by an ellipsoid and calculated its center and diameter as well as the positions of the Purkinje reflexes.

ANALYSIS

Joystick data

Data were smoothed by Gaussian filtering (half-width = 120 ms) to reduce noise. Start and end of the joystick movement were defined, for constrictions, as the negative and positive peak of the second derivative, respectively; hence both start and end of the movement were objectively determined. The slope midpoint is defined as half the time between start and end of the movement. This midpoint is supposed to correspond to the time of the button press. Indeed, these two measures correspond nicely to each other if they are compared on the basis of the corresponding pupil responses. Joystick movements that did not reach at least 50% of the maximum joystick amplitude were counted as partial or incomplete transitions and those below 60% were not included in the analysis of pupil responses (see Figure S5 in Supplementary Material). Transitions with small discontinuities of movement but without a change in direction were considered as one (slower) movement. The data were epoch-based z-transformed and averaged. The following analysis was the same as for the pupil data.

Pupil

Data points lost for example due to eye blinks were extrapolated by a polynomial function. No data points were discarded. Subsequently the whole data set was smoothed with a 7 point median filter. Averaging into "epochs" was relative either to the button response or the midpoint of the joystick movement, supplying means, and SEs of the means of pupil size for the two types of pupil transitions caused by rivalry or stimulus changes. Each epoch was normalized via z-transformation (z-score), see Figure S1a in Supplementary Material. A polynomial function was fitted to the averaged data, separately for transitions from dark to bright versus bright to dark. The second derivative of the fit function served to identify the exact start of the pupil response. z-Scores of pupil diameter were finally transformed to arbitrary units for better comparability in the graphs by setting the difference between maximum and minimum values for the averaged epoch to "unity."

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at http://www.frontiersin.org/human_neuroscience/10.3389/fnhum.2011.00120/abstract

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Callosal connections of primary visual cortex predict the spatial spreading of binocular rivalry across the visual hemifields

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In binocular rivalry, presentation of different images to the separate eyes leads to conscious perception alternating between the two possible interpretations every few seconds. During perceptual transitions, a stimulus emerging into dominance can spread in a wave-like manner across the visual field. These traveling waves of rivalry dominance have been successfully related to the cortical magnification properties and functional activity of early visual areas, including the primary visual cortex (V1). Curiously however, these traveling waves undergo a delay when passing from one hemifield to another. In the current study, we used diffusion tensor imaging (DTI) to investigate whether the strength of interhemispheric connections between the left and right visual cortex might be related to the delay of traveling waves across hemifields. We measured the delay in traveling wave times (ΔTWT) in 19 participants and repeated this test 6 weeks later to evaluate the reliability of our behavioral measures. We found large interindividual variability but also good test–retest reliability for individual measures of ΔTWT. Using DTI in connection with fiber tractography, we identified parts of the corpus callosum connecting functionally defined visual areas V1–V3. We found that individual differences in ΔTWT was reliably predicted by the diffusion properties of transcallosal fibers connecting left and right V1, but observed no such effect for neighboring transcallosal visual fibers connecting V2 and V3. Our results demonstrate that the anatomical characteristics of topographically specific transcallosal connections predict the individual delay of interhemispheric traveling waves, providing further evidence that V1 is an important site for neural processes underlying binocular rivalry.

Keywords: traveling waves, interhemispheric integration, binocular rivalry, diffusion tensor imaging, corpus callosum, primary visual cortex, radial diffusivity

INTRODUCTION

The phenomenon of binocular rivalry has been studied for almost 200 years now (Wheatstone, 1838) and has recently inspired the search for the neural correlates of conscious perception (Logothetis, 1998; Tong, 2003). During rivalry, visual stimuli presented separately to the two eyes compete for dominance in subjective awareness, such that the interpretation of the visual display alternates between the two monocular images. In transition periods, perceptual change often starts at one location and spreads to the other parts of the scene, a phenomenon termed "traveling waves" (Wilson et al., 2001). Using psychophysical estimates of wave speed for differently sized rival stimuli, Wilson et al. (2001) found that these traveling waves of changing perceptual dominance spread over space with a characteristic speed well predicted by the cortical magnification factor for primary visual cortex (V1). In a series of follow-up studies, Lee et al. (2005, 2007) used functional magnetic resonance imaging (fMRI) to demonstrate a neural correlate of traveling waves in early visual cortex (V1–V3). Specifically, they found that peak activity along the cortical representation of the rival stimulus was systematically shifted in time, thus implying that traveling wave generation may indeed arise within V1 as suggested by earlier psychophysical results.

Interestingly, the original paper (Wilson et al., 2001) also found that observers reported a longer travel time for waves that crossed the visual midline (mean difference of about 170 ms). They surmised that this could arise from the interhemispheric transfer of visual information that is necessary for stimuli crossing between the left and right hemispheres of the visual cortex. Long-range connections between hemispheres through the corpus callosum (CC) or subcortical structures might introduce a slow-down in neural transmission. The aim of our study was twofold. First, we tested whether individuals show reliable differences in their delay of traveling wave times (ΔTWT) for rivalry propagating across the visual hemifields, by evaluating test–retest reliability across experimental sessions separated by several weeks. Second, using fMRI and diffusion tensor imaging (DTI), we investigated whether specific anatomical characteristics of the CC that linked the left and right portions of the early visual areas would be able to predict the individual ΔTWT values.

MATERIALS AND METHODS

PARTICIPANTS

Nineteen participants whose ages ranged from 21 to 34 (mean age, 24; 10 males; 7 with a left eye dominance) took part in the study. All participants were right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971) and none had any history of psychiatric or neurological disorders. Ocular dominance was determined using the Miles test (Chaurasia and Mathur, 1976). All participants had normal or corrected-to-normal vision and were either paid for participation or received course credit. Written informed consent was obtained from all participants. Only individuals who reliably perceived traveling waves in the practice runs were used in the main experiment; this group comprised about 70% (19 out of 28) of those initially screened. Psychophysical tests took place in two sessions, with an interval of about 6 weeks between test and retest. We acquired DTI data and standard fMRI retinotopic mapping scans from all participants.

STIMULI

We used two monocular, annularly shaped gratings similar to those described by Wilson et al. (2001) and Lee et al. (2005). The rivalry display consisted of a high-contrast spiral pattern of 50% Michelson contrast shown to one eye (see **Figure 1A**), and a low-contrast radial pattern display shown at 12% contrast to the other eye (see **Figure 1B**). The high-contrast spiral pattern had a pitch angle of 45° and a spatial frequency of 3.64 cycles/degree, with a faint greenish hue added to enhance the perceptual salience of the traveling wave (luminance: 7.7 cd/m^2; luminance of the dark phase: 2.54 cd/m^2). The spatial frequency of the grayish radial grating was 2.55 cycles/degree (luminance of the dark phase: 31.5 cd/m^2; of the bright phase: 39.27 cd/m^2). The diameters of the outer edge of the two monocular annuli were 10 cm, corresponding to a visual angle of 7.85°. The annuli were 2 cm wide (1.6°). The inner edge had a diameter of 6 cm or 4.7° in visual angle. In the center of the annuli was a bull's eye-like fixation point. The spatial configuration of these narrow, annularly shaped rival targets effectively constrains the path of perceptual traveling waves, making it straightforward to induce the waves and measure their speed.

Stimuli and experimental procedure were generated in MATLAB 7.3.0 (R2006b) using Psychtoolbox 3.0.8 (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 19″ CRT monitor (1,024 × 768 resolution, 120 Hz refresh rate). For the monocular projection of different images to the two eyes, participants wore Stereo Graphics Shutter Glasses that were synchronized with the monitor's refresh rate by a Crystal Eyes Workstation (RealD, Beverly Hills, CA, USA)[1].

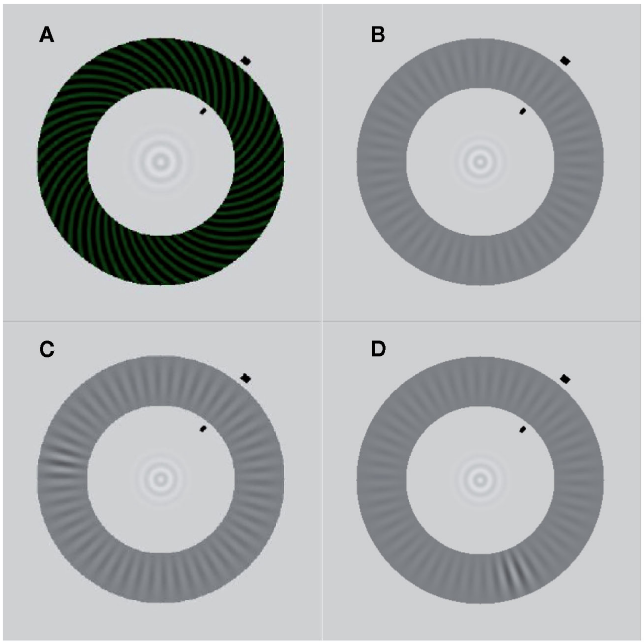

FIGURE 1 | Stimuli. (A) High-contrast spiral pattern (dominant stimulus). **(B)** Low-contrast radial pattern (target stimulus). **(C)** Contrast increment in the upper left quadrant of the target stimulus. The induced wave that propagates along the shorter section between trigger and arrival point (black lines) travels along the interhemispheric path. **(D)** Contrast increment in the lower right quadrant of the target stimulus. The induced wave that propagates along the shorter section between trigger and arrival point travels along the intrahemispheric path.

EXPERIMENTAL PROCEDURE

During the experiment, participants' head position was stabilized using a chin rest at a distance of 73 cm to the screen. Participants were asked to maintain strict fixation on the bull's eye at the center of the annuli. We used the interocular flash-suppression technique introduced by Wolfe (1984). On each trial, the low-contrast radial pattern (the "target") was presented to one eye and, then 1.25 s later, the high-contrast spiral pattern was presented to the corresponding retinal location of the other eye. This sequence typically resulted in perceptual suppression of the target stimulus. After 0.83 s, an abrupt, local increment in the contrast of the radial target stimulus appeared for 0.375 s. The size of the increment was three spatial cycles (1.18°) of the radial grating and it increased the contrast of the low-contrast grating locally from 12 to 27% (luminance of the dark phase: 23.03 cd/m^2, of the bright phase: 40.1 cd/m^2). As expected (Wilson et al., 2001), the abrupt onset of this increment triggered a change in perceptual dominance, causing the previously suppressed target pattern to become perceptually dominant immediately at the location of the trigger, which, in turn, tended to induce a wave of spreading dominance of the target that traveled around the annulus. Participants were instructed to press a button as soon as the wave reached an arrival point that was clearly designated by two short, black lines at the inner and outer boundaries of the annuli. Participants were asked to respond only to the wave that traveled along the shorter section between trigger and arrival point

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[1] http://www.reald.com/Content/Crystal-Eyes-3.aspx

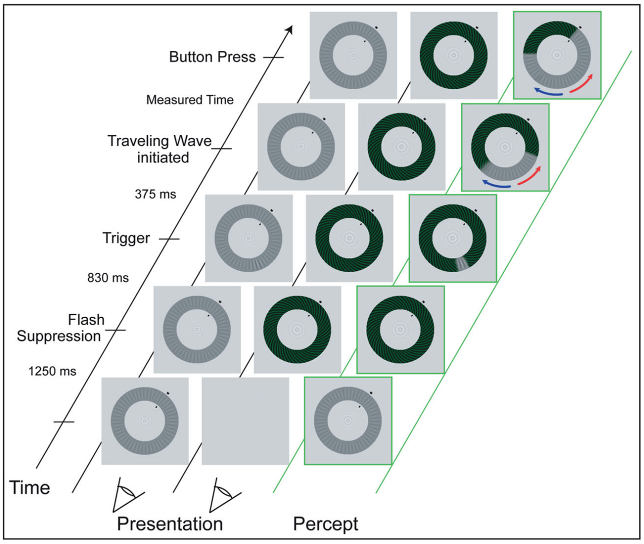

FIGURE 2 | Experimental procedure of the psychometric measurements (see text for a detailed description). While maintaining fixation on the small, central bull's eye figure, participants monitored the perceptual wave that traveled along the shorter section between trigger location and arrival point (red arrow). The two columns to the left show the dissimilar images that are presented monocularly, while the green right column illustrates the resulting percept.

(see **Figure 2**). The background remained light gray (luminance: 91.8 cd/m^2). The arrival point position varied between blocks of trials, and arrival point markers were presented at one of four positions (50°, 130°, 230°, 310° in relation to the 3 o'clock position in the annuli). These positions were chosen to cover all quadrants and to ensure that waves induced by the triggers traveled either along an intra- or interhemispheric path. Per arrival point, there were two possible trigger points, located at a distance of 120° to both sides of the arrival point (see **Figures 1C,D**).

The time the wave needed to travel the distance of 7.38° in visual angle along the shorter path was measured based on the time elapsed from the appearance of the trigger to the participant's button press indicating that the wave had reached the arrival point. After each trial, participants verified whether they had actually seen the trigger-induced wave traveling toward the arrival point and whether they had reacted in time by pressing a "yes" or "no" key. Runs consisted of at least 12 positive trials per trigger point, with negative trials (i.e., trials when waves were unsuccessfully triggered or when triggered waves dissipated before reaching the arrival point) discarded from further analysis. Participants had to complete eight runs in total, two runs per arrival point position. To control for participants' ocular dominance, the number of runs in which the target stimulus was presented to the right eye was equal to the number of runs in which it was presented to the left eye. In total, participants had to complete at least 192 trials in one session. Participants were familiarized with the instructions and the stimuli in eight test trials, which preceded the actual experiment. The same procedure was repeated after 6 weeks.

ANALYSIS OF BEHAVIORAL DATA

Correlation and regression analyses were performed using R, version 2.10.1[2] and the car package[3]. For all analyses, linear parametric methods were used, i.e., Pearson coefficients for correlation and the general linear model for multiple regression. Statistical tests were performed using two-tailed tests with an α-level of 0.05. Data from the psychophysical measurements were corrected for outliers by removing trials with speed estimates outside the range of 2 SD from the mean for each individual.

Means were computed for interhemispheric traveling wave times (interTWT; wave start and end points in different visual hemifields) and intrahemispheric traveling wave times (intraTWT; wave start and end points in the same visual hemifield). To estimate the amount of time required for interhemispheric transfer of the traveling wave, we calculated the difference between these two measures (ΔTWT = interTWT − intraTWT). The intraTWT, interTWT, and ΔTWT estimates from the two test periods (separated by 6 weeks) were correlated to determine test–retest reliability. Since we controlled for participants' ocular dominance, we were able to estimate intraTWT, interTWT, and ΔTWT separately for both eyes. This allowed us to determine a version of parallel-test or split-half reliability for the different measures. We estimated an average intraTWT across the two time points for each eye and then correlated the intraTWT of the left eye with the intraTWT of the right eye. The same procedure was performed for interTWT and ΔTWT. For regression analyses of the relationship between ΔTWT and measures of microstructural integrity, the average ΔTWT of the two time points was entered as dependent variable and the different measures derived from the diffusion data were entered as independent variables, either individually or in multiple-regression analyses.

ACQUISITION OF IMAGING DATA

All data were acquired at the Brain Imaging Center Frankfurt am Main, Germany using a Siemens 3-T Trio scanner (Siemens, Erlangen, Germany) with a eight-channel head coil and maximum gradient strength of 40 mT/m.

Anatomical imaging

For coregistration and anatomical localization of functional and diffusion tensor data, a T1-weighted anatomical image of 1 mm × 1 mm × 1 mm was acquired in each of the two sessions (MP-RAGE, TR = 2250 ms, TE = 2.6 ms, flip angle: 9°, FoV: 256 mm).

Diffusion tensor imaging

The diffusion-weighted data were acquired using single-shot spin-echo echo-planar-imaging (EPI; TR = 8200 ms, TE = 99 ms, slice thickness = 2 mm, FoV = 192 mm, voxel size = 2.0 mm × 2.0 mm × 2.0 mm, matrix size = 96 × 96). Diffusion weighting was isotropically distributed along 60 directions using a *b*-value of 1000 s/mm^2. Additionally, 10 data sets with no diffusion weighting were acquired initially as anatomical reference for motion correction and for computation of diffusion coefficients during

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[2] http://www.R-project.org

[3] http://CRAN.R-project.org/package = car

the diffusion sequence. To increase signal-to-noise, we acquired three consecutive scans that were subsequently averaged. Total acquisition time for diffusion imaging was 30 min.

Retinotopic mapping

Participants were presented with both eccentricity and polar-angle stimuli. However, only the data of the polar-angle mapping experiment were used for further analysis. Stimuli were generated with a custom-made program based on the Microsoft DirectX library (Muckli et al., 2005) and presented using a MR-compatible goggle system with two organic light-emitting-diode displays (MR Vision 2000; Resonance Technology, Northridge, CA, USA). In the polar-angle mapping experiment, a wedge-shaped checkerboard pattern subtending up to 30° visual angle was presented. The wedge started at the right horizontal meridian and slowly rotated clockwise around the fixation point for a full circle of 360°. The mapping experiment consisted of 12 repetitions of rotation, each cycle lasting for 64 s. Participants had no further task but to fixate on the central fixation point. For the polar-angle mapping experiment, a gradient-recalled EPI sequence with the following parameters was applied: 33 slices, TR = 2000 ms, TE = 30 ms, flip angle = 90°, FoV = 192 mm, slice thickness = 3 mm, gap thickness = 0.3 mm, voxel size = 3.0 mm × 3.0 mm × 3.0 mm. The acquisition time for the retinotopic mapping was 22 min.

ANALYSIS OF FUNCTIONAL DATA

Functional data to localize the retinotopic neural representation of visual space were analyzed using BrainVoyager QX 2.0.8 software (Brain Innovation, Maastricht, the Netherlands)[4]. Pre-processing steps included motion correction, linear trend removal, and temporal high-pass filtering. The analysis of the polar-angle mapping experiment was conducted by the use of a cross-correlation analysis (Muckli et al., 2005). The boundaries of retinotopic cortical areas V1, V2, and V3 were estimated manually on the inflated cortical surface generated from each participant's anatomical data set. After the selection of the cortical areas V1, V2, and V3 on the inflated cortical surface, the area was projected back into the three-dimensional participant-specific native space by selecting voxels with a maximum distance of 2 mm from the gray/white matter boundary. The V1, V2, and V3 three-dimensional masks were generated for each hemisphere for a total of 38 hemispheres. These masks were exported out of Brain Voyager QX using a NIfTI converter developed by Brain Innovation (Maastricht, the Netherlands) to continue the analysis in FSL[5]. Using FLIRT, part of the FSL toolbox, these masks were transformed into diffusion space for tractography analysis. Data from each participant were visually inspected to confirm that the transformation procedure was successful. The sizes of the V1, V2, and V3 masks averaged 1000 voxels (8000 mm^3) in diffusion space for each hemisphere.

ANALYSIS OF DIFFUSION DATA

Diffusion tensor modeling and probabilistic tractography were performed using FDT (FMRIB's Diffusion Toolbox) implemented in FSL. Pre-processing steps included (i) correction for eddy current and head motion, (ii) correction of the gradient direction for each volume using the rotation parameters from the head motion. For the evaluation of white-matter microstructure, three maps of quantitative diffusion parameters were calculated with the resulting three eigenvalues (λ_1, λ_2, and λ_3) in each voxel, namely the fractional anisotropy (FA), axial diffusivity (AD), and radial diffusivity (RD). FA maps were obtained using the equation provided by Basser and Pierpaoli (1996). AD maps were computed as the first eigenvalue (λ_1), which represents the main diffusion direction, corresponding to the main fiber axis (left–right) in the CC. RD maps were obtained using the mean of the eigenvalues λ_2 and λ_3 with high values indicating high diffusion in the direction perpendicular to the main fiber direction.

Masks for V1, V2, and V3 in both hemispheres were defined in diffusion space to serve as target regions for fiber tracking. To define the seed region, a mask covering the whole CC was created separately for each participant. This was done by drawing manually onto the CC in diffusion space, starting from the mid-sagittal plane and then expanding the mask by two voxels to the left and to the right, respectively, in total covering five voxels of the CC along the x-axis. Estimation of tracts was performed using probabilistic tractography using published methods in the FSL environment; the details of the procedure have been described elsewhere (Behrens et al., 2003). We used a dual-fibers model as implemented in the latest version of bedpostX. The model allows for the representation of two fiber orientations per voxel when more than one orientation is supported by the data. This allows modeling of crossing fibers, and produces more reliable results compared to single-fiber models (Behrens et al., 2007). The result is a brain image where all voxels have a value that represents the connectivity between that voxel and the voxels in the seed region. Fiber tracking was done probabilistically in each participant's diffusion space, using 25000 tract-following samples at each voxel; the step length was set to 0.5 mm and curvature threshold of 0.2 was chosen. Tracts were generated from each seed voxel within the CC mask, and only tracts entering the target masks were retained. Target masks were also set as waypoint and termination masks to prevent the tract from projecting into other areas. For each participant, six different tracts were calculated (see **Figures 3A,B**), each connecting a pair of masks consisting of: (1) the CC mask and the left V1, (2) the CC mask and the right V1, (3) the CC mask and the left V2 mask, (4) the CC mask and the right V2 mask, (5) the CC mask and the left V3, (6) the CC mask and the right V3. To remove spurious connections, the raw V1, V2, and V3 tracts of individual participants were thresholded to include only voxels that had at least 12500 samples passing through them (probability threshold of 0.5). The reason for applying such high thresholds in the generation of the V1, V2, and V3 tracts was to differentiate callosal segments most likely connecting V1, V2, and V3.

To determine the microstructural integrity of the specific CC segment that interconnects left and right V1, a combined tracking approach was used (Westerhausen et al., 2009). After calculating the sum of the thresholded tracts connecting the CC with the left and right V1, only those voxels in the CC containing fiber projections of V1 of both hemispheres were selected. From the identified V1 CC segment, quantitative diffusion parameters (FA,

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[4] www.brainvoyager.com

[5] www.fmrib.ox.ac.uk/fsl

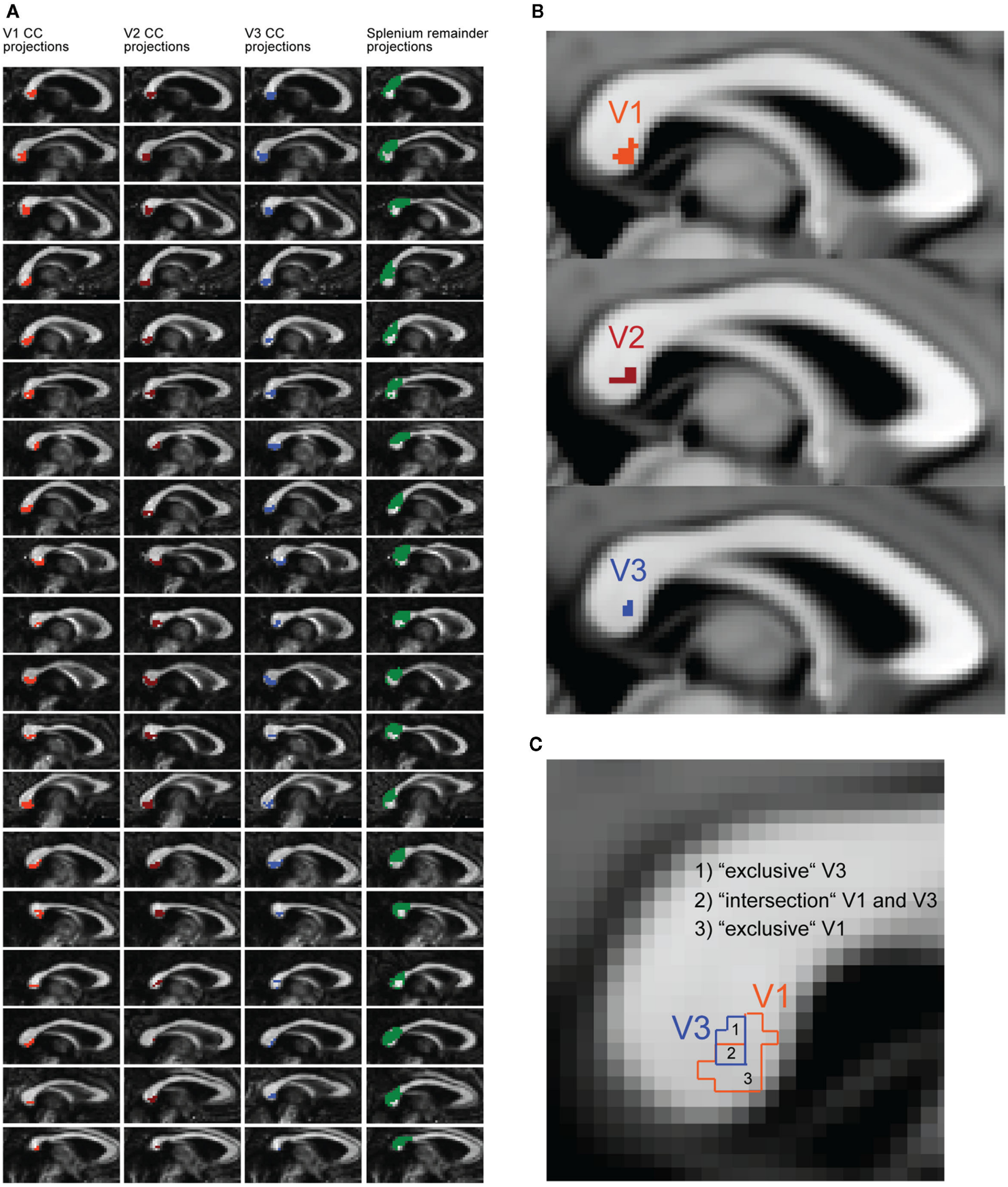

FIGURE 3 | Tractography results and schematic description of the parcellation logic for the transcallosal fibers. (A) Midsagittal tracking results of every participant overlaid on each individual's corpus callosum (CC). Transcallosal fiber connections are plotted for regions that project to functionally localized regions of V1 (orange), V2 (dark red), and V3 (blue). The green area represents the splenium, anatomically defined, excluding the projections from V1, V2, and V3 (splenium remainder). **(B)** Display of the group-analysis results for V1 (orange), V2 (dark red), and V3 (blue) CC segments. Individual CC segments were non-linearly transformed into MNI space. Only voxels are displayed that were part of V1, V2, V3 CC segments in at least 14 out of 19 participants. **(C)** Schematic description of subregions in the CC. The subregions for V1 (orange) and V3 (blue) were defined according to the fiber tracking results. Because the V1 and V3 subregions overlapped in most participants, an additional regression was performed with the "intersection" and "exclusive" segments of V1 and V3.

RD, AD) were extracted and averaged for the subsequent correlation analysis. The same tracking procedure was also applied for V2 and V3.

Additional analysis of V1 fiber tract

Position and size of the V1 CC segment were determined by the applied probability threshold for the tracts between the CC and the target area V1. Here, lower threshold values will increase and higher values will decrease the size of the CC segments. Thus, in order to rule out potential influences of the thresholding procedure on the extracted microstructural properties of the V1 CC segment and the resulting estimates of the correlation between structural variables and behavior, a different probability threshold value of 0.25 was applied for the V1 tracts (i.e., at least 6250 samples passing through a voxel) to extract an alternative (and larger) V1 CC segment for each participant. The resulting segment was significantly larger than the previous one, $t(18) = -14{,}30$, $p < 0.001$ (size "0.5 probability threshold" in voxels, $M = 37$, SD = 13; size "0.25 probability threshold" in voxels, $M = 55$, SD = 15). All analyses were also performed for this second V1 segment.

Sub-parcellation procedure for the visual corpus callosum segments

It was found that the V1 CC segment was partially overlapping with the V3 CC segment. To create CC segments that exclusively represented a given cortical projection, the identified CC segments were separated into an "exclusive" and an "intersection" sub-segment (see **Figure 3C**). Two "exclusive" segments (V1 without V3; V3 without V1) and one "intersection" segment (V1 and V3 overlapping) were created. Again, the revealed sub-segments were transferred to the maps of the quantitative diffusion parameters to extract the microstructural properties for correlation analysis.

Geometry-based tract segmentation

To compare the tractography-based tract segmentation with the traditional approaches for the quantification of callosal variability, we also performed a standardized geometrical parcellation of the CC. For this purpose, the midsagittal length of the maximal anterior–posterior extent of the CC mask of each participant in diffusion space was measured and a splenium mask was created manually according to the Witelson (1989) scheme. As defined by the scheme, the splenium is the posterior fifth of the CC in relation to its length along the y-axis. We performed the same correlation analysis on the splenium mask to determine whether the quantitative diffusion parameters in this structure might account for interhemispheric delays in the spatial spreading of rivalry dominance. Additional control analyses were performed using a splenium sub-segment, in which the V1, V2, and V3 CC segments were excluded from the splenium (splenium remainder).

RESULTS

BEHAVIORAL DATA

We computed traveling-wave times for the intrahemispheric (intraTWT) and interhemispheric (interTWT) spread of dominance. Traveling times for interTWT ($M = 1907$ ms, SD = 865 ms) were longer than for intraTWT ($M = 1854$ ms, SD = 840 ms), although the mean difference between interTWT and intraTWT of 53 ms (SD = 148 ms) was not significant in our sample [$t(18) = 1.56$, $p = 0.07$, one-tailed, 95% CI: -18.6 to 124.6]. Analyses indicated large interindividual variability of both indices, but high test–retest reliability for individual participants over 6 weeks for the intraTWT [$r(17) = 0.79$, $p < 0.001$] and interTWT [$r(17) = 0.77$, $p < 0.001$; **Figure 4A**]. Since eye of presentation for the rival patterns was varied between runs, we were also able to calculate parallel-test reliabilities between eye configurations (averaged across the two time points). For both measures, reliabilities were at ceiling level [intraTWT, $r(17) = 0.98$, $p < 0.001$; interTWT, $r(17) = 0.98$, $p < 0.001$, **Figure 4B**]. No significant sex differences were found for the average intraTWT [$t(18) = 1.56$, $p = 0.07$, two-tailed] or interTWT [$t(18) = -0.09$, $p = 0.73$, two-tailed].

For the difference between interTWT and intraTWT (ΔTWT), we also found large interindividual variability, which was not significantly correlated with interTWT [$r(17) = 0.26$, $p = 0.29$] or intraTWT [$r(17) = 0.09$, $p = 0.72$]. Given that ΔTWT is a difference measure, we evaluated test–retest [$r(17) = 0.62$, $p = 0.004$] and parallel-test reliabilities [$r(17) = 0.65$, $p = 0.002$, **Figures 4A,B**] and found that these were high. Again, no sex differences were found for the average ΔTWT [$t(17) = 1.03$, $p = 0.38$] over the two time points. The behavioral results showed that the speed of traveling waves of dominance and the delay for transfer between hemispheres are stable traits of individual visual processing in participants.

fMRI AND DTI DATA

The most commonly used measure of microstructural integrity for DTI measures of white matter is FA. It represents the directional distribution of water diffusion in the respective part of the brain. FA reaches a high value when diffusion is predominantly in one direction and reaches the lowest possible value for equal diffusion in all directions. We found significant correlations between ΔTWT and the FA of those CC segments that interconnect left and right V1 [$r(17) = 0.74$, $p < 0.001$]. We also looked at the component measures from which FA is computed (see also Materials and Methods). In tissue as highly organized as the CC, the second and third eigenvalues can be averaged to characterize diffusion perpendicular to the main fiber direction (RD). Diffusion in the main fiber direction (left–right in the CC) corresponds to the first eigenvalue (AD). In accordance with a previous paper (Dougherty et al., 2007), we found that AD did not contribute significantly to ΔTWT prediction [$r(17) = -0.35$, $p = 0.14$], but there was a strong correlation with RD [$r(17) = -0.72$ and $p < 0.001$; **Figure 5**]. In hierarchical regression analyses, we confirmed that neither adding AD nor FA as predictors in a regression of ΔTWT on RD provided a significant increase in explained variance for the regression model [adding AD: $F(1,16) = 0.54$, $p = 0.47$; adding FA: $F(1,16) = 2.55$, $p = 0.13$]. Therefore, further analyses focused on RD as a measure of callosal microstructure.

To examine the extent to which these structure–function relations are topographically specific within the CC, we compared correlations between ΔTWT and anatomical measures not only for the callosal segment linking V1 but also for the segments linking V2, V3, and parts of the posterior CC not covered by the V1–V3 segments (splenium remainder, see Materials and Methods). In a combined multiple-regression analysis with segment RDs as independent variables and ΔTWT as dependent variable, RD of the V1 and V3 CC segments were the only variables providing unique contributions to ΔTWT prediction [V1 segment, $\beta = -1.08$, $t(14) = -5.927$, $p < 0.001$; V3 segment, $\beta = 0.663$, $t(14) = 3.569$, $p = 0.003$; other predictors, $p > 0.53$]. However, separate bivariate analyses for the CC segments showed that only

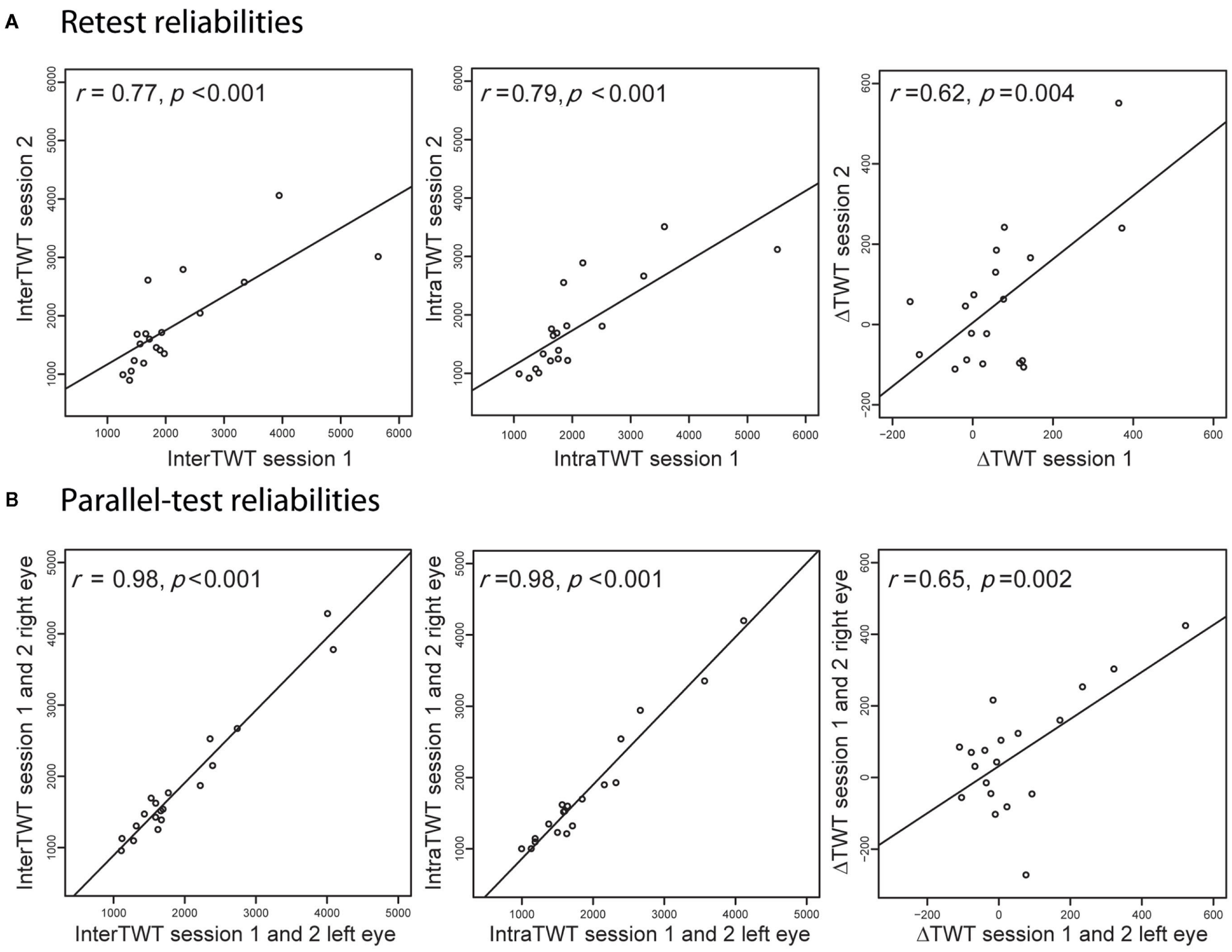

FIGURE 4 | Reliability of the behavioral measures. (A) Analyses show high retest reliabilities for interhemispheric traveling wave time, intrahemispheric traveling wave time and the difference of the two indices (ΔTWT). **(B)** Analyses also show high parallel-test reliabilities for the same psychometric indices, indicating that these psychophysical measures are stable features in humans.

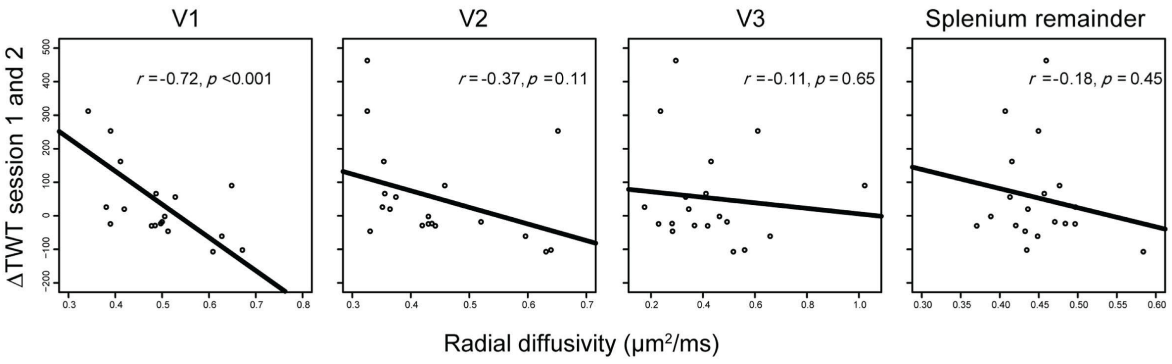

FIGURE 5 | Correlations between interhemispheric delays and fiber properties of different callosal projections. Only radial diffusivity (RD) of V1 callosal projections predicted behavioral variance in ΔTWT; no reliable relationships were found between ΔTWT and RD in callosal projections of V2, V3, or the splenium remainder.

RD of the V1 CC segment correlated significantly with ΔTWT [V1 segment, $r(17) = -0.72, p < 0.001$]. No significant correlation was found between ΔTWT and RD of the other CC segments [V2, $r(17) = -0.37$, $p = 0.11$; V3, $r(17) = -0.11$, $p = 0.65$; splenium remainder, $r(17) = -0.21$, $p = 0.38$; see **Figure 5**]. A situation in which an independent variable shows no bivariate correlation with the dependent variable, but makes a significant contribution in the context of a multiple-regression analysis with other variables, is called "suppression" in statistics. The variable suppresses noise variance in other independent variables and thereby enhances predictive power of the variable set as a whole. In our data set, V3 RD seems to act as a suppressor variable, since it is only weakly related to ΔTWT on its own. Therefore, only RD of the V1 segment is directly associated with ΔTWT.

Correlation coefficients can be strongly influenced by a few exceptional cases. Therefore, we eliminated the most prominent outliers (Cook's $D > 0.10$) from the analysis, both as a group and individually. For the V1 CC segment, we calculated correlation coefficients with various outliers removed, and repeatedly observed a strong relationship with *r* values ranging from −0.50 to −0.77, which were all significant at an alpha level of 0.05 (**Table 1**). Results for the control CC segments were non-significant in all cases [$p(\text{V2}) > 0.10$; $p(\text{V3}) > 0.36$; $p(\text{Spl}) > 0.23$].

We also considered the fact that our measures of ΔTWT revealed considerable variability in interhemispheric delay times across participants. Although the mean ΔTWT was 53 ms, a large number of participants had negative values in our data (see **Figure 5**). Looking more closely at the measurements for the first and second sessions (**Figure 4**, right panel), it can be seen that only four participants had negative ΔTWT values across both sessions, eight showed positive values in both sessions, and seven showed mixed results. Therefore, the overall trend in our data is in the same direction as the original study by Wilson et al. (2001), which reported a mean ΔTWT of 173 ms based on detailed psychophysical measurements of two experienced visual observers. A more extensive study would be needed to estimate the actual distribution of ΔTWT in the broader population. Nevertheless, in the present study one could ask whether the observed relationship between V1 callosal anatomy and behavioral estimates of interhemispheric delay might depend on a subset of participants exhibiting positive or negative ΔTWT values. After separating participants into the two subgroups, those with positive or negative ΔTWTs, we found that the correlation with V1 RD was strong and statistically significant in both subgroups, despite the splitting of the sample size [$\Delta\text{TWT} > 0$: $r(7) = -0.67$, $p = 0.049$; $\Delta\text{TWT} < 0$: $r(8) = -0.80$, $p = 0.005$].

To control for the effects of age and sex on the regression analyses, we performed a combined multiple-regression analysis with RD in the V1 CC segment, age and sex as independent variables and ΔTWT as dependent variable. The strong and unique relationship between V1 RD and ΔTWT remained stable [$\beta = -0.61$, $t(15) = -3.09$, $p = 0.005$; other predictors, $p > 0.19$].

Since our results are based on correlations between variables, we cannot exclude the existence of additional factors that might affect or drive the association between behavior and callosal microstructure. In a multiple-regression analysis, we included a number of control variables that are plausible candidates for alternative explanations. We considered the size of V1, the (logarithm of the) size ratio between left and right V1, the size of the callosal segments connecting V1, and the average probability values in the callosal V1 segments from the probabilistic tracking. The strong and unique relationship between V1 RD and ΔTWT remained stable even when these other predictor variables were partialed out [$\beta = -0.76$, $t(13) = -3.66$, $p = 0.003$]. Only the size of the callosal V1 segments made a marginal contribution to ΔTWT ($p = 0.07$, other predictors: $p > 0.28$).

Since the V1 and V3 CC segments showed some degree of overlap and both made significant contributions in the multiple-regression analysis, we created two CC segments of V1 and V3, respectively, that excluded the intersection of the two segments, and performed correlation analyses for these two newly defined segments as well as their intersection (see **Figure 3C** and Materials and Methods). Only RD in the "exclusive" V1 CC segment showed a significant correlation with ΔTWT [$r(17) = -0.61$, $p = 0.005$]. There was neither a significant effect in the intersection CC segment [$r(17) = -0.33$. $p = 0.17$] nor in the "exclusive" V3 CC segment [$r(17) = 0.07$, $p = 0.74$].

Defining the V1 CC segment by a more liberal tract threshold (value = 0.25) also did not affect the outcome (see Materials and Methods). A separate correlation analysis with the RD of the "liberal" V1 CC segments and ΔTWT showed that the relationship between microstructure and behavior remained statistically significant [$r(17) = -0.60$, $p = 0.007$]. One reason for the weakening of correlations could be the expanded size of the V1 CC segments (size "0.5 threshold" in voxels, $M = 37$, SD = 13; size "0.25 threshold" in voxels, $M = 55$, SD = 15), which might reduce the accuracy of isolating V1-specific projections in the CC.

Table 1 | Robustness of results with elimination of outliers.

Cases excluded	Cook's *D*	*r*	df	*t*	*p*	Slope	Intercept
LAA30 (ΔTWT = 463 ms)	0.92	−0.50	16	−2.29	0.04	−678	371
TGA01 (ΔTWT = 90 ms)	0.52	−0.77	16	−4.87	<0.001	−1337	689
RKL25 (ΔTWT = −24 ms)	0.14	−0.71	16	−4.04	<0.001	−1163	636
FDN14 (ΔTWT = 312 ms)	0.13	−0.61	16	−3.11	0.007	−972	524
LAA30, TGA01, RKL25, FDN14	–	−0.67	13	−3.28	0.006	−888	458

Correlations between ΔTWT and radial diffusivity (RD) of the V1 segment for different subgroups excluding varying sets of outliers (Cook's D > 0.10).

We focused our analyses on RD because, in accordance with a previous study (Dougherty et al., 2007), we found that the first eigenvalue did not contribute to the correlation between microstructure and ΔTWT, which also affects correlations with FA. Nevertheless, since FA is widely used as a main marker of microstructural integrity, we performed the main analyses with FA values. With regard to the anatomical specificity of results, we performed multiple-regression of ΔTWT on FA values of the V1, V2, V3, and splenium remainder CC segments. FA of the V1 and V3 CC segments were the only variables providing a unique contribution to ΔTWT prediction [V1 segment, $\beta = 0.97$, $t(14) = 4.85$, $p < 0.001$; V3 segment, $\beta = -0.52$, $t(14) = -2.31$, $p = 0.03$; other predictors, $p > 0.56$]. But again, separate correlation analyses for the segments showed that only FA of the V1 CC segment contributed to ΔTWT prediction [V1 segment, $r(17) = 0.74$, $p < 0.001$]. No correlation was found between FA of the V3 CC segment and ΔTWT [V3 segment, $r(17) = 0.17$, $p = 0.48$]. Also, separate correlation analyses between the two additional control segments and ΔTWT did not reveal significant effects [V2 segment, $r(17) = 0.41$, $p = 0.07$; splenium remainder, $r(17) = 0.22$, $p = 0.36$].

DISCUSSION

Our results demonstrate that the propagation times of traveling waves during binocular rivalry within and across hemispheres are stable characteristics of visual processing. In addition, we found that the individual delay introduced by interhemispheric transit (ΔTWT) also has a high reliability, although lower than the absolute travel times. We investigated the relationship between ΔTWT and microstructural values of specific CC segments connecting early visual areas in healthy humans, which revealed a very specific association of ΔTWT with the CC segments connecting V1 of the two hemispheres. No significant correlations were found for neighboring CC segments (V2, V3, and splenium remainder) in the posterior part of the CC.

The observed stability of the propagation time of traveling waves in our study is in accordance with findings of other studies focusing on the alternation rate during binocular rivalry (Pettigrew and Miller, 1998; Miller et al., 2010; Shannon et al., 2011). The alternation rate for a given observer is the average rate of switches (in Hz) between the two possible percepts for prolonged stimulation. Previous studies have found that the alternation rate is highly reliable (≥ 0.80) over time when tested weeks or even months later. Interestingly, there is also evidence for a substantial genetic contribution to individual variation in alternation rate (Miller et al., 2010; Shannon et al., 2011) and, moreover, the alternation rate for binocular rivalry is correlated with alternation rates of other bistable phenomena (Shannon et al., 2011). Considered together, these patterns of results suggest the existence of a global genetic factor governing visual bistability.

In general terms, perceptual alternation during binocular rivalry is thought to result from inhibitory interactions between neural representations of the different percepts (Lehky, 1988). Early models mainly focused on competition between eye-specific channels (Blake, 1989), but recent evidence suggests that rivalry can occur on multiple levels of the visual hierarchy (Blake and Logothetis, 2002; Wilson, 2003; Tong et al., 2006). Apart from random fluctuations, changes in perceptual dominance over time are caused by increasing adaptation of the dominant representation with concurrent release from inhibition for the suppressed stimulus (Alais et al., 2010). Traveling wave propagation, too, can be modeled with mutually inhibitory, adaptable neural ensembles (Wilson et al., 2001). In this model, wave propagation is introduced through laterally spreading inhibition between ocular dominance columns. To account for the influence of collinear facilitation on wave speed, long-range excitatory connections are required as an additional element. It is interesting to note that individuals who tend to experience fast traveling waves also tend to exhibit faster rates of rivalry alternations, suggesting that traveling waves and alternation rate may have common neural bases (Kang et al., 2009).

In binocular rivalry research, there is long-standing debate on where within the cortical hierarchy neural competition between rivaling interpretations is initiated and where it is resolved (Blake, 1989; Logothetis, 1998; Leopold and Logothetis, 1999; Blake and Logothetis, 2002). Resolution of that debate may in turn have implications for identifying the neural correlates of conscious perception (Rees et al., 2002; Tong, 2003; Knapen et al., 2011). Due to the separated inputs to the two eyes, early models assumed that rivalry is determined by eye-specific channels especially in V1 (Blake, 1989) and imaging studies found activation patterns in V1 (Polonsky et al., 2000; Tong and Engel, 2001; Lee and Blake, 2002) and even the lateral geniculate nucleus (Haynes et al., 2005; Wunderlich et al., 2005) corresponding to the conscious perception of observers. But electrophysiological studies in macaque monkeys (Logothetis and Schall, 1989; Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997) and psychophysical studies in humans (Kovács et al., 1996; Logothetis et al., 1996; Ngo et al., 2000) suggested that, at least for specific stimuli, interactions at higher levels of visual processing are relevant for the resolution of perceptual conflict. For the traveling wave, activation patterns in early visual areas V1–V3 have been found to correlate with the perceived wave propagation time (Lee et al., 2005). In V1 this correspondence is preserved even when attention is drawn away from the stimulus and conscious awareness of the wave propagation is presumably absent (Lee et al., 2007), pointing to V1 as a lynchpin locus of the neural circuitry associated with traveling waves. Psychophysical evidence also points to V1 as the main correlate even for waves in complex images (Arnold et al., 2009), although there are certain wave features that cannot be exhaustively explained by characteristics of early visual cortex (Naber et al., 2009). Our data support the view that V1 is integrally involved in traveling waves, showing a very specific effect for V1 connections between hemispheres.

In our analysis, we correlated different DTI parameters with our behavioral measure. For any given DTI voxel, diffusion can be represented by the three orthogonal main diffusion directions of the diffusion ellipsoid called "eigenvalues." AD corresponds to the first eigenvalue (λ_1) and represents the dominant diffusion direction. RD is the average of the two remaining eigenvalues (λ_2 and λ_3) representing diffusion in the plane orthogonal to the main diffusion direction. Especially in the CC, combining λ_2 and λ_3 is justified by the fact that the two values are highly correlated ($r > 0.9$; Dougherty et al., 2007; Genç et al., 2011). We found that only RD and FA were significant predictors of ΔTWT, but not AD. Also, neither FA nor AD explained variance in addition to RD in a hierarchical regression model. Since FA is a non-linear combination of the three eigenvalues (Basser and Pierpaoli, 1996) and therefore of AD and RD, it inherits the predictive weakness of AD and apparently does not gain predictive power by the non-linear combination of the components. Other studies have also found correlations with behavioral variables specific to RD in the CC (Dougherty et al., 2007), as well as the arcuate fasciculus (Yeatman et al., 2011). It is unknown why AD was not reliably correlated with the behavioral measures in these studies. Danielian et al. (2010) investigated the reliability of DTI parameters in repeated measurements separated by up to one year. They found very high reproducibility for FA and RD, but not for AD. Interestingly, along the same lines, another study found a high heritability for FA and RD in a large sample of participants, and a low heritability for AD (Kochunov et al., 2010). This suggests that the AD measure is either unreliable and/or does not correspond to a behaviorally relevant feature of white-matter connections.

There are a number of physiological factors that potentially influence diffusion measures of white-matter microstructure including axon diameter, fiber density, myelination, and fiber-orientation distribution (Beaulieu, 2002; Le Bihan, 2003). The relationship between ΔTWT and RD in our data revealed a strong negative correlation. A plausible interpretation of our results is that greater RD values are produced by larger axon diameters in the V1 callosal segment (Takahashi et al., 2002; Barazany et al., 2009) and therefore afford a faster nerve-conduction velocity in those connections (Caminiti et al., 2009). Faster nerve-conduction velocity, in turn, would lead to a reduced delay in the interhemispheric transfer of the traveling wave. A number of previous studies found correlation signs that are in agreement with our physiological interpretation (Westerhausen et al., 2006; Dougherty et al., 2007; Imfeld et al., 2009; Jäncke et al., 2009; Hänggi et al., 2010; Elmer et al., 2011; Genç et al., 2011), but there are also many other studies with correlation signs that are better explained by differences in myelination and fiber density (Bengtsson et al., 2005; Boorman et al., 2007; Johansen-Berg et al., 2007; Wahl et al., 2007; Rudebeck et al., 2009; Scholz et al., 2009; Fleming et al., 2010; Kanai et al., 2010; Tomassini et al., 2010), and a few studies show both correlation directions for different relevant structures (Schmithorst and Wilke, 2002; Tuch et al., 2005; Roberts et al., 2010; Voineskos et al., 2010). In the visual domain, Westerhausen et al. (2006) found that higher mean diffusivity in the posterior CC is correlated with faster interhemispheric transfer, in line with our results, but other studies with a similar design could not support their finding (Schulte et al., 2005; Whitford et al., 2011). For the future, a promising DTI measure that might arbitrate between the possible physiological interpretations is the recently described "bound pool fraction" (Stikov et al., 2011), which is a more direct measure of myelin content and would help to disambiguate between the possible interpretations.

Our tracking results for CC connections of early visual cortex are in good agreement with previous work (Dougherty et al., 2005; Putnam et al., 2010; Saenz and Fine, 2010). Tracer studies in humans and other animals showed that interhemispheric connections between left and right V1 are confined to the border region between V1 and V2, where the vertical meridian of the visual field is represented (Choudhury et al., 1965; Clarke and Miklossy, 1990). It is therefore difficult to strictly separate V1 and V2 interhemispheric connections with DTI methodology, whereas the separation is clearer for V3 (Clarke and Miklossy, 1990). This might explain why values for V2 showed a trend toward significance for the correlations with interhemispheric delay. V3 made a significant contribution in the multiple-regression analysis, but the bivariate correlation with ΔTWT was very weak, suggesting that the V3 contribution is only due to suppression of noise variance in other predictors. The suppression effect can most likely be explained by the overlap between the CC segments of V1 and V3. Despite the caveats, the degree of anatomical specificity in our results is quite striking and provides strong evidence for a highly selective V1 effect in our DTI measures of the early visual cortex.

In conclusion, we found that the properties of V1 interhemispheric connections are a good predictor of the individual delay in traveling waves crossing the midline of the visual field. This supports the claim that V1 is a vital hub for the neural mechanisms underlying binocular rivalry and propagation of traveling waves and shows that an important part of the interhemispheric transmission in early visual areas is accomplished through the CC in healthy individuals. In addition, we established that propagation speed and interhemispheric delay of the traveling wave are stable measures of subjective experience in observers.

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Increased readiness for adaptation and faster alternation rates under binocular rivalry in children

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Binocular rivalry in childhood has been poorly investigated in the past. Information is scarce with respect to infancy, and there is a complete lack of data on the development of binocular rivalry beyond the first 5–6 years of age. In this study, we are attempting to fill this gap by investigating the developmental trends in binocular rivalry in pre-puberty. We employ a classic behavioral paradigm with orthogonal gratings, and introduce novel statistical measures (after Pastukhov and Braun) to analyze the data. These novel measures provide a sensitive tool to estimate the impact of the history of perceptual dominance on future alternations. We found that the cumulative history of perceptual alternations has an impact on future percepts, and that this impact is significantly stronger and faster in children than in adults. Assessment of the "cumulative history" and its characteristic time-constant helps us to take a look at the adaptive states of the visual system under multi-stable perception, and brings us closer to establishing a possible developmental scenario of binocular rivalry: a greater and faster relative contribution of neural adaptation is found in children, and this increased readiness for adaption seems to be associated with faster alternation rates.

Keywords: multi-stable perception, binocular rivalry, human development, adaptation, cumulative history, dominance time

INTRODUCTION

Binocular vision or stereopsis provides precise depth perception by aligning the two eyes' views. Under the eye-specific stimulation of binocular rivalry, the mature visual system enters into a continuous fluctuation between two or more perceptual states, not yielding stereopsis. While cortical binocularity in humans seems to have a relatively abrupt onset (at around 3.5 months) during ontogeny (Braddick et al., 1980; Petrig et al., 1981), driven by experience-dependent mechanisms (Kovacs et al., 2011), little is known about the onset time of binocular rivalry and its further development. Here we review information with respect to the human development of binocular rivalry, and make an attempt to assess its maturity before puberty in a behavioral experiment. We interpret our data in the wider framework of neural adaptation.

The nature of binocular vision of human infants before the occurrence of binocular 3D perception has been debated. This issue was mainly investigated in preferential looking paradigms, employing stimuli that induce binocularly rivalry in adults. Shimojo et al. (1986) found that infants younger than 3.5 months of age preferred to look at the dichoptic (interocularly orthogonal) pattern. However, at an average age of 3.5 months, a sudden shift of preference occurred from the rivalrous pattern to the fusible stimulus. They interpret this result as a preference for a blended stimulus, resulting in a grid-like pattern, which is more complex than the monocularly projected simple lines. However, from the time by which binocular functions have further developed (3.5 months of age), the two patterns begin to oscillate, which might be aversive for infants. This would account for the shift in the preference for binocularly fusible stimuli, and would suggest that pre-stereoscopic vision blends those images that are rivalrous for adults. However, these results could not be replicated (Brown and Miracle, 2003). Nor did Brown et al. (1999) find any physiological evidence for binocular rivalry using a visually evoked potential paradigm with 5- to 15-month-old infants. They attribute their result to the immaturity of dichoptic suppression.

Even less data have accumulated so far concerning the development of rivalry following infancy. In a study that aimed to compare binocular interactions of children aged 6–14 years to normal and amblyopic adults, it was found that binocular summation decreased with age in a dichoptic visual acuity task (Vedamurthy et al., 2007). The acuity of the dominant eye did not improve significantly in children in the dichoptic viewing condition compared to the monocular condition. In this respect, the performance of children was similar to that of adults. However, they found a significant negative correlation with age in the improvement of acuity of the non-dominant eye in the dichoptic condition compared to the monocular one, indicating that developmental trends in binocular interactions are present after infancy, until at least pre-puberty.

The development of binocular rivalry was investigated in 5- to 6-year-old children (Kovacs and Eisenberg, 2005). They found that children alternated significantly more quickly than adults. Verbal reports of the subjects also indicated that children perceived a patchwork of the two images more frequently than adults. On this basis, the conclusion was drawn that the visual system of 5- to 6-year-old children is not sufficiently mature to integrate entire images spatially, thus they experience more piecemeal rivalry than adults. This is in line with their earlier findings in contour integration (Kovacs et al., 1999; Kovacs, 2000) and spatial integration (Káldy and Kovacs, 2003).

Binocular rivalry shares several features with the perception of ambiguous figures, such as the Necker cube. Common features are gamma distribution of the dominance times of each percept, the high inter-subject variability of the frequency of reversals, the significant influence of stimulus properties on reversal rates, or the fact that both can be influenced by the voluntary control of the subject (see Kornmeier and Bach, 2005).

According to the findings reviewed by Leopold and Logothetis (1999), stimulus properties, such as brightness, contrast, and spatial-frequency content can have a significant impact on the balance of dominance and suppression. In addition, high-level properties of the stimuli can also modify dominance periods in multi-stable perception. Such properties include recognizability or semantic content. For instance, if a recognizable figure is inverted, then its perceptual dominance might significantly be altered in both figure/ground stimuli and binocular rivalry.

Voluntary control is another modifying factor of multi-stable perception. The influence of voluntary control of the subject was found to be stronger in the case of ambiguous figures than for binocularly presented rivalrous stimuli (van Ee et al., 2005). Taddei-Ferretti et al. (2008) also point out that the rivalry between the two possible percepts of an ambiguous figure is less automatic than the competition between two different images presented binocularly. An additional common feature of binocular rivalry and ambiguous figures that Taddei-Ferretti et al. (2008) mention is that both are influenced by eye movements (Ellis and Stark, 1978; Sabrin and Kertesz, 1980). Leopold and Logothetis (1999) consider exclusivity, inevitability, and randomness as the three most fundamental common features of multi-stable perception including binocular rivalry and ambiguous figures. Exclusivity means that only one percept is present at one time, while inevitability implies that "perception can never become 'locked' onto a single solution" (p. 261): perceptual hypothesizes are constantly changing concerning the presented stimuli. These attributes are characteristics of both binocular rivalry and ambiguous figures.

Reese and Ford's (1962) pioneering study intended to investigate developmental aspects of ambiguous figure perception. Nursery-school children were shown a series of six pictures of either animals or human faces. Their task was to name each. After that, they were asked to state an expectancy about the next picture. The result was that when they were shown the Bugelski rat-man ambiguous figure, it was easier for them to provide the "animal" interpretation than the "human face" interpretation, which means that the animal interpretation was easier to prime by the previously shown pictures. This might be considered evidence of stimulus-dependency even at such an early age. However, 3- to 5-year-old children also show significant performance differences even in this short age range. Doherty and Wimmer (2005) found that 3-year-old children cannot even report both interpretations of such ambiguous images as the duck–rabbit or the man–mouse figures. However, 4-year-old children can easily interpret the ambiguous figures in both ways. Nonetheless, spontaneous reversals occurred only at the age of 5. The conclusion of this study is that understanding that the perception of the same physical image might reverse is not sufficient for spontaneous reversals to occur.

The foregoing review of the literature indicates that binocular rivalry in childhood has been poorly investigated in the past, and the case is similar concerning the broader sense of bistable or multi-stable perception. Some studies focused on changes in binocular rivalry during adulthood. In these studies, it was found that domination times became longer with age. Jalavisto (1964) for instance, investigated binocular oscillations in the age range of 40–93. It was found that the frequency of oscillation decreased with age in a regular manner, and a total lack of change became prevalent in the oldest age classes. In a more recent study, similar results were obtained (Ukai et al., 2003), in which the alternation rates in three age-groups were compared: 20–34, 35–49, and 50–64-year-old subjects were investigated. In line with the results of Jalavisto (1964), they found a prolongation in alternation time as a function of age. Information is still scarce with respect to infancy, and there is a complete lack of data on the development of binocular rivalry beyond the first 5–6 years of life in childhood. In this study, we are attempting to fill this gap by investigating the developmental trends in binocular rivalry in pre-puberty. We employ a classic behavioral paradigm with orthogonal gratings, and introduce novel statistical measures to analyze the data. These novel measures were developed by Pastukhov and Braun (2011), and they provide a sensitive tool to estimate the impact of the history of perceptual dominance on future percept durations. The Pastukhov and Braun (2011) method used here reveals a significant correlation between past perceptual history and future dominance duration, which does not become evident with conventional measures such as sequential correlations of dominance durations (Fox and Herrmann, 1967; Borsellino et al., 1972; Walker, 1975; Lehky, 1995). Assessment of the "cumulative history" and its characteristic time-constant helps us to take a look at the adaptive states of the visual system under multi-stable perception, and brings us closer to establishing a possible developmental scenario for binocular rivalry.

MATERIALS AND METHODS

SUBJECTS

A total of 59 observers participated in the experiment: 9-year-olds ($n = 23$; mean age = 116.4 months; SD = 4.6); 12-year-olds ($n = 19$; mean age = 151.4 months; SD = 4.4); 21-year-olds ($n = 17$; mean age = 249.1 months; SD = 27.9). All subjects had normal or corrected-to-normal vision and were naive to the purpose of the experiment. Approval of the Budapest University of Technology and Economics (Faculty of Economics and Social Sciences) Ethical Board was obtained. Informed consent was obtained from adult participants or from the parent/caregiver of the child. Observers were not paid for their contribution.

APPARATUS

Stimuli were generated in real-time and displayed on a 15″ LCD screen, with a spatial resolution of 1366 × 768 pixels and a refresh rate of 60 Hz. The viewing distance was 60 cm, so that each pixel subtended approximately 0.024°. Anaglyph glasses (red/green) were used for the dichoptic presentation. Responses were obtained by means of a joystick, whose tilt was recorded by a MATLAB program controlling the experiment.

STIMULI

The binocular rivalry stimulus consisted of two gratings presented dichoptically: radius, 3°; spatial frequency 0.6 cycles/degree; contrast 50%. One grating was tilted leftward by 45° and the other rightward by 45°. To minimize inter-block effects, tilt for left and right eye was exchanged in every block, and grating-phase was changed by 180° in every second block (**Figure 1A**).

PROCEDURE

Data were collected in a normally lit, quiet room. Initially, subjects were provided anaglyph glasses and invited to view the computer screen with the rivalrous gratings. When asked about their percept, all subjects reported alternating percepts. After this introduction to the stimulus, observers reported their perceptual state continuously using a joystick. The joystick allowed them to report three different percepts (leftward tilt, rightward tilt, and mixed), and in the case of dominant gratings with a particular tilt, the degree of dominance was indicated by the degree of movement. Dominant gratings were indicated by tilting the joystick in the corresponding direction, while subjects were asked to keep the joystick at the center in the case of a mixed percept. The experimental program recorded the joystick tilt at 50 Hz sampling frequency. The experiment comprised five blocks; each block lasted 5 min. Each block was followed by a 1-min interval, during which subjects were asked to rest (**Figure 1B**).

STATISTICAL ANALYSIS

In order to extract perceptual dominance phases from sampled continuous responses, inputs were discretized into left and right percepts using 75% threshold of maximal joystick tilt (i.e., a percept was labeled as left if joystick was over −75% and it was labeled as right if it was over +75% of horizontal tilt). Mean dominance time (T_{dom}) was computed from the sequence of discrete dominance periods T_{i}.

As a measure of history dependence for multi-stable displays we have used a coefficient of correlation with cumulative history c_H (Pastukhov and Braun, 2011), which was computed as follows. Let $S_x(t)$ be a record of perceptual experience x as a function of time t, defined as unity while percept x dominates, 0.5 during a mixed or patchy percept, and zero when percept x is suppressed. The cumulative history $H_x(t)$ computed using a leaky integrator (Tuckwell, 2006) is then given by

$$H_x(t) \approx \frac{1}{\tau_H}\int_0^t S_x(t')\cdot \mathrm{e}^{\frac{(t-t')}{\tau_H}}\,dt' \qquad (1)$$

where $x \in \{\text{red/green}\}$ denotes a uniform percept and τ_H is a time-constant to be determined empirically. This assumes that the contribution of prior experience decays exponentially, multiple contributions of same percept combine additively, and there is no contribution from competing percept (see **Figure 2** for an

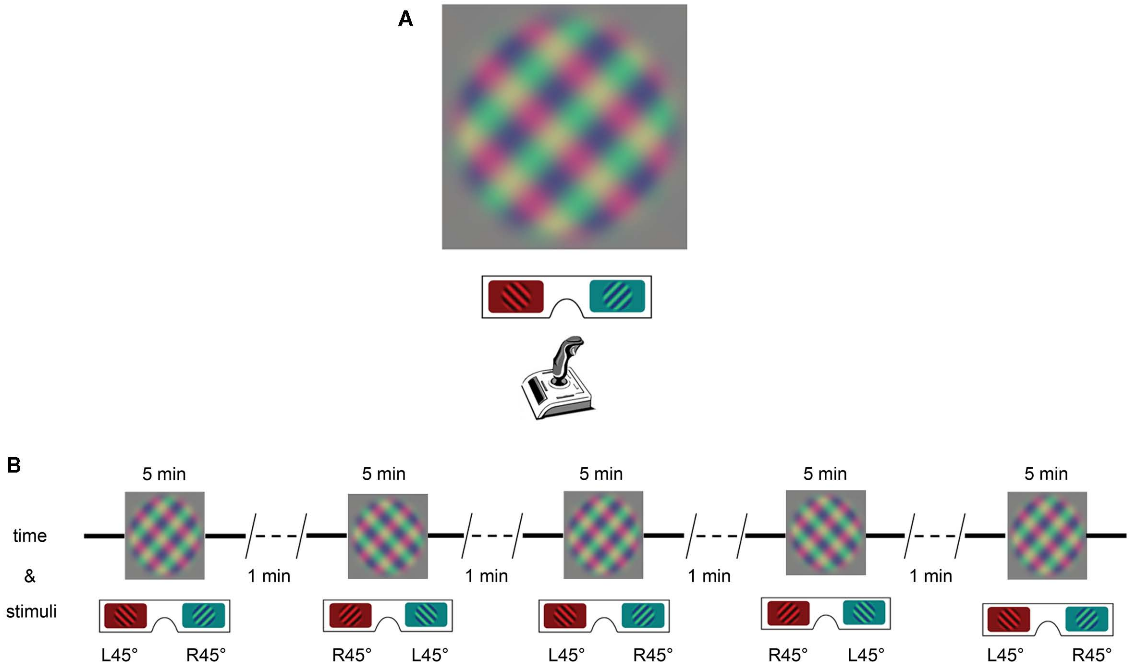


FIGURE 1 | Stimulus and procedure. (A) The orthogonal grating stimuli presented to the two eyes were viewed through anaglyph glasses. Subjects had to indicate the tilt of the perceived grid by tilting the joystick correspondingly. They kept the joystick in the center position in case of mixed percepts. **(B)** The experiment comprised five blocks of 5-min stimulus presentations, with a 1-min interval following each block. Eye of origin for the orthogonal gratings was exchanged in each block.

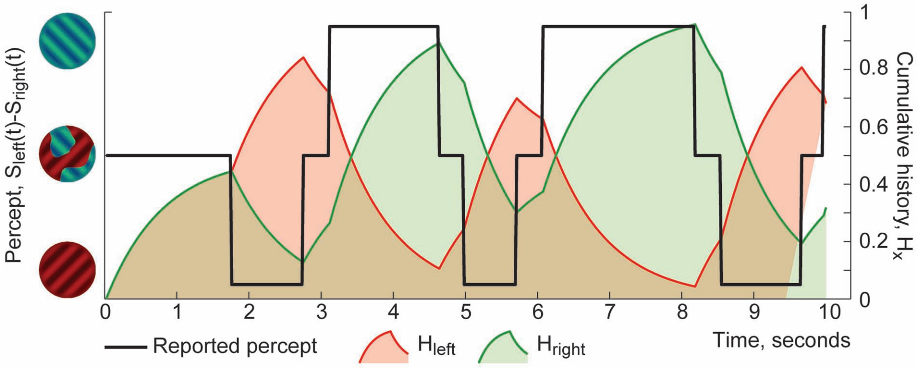


FIGURE 2 | Example of cumulative history traces for series of dominance phases of visual appearances (9 years old). Black trace indicates reported visual appearance ("green/left eye," "red/right eye," or "patchy"). Color traces illustrate hypothetical cumulative histories (correspondingly, green for "green/left eye" percepts and red for "red/right eye"), computed with $\tau_H = 0.5 \cdot T_{\text{dom.}}$

illustration on cumulative history computed from a sequence of perceptual dominance phases).

After computing the cumulative histories H_{left} and H_{right} for two alternative percepts from a sequence of dominance periods up to time t, we computed linear correlation coefficients with the immediately following dominance period T_{i} ($H_{\text{left}} \times T^{\text{left}}$, $H_{\text{left}} \times T^{\text{right}}$, $H_{\text{right}} \times T^{\text{left}}$, and $H_{\text{right}} \times T^{\text{right}}$). Specifically, we computed linear correlations between logarithm of its normalized duration and cumulative history for the same and opposite percept, e.g., when left eye is dominant, $S_{\text{left}}(t) = 1$; $c_H^{\text{same}} = r(\ln(T_{\text{i}}/T_{\text{dom}}), H_{\text{left}})$ and $c_H^{\text{diff}} = r(\ln(T_{\text{i}}/T_{\text{dom}}), H_{\text{right}})$. Note that cumulative histories of two competing percepts approach unity ($H_{\text{left}} + H_{\text{right}} \approx 1$) only in the absence of "patchy" percepts, we have used both to compute an average absolute correlation:

$$c_H = \frac{\left|c_H^{\text{diff}}\right| + \left|c_H^{\text{same}}\right|}{2} \tag{2}$$

To determine the characteristic time-constant (τ_H), we computed average absolute correlations for values of τ ranging from 0.01 to 60 s. The maximal correlation obtained was taken as the value of c_H, and the τ yielding this maximal correlation was taken as the value of τ_H. In sum, c_H stands for the measure of adaptation taking into account the entire stimulus presentation up to time t, while τ_H indicates how fast the adaptation is built up. Note that for small τ_H cumulative history assumes intermediate values only after one or more short dominance periods. The higher the τ_H value is, the slower the subject adapts to each percept; while a higher c_H value indicates a larger extent of adaptation.

After computing the above-mentioned variables, outliers were excluded from each group. The criterion for exclusion was identical for each group. The SD of each subject was computed for each variable across the blocks. The mean SD of each group was also computed from the individual SDs. The individual SDs here indicate the reliability of the perceptual reports of the particular subject: the responses of subjects who show a high SD among a given observable, can be considered as inconsistent, which might be due to either lack of attention or fatigue. Therefore, subjects, whose SD along any of the investigated variables approached the 4 SD distance from the average SD of the group, were excluded from the analysis. This criterion was re-checked following each exclusion. A total of eight subjects were excluded.

After removing extreme outliers, independent sample t-tests were conducted between all groups for all the five variables, and correlations were computed between age-groups and observables.

RESULTS

The t-test yielded a marginally significant difference in average dominance times (T_{dom}) between 9-year-olds and adults (for means and t-values see **Figure 3A**). Each percept tends to persist for a longer period in adults than in 9-year-old children (**Figure 3B**). There was no significant difference between 9- and 12-year-olds, and between 12-year-olds and adults. However, the developmental trend in **Figure 3B** seems to be clear: dominance times increase with age. The same tendency was found earlier in 5- to 6-year-olds as compared with adults (Kovacs and Eisenberg, 2005).

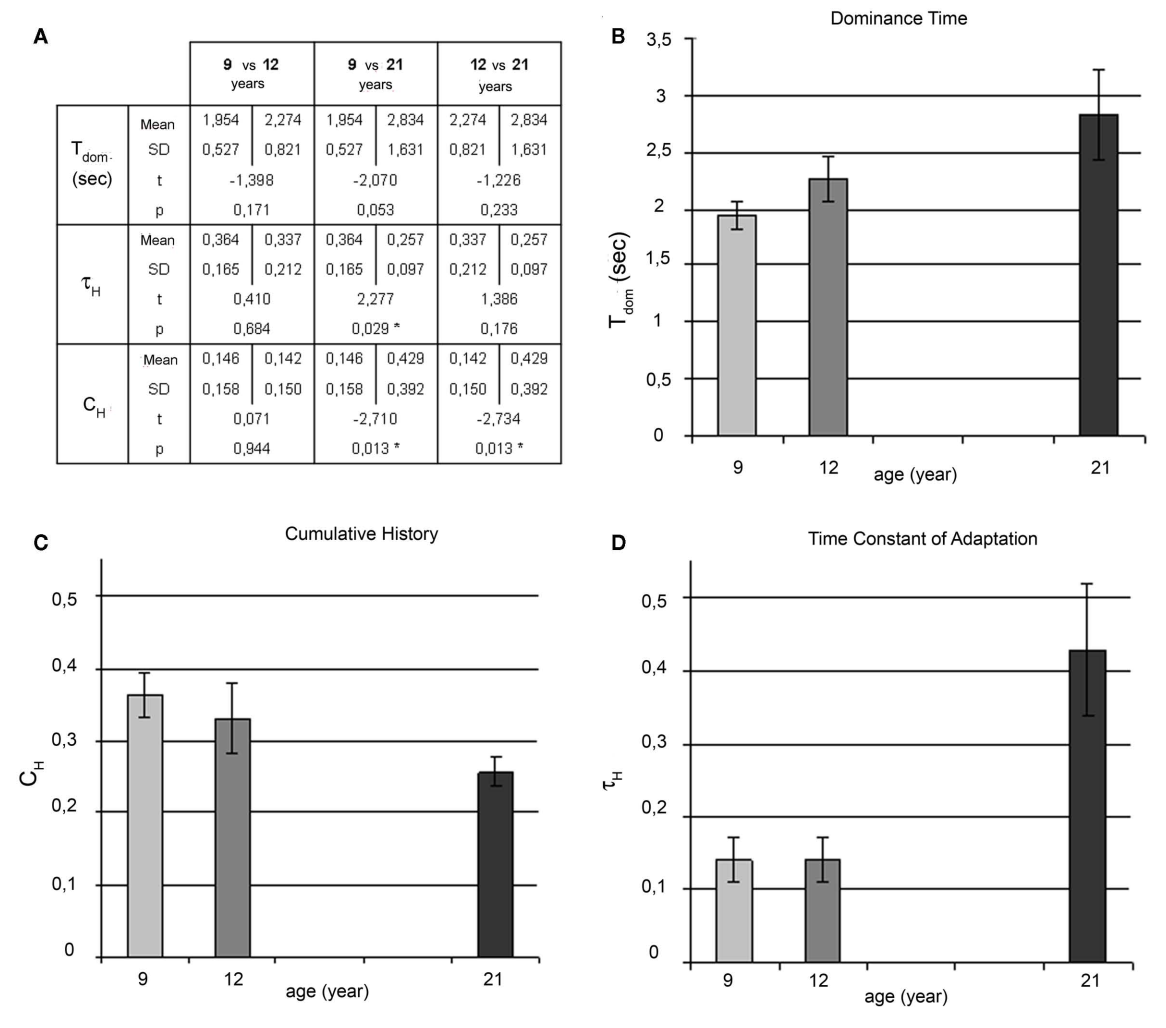
The c_H value is significantly higher in 9-year-olds than adults, i.e., the length of the subsequent dominance period of a particular percept shows a higher correlation with the previous dominance time ratio of the other percept in 9-year-olds than in adults (**Figures 3A,C**). This means that 9-year-olds and adults show a significant difference in their extent of adaptation to each percept. There was no significant difference between 9- and 12-year-olds, and between 12-year-olds and adults.

The time-constant of the build-up of the adaptation (τ_H) produced significant differences both between 9-year-olds and adults as well as 12-year-olds and adults (**Figures 3A,D**). There was no significant difference between 9- and 12-year-olds. The τ_H value of adults is significantly higher than that of 9- and 12-year-old children, showing that the build-up of adaptation is slower in adults.

These differences were also indicated by correlations between age-groups and the observables (see **Table 1**).

DISCUSSION

Our results indicate that 9-year-old children are not exactly adult-like in terms of alternation rate which is a conventional measure



		9 vs 12 years		9 vs 21 years		12 vs 21 years	
T_{dom} (sec)	Mean	1,954	2,274	1,954	2,834	2,274	2,834
	SD	0,527	0,821	0,527	1,631	0,821	1,631
	t	-1,398		-2,070		-1,226	
	p	0,171		0,053		0,233	
τ_H	Mean	0,364	0,337	0,364	0,257	0,337	0,257
	SD	0,165	0,212	0,165	0,097	0,212	0,097
	t	0,410		2,277		1,386	
	p	0,684		0,029 *		0,176	
C_H	Mean	0,146	0,142	0,146	0,429	0,142	0,429
	SD	0,158	0,150	0,158	0,392	0,150	0,392
	t	0,071		-2,710		-2,734	
	p	0,944		0,013 *		0,013 *	

FIGURE 3 | Results. (A) Means, SDs, *t*-, and *p*-Values for each variable. T_{dom} is mean dominance time; Coefficient of correlation with cumulative history c_H is a measure of history dependence; Characteristic time-constant τ_H indicates how fast the adaptation is built up. **(B)** Dominance times (T_{dom}) within age-groups. **(C)** Cumulative history (c_H) within age-groups. **(D)** Time-constant of adaptation within age-groups. Error bars indicate SE.

Table 1 | Correlations between age-groups and the investigated observables.

Correlations	T_{dom}	τ_H	c_H
AGE-GROUP			
Pearson correlation	0.329	0.457	−0.273
Sig. (two-tailed)	0.018	0.001	0.053
N	51	51	51

of binocular rivalry. Children seem to have shorter average dominance times than adults. This is consistent with an earlier study by Kovacs and Eisenberg (2005) that showed that 5- to 6-year-old children are alternating very quickly. Our findings are also in line with the results of Jalavisto (1964) and Ukai et al. (2003), who found that alternation rate decreased with age in adulthood. Although the developmental curve is not complete yet, and there are several further age-groups to be tested, it can be concluded that the development of binocular rivalry, as measured by its most salient feature, is not complete by the end of the first decade in life. That draws a conspicuously slow developmental trajectory which is not yet supported by explanatory anatomical or physiological data.

In addition, we have applied two novel measures of the effect of neural adaptation, recently suggested by Pastukhov and Braun (2011). The first such measure (c_H) was the correlation between dominance times and accumulated prior dominance history and the second (t_H) was the effective time-constant of this accumulation. To appreciate the import (and limitations) of these measures, one has to consider that perceptual reversals may have several contributing causes (Wolfe, 1984; Nawrot and Blake, 1989; Petersik, 2002; van Ee, 2009; Alais et al., 2010; Kang and Blake, 2010; Pastukhov and Braun, 2011).

Firstly, neural adaptation of the dominant representation is thought to progressively destabilize the dominant percept by both the adaptation of the dominant percept, and the recovery from adaptation of the suppressed percept. Secondly, spontaneous activity fluctuations in perceptual representations as well as external transients such as eye movements or eye blinks curtail the duration of dominance periods. Thirdly, internal transients such as shifts in attention or in other volitional processes may trigger reversals. The measure c_H is a correlative measure and estimates only the relative contribution of neural adaptation to reversal timing, that is, relative to all other possible factors. We emphasize that it should not be taken to estimate the absolute strength of neural adaptation.

Specifically, our finding that dominance durations are more correlated with prior history in children than in adults, implies simply a greater relative contribution of neural adaptation. This could either be because adaptation is more pronounced, or because other factors (e.g., neural noise, attention shifts) are less pronounced in children. Our observations that shorter dominance phase duration in children are accompanied by shorter time-constants of reconstructed neural adaptation are consistent with predictions of models of multi-stable perception (Wilson, 2007; Shpiro et al., 2009), where mean dominance duration is directly proportional to the adaptation time-constant. A related possibility is that, due to the generally shorter dominance times of children, stochastic factors such as neural noise or attention shifts simply have fewer opportunities for triggering a perceptual reversal. Voluntary control over binocular rivalry is limited (Chong et al., 2005; Hancock and Andrews, 2007) and in fact less than for other bistable displays (Meng and Tong, 2004). Rivalrous displays undergo perceptual reversals even when attention is diverted (Lee et al., 2007). Nevertheless, we cannot rule out the possibility that our findings reflect differences in attentional characteristics between children and adults.

Although our study provides the first articulate view on the human developmental trajectory of binocular rivalry, more age-groups, and the underlying factors behind the protracted developmental curve need to be further investigated.

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An integrated framework of spatiotemporal dynamics of binocular rivalry

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Fluctuations in perceptual dominance during binocular rivalry exhibit several hallmark characteristics. First, dominance switches are not periodic but, instead, stochastic: perception changes unpredictably. Second, despite being stochastic, average durations of rivalry dominance vary dependent on the strength of the rival stimuli: variations in contrast, luminance, or spatial frequency produce predictable changes in average dominance durations and, hence, in alternation rate. Third, perceptual switches originate locally and spread globally over time, sometimes as traveling waves of dominance: rivalry transitions are spatiotemporal events. This essay (1) reviews recent advances in our understanding of the bases of these three hallmark characteristics of binocular rivalry dynamics and (2) provides an integrated framework to account for those dynamics using cooperative and competitive spatial interactions among local neural circuits distributed over the visual field's retinotopic map. We close with speculations about how that framework might incorporate top-down influences on rivalry dynamics.

Keywords: binocular rivalry, dynamics, dynamic network models

The brain is often portrayed as a complex, dynamical system (e.g., Friston and Price, 2001), and the phenomenon of binocular rivalry – the topic of this special Frontiers issue – certainly fits with that portrayal. Faced with conflicting monocular inputs, the visual system lapses into a state of instability in which those conflicting inputs compete for perceptual dominance. While one input dominates, the other is suppressed from awareness, a characteristic that makes rivalry attractive to those interested in the neural correlates of consciousness (e.g., Rees et al., 2002). But equally fascinating, perceptual dominance fails to settle into a single, stable state and, instead, fluctuates unpredictably over time. Because of this aspect of rivalry, the phenomenon represents a potentially revealing window onto neural events underlying brain dynamics (Kim and Blake, 2005). For the last several years we have focused intensely on the nature of the mechanisms responsible for perceptual instability during rivalry, and this paper provides a progress report on our thinking about this question. From the outset, we stress that much of our work is stimulated by recent publications out of other laboratories, and we are pleased to acknowledge their influence throughout this paper.

Our approach to understanding the dynamics of binocular rivalry is centered around its three hallmark characteristics. First, fluctuations in perception during binocular rivalry are stochastic, meaning that it is impossible to predict exactly when the next perceptual switch will occur. This characteristic shows up in the unimodal distributions of dominance durations that are skewed toward a longer tail (Levelt, 1965; Fox and Herrmann, 1967; Logothetis et al., 1996; Brascamp et al., 2005). Second, despite its stochastic nature, variations in physical characteristics of rival stimuli including contrast (Fox and Rasche, 1969; Blake et al., 1971; Hollins and Hudnell, 1980; van Ee, 2009), luminance (Kakizaki, 1960), and spatial frequency (Fahle, 1982) produce predictable changes in average dominance durations of binocular rivalry. Third, perceptual alternations during binocular rivalry are spatiotemporal in nature, meaning that perceptual dominance can arise locally within a region of rival stimulus and spread over time to culminate in dominance of the entire rival stimulus (Wheatstone, 1838; Meenes, 1930). The spatiotemporal nature of rivalry transitions is highlighted by traveling waves of binocular rivalry in which a perceptual switch within a local region propagates like a wave (Wilson et al., 2001).

Any comprehensive account of binocular rivalry dynamics needs to explain these three hallmark characteristics. In the following sections, we highlight recent advances, made by us and others, that provide a framework for such an account. We then sketch the outlines of a network model of rivalry that accounts for these three hallmark characteristics. We conclude by briefly considering how other factors influencing rivalry dynamics may be integrated into this framework.

WHY DOMINANCE ALTERNATES DURING BINOCULAR RIVALRY

The most popular class of models seeking to explain perceptual alternations during binocular rivalry are built on the concepts of mutual inhibition, an idea dating back over a century (Breese, 1899). While the details vary among models, the general idea is that pools of neurons representing possible alternative stimulus representations compete for dominance via mutual inhibition, with the winner of this competition inhibiting the activity associated with the losing representation (**Figure 1A**). Compared to other classes of models such as those based on a clocklike neural oscillator (Pettigrew, 2001) or on cognitive inference (Walker, 1978), the mutual inhibition model parsimoniously accounts for a wide range of results showing systematic changes in rivalry dynamics dependent on sensory properties such as contrast. The model is agnostic with respect to the nature of the site at which these inhibitory interactions take place, meaning the model works in the context of eye-based rivalry (Matsuoka, 1984) or object-based rivalry (Dayan, 1998; Wilson, 2003). In addition, top-down factors such as attention (e.g., Lack, 1978; Meng and Tong, 2004), and affective connotation (e.g., Alpers and Pauli, 2006) can be incorporated into this reciprocal inhibition account, a point we return to at the end of this article.

In this model, inhibition is responsible for exaggerating differences in activation levels between the competing neural representations, allowing one competitor to gain the upper hand. To account for switches in the dominant neural representation and, hence, fluctuations in perception, the mutual inhibition requires an additional mechanism, and in many instantiations of this model that mechanism is neural adaptation (Lehky, 1988; Kalarickal and Marshall, 2000; Laing and Chow, 2002; Wilson, 2003; Lankheet, 2006). According to this idea, the neural representation of the currently dominant stimulus weakens over time owing to slow adaptation, thereby reducing its inhibitory impact on the weaker, non-dominant representation. Eventually the two representations reach the point of equivalence causing an abrupt change in state. Those models typically produce variability in the durations of rivalry states by incorporating noise in the volley of neural signals representing rival stimuli, although one recent instantiation of the model successfully simulated rivalry alternations using noise just in the slow adaptation component (van Ee, 2009). There have also been attempts to model rivalry alternations primarily on the basis of noise, with adaptation playing a secondary role at best (e.g., Kim et al., 2006; Moreno-Bote et al., 2007).

Schematically, these two accounts, one based on adaptation and the other on noise, can be represented by an energy landscape (Brascamp et al., 2006; Kim et al., 2006; Moreno-Bote et al., 2007; see Seely and Chow, 2011, for a discussion of the relation between energy models and mutual inhibition models). As illustrated in **Figures 1B,C**, two alternative perceptual states are represented by two wells, and the current perceptual state is represented by the position of an object within one of those wells. In this scheme, the energy landscape comprises a gradient that governs the movements of the object within that landscape. In the absence of any other forces, the object settles into a location within the landscape where the energy level is locally minimal. The object remains at that location (meaning the perceptual state remains unchanged) until other forces act upon that object or upon the landscape. In the case of binocular rivalry two such forces leading to state changes have been proposed. In adaptation-based models, the gradient of the landscape itself changes such that the depth of the well in which the object is currently located decreases over time, eventually minimizing the depth of the well to the point where the object rolls into the other well; this corresponds to a switch in perceptual state (**Figure 1B**). In noise-based models, the depths of the two wells remain unchanged and noise provides the impetus that moves the object from its currently occupied well to the other one. A perceptual switch occurs when noise is sufficiently strong to boost the object over the energy barrier into the neighboring well (**Figure 1C**).

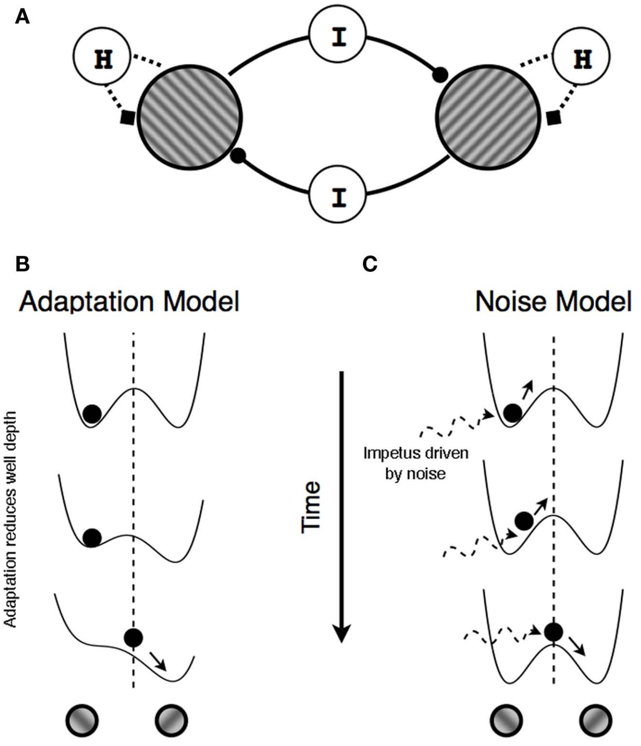

FIGURE 1 | Mechanisms producing perceptual alternations. (A) Schematic illustration of reciprocal inhibition network in which neurons representing the left- and the right-titled tilted gratings mutually inhibit one another (components labeled I) and, at the same time, undergo self-adaptation (the components labeled H). **(B,C)** Double well potential landscape of the two models of rivalry alternations in which the position of the ball represents perceptual state at a given moment. **(B)** In adaptation models, potential landscape changes over time due to adaptation and a perceptual switch occurs when double well potentials temporarily form a single well potential owing to the reduced depth of the well in which the ball currently resides (adaptation). **(C)** In noise models, the two potential landscape remain unchanged but random fluctuations in the ball's location within a given well eventually provide sufficient impetus to project that ball into the other well.

Which of these forces is primarily responsible for alternations in rivalry state, adaptation or noise? Strictly speaking, this represents an ill-posed question, for noise is almost certainly inherent in all neural events including those involved in binocular rivalry (e.g., Brascamp et al., 2006). The more tractable (i.e., empirically testable) question is to ask whether adaptation plays a significant role in the production of perceptual alternations, for once this question is answered one can then evaluate the relative contribution of noise. Until recently, however, evidence bearing on the importance of adaptation in rivalry alternations was equivocal. For one thing, adaptation predicts that a particularly long dominance duration should be associated with especially strong adaptation and, therefore, should be followed by an unusually brief duration of dominance of that stimulus; in other words, there should be evidence for sequential dependencies among successive state durations (van Ee, 2009). Whereas earlier studies failed to find robust correlations among successive dominance durations (Fox and Herrmann, 1967; Walker, 1975; Lehky, 1995; Logothetis et al., 1996), recent work using more refined methods have obtained evidence for significant, non-zero serial correlations (Gao et al., 2006; van Ee, 2009). Furthermore, computational modeling by van Ee (2009) reveals that the sequential dependencies producing those correlations can be simulated by the addition of noise to the process responsible for neural adaptation but not by noise added to mutual inhibition dynamics. Also of relevance to the question of adaptation's involvement in rivalry are studies that sought directly to examine whether rivalry dynamics can be altered by adaptation to a rival stimulus (Blake and Overton, 1979; Hollins and Hudnell, 1980; Wade and de Weert, 1986; Blake et al., 1990; van Boxtel et al., 2008). While broadly consistent with such an influence, the conditions of adaptation employed in those studies did not mimic the actual conditions arising during continuous viewing of rival stimuli: the average dominance durations during binocular rivalry last only a few seconds at a time whereas those studies employed long periods of adaptation prior to rivalry testing. While prolonged adaptation can temporarily reduce dominance durations of a subsequently viewed rival stimulus, prolonged adaptation probably produces saturated levels of adaptation that are unlikely to be achieved during ordinary rivalry.

We set out to create a more realistic set of conditions to test whether adaptation might indeed be involved in triggering changes in perceptual state during rivalry (Kang and Blake, 2010). Unlike previous studies that assessed rivalry durations following a single, prolonged period of monocular adaptation, our technique inserted relatively short episodes of monocular adaptation into a much longer, ongoing period of rival stimulation during which observers tracked alternations in dominance. Moreover, the durations of monocular adaptation inserted into ongoing rivalry were equivalent to previously estimated durations of dominance phases of binocular rivalry. By systematically varying the durations of these periods of adaptation inserted into ongoing rivalry, we confirmed that dominance durations are inversely related to the immediately preceding duration of monocular exposure to a rival stimulus, as predicted by adaptation theory. Short-term adaptation of the sort implicated in our procedure is also very likely the source of the localized breakouts of dominance within regions of a rival target where the local strength (e.g., contrast) of the currently suppressed stimulus is higher than elsewhere in that stimulus (Paffen et al., 2008). Short-term adaptation probably also accounts for the propensity for local breaks in suppression following variable periods of monocular suppression in a flash suppression paradigm (van Ee, 2011).

The online-adaptation procedure described in the last paragraph also offers one way to ask how adaptation and noise might interact to trigger state changes in rivalry, because adaptation- and noise-based models predict very different, characteristic distributions of dominance durations. Adaptation-based models generate periodic alternations of perception and, thus, highly similar dominance durations when the stimulus energy levels of the two rival stimuli are identical. In contrast, noise-based models produce irregular alternations of perception that accrue to create an exponential distribution of dominance durations (Shpiro et al., 2009). These two distinct distributions can be indexed using the coefficient of variation (CV), an index calculated by dividing the SD of the dominance durations by the mean of those durations. For adaptation-based models, CV should approach 0 because the SD of the distribution of durations is very small; CV predicted by noise-based models should approach 1, the hallmark characteristics of an exponential distribution. With this in mind, we calculated the CV from measured dominance durations associated with different durations of adaptation. We found that CV was approximately 0.5 when there were no periods of inserted adaptation, and CV increased with increasing adaptation, approaching a value of 1 when adaptation duration was equivalent to the mean dominance durations for given observer. This result implies that noise plays a more important role in producing perceptual alternations with increasing adaptation.

Putting our findings together with other empirical and modeling results (Kim et al., 2006; Moreno-Bote et al., 2007; van Ee, 2009), the following picture emerges within the framework of the double well energy landscape. Immediately following a perceptual state change, a second change is highly unlikely because the depth of the energy well associated with the newly dominant stimulus is considerably deeper than the random, noise-produced fluctuations in the strength of that stimulus. The noise, in other words, is too weak to produce a random bounce sufficient to jump the initially high energy barrier. However, as the depth of the well decreases due to adaptation the energy barrier becomes effectively smaller and, thus, increases the probability that noise will be sufficiently strong to overcome the barrier and trigger a switch to the other well. This conceptualization, together with insight concerning the role of noise in adaptation (van Ee), helps us understand why studies tend to find only weak correlation between successive dominance durations, a finding that heretofore was a thorn in the side of the adaptation model: short and intermediate duration dominance states are predominantly determined by adaptation, with a significant contribution from noise reflected only in relatively long dominance durations that occur infrequently.

LEVELT'S SECOND PROPOSITION AND WHY IT IS SOMETIMES VIOLATED

While inherently variable, dominance durations still vary systematically with changes in the strength of one or both of the rival stimuli. For example, it is well known that dominance durations vary with stimulus contrast, luminance, spatial frequency, and motion, to give examples (see review by Blake, 2001). The relation between rivalry's time course and the strength of rival stimulation was formalized by Levelt (1965) as a set of four propositions. The first proposition states that the total percentage of time that a given stimulus is dominant in rivalry increases with the strength of that stimulus, and the third and fourth propositions state that rivalry alternation rate increase with unilateral or bilateral increases in the strength of the rival stimuli. To our knowledge there is no evidence contradicting any of those three propositions. The second proposition asserts that increases in the stimulus strength of a given rival stimulus reduce its durations of suppression but have no effect on its durations of dominance. This second proposition seems counterintuitive, for one would think that strengthening a stimulus would cause it to remain visible for longer periods of time. This proposition is also controversial, for some studies report evidence supporting it (Levelt, 1965; Fox and Rasche, 1969; Blake, 1977; Logothetis et al., 1996; Meng and Tong, 2004) but others report evidence that violate it (Mueller and Blake, 1989; Bossink et al., 1993; Brascamp et al., 2006).

Several factors have been mentioned as possible sources contributing to these mixed results, including the range of contrast values tested (Brascamp et al., 2006), the contaminating effect of mixed dominance states (Mueller and Blake, 1989) and the existence of return transitions where an exclusively dominant stimulus transitions to the mixed state but then reverts to complete dominance (Brascamp et al., 2006). A re-examination of the relevant literature by one of us (Min-Suk Kang) led to the realization that stimulus size might be a crucial factor governing whether or not Levelt's second proposition is violated (see **Table 1**). That motivated a study in which rivalry alternations were measured for different sized rival stimuli whose contrast levels were varied parametrically (Kang, 2009). To assess the contribution of mixed dominance, results using two tracking strategies were compared (**Figure 2A**). In the *whole tracking procedure*, observers reported rival alternations only when one entire, spatially extended rival figure was exclusively dominant, with no hint of partial dominance of the other rival stimulus. In the *partial tracking procedure*, observers reported rivalry alternations within a small, central region of the larger rival stimuli. If mixed dominance contributes to the contrast-invariance of dominance durations dictated by Levelt's second proposition, we would expect that these two tracking procedures, when implemented using different contrast values, should produce different conclusions concerning the validity of the proposition.

Stimulus size indeed mattered: dominance durations were invariant with changing contrast when stimulus size was large but were variable when stimulus size was small (**Figure 2B**). Moreover, rivalry dynamics associated with return transitions could not explain the difference of the rivalry dynamics between the small and large stimulus size: dominance durations associated with perceptual switches were similar to dominance durations associated with return transitions for the same sized stimulus. In addition, when rival stimuli were large, contrast-invariant dominance durations were found for both tracking strategies, indicating that mixed dominance was not responsible for violation of that proposition. As an aside, it is interesting to note that van Ee (2009) found that mixed dominance also has no influence on the stochastic properties of rivalry alternations as indexed by serial correlations over successive dominance durations.

Table 1 | Summary of previous literature.

Study	Stimulus	Size	Result
Levelt (1965)	Reversed luminance contrast	6.00°	O
Fox and Rasche (1969)		3.24°	O
Bossink et al. (1993)		1.32°	X
Meng and Tong (2004)	Sine wave grating	6° × 2°	O
Logothetis et al. (1996)		3°	O
Blake (1977)		1.25°	O
Mueller and Blake (1989)		0.80°	X
Brascamp et al. (2006)		0.62°	X

In the Result column, O indicates the result of the study supporting Levelt second proposition and X indicates the violation of Levelt second proposition. This table is reproduced from Kang (2009), with permission from Journal of Vision.

Having solved that riddle, however, we were left with a new one: how can we explain why stimulus size influences the time course of rivalry alternations? From earlier research, we know that binocular rivalry dynamics are spatiotemporal in nature, meaning that rivalry appears to occur within local zones of the visual field (Blake et al., 1992), with neighboring zones influencing one another (Alais et al., 2006). These properties of rivalry can be embodied in a model whose simulated dynamics provide a test of the boundary conditions under which Levelt's second proposition would hold up. Accordingly, we constructed such a model in which rivalry transpires within local, interacting networks each representing neighboring region of the visual field. (Within the energy landscape framework, those local networks could be construed as set of neighboring energy landscapes whose dynamics spread among the set.) The combined outputs from those local networks could be any of the three interdependent perceptual states associated with spatially extended rival stimuli. By appropriate adjustment of the interaction terms, this model reproduced the contrast-invariance of dominance durations predicted by Levelt's second proposition, even though the model's output at each individual location violated that contrast-invariance (**Figure 2C**). This happens because the spatial interactions promote attraction between neighboring neural states, pulling them into synchrony. It is worth noting that these same mechanisms could also govern the dynamics of other forms of perceptual bistability including ambiguous structure from motion, which exhibits invariant dominance durations when stimulus strength is manipulated (Klink et al., 2008a).

These empirical findings and model simulations demonstrate that spatial interactions play an important role in the control of rivalry dynamics evidenced by spontaneous perceptual alternations. Those interactions are not just necessary add-on components to account for traveling waves (Wilson et al., 2001) or the spread of perceptual suppression (Maruya and Blake, 2009; Nichols and Wilson, 2009). This realization leads naturally to our next hallmark characteristic of rivalry, the spatial spread of perceptual dominance as exemplified by traveling waves.

SPATIOTEMPORAL DYNAMICS OF BINOCULAR RIVALRY

In this section we show how it is possible to tie together binocular rivalry dynamics associated with spontaneous perceptual alternations with the dynamics associated with transitions in dominance that arise locally and spread throughout a previously suppressed rival stimulus. As pointed out earlier, these transitions often resemble traveling waves of dominance, i.e., a series of perceptual switches over space and time. Moreover, Wilson et al. (2001) have demonstrated that it is possible to create stimulus conditions where these waves can be produced and measured in a controlled manner with brief, discrete episodes of rivalry. But for our purposes, we needed to harness the control provided with this traveling wave technique while, at the same time, being able to measure spontaneous perceptual alternations during extended periods of binocular rivalry.

To achieve this, we devised a periodic perturbation technique in which we could measure these two types of rivalry dynamics using the same procedure (Kang et al., 2009). Here is how it works (see **Figure 3A**). We created spatially extended rivalry targets containing a small monitoring region within the middle of the rival targets, and observers reported the fluctuations in perceptual state

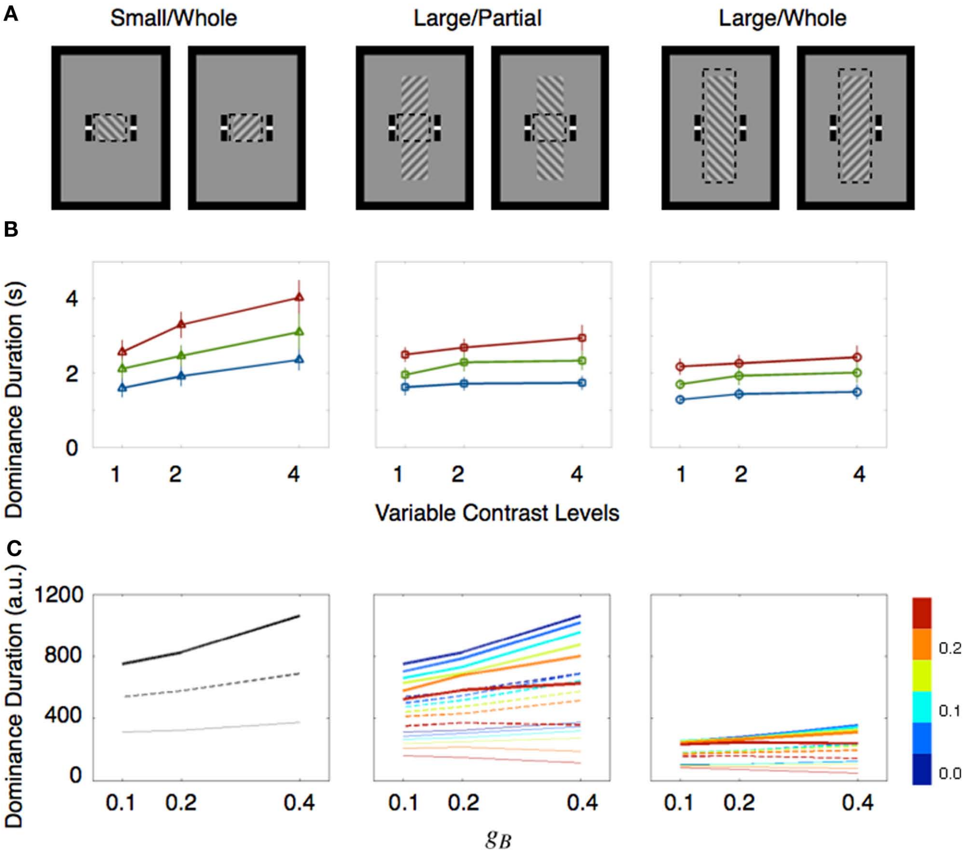

FIGURE 2 | Size dependent rivalry dynamics. (A) Stimulus conditions are illustrated. Observers report the perceptual state within the monitoring region which is depicted with dashed boxes. These dashed boxes were not shown during the experiments. **(B)** Mean dominance durations of the ipsilateral stimulus are plotted as a function of the contrast of the ipsilateral stimulus. The contrasts are represented as multiples of the lowest contrast level. The contrast values of the contralateral stimulus (expressed as multiples relative to the lowest value) are drawn with three separate lines (red line for 1X; green line for 2X; blue line for 4X). Error bar equals ± 1 SE. **(C)** Mean dominance durations (arbitrary unit) of simulated binocular rivalry are shown as **Figure 2B** in which contrasts of two rival stimuli were manipulated with potential landscape parameters g_A and g_B. Three distinct line styles indicate the dominance durations at a given g_A (thick line for $g_A = 0.1$; dotted line for $g_A = 0.2$; thin gray line for $g_A = 0.4$). Strength of spatial interactions were manipulated with the coupling strength parameter represented by different colors shown in the color bar at right. These figures are reproduced from Kang et al. (2009), with permission from Journal of Vision.

within that monitoring region. (This is essentially the same partial tracking procedure described in the previous section.) Now, to measure traveling wave dynamics, we introduced abrupt contrast increments within small regions located at the opposite ends of the two elongated rival stimuli (**Figure 3A**). Thus, for example, a trigger would appear at the upper region of one eye's stimulus and a lower region of the other eye's stimulus, and these contrast pulses – perturbations we dubbed them – are presented periodically in antiphase to the two eyes. With the pulses are appropriately timed, observers tend to perceive upward and downward traveling waves of binocular rivalry that alternate periodically over time. Using a statistical technique based on reverse correlation, we can characterize the probability and the speed of these traveling waves based solely on the records of dominance durations measured at the monitoring region, and we can evaluate the relation between spontaneous rivalry alternations and the dynamics of the traveling waves. This allowed us to answer two questions: (1) do observers who experience relatively slow rivalry alternations (slow alternators) tend to experience slow traveling waves compared to the wave speed experienced by observers who exhibit relatively fast rivalry alternations (fast alternators), and (2) does the configuration of the stimulus patterns carrying the traveling waves jointly influence the speed of those waves and the time course of spontaneous alternations?

Using vertically elongated rival stimuli consisting of left- and right-tilted contours (**Figure 3A**), we measured the speed of traveling waves and alternation rate within the monitoring region. As shown in **Figure 3B**, alternation rate was strongly correlated with traveling wave speed within our sample of seven observers. With a sample of 12 observers, alternation rate was also correlated with latency, an indirect measure of speed of traveling waves (**Figure 3C**). This pattern of results means that fast alternators see fast traveling waves, which explains why fast alternators tend to experience difficulty seeing traveling waves: their spontaneous perceptual alternations more nearly resemble traveling waves than do the state changes experienced by slow alternators.

In another study (Kang et al., 2010), we asked whether the speed of traveling waves and the durations of dominance of a rival stimulus are both influenced by contour collinearity, a stimulus property

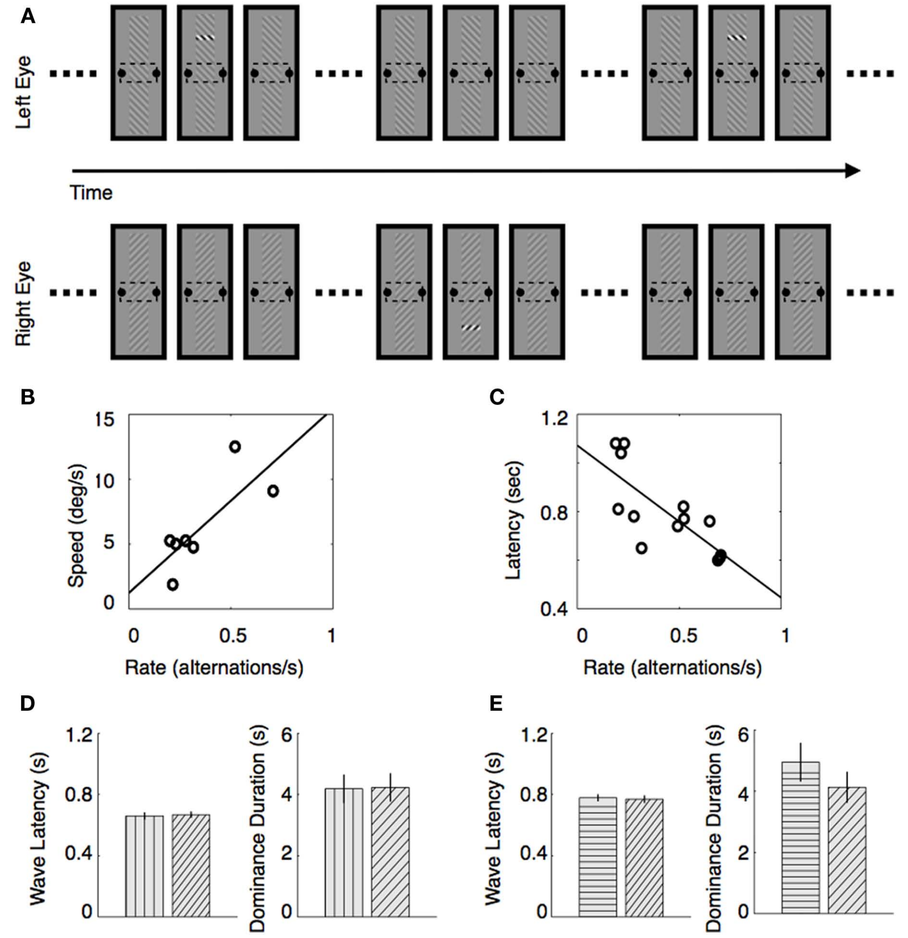

FIGURE 3 | Relation between traveling wave dynamics and dominance durations accompanied with spontaneous perceptual alternations. **(A)** Stimulus conditions that implement the periodic perturbation technique. While observers are reporting perceptual alternations within the monitoring region during an extended viewing period of binocular rivalry, triggers are presented periodically in antiphase. A trigger comprises a brief contrast increment within a small region of rival figure. Trigger locations are different for the two rival stimuli: one is presented at the upper region and the other one is presented at the lower region of the two rival stimuli, respectively. **(B,C)** Traveling wave speed covaries with alternation rate. **(B)** Estimated traveling wave speed of each observer is plotted as a function of alternation rate. **(C)** Estimated traveling wave for each observer is plotted as a function of alternation rate. **(D,E)** Latency of the traveling waves and dominance durations when rival stimuli of different collinearity are presented. **(D)** Result when the vertical and diagonal gratings are presented: mean latency (Left) and mean dominance duration (Right). Pattern filled within the bar indicates the stimulus pattern either carrying traveling waves that emerges from suppression (Left) or being associated with perceptual dominance (Right). **(E)** Result when the horizontal and diagonal gratings are presented. These figures are reproduced from Kang (2009), Kang et al. (2010), with permission from Journal of Vision.

shown by others to influence both wave speed (Wilson et al., 2001) and concurrent rivalry alternations among multiple, neighboring rival targets (Alais et al., 2006). If stimulus collinearity increases neural activity via recurrent excitation, one would predict that a rival stimulus with high collinearity will be dominant longer, on average, when it competes against a rival stimulus of low collinearity. In addition, a highly collinear rival stimulus should exhibit faster traveling waves as it emerges from suppression when that highly collinear stimulus is in rivalry with a weakly collinear rival stimulus; at the same time, the weakly collinear stimulus should emerge from suppression more slowly when in rivalry with the highly collinear stimulus.

When we measured those aspects of rivalry, however, the results did not conform to these predictions. Specifically, we prepared two pairs of vertically elongated rival stimuli like those illustrated in **Figure 3A**: in one pair a vertical grating seen by one eye rivaled with a diagonal grating seen by the other eye. The elongated vertical grating, it is safe to assume, possesses high collinearity relative to the diagonal grating. Contrary to our prediction, traveling waves propagated with similar speed whether they emerged from the vertical grating or from the diagonal grating, and, moreover, dominance durations of the two rival stimuli were also comparable (**Figure 3D**). The same was true when a horizontal grating was in rivalry with a diagonal grating (**Figure 3E**).

This result implies that the dynamics of traveling waves behave in a similar fashion as do the dynamics of spontaneous perceptual alternations, but we are left to explain the counterintuitive influence of stimulus collinearity. As we did to explain the emergent property of the Levelt's second proposition of the large stimulus, we turned to computer simulations, this time modifying extant network models of traveling waves (Wilson et al., 2001; Stollenwerk and Bode, 2003; Bressloff and Webber, 2011) to develop and test a hypothesized mechanism: renormalization of overall stimulus strength by pattern dependent adaptation while retaining recurrent excitation dependent on stimulus collinearity. This refinement of the network model of rivalry outlined in the previous section (i.e., distributed, interdependent local zones of rivalry) successfully reproduced dynamics of traveling waves and dominance durations for all combinations of rival stimulus patterns (Kang et al., 2010).

AN INTEGRATED FRAMEWORK: NETWORK MODELS OF BINOCULAR RIVALRY

This series of studies together with important work by others interested in rivalry has taught us the importance of framing seemingly incompatible psychophysical results within the context of a computational model. In the case of rivalry alternations, recent modeling efforts underscore that the question is not one of noise versus adaptation but, instead, a question of the degree of balance between these two forces. Those models inspired us to perform experiments that revealed the unfolding roles of noise and adaptation during the time course of a given rival state. And in the case of rivalry's dependence on stimulus strength, we see that violations of Levelt's second proposition, rather than failing to replicate results supporting the proposition, in fact reveal an important characteristic of neural mechanisms underlying rivalry: cooperative and competitive spatial interactions provide the key to understanding the conditions under which the contrast-invariance of dominance durations is observed, consistent with Levelt's second proposition, and the conditions under which that invariance rule is violated. And finally, the model refinements that explain Levelt's second proposition also reproduce the dynamics of both traveling waves and ongoing perceptual alternations. This outcome is particularly noteworthy in that those two forms of dynamics differ by an order of magnitude different in terms of their time scales: traveling waves occur within a few hundreds milliseconds and spontaneous perceptual alternations occur over a few seconds.

Our work is not done, however. Interest in binocular rivalry has grown considerably in recent years, the result being new findings that bring surprises and fresh challenges for extant models. We know now, for example, that the time course of rivalry alternations can be influenced by the affective connotation of the rival stimuli (e.g., Alpers and Pauli, 2006; Anderson et al., 2011), by the learned affordance of a rival stimulus (Chopin and Mamassian, 2010), by manipulations that engage visual attention (Neisser and Becklen, 1975; Ooi and He, 1999; Mitchell et al., 2004; Chong et al., 2005; Chong and Blake, 2006; Klink et al., 2008b; Paffen and Van der Stigchel, 2010), and by the activity being executed at the time rivalry is being observed (Maruya et al., 2007). Rivalry dynamics are also affected by sensory signals arising in other modalities including hearing (Kang and Blake, 2005; van Ee et al., 2009; Conrad et al., 2010), touch (Lunghi et al., 2010), and smell (Zhou et al., 2010). Moreover, there are bottom-up influences, too, that must be incorporated into models of rivalry, including eye movements, which are indeed capable of increasing the incidence of rivalry alternations (van Dam and van Ee, 2006). For that matter, eye movements could be involved in some of the putative top-down effects on rivalry, because eye movements are sensitive to top-down, cognitive influences such as memory load in a visual working memory task (Ehrlichman et al., 2007). We would not want to conclude that a given cognitive factor (e.g., memory load) influences rivalry before ruling out an involvement of eye movements. Finally, models of rivalry must be able to account for the large range of individual differences in rivalry dynamics (Carter and Pettigrew, 2003) that appear to have a significant genetic component (Miller et al., 2010; Shannon et al., 2011).

We are confident that these additional findings on rivalry dynamics can be incorporated into a refined version of existing network models of binocular rivalry. For example, individual differences in rivalry alternation rate may well stem from individual differences in gain control mechanisms that govern neural adaptation, with the additional possibility of inherent differences in noise levels. Furthermore, the cooperative and competitive spatial interactions implicated in our studies of Levelt's second proposition probably play key roles in promoting coherent dominance of a figure defined by stimulus features distributed between the two eyes (Whittle et al., 1968; Kovacs et al., 1996; Lee and Blake, 2004). As for top-down influences related to attention, affect, expectation, and action planning, these could be embodied in feedback signals onto neural representations of the competing rival stimuli. For example, it is well known that feature-based attention is spatially extensive throughout the visual field (Saenz et al., 2002; Hayden and Gallant, 2005) and, therefore, attention to a particular feature could strengthen the excitatory drive of that feature wherever it appears within the visual field. At the same time, spatial attention, being focused on a given location in visual space, could increase the strength of neural representations of both rival stimuli since both are imaged within the attended spatial region, resulting in increases in alternation rate. Recent advances in development of connectivity maps provide tantalizing circuitry for achieving these kinds of modulatory influences (Martin, 2011).

CONCLUDING REMARKS

In this review, we summarized recent progress in understanding binocular rivalry dynamics and provided an integrated framework that can readily incorporate other empirical findings. Considering that binocular rivalry is a model system for studying perceptual multistability, implications of this advancement in rivalry dynamics may well extend to perceptual multistability arising from neural representations of competing figure/ground (face/vase), depth, and object interpretations.

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Ambiguous figures – what happens in the brain when perception changes but not the stimulus

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During observation of ambiguous figures our perception reverses spontaneously although the visual information stays unchanged. Research on this phenomenon so far suffered from the difficulty to determine the instant of the endogenous reversals with sufficient temporal precision. A novel experimental paradigm with discontinuous stimulus presentation improved on previous temporal estimates of the reversal event by a factor of three. It revealed that disambiguation of ambiguous visual information takes roughly 50 ms or two loops of recurrent neural activity. Further, the decision about the perceptual outcome has taken place at least 340 ms before the observer is able to indicate the consciously perceived reversal manually. We provide a short review about physiological studies on multistable perception with a focus on electrophysiological data. We further present a new perspective on multistable perception that can easily integrate previous apparently contradicting explanatory approaches. Finally we propose possible extensions toward other research fields where ambiguous figure perception may be useful as an investigative tool.

Keywords: ambiguous figures, multistable perception, Necker cube, old/young woman, EEG/ERP, event-related potentials, reversal positivity, reversal negativity

INTRODUCTION

Normally we experience our visual world as stable and unambiguous – it seems to be as we see it. Numerous optical illusions (Bach, 1997), however, demonstrate that the information provided via our eyes is restricted, thus incomplete and often ambiguous. Our perceptual system needs to disambiguate and interpret it in order to construct stable unambiguous percepts that allow us to successfully act in our environment. Extreme cases are ambiguous figures, like the classical Necker cube (**Figure 1A**, Necker, 1832) or Borings Old/Young woman (**Figure 1C**, Boring, 1930), designed to render two (or even more) perceptual interpretations about equally probable (indicated in **Figures 1B,D**). Another example is binocular rivalry, where the observer's two eyes see different images (Blake, 1989, 2001). In all of these cases the brain states corresponding to the two interpretations become unstable and spontaneous perceptual reversals can occur although the external stimulus stays unchanged.

Ambiguous figures can be found in any textbook about cognitive sciences and neuroscience. The perspective to experimentally separate perceptual interpretation – which changes periodically – from the earliest steps of visual processing – which should stay unchanged, like the visual input – has attracted scientists from various disciplines in the field. It is believed that understanding the mechanisms underlying the perceptual reversal or finding the location(s) of the switch between sensory and perceptual processing may help to understand how the activity pattern of sensory receptors is translated into a complex representation of the perceptual world (perceptual organization, e.g., Pomerantz and Kubovy, 1981), how this representation is realized neurally (object representation) and how it gets conscious (e.g., Crick and Koch, 1998; Blake and Logothetis, 2002; Dehaene and Changeux, 2011).

We will here review the findings from physiological studies on ambiguous figures with a specific focus on EEG studies. Based on the results available so far we will propose a new perspective on the phenomenon, which easily integrates approaches that appeared to be contradictory so far.

Scientific studies of perceptual instability phenomena have been carried out for nearly 200 years and explanations so far followed two main traditions, namely the bottom-up (or sensory) and the top-down (or cognitive) explanatory approaches.

The bottom-up approach assumes that perceptual reversals result from cycles of passive adaptation, recovery, and mutual inhibition of competing neural units or channels in early visual areas (e.g., Köhler, 1940; Toppino and Long, 1987). There is plenty of experimental evidence for this approach and some key findings are listed below:

Several studies demonstrated local (retinotopic) adaptation effects (e.g., Howard and Durham, 1961; Long et al., 1992; Long and Olszweski, 1999), effects of stimulus features (e.g., Washburn et al., 1931; Ammons and Ammons, 1963), and of presentation mode (e.g., Orbach et al., 1963; Kornmeier et al., 2007) on the initial percept and the reversal dynamics of ambiguous figures.

The top-down approach, in apparent contrast, assumes perceptual reversals as the result from active high-level/cognitive processes like attention, expectation, decision-making, and learning (Gregory, 1974; Rock et al., 1994b; Leopold and Logothetis, 1999). Some key findings supporting this approach are: (1) Although the bottom-up approach implies regular oscillations between the two interpretations, the durations of successive

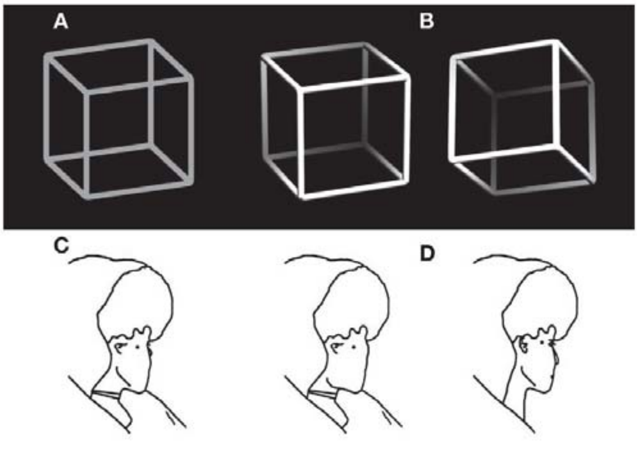

FIGURE 1 | Examples of ambiguous figures and their disambiguated variants. (A) The Necker cube (Necker, 1832) and **(B)** disambiguated versions with depth cues and a lightning model. **(C)** Outline version of Borings Old/Young woman figure (Boring, 1930) adapted from Gale and Findlay (1983) and **(D)** disambiguated old (left) and young woman figure (right).

intervals of transiently stable percepts ("dwell times") are unpredictable and show characteristics of a stochastic process (e.g., fit to gamma distribution, Borsellino et al., 1972; Murata et al., 2003; Brascamp et al., 2005). According to Leopold and Logothetis (1999) this is a signature of high-level exploratory behavior. (2) Perceptual reversals are very rare or even absent, when observers do not know that alternative interpretational possibilities exist (e.g., Girgus et al., 1977; Rock et al., 1994a), a finding hard to reconcile with fully automatic adaptation processes. Further, the rate of reversals can be modulated volitionally, although they cannot be prevented totally (e.g., Liebert and Burk, 1985; Strüber and Stadler, 1999).

While most of the authors so far exclusively favored either a bottom-up or a top-down explanation, more and more studies indicate that both classes of factors play important roles and must be integrated in an explanation of the phenomenon (e.g., Hochberg and Peterson, 1987; Blake and Logothetis, 2002; Tong et al., 2006; Kornmeier et al., 2009; Bartels and Logothetis, 2010).

EEG STUDIES AND THE TIME REFERENCE PROBLEM

The EEG allows millisecond resolution of neural processes underlying perceptual reversals and thus may provide the necessary temporal precision to resolve the debate about whether low-level bottom-up or high-level/cognitive processes are at work. However a precise time reference is necessary for EEG analysis but difficult to establish because of the endogenous character of the reversal event. Two major strategies have evolved to circumvent this problem, both with advantages and disadvantages. In the following we will discuss the relevant studies and relate their results to each other.

THE "MANUAL RESPONSE PARADIGM" – USING MANUAL RESPONSE AS TIME REFERENCE

The principal idea is to present an ambiguous stimulus continuously and use participants' manual indications of perceptual reversals as time reference to analyze the data in a certain interval backward in time. Typical control intervals in manual response studies were periods of stable percept (e.g., Basar-Eroglu et al., 1996) and spontaneous EEG intervals during fixation of a fixation target (e.g., Strüber et al., 2001). Spontaneous key presses not related to perceptual reversals were considered as control for EEG components related to motor preparation and execution (Basar-Eroglu et al., 1993). This paradigm has been applied in a number of studies and the results are summarized in the following:

P300-like parietal positivity

A positive event-related potential (ERP) with a right parietal maximum (P4 electrode, "parietal positivity") occurred ≈250 ms before key press with reversals of motion direction of the stroboscopic alternative motion (SAM) stimulus (Schiller, 1933; Basar-Eroglu et al., 1993; Strüber and Herrmann, 2002) and with orientation reversals of the Necker cube (Strüber et al., 2001; Mathes et al., 2006). This parietal positivity was interpreted as a variant of the well-known cognitive P300 ERP component (e.g., Pritchard, 1981; Verleger et al., 2005) and thus taken as evidence for top-down processes. Strüber and Herrmann (2002) compared MEG activity during endogenous motion reversals of the SAM with exogenously induced motion reversals of disambiguated SAM variants (the two dots moved concurrently either horizontally or vertically in the same direction). They found a reversal-related parietal positivity both for endogenous as well as for exogenously induced motion reversals. Given reaction times from their unambiguous stimulus conditions of about 550 ms, the authors assumed that their parietal positivity occurs subsequent to the motion reversal and reflects its conscious recognition.

Alpha-band power decrease

İşoğlu-Alkaç (2000) used the Necker cube in their study and reported a decrease of alpha-band power in the time range of the parietal positivity compared to alpha activity during a time range immediately before. The authors argue that because alpha-power decrease occurs with active brain states while alpha-power increase with passive states of decreased cortical excitability, alpha power (8–16 Hz) decrease together with the P300-like positivity indicate active cognitive processes during perceptual reversals (İşoğlu-Alkaç et al., 2000). Strüber and Herrmann (2002) found a relatively constant value of alpha oscillation (10 Hz) until it suddenly drops between 300 and 200 ms before button press for exogenously induced SAM-motion reversal, and a continuous decrease in alpha activity within 1000 ms before key press for endogenous reversals. They interpreted the latter as evidence for a slow bottom-up destabilization of the active perceptual interpretation compared to a sudden exogenously driven destabilization. İşoğlu-Alkaç and Strüber (2006) recently found that alpha-power decrease is restricted to the lower alpha bands (6–10 Hz) whereas the upper alpha band (10–12 Hz) was unaffected.

Gamma-band power increase

Basar-Eroglu et al. (1996) found (non-phase-locked) EEG gamma band (30–50 Hz) enhancement within 1000 ms before key press related to SAM reversals compared to perceptual stability (during a time interval after key press) most prominent at the right frontal electrode position (F4). The results were interpreted as evidence for cognitive destabilization processes underlying perceptual reversals. Strüber et al. (2000) found higher SAM reversal-related gamma activity (28–48 Hz) for participants with high reversal rates (reversals per time unit) compared to participants with low reversal rates. The authors interpret their results as further support for the involvement of attentional top-down processing during endogenous motion reversals. Strüber et al. (2001) confirmed these results for the Necker cube.

In Mathes et al.'s (2006) study participants had to volitionally either speed up or slow down the reversal rate or keep a passive attitude toward a Necker cube stimulus. The authors reported higher amplitude of the P300-like positivity and higher gamma activity (28–48 Hz) during the slow down condition than during the speed up condition.

Summary

Taking the above studies together, gamma power increases and alpha-power decreases in a time interval 1000 ms before participants' manual indication of perceptual reversals of an ambiguous figure. Between 500 and 250 ms before key press a parietal positivity occurs which is interpreted as indicating conscious recognition of a perceptual reversal. The reversal event itself then must have occurred earlier.

PROBLEMS OF THE MANUAL RESPONSE PARADIGM

EEG results from the manual response paradigm suggest that endogenous perceptual reversals take place between 1000 and 550 ms before observers' manual response. However, the available data can easily be interpreted either in bottom-up or top-down direction.

Further, as the authors emphasize, manual reaction times strongly vary both intra-individually and inter-individually (Strüber et al., 2000; Strüber and Herrmann, 2002). Recently we estimated the amount of reaction time variance related to orientation reversals of a Necker cube (Kornmeier and Bach, 2004b) in the following way: using depth cues, we created two unambiguous and thus perceptually stable variants of the Necker cube (**Figure 1B**). These appeared in random order, and participants indicated perceived orientation reversals with a key press. Median reaction time from five subjects was 616 ms with an interquartile range from 530 to 733 ms. ERP example traces (±SEM) from the occipital location (Oz) of one participant are seen in **Figure 2A**: When the EEG is averaged with respect to the exogenous stimulus reversal (continuous vertical line), sharply defined ERP components result (dashed vertical line indicates the median reaction time). **Figure 2B**: When the same EEG is "backward averaged" with respect to the participant's response, the early visual ERP components are largely obliterated. It is thus likely, and indeed we will show that endogenous reversals are accompanied by ERP structures earlier than the parietal positivity that can be indentified only with a more precise time reference.

THE ONSET PARADIGM: STIMULUS ONSET AS TIME REFERENCE

The onset paradigm goes back to the work of the Orbach group (e.g., Orbach et al., 1963; Orbach et al., 1966). They presented a Necker cube discontinuously, varied presentation time and interstimulus interval (ISI) and found that reversal rates are modulated in a non-monotonic manner mainly as a function of ISI. **Figure 3** depicts their data together with data from our own lab (Kornmeier et al., 2002).

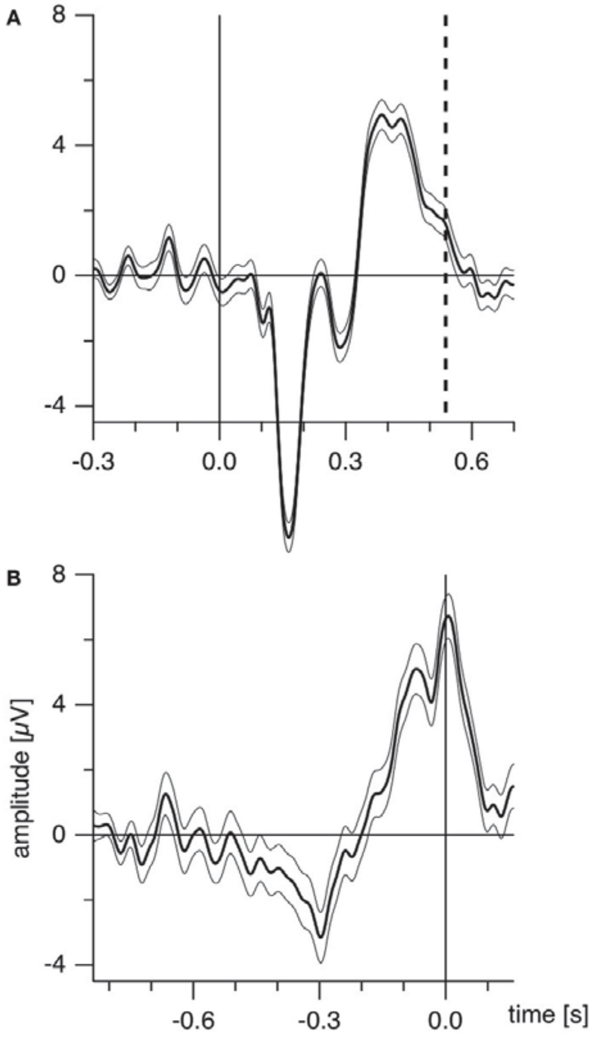

FIGURE 2 | Estimating manual reaction time variance. Participants observed unambiguous cubes (similar to **Figure 1B**) that randomly reversed (16 times per minute on the average) and indicated manually each perceived orientation reversal. **(A)** ERP traces (±SEM) from the occipital location of one participant with the exogenous reversal instance as time reference for averaging (vertical line) are seen. Sharply defined early ERP components result; the reaction time is widely scattered (200 ms interquartile range; dashed line indicates median reaction time). **(B)** The same EEG data averaged backward with reaction times as time references (vertical line). The early visual ERP components are largely obliterated. Only the late positivity is roughly similar to **(A)**. The Onset Paradigm (**Figure 4**) avoided this problem.

As can be seen, for ISIs shorter than about 400 ms reversal rates increase monotonically up to more than twice the rate during continuous observation. After 400 ms a monotonic decrease of reversal rates can be observed. Reversals can even be brought to stand still with ISIs in the range of seconds (Leopold et al., 2002; Maier et al., 2003). Most relevant for EEG studies is that reversals occurred typically near stimulus onset if the presentation

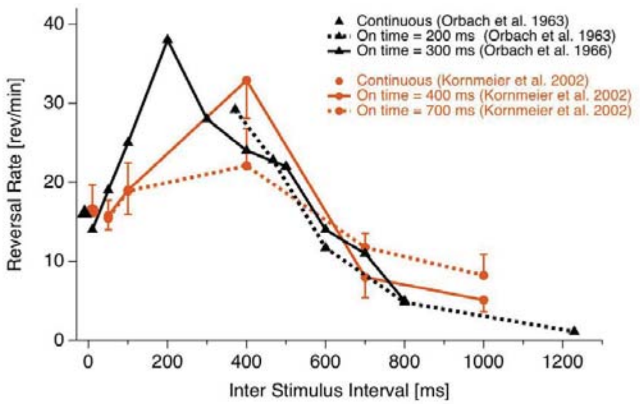

FIGURE 3 | Reversal rate as a function of ISI. Reversal rates with continuous and discontinuous presentations of ambiguous Necker stimuli from different studies. Reversal rates behave non-monotonically, increasing with ISI up to 400 ms. Thereafter they decrease with further increasing ISIs. (Fig from Kornmeier et al., 2007, modified).

time was short enough (Orbach et al., 1966). Stimulus onset thus promised to be a more precise time reference of the reversal event than reaction times.

O'Donnell et al. (1988) were the first study to use stimulus onset as time reference for averaging EEG data. In two conditions participants viewed the ambiguous Necker cube and (apparently) unambiguous cube variants for 700 ms followed by ISIs of 3300 ms. After each stimulus offset they indicated their previous percept by pressing one of two possible keys. In the case of the ambiguous Necker cube, perceptual reversals between two successive stimulus presentations were purely endogenous, whereas in the case of the unambiguous cube variants perceptual reversals were regarded as exogenously induced by stimulus alternations. The authors compared reversal trials with non-reversal trials and found a late parietal/frontal positivity for both exogenously induced and endogenous perceptual reversals. In the case of exogenously induced reversals this positivity was larger and occurred earlier (around 550 ms after stimulus onset) compared to endogenous reversals (around 650 ms after onset).

Identifying O'Donnell et al.'s (1988) positivity with the positivity found with the Manual Response Paradigm and accepting Strüber and Herrmann's (2002) hypothesis about the positivity as an index of conscious realization of the reversal, O'Donnell et al.'s data restrict the reversal event to a time window of 650 ms between stimulus onset and the late positivity. Further, the similar results of O'Donnell et al.'s (1988) illusory and physical reversal conditions suggest similar processes underlying endogenous and exogenously induced perceptual reversals.

O'Donnell et al.'s (1988) data provide a sizable improvement on temporal precision, but some limitations have to be faced: (1) Their "unambiguous" cube variants are not really unambiguous. They can easily be perceived in two different orientations as either inside or outside corners of a box. (2) The non-monotonic character of the reversal rate as a function of ISI (**Figure 3**) suggests two separate processes, one responsible for the increasing part of the function (reversals during continuous observation and with short interruptions, **Figure 3**, left part), and another responsible for the decreasing part (perceptual reversals with long ISIs, **Figure 3** right part). O'Donnell et al.'s choice of 3300 ms ISI places their reversals to the second type and thus raises doubts about whether they are a good model for the continuous case (see also below).

(3) A perceptual reversal during continuous observation of an ambiguous figure involves an implicit comparison of the current with the previous (different) percept, thus working memory may play a role (e.g., Pearson and Brascamp, 2008). In O'Donnell et al.'s (1988) study participants were instructed to report their percept of each presentation. Comparisons across presentations were not necessary. This task together with the relatively long ISIs may have allowed separate percepts of cube stimuli at each stimulus presentation instead of perceptual reversal experiences.

We adopted O'Donnell et al. (1988)'s paradigm but modified it in the following ways (**Figure 4**):

(a) Optimizing presentation time and ISI: We shortened our ISI to 400 ms to be as close to the continuous viewing condition as possible while concurrently enabling manual responses within the ISI. Presentation time was set to 800 ms, long enough to allow the full development of a P300-like positivity and short enough to keep the probability of additional perceptual reversals later during the presentation interval low.
(b) Comparison task across presentations: Our participants compared in a go/nogo task the perceived front-back orientation of the current Necker lattice (a combination of nine Necker cubes, **Figure 4**) with that of the preceding one in two experimental conditions. In one condition they pressed a key whenever the currently perceived orientation differed from the preceding one ("reversal condition"). The second, control condition was identical except that the task was the opposite: participants indicated when they perceived orientation of the stimulus as remaining the same ("stability condition"). All manual responses were executed in the ISI after the relevant percept in order to keep neural activity related to motor-preparation and -execution as far away as possible from the critical time interval of the reversal. Any ERP signature related to lower-level stimulus processing, afterimages, or motor preparation should be identical in the two conditions and should disappear after subtraction of the related ERP traces from each other.
(c) Like O'Donnell et al. (1988) we exogenously induced orientation reversals of unambiguous stimulus variants in a second experiment. Our unambiguous cube variants contained depth cues, like shading, central perspective, and a lighting model (**Figure 1B**, Woo et al., 1998).

Four types of ERP traces were calculated, related to (1) endogenous perceptual reversals and (2) endogenous perceptual stability of ambiguous Necker stimuli, (3) exogenously induced perceptual reversals, and (4) exogenously induced perceptual stability of disambiguated stimulus variants.

THE PROCESSING CHAIN OF PERCEPTUAL REVERSALS

According to our null hypothesis, the EEG traces from the reversal and stability conditions should not differ, because both conditions

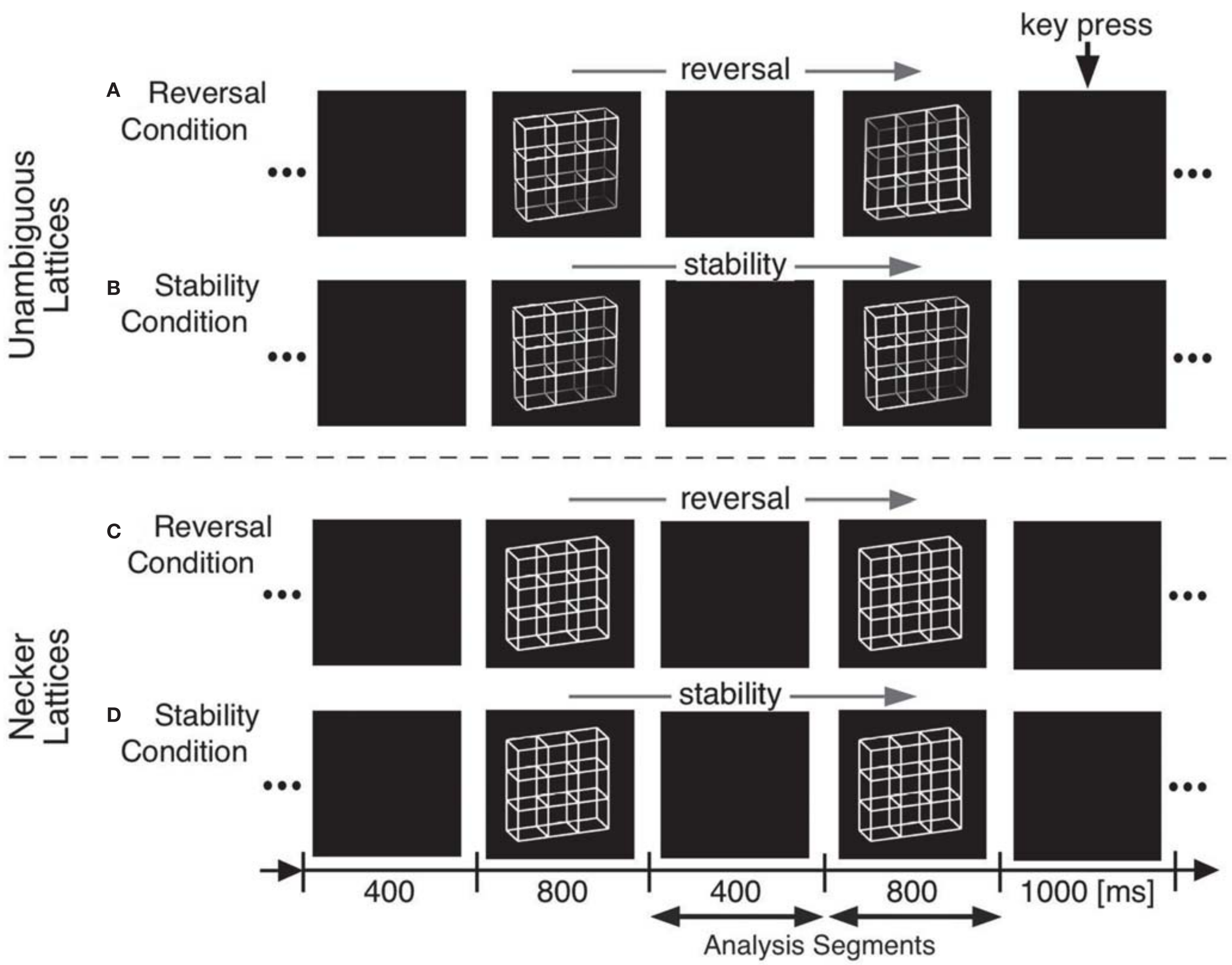

FIGURE 4 | Onset paradigm. Participants viewed in different experiments either unambiguous lattices **(A,B)** or ambiguous Necker lattices **(C,D)** and compared the 3D perspective of successively presented stimuli. In separate experimental conditions they indicated in a go/nogo task either a perceived perspective reversal [reversal conditions in **(A,C)**] or perceived stability [stability conditions in **(B,D)**] across two successive stimulus presentations by a key press in the ISI following the respective perceptual event. Each key press extended the current ISI from 400 to 1000 ms.

contain identical stimuli, a comparison task, a mental decision, and aspects of response preparation. Further, the amount of required attention to execute the task should be equal in the two conditions.

The difference traces ("dERP," reversal condition minus stability condition) should thus be flat and any residuum would be related to the perceptual reversal aspect. Indeed we did find a series of reversal related modulations in lower (dERP) as well as higher frequencies. **Figure 5A** presents the ERP traces from perceptual reversal trials (interrupted lines) and perceptual stability trials (continuous lines) on a schematic head (data from Kornmeier and Bach, 2004b). **Figure 9** presents the related (induced) modulations at higher frequencies. Like in **Figure 5**, for each electrode position a pair of graphs depicts data from the unambiguous lattice variants on bottom on a gray background and data from the ambiguous lattices on top on a white background. The electrode positions are indicated schematically in **Figures 5B** and **9B**. At a first glance ERP traces (**Figure 5A**) are very similar across stimuli and conditions. Especially the P100 components as the earliest visual responses after stimulus onset are roughly identical (**Figure 6**). The subsequent components match in latency but differ in amplitude. These differences are better seen in the difference traces (dERPs, **Figure 5C**) and their temporal relations are schematically presented in **Figure 8**. Likewise modulations at higher frequency are very similar across averaged conditions and experiments, and are depicted in the time–frequency charts in **Figure 9A**. Most conspicuous is an initial power enhancement in the alpha to beta range immediately after onset that quickly shifts to the theta and lower alpha range where it sustains. Further, a sustained beta deactivation starts about 100 ms after stimulus onset and spreads to the whole beta and upper alpha band. Differences in higher frequency power between conditions and experiments are

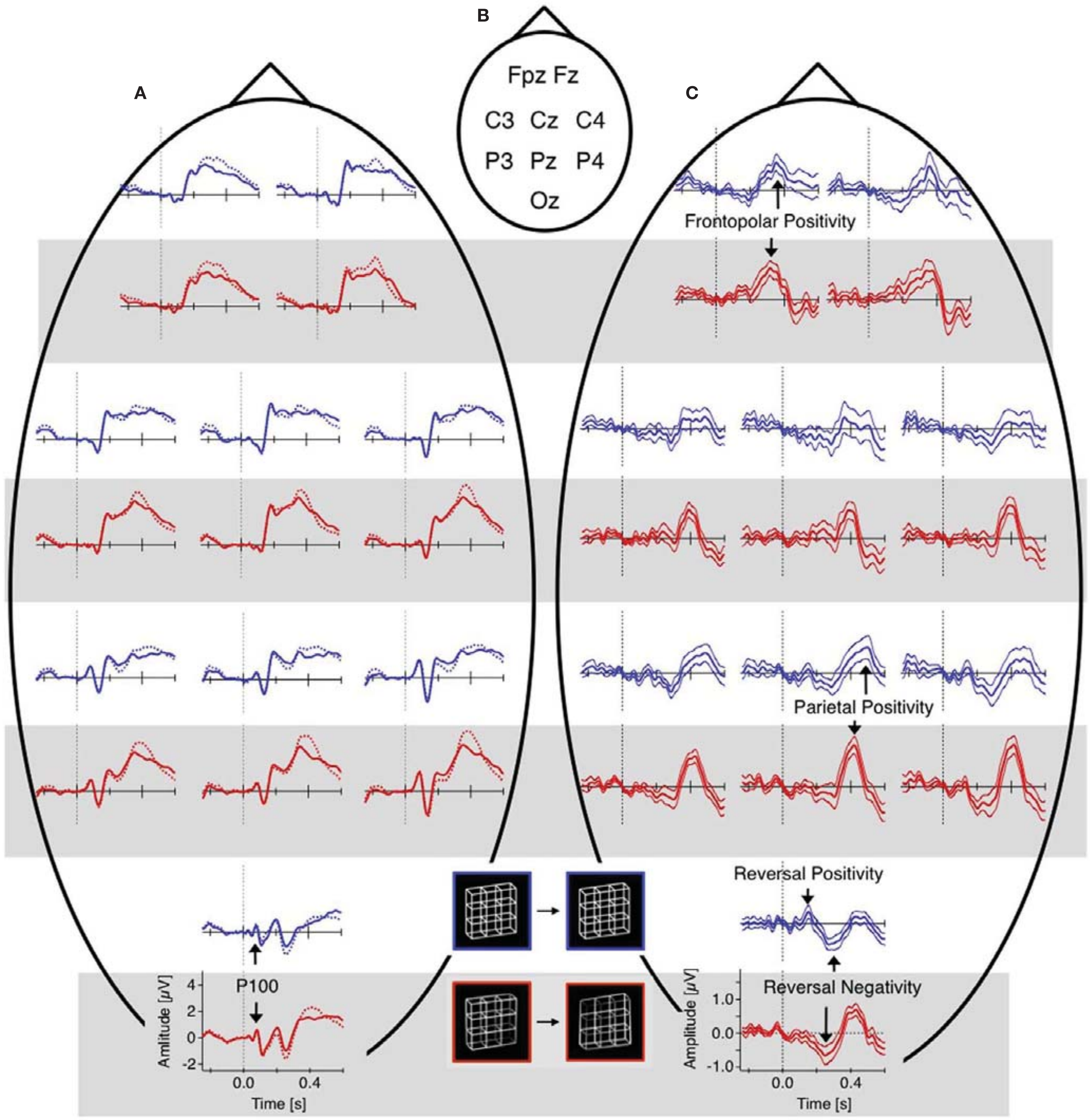

FIGURE 5 | Grand mean ERPs (16 participants, baseline −60 to +40 ms). For each electrode position a pair of graphs contain data from the unambiguous lattice variants in red on bottom on a gray background and the data from the ambiguous lattices in blue on top on a white background. Dashed vertical lines indicate stimulus onset, electrode positions are indicated schematically in **(B)**. **(A)** Raw ERPs before subtraction. The global shapes of the ERP traces at each electrode are very similar across conditions (reversal, dotted traces, and stability, continuous traces) and across experiments (ambiguous and unambiguous stimuli). This is especially true for the early visual ERP components at the occipital electrode position). **(C)** Difference traces (reversal minus stability). Differences ERPs (dERPs) are very similar between ambiguous and unambiguous stimuli with two exceptions: (1) All dERPs found with unambiguous stimuli occur earlier and (2) the early occipital Reversal Positivity (RP) is restricted to endogenous perceptual reversals of ambiguous Necker lattices. Data from Kornmeier and Bach (2004b).

better seen in the difference time–frequency charts in **Figure 9C** and their temporal relation schematically in **Figure 10**.

In the following we will discuss the individual dERP components and related modulations at higher frequencies separately:

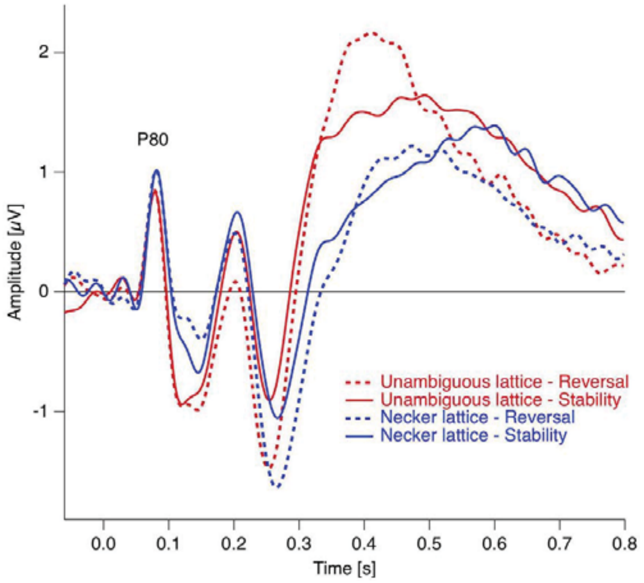

FIGURE 6 | Grand mean ERP traces from the occipital electrode position. As can be seen, the early visual ERP components are very similar across conditions (reversal, dotted traces and stability, continuous traces) and experiments (Necker lattices, blue, and unambiguous variants, red). Data from Kornmeier and Bach (2004b).

SIGNATURES SPECIFIC FOR ENDOGENOUS REVERSALS OF AMBIGUOUS FIGURES

Reversal positivity

The reversal positivity (RP) occurs around 130 ms after stimulus onset, is most prominent at occipital electrode positions and restricted to endogenous reversals of the ambiguous stimuli. So far it has been reported by studies using the Onset Paradigm with Necker lattices (Kornmeier and Bach, 2005, 2006; Kornmeier et al., 2007; Britz et al., 2009), with the classical Necker cube (Kornmeier et al., 2011), with Borings (1930) Old/Young Woman (**Figure 1C**, Kornmeier and Bach, 2004a) and recently even with binocular rivalry stimuli (Britz and Pitts, 2011). Pitts et al. (2007) found modulations in the P1 ERP component during reversals of the Vase/Face stimulus and Schroeder's staircase stimulus fitting with polarity and time window of the RP. Britz and Pitts recently discussed the RP as a modulation of the P1 component and localized it in "primary visual areas" (Britz and Pitts, 2011). Recent evidence from our lab suggests, however, that P1 and RP are different components (Kornmeier et al., 2011) suggesting that the P1 effect in Pitts et al. (2007) may be a superimposed RP. Pitts et al. (2008) and Intaite et al. (2010) did not find a significant RP with perceived reversals of the Necker lattice. In the latter study a strongly modified variant of the Onset Paradigm (e.g., reversals from unambiguous to ambiguous lattices) may be the reason. Pitts et al. (2009) did not analyze the data in the RP time window.

A possible explanation for the remaining inhomogeneity of results may be the following: The RP is a small component typically with amplitudes around or even below 1 µV (e.g., Kornmeier and Bach, 2005; Kornmeier and Bach, 2006; Britz et al., 2009). A critical parameter for its statistical validity is the signal-to-noise ratio and thus the number of EEG trials per subject that enter the ERP calculation. This was between 100 and 120 per condition in our studies. Britz et al. (2009) reported about 52 trials per condition and participant on average. In Pitts et al.'s (2007, 2008) studies the number of trials was down to 30 and below. Their absolute number of trials (not reported) may have been large enough to let a positive deflection appear but too low to render it significant[1] (Luck, 2005; Pitts et al., 2007).

In studies using the Manual Response Paradigm the RP was probably obliterated due to reaction time variability. This would imply that reaction times are considerably less precise compared to stimulus onset as time reference. We estimated the precision of the Onset Paradigm in the following way: The earliest ERP response after stimulus onset, the P100, occurred in our data 80 ms after onset with a peak width of ±20 ms and was regarded as a low-level ERP and fully synchronized to stimulus onset. In comparison, the RP is the earliest reversal-related dERP component has a peak width of about ±35 ms. Let us now assume that it results from a convolution of the variance producing the P100-width with the variance producing the Reversal Positivity. Assuming a Gaussian peak shape, the unknown width of the temporal variance would be equal to:

$$\text{Temporal variance of the reversal instance} = \sqrt{\left(35^2 — 20^2\right)} \approx 30$$

(based on additivity of variances)

Thus endogenous perceptual reversals were synchronized with stimulus onset with a precision of about ±30 ms, an improvement of more than a factor of three over the manual response reference (**Figure 7**).

Early alpha modulations

A left-hemispheric power reduction in the alpha band (8–15 Hz) ranging from the occipital to frontopolar electrode (Component A5 in **Figures 9** and **10**) shows some similarities to the RP and may thus be related: Both (1) start around 130 ms, (2) are restricted to endogenous reversals, and (3) have an opposite sign as the subsequent components.

Interpretation of the RP: decision conflict during interpretation of ambiguous information. In summary, the RP shows three interesting features:

(1) It is restricted to endogenous reversals.
(2) It occurs relatively "early" during visual processing, which is reflected in its latency and its spatial distribution at occipital electrodes. For discontinuous stimulus presentation, early is well defined as occurring with short latency after stimulus onset. But what would early mean for perceptual reversals during continuous observation? Here early and late can be alternatively defined as temporal distance from reaction time. Reaction times can be estimated with ambiguous figures using the Onset Paradigm and instructing participants to respond

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[1] The multiple testing problem is inherent to the analysis of EEG data. Depending on the number of tests, corrections for alpha-error-inflation can strongly reduce test-sensitivity, especially in cases of small signals like with the Reversal Positivity.

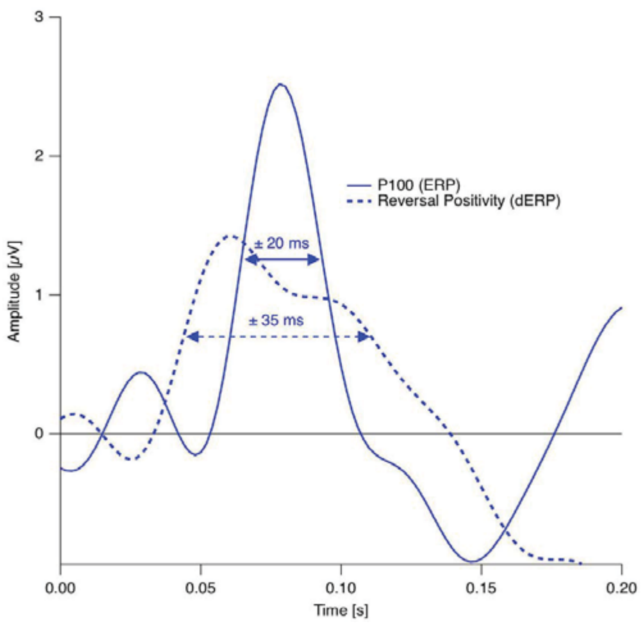

FIGURE 7 | Estimation of the temporal precision with the Onset Paradigm. Continuous trace: Grand mean ERP trace from the occipital electrode in the reversal condition in the P100 time window. Dotted trace: Grand Mean dERP trace from the occipital electrode position in the time window of the RP. The dERP trace is shifted on the time scale in order to align the RP with the P100 and thus to simplify peak-with comparison. Data from Kornmeier and Bach (2005).

immediately after perceived reversals. Substituting the reversal instance with stimulus onset and assuming that reversals occur only after stimulus onset, the upper limit of reaction time to endogenous reversals is in the range of 600 ms (Kornmeier and Bach, 2006). Thus the RP occurs roughly 470 ms before the manual indication of a perceived reversal (Kornmeier and Bach, 2006). In perceptual processing times 470 ms is very long and thus the RP can also be labelled as early from this point of view.

(3) The RP occurs with different types of ambiguous stimuli (Necker cube, Necker lattice, Old/Young woman stimulus and even with binocular rivalry stimuli). This indicates generality across low-level stimulus features and across stimulus types. Further, the RP differs from the spatiotemporal close P1 (Kornmeier et al., 2011).

Currently we regard the RP as an indicator of the visual system's "detection" of ambiguity, or the related decision conflict at a certain processing level during perceptual organization (Pomerantz and Kubovy, 1981) where the ambiguity gets evident. For the Necker cube the identification of line orientations and their binding together would be low-level steps and perhaps related to the C1 and P1 ERP components (discussed in Kornmeier et al., 2011). Ambiguity occurs subsequently during the interpretation of acute and obtuse angles as orthogonal and the allocation of depth values to the different square planes. Here a perceptual decision has to be made and the RP may reflect the related conflict or its detection.

Two questions arise immediately from this speculation:

(1) In the case of the Necker cube the stimulus information is always ambiguous. Why should there be a difference in dealing with this ambiguity in reversal and stability trials (remind that the RP is a dERP, resulting from the subtraction of stability ERP traces from reversal ERP traces)? A possible answer to this question may be the following: All sensory information is incomplete and to some degree ambiguous. Our perceptual system uses (amongst other strategies) past perceptual experiences (on various time scales) to disambiguate and interpret this information. Several adaptation and priming studies support this view (e.g., Long et al., 1992; Woerner et al., 2009). The above mentioned decision conflict need not occur if the perceptual system is already strongly biased in favor of one (e.g., the previous) percept at the moment the ambiguous stimulus appears. This may be the case in our stability trials. We have estimated the disambiguation time in the case of a decision conflict with the Necker lattice as 40–70 ms (Kornmeier and Bach, 2006, see also below). If our above speculation is correct, then reaction times should be delayed by this amount in the reversal trials, where a conflict arises and disambiguation is necessary, compared to the stability trials without conflict. This is indeed what we recently found (Kornmeier et al., 2011).

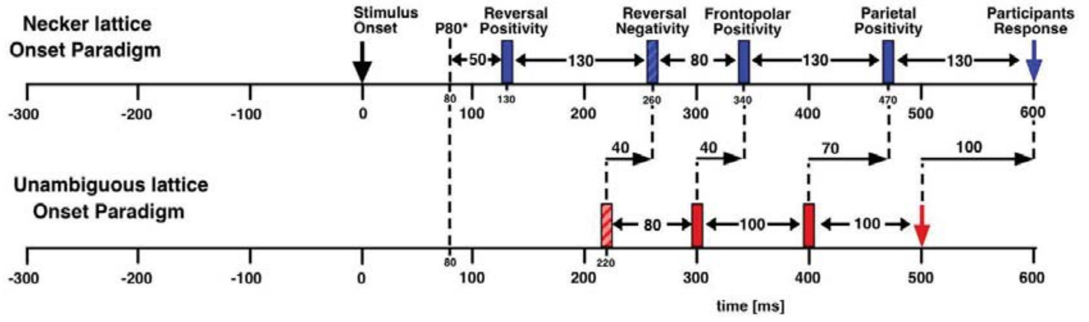

FIGURE 8 | Schematic time scale of endogenous and exogenous dERP components. dERP components are indicated by rectangles. The vertical dashed line indicates the P100 as earliest occipital ERP component before subtraction. Negative values on the time axis reflect the time period of the ISI before stimulus onset. Data from Kornmeier and Bach (2004b, 2006).

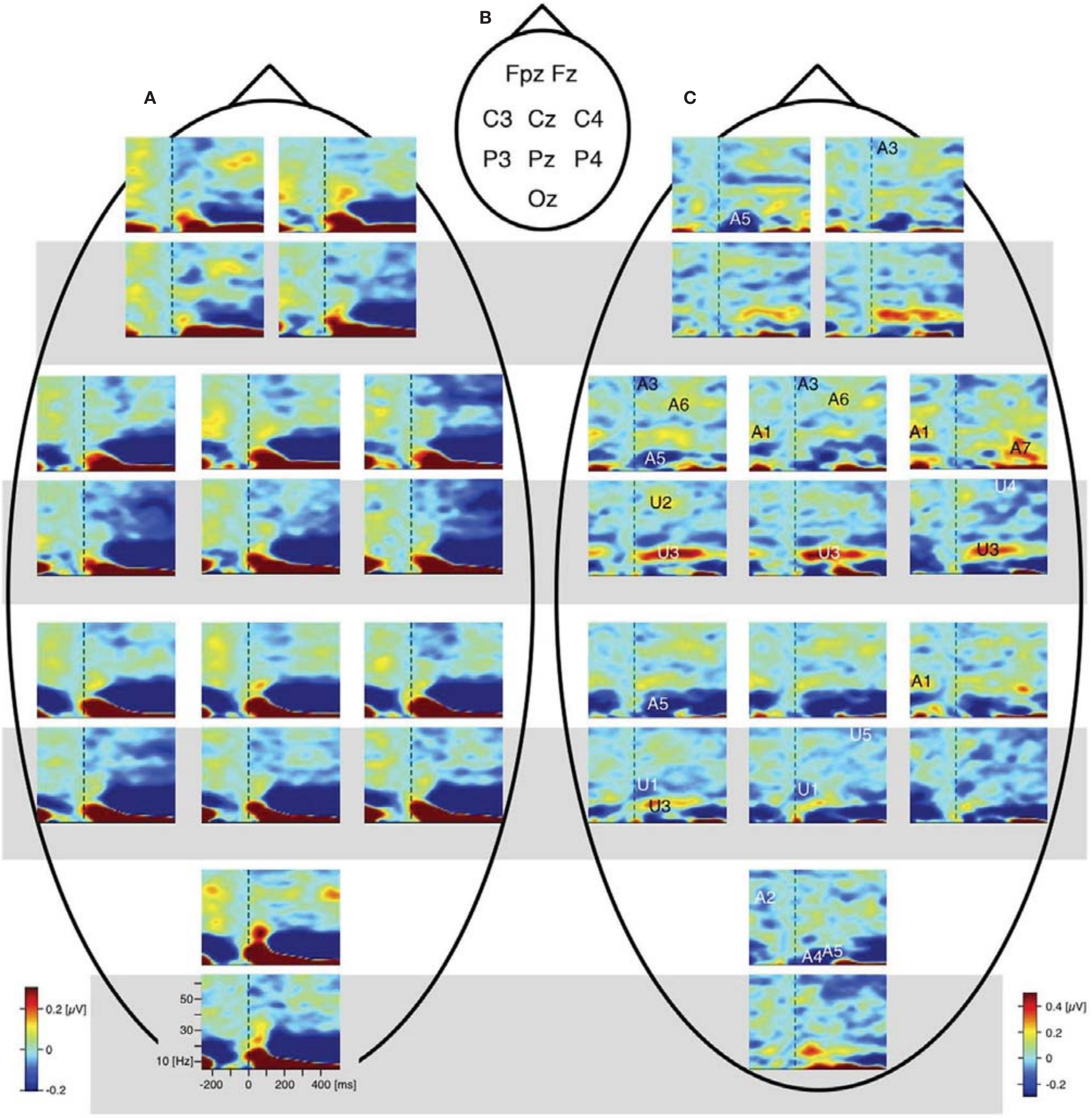

FIGURE 9 | Grand mean EEG time–frequency charts. For each electrode position a pair of time–frequency charts contain data from the unambiguous lattice variants (bottom, grey background) and the data from the ambiguous lattices (above, white background). Dashed vertical lines mark the stimulus onset. **(A)** Raw time–frequency charts. Grand mean time–frequency charts were obtained by averaging data across participants and conditions. Electrode positions are indicated schematically in **(B)**. **(C)** Differences of grand mean EEG time–frequency charts (reversal minus stability). Entries in **(B)** (e.g., A1, U2, . . .) indicate the position of significant deflections from zero in the time–frequency plane. A, ambiguous; U, unambiguous; numbers indicate the temporal order of effects; black/white colouring of the numbers and letters is only for saliency. Most remarkable is the gamma band modulation before onset of the ambiguous Necker stimulus (deflection A1 at electrodes P4 and C4 and Cz; and deflection A2 at electrode Oz). No such modulation occurs with the unambiguous stimulus variants. (from Ehm et al., 2011, **Figure 2**).

(2) Disambiguation of incoming information as described above makes sense if the stimulus reappears periodically after a blank screen interval and a percept has to be created. But how can this be translated to the continuous case? There is accumulating evidence that perception is discontinuous and that our impression of perceptual continuity is an illusion (e.g., Dubois and Vanrullen, 2011). According to this view some neural instances would "perceive" a discontinuously

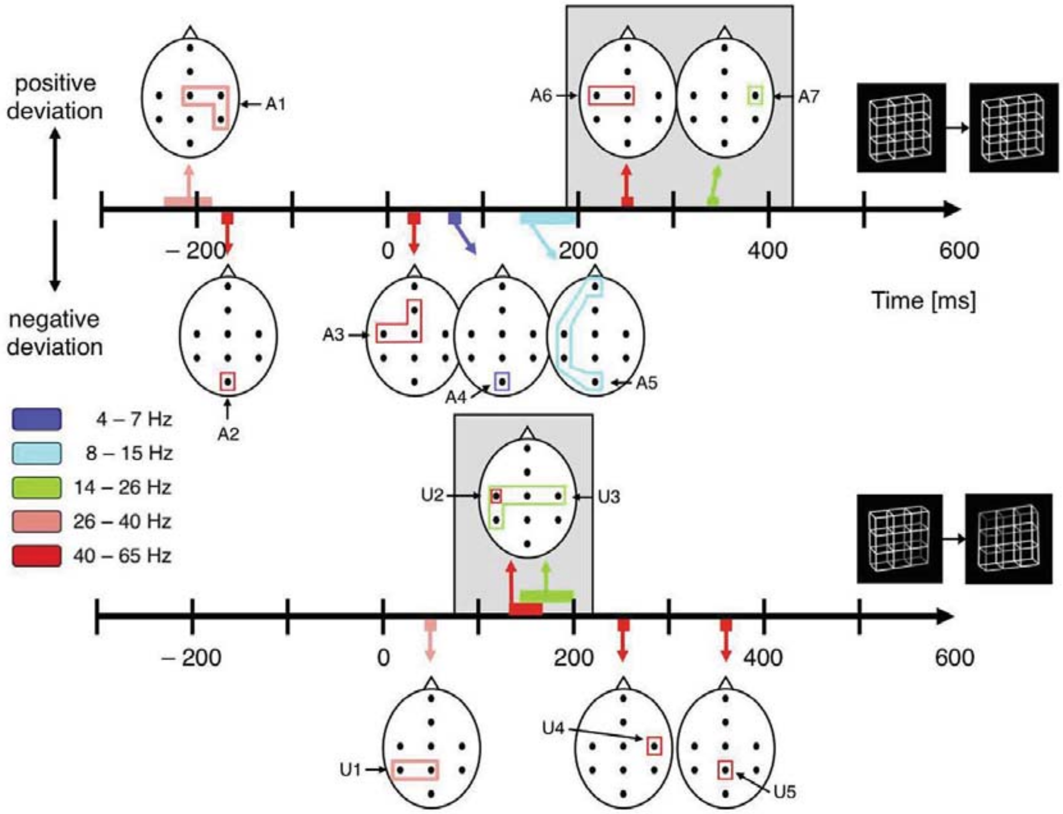

FIGURE 10 | Schematic display of significant components from the time–frequency analyses. The black dots within the schematic heads mark electrode positions. The closed polygons surrounding electrode positions mark significant test results, their color indicates the corresponding frequency range. Head positions on the time axes indicate peak time. Positive and (negative) excursions appear above (below) the time axes. Top: Necker stimulus; bottom: unambiguous stimulus. Gray backgrounds highlight analogies between ambiguous and unambiguous stimuli. Their temporal difference is consistent with dERP results. Pre-onset gamma modulations (A1 and A2) are restricted to the Necker stimuli.

presented stimulus similarly to a continuously presented stimulus (given a certain frequency). Some (potentially higher level) updating instance may periodically re-evaluate and re-interpret the visual input in order to notice environmental changes. Thus, periodic decisions and decision conflicts may also arise during continuous observation of an ambiguous figure. Such a concept had already been proposed in top-down explanation approaches (e.g., Vickers, 1972; Leopold and Logothetis, 1999) and also in a recent Necker-Zeno Model for Bistable Perception (Atmanspacher et al., 2004, 2008). Accordingly, the RP should not only occur with the Onset Paradigm but also with spontaneous reversals of a continuously presentated ambiguous figure. And it should be detectable if a sufficiently precise time reference were available with continuous stimulus presentation. Additional experiments with ambiguous figures from other categories (e.g., apparent motion, figure-background stimuli) need to further test the generality of the RP.

Interpretation of the alpha-power reduction: disambiguation time. The left-hemispheric reduction of alpha-power starts at the latency of the RP (130 ms), it extends from posterior to anterior sites and lasts for about 60 ms (**Figures 9** and **10**). Modulation of alpha activity is discussed in the contexts of change from a resting state to excitation/activation, attention and top-down modulation of perceptual processing, execution of cognitive tasks or temporal segmentation of perception and consciousness (for a review, see Palva and Palva, 2007). In the current experiment the alpha reduction may indicate recurrent activity between occipital and frontal areas to resolve the ambiguity and the related decision conflict indicated by the RP. It may thus reflect a disambiguation time of roughly 60 ms in the case of the Necker lattice. Interestingly, Foxe and Simpson (2002) indicated that in humans visual information needs only about 30 ms from striate to prefrontal cortex. Two loops of recurrent activity thus seem to be sufficient to disambiguate the Necker lattice.

SIGNATURES OCCURRING WITH BOTH EXOGENOUSLY INDUCED AND ENDOGENOUS REVERSALS

Reversal negativity

The reversal negativity (RN) is the first dERP component found with both endogenous reversals of the Necker lattices and exogenously induced reversals of the unambiguous lattice variants. It occurs roughly 220 ms after stimulus onset with exogenously induced reversals and about 40 ms later at 260 ms with endogenous reversals (Kornmeier and Bach, 2006; Intaite et al., 2010; **Figure 8**).

This component has been reported in all studies using the onset paradigm (Kornmeier and Bach, 2004b, 2005, 2006; Kornmeier et al., 2007, 2011; Pitts et al., 2007, 2008, 2009; Britz et al., 2009; Intaite et al., 2010; Britz and Pitts, 2011). Source analysis revealed locations in the lateral occipital and inferior temporal areas (Pitts et al., 2009; Britz and Pitts, 2011).

There are, however, some differences concerning the temporal extent and the spatial distribution of the RN. These differences may be traced back to differences in the experimental paradigm concerning the time window of participants' responses. In some studies the participants were allowed to respond immediately after a perceived reversal, i.e., already during the stimulus presentation period. In those cases the negative dERP component was both temporally and spatially extended (e.g., Pitts et al., 2008; Intaite et al., 2010; Kornmeier et al., 2011) compared to the case when responses were only allowed in the ISI following a perceived reversal. In the latter case the negative dERP component was shorter and restricted to occipital/parietal locations (e.g., Kornmeier and Bach, 2004b; Kornmeier and Bach, 2005). Kornmeier et al. (2007) demonstrated that in the cases of immediate responses (already in the stimulus presentation interval) the occipital/parietal RN is superimposed by a residual Bereitschaftspotential, which occurs later (at about 300 ms after onset) and which has a distribution from parietal to frontal positions. Elbert et al. (1985) have previously shown influence of psychological variables on the Bereitschaftspotential in the context of perceptual reversals of the Necker cube.

Interpretation of the RN. So far the functional role of the RN is unclear. It's role as an indicator of top-down influence of the reversal process (e.g., Pitts et al., 2008) and its potential identity with the spatiotemporally very similar Selection Negativity (Anllo-Vento and Hillyard, 1996) are in discussion (Kornmeier and Bach, 2004b; Pitts et al., 2008; Intaite et al., 2010). A specific role for the RN in endogenous perceptual reversals can be ruled out by the fact that it also occurs when perceptual reversals are exogenously driven by a physical stimulus change (Kornmeier and Bach, 2006). Interestingly, the RN's spatial location seems to be related to the stimulus type. It is most prominent at occipital/parietal locations with cube type stimuli whereas it seems to be more dominant at temporal locations in the case of Boring's old/young woman (Kornmeier and Bach, 2004a).

Frontopolar and parietal positivities

The Frontopolar Positivity follows the RN. It is most prominent at the frontopolar electrode and occurs 300 ms after stimulus onset in the case of exogenously induced reversals, and 40 ms later at 340 ms in the case of endogenous reversals (**Figures 5C** and **8**). No source analysis of this component has been done so far.

The Parietal Positivity follows the Frontopolar Positivity. It is maximal at parietal electrodes and occurs 400 ms after stimulus onset with exogenously induced reversals and about 70 ms later at 470 ms in the case of endogenous reversals. Most of the ERP studies using the Onset Paradigm reported a reversal-related parietal positivity with very similar spatiotemporal patterns (e.g., Kornmeier and Bach, 2004b; Pitts et al., 2008; Britz et al., 2009). It was recently localized in the bilateral superior and middle temporal as well as left inferior frontal areas (Britz and Pitts, 2011). Some studies did not discern between Frontopolar and Parietal Positivities and regarded them as one and the same component with a parietal to frontopolar extent (e.g., Britz et al., 2009; Britz and Pitts, 2011). Pitts et al. (2008) reported a frontal positive component at around 300 ms and interpreted it as a "selection positivity," i.e., a sign-inverted frontal counterpart of the occipital/parietal Selection Negativity (Anllo-Vento and Hillyard, 1996).

Interpretation of the frontopolar positivity. Recently we found in our data strong evidence in support of two separate positive components: With our go–nogo variant of the Onset Paradigm we were able to differ between manually indicated reversal events (reversal percepts in the reversal condition, i.e., go trials) and reversal events without indication (reversal percepts in the stability conditions, i.e., nogo trials) – and with the same logic corresponding stability events. The dERPs from the go trials showed a decrease of a positivity at 400 ms and a increase of a positivity at 300 ms from parietal to frontopolar electrode positions in the case of the unambiguous lattices (**Figure 11C**: from bright to dark colors). This is similarly indicated but less pronounced with the ambiguous lattices with the above mentioned latency shifts (**Figure 11A**). In contrast, the dERPs related to the nogo trials showed a simple amplitude reduction from parietal to frontopolar electrodes without any difference in latency (**Figures 11B,D**). Thus, the Frontopolar Positivity is absent in the nogo trials. This observation decouples the Frontopolar Positivity both from the Parietal Positivity and the RN and may indicate a role of working memory related to the delayed response in the subsequent ISIs of the go trials – no delayed response and thus no related memory is necessary in the nogo trials. This interpretation suggests that some response-related brain instance must already know about the perceptual outcome at 300 ms (unambiguous lattices) or 340 ms (ambiguous lattices). More research is necessary to test this interpretation of the Frontopolar Positivity.

Interpretation of the parietal positivity. So far all electrophysiological studies on ambiguous figures report a slow positivity with parietal to frontal dominance. With the Onset Paradigm such a positivity occurs between 400 and 500 ms after stimulus onset and between 100 and 150 ms before the manual response (e.g., Kornmeier and Bach, 2006; Pitts et al., 2009). With the Manual Response Paradigm a slow positivity peaks roughly 250 ms before the manual response. Assuming that both paradigms identified the same component, the mismatch between latencies of about 100 ms may result from (1) different time references for averaging (stimulus onset or reaction instances) together with a temporal coupling asymmetry of this component to the two time references and (2) a merging of the Frontopolar with the Parietal Positivity in the case of backward averaging from manual responses.

Several authors identified the Parietal Positivity with the well-known P3b component, which typically occurs in oddball paradigms (Picton, 1992), and indeed Verleger et al. (2005) demonstrated the persistence of the classical P3b across onset and reaction time as time references for averaging. The interpretations of the Parietal Positivity range from (1) indication of attentional and cognitive processes during a perceptual reversal (O'Donnell et al., 1988) or (2) following it (İşoğlu-Alkac et al., 2000), (3) closure

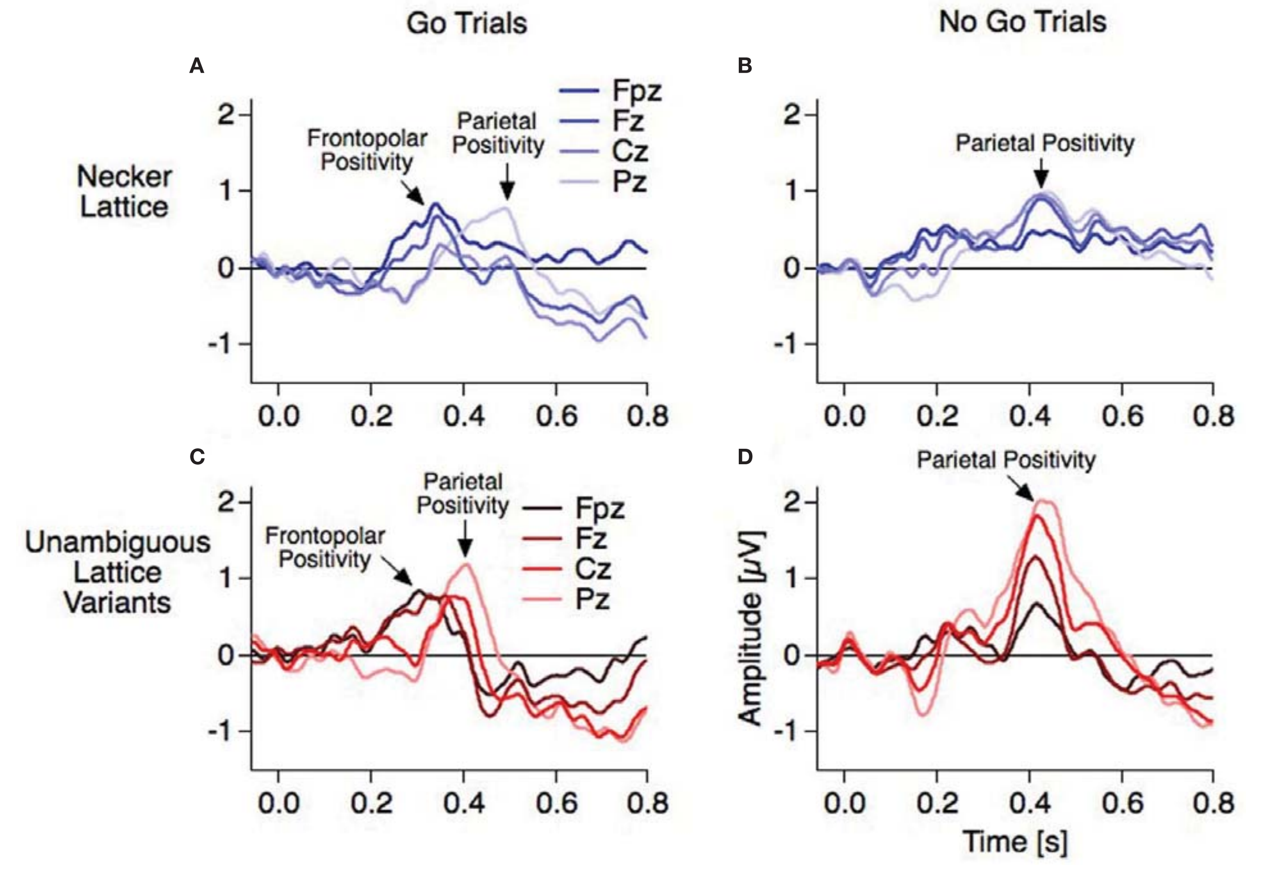

FIGURE 11 | Parietal and frontopolar positivities (dERPs) along the midline electrodes. (A,C) Temporally and spatially separated Parietal and Frontopolar Positivities occur in the go trials. **(B,D)** The Frontopolar Positivity, however, is absent in the no–go trials. Instead, the amplitude of the Parietal Positivity decreases from parietal to frontopolar positions, while its latency stays unchanged (Data from Kornmeier and Bach, 2004b).

of the switching process (Strüber et al., 2001), or (4) cognitive/conscious recognition or appraisal of the reversal (Strüber and Herrmann, 2002; Kornmeier and Bach, 2006; Britz and Pitts, 2011). The following consideration supports the cognitive appraisal/visual awareness hypothesis from above: The minimal reaction time with the simplest auditory task (faster than visual) is in the range of 150 ms (Debecker and Desmedt, 1970). This gives an upper limit for a pure motor execution after the conscious response decision has taken place. It fits well with our average temporal distance between the Parietal Positivity and the manual reaction and thus may place the moment of conscious experience of the perceptual change (and the decision to indicate this) roughly at the latency of the Parietal Positivity. Further support comes from several ERP studies on ERP correlates of consciousness. There, a P3b occurs if perceptual processing of a stimulus reaches consciousness, whereas this component is absent, when the stimulus stays subliminal (Dehaene and Changeux, 2011, for a recent review).

Beta and gamma modulations common to both endogenous and exogenously induced reversals

All dERP components found with exogenously induced reversals seem to occur also with endogenous reversals, however with a temporal delay. A similar pattern of results can be observed in the beta and gamma frequency range. In the case of exogenously induced reversals a left-central increase in gamma activity at about 150 ms (40–65 Hz, **Figures 9** and **10**, component A6) followed by a bilateral central increase in beta activity (14–26 Hz, **Figures 9** and **10**, component A7) at around 260 ms can be observed. Correspondingly, in the case of endogenous reversals a left-central gamma increase starts at about 250 ms and thus 100 ms later than the exogenous counterpart (**Figures 9** and **10**, component U2). An increase in beta activity follows at around 320 ms (**Figures 9** and **10**, component U3). Significance for the latter, however, is restricted to the right-central electrode position. Although the pattern of results agrees less well than the dERP components, which might partly be due to the lower temporal resolution of time–frequency analyses compared to ERPs, component A6 might be associated with component U2 and the same may apply to components A7 and U3 (indicated by a gray shading in **Figure 10**) and the temporal delay between these components has the same sign as with the dERP components.

Several studies using the Manual Response Paradigm reported enhanced frontal gamma activity within 1000 ms before the manual response (e.g., Basar-Eroglu et al., 1996; Strüber et al., 2000).

The gamma enhancement found with the Onset-Paradigm lies within the above 1000-ms time interval and may reflect the same neural processes. The spatial differences between gamma enhancements and the missing beta effect with the Manual Response Paradigm may be explained by different control conditions.

Interpretation of the beta and gamma modulations. The gamma-band modulation at 250 ms is the earliest signature at higher frequencies in the case of endogenous reversals with a corresponding component from exogenously induced reversals. Interestingly, its start matches well the latency of the RN, the earliest dERP component common to both types of reversal. According to Kornmeier and Bach (2006) these findings indicate that at least 250 ms after stimulus onset, the "decision" about the perceptual outcome has taken place. Thus all signatures at 250 ms and later must be of secondary order and subsequent to the reversal process, and the underlying processes must be very similar if not identical for the two types of stimuli. Their detailed functional roles have to be discovered in future experiments.

IS IT VALID TO ANALYZE COMPONENTS FROM DIFFERENCE TRACES?

Amplitude modulations in an ERP difference trace can result from a modulation in strength of components before subtraction or they are simple artifacts from differential latency shifts of the underlying components in the two conditions. A combination of both is also possible. **Figures 5A** and **6** show roughly equal latencies of our raw ERP traces (before subtraction) across reversal and stability conditions for each of the two stimulus types. Analyzing the dERPs thus seems to be valid.

Any EEG deflection, however, is a spatial summation of an unknown number of differing generators. A component of a difference trace can thus result from a complex and differential interplay of different underlying generators in the two conditions. Britz and Pitts (2011) thus additionally compared current density maps and source images of raw ERPs and of dERPs. Further they identified clusters of brain microstates (Lehmann and Skrandies, 1980; Michel et al., 2004) with temporally stable global field power (spatial SD of the potential field) and compared them between the reversal, stability and difference traces. In summary they found converging evidence that all the reversal-related signatures reported above result from strength-based modulations of stimulus-related neural generators. This qualifies the stability condition as a valid control and further validates the analysis of the signatures from the difference traces.

ARE PERCEPTUAL REVERSALS DURING DISCONTINUOUS STIMULUS PRESENTATION A GOOD MODEL FOR THE CONTINUOUS CASE?

The gain in temporal resolution of the endogenous reversal process, allowing a high temporal resolution of ERP components, comes at the cost of the periodical interruption of the stimulus presentation. Noest et al. (2007) recently discussed extensively whether the basic mechanisms of reversals induced by these interruptions resemble or differ from the reversal mechanism during continuous observation. They distinguished between "percept switch" events during continuous presentation and "percept choice" events during discontinuous presentation of an ambiguous figure and present a model for the latter. A percept choice was considered as a kind of perceptual decision about the representation of an ambiguous stimulus appearing (and then disappearing) on a blank screen. The underlying mechanisms were assumed to differ from those of percept switch mechanisms, i.e., reversals during continuous observation of an ambiguous figure.

According to Noest et al. (2007), all findings with the Onset Paradigm belong to the latter reversal type. It is not entirely clear, however, how and when exactly (at which ISI) the transition between percept choice and percept switch takes place. Based on the following theoretical and empirical arguments, including the data presented above, we argue that reversals during interrupted stimulation with short ISIs (e.g., <400 ms) may still belong to the percept switch events and that the above-presented results from the Onset Paradigm may also apply to the continuous case.

1. The empirical data show a non-monotonic modulation of reversal rates mainly as a function of ISIs with a maximum around an ISI of 300 ms (Orbach et al., 1963, 1966; Kornmeier et al., 2002), an asymptotic decrease toward zero reversals for longer ISIs (e.g., Orbach et al., 1963; Orbach et al., 1966; Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003), and a smooth monotonic decrease of reversal rates toward the continuous case for shorter ISIs (Orbach et al., 1963, 1966; Kornmeier et al., 2002, 2007; see also **Figure 3**). This non-monotonic behavior of reversal rates provides evidence for the existence of two different processes and suggests an estimate of roughly 400 ms for the transition point. For shorter ISIs the underlying processes may be similar to the continuous case to which the observed reversal rates converge (switch events). For ISIs above 400 ms, perceptual reversals may be simply separate percepts (choice events). The recently proposed Necker-Zeno model of bistable perception (Atmanspacher et al., 2004, 2008) lends additional, theoretical support to this view. It successfully models the non-monotonic behavior of reversal rates with discontinuous stimulus presentations and predicts a simple relation between three basic time scales in cognitive neuroscience. ISIs of 300 ms and longer can be identified with one of these time scales, while for ISIs smaller than 300 ms this is not the case. A most recent summary of the results obtained with the Necker-Zeno Model can be found in Atmanspacher and Filk (2010).
2. The RP, as a dERP component specifically related to endogenous reversals, has been reported so far in several studies with discontinuous presentation of ambiguous figures using small ISIs: from 14 to 390 ms in Kornmeier et al. (2007), and even 600 ms in Britz et al. (2009)[2]. It is invariant in amplitude and

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[2] Psychophysical data collected with the Necker cube indicate a transition point between switch reversals and choice reversals at ISIs between 300 and 400 ms (Orbach et al., 1963). Kornmeier et al. (2007) presented a more complex Necker lattice, composed of nine simple cubes, and found a rising reversal rate together with a unchanged RP in a ISI-range between 10 and 400 ms. Britz et al. (2009), presenting a lattice composed of four Necker cubes, identified the RP even with an ISI of 600 ms, which indicates a discrepancy between a physiological and a psychophysical estimate of the transition point. Results from Kornmeier et al. (2002) however indicate that the transition point in the case of more complex Necker lattices are at larger ISIs compared to the simple Necker cubes.

latency within an ISI-range at least up to 400 ms (Kornmeier et al., 2007). Interestingly, O'Donnell et al. (1988), presenting their Necker cubes discontinuously with ISIs as long as 3300 ms, did not find a RP. We would agree with Noest et al. (2007) that, given such long ISIs, they observed perceptual choices rather than perceptual switches.

3. A typical eye-blink roughly lasts 200 ms, occurs every 4 s on average (e.g., Caffier et al., 2003) and interrupts continuous stimulus presentation. Thus even the continuous case (perceptual switch event) is full of short perceptual interruptions.

In summary, it seems appropriate to systematically distinguish between percept choice and percept switch events. However, both empirical and theoretical arguments indicate that the mechanisms underlying perceptual reversals during discontinuous stimulus presentations with short ISIs are very similar – if not identical – as during continuous observation. We thus expect that the RP as the earliest ERP correlate of perceptual reversals during discontinuous presentation of ambiguous figures would also be identified in the continuous case if the necessary temporal resolution were available. The exact transition point between percept switch and percept choice events may depend on the type of ambiguous stimulus used.

SUMMARY AND PREDICTIONS

The Onset Paradigm successfully synchronizes endogenous perceptual reversals of ambiguous figures with stimulus onset with a precision of about ±30 ms. It provides a series of EEG signatures related to endogenous reversals which is very similar to a series of EEG signatures related to exogenously induced reversals of unambiguous stimulus variants with three exceptions:

(1) An occipital RP 130 ms after stimulus onset and (2) a left-hemispheric occipital to frontopolar decrease in alpha-band activity, starting at the same time and lasting for about 60 ms, are restricted to endogenous reversals of ambiguous figures. (3) All subsequent signatures are delayed with endogenous compared to exogenously induced reversals.

The smallest delay lasts roughly 40 ms and is visible in the earliest component occurring with both types of reversals, the occipital/parietal RN, starting at 260 ms with endogenous reversals and at 220 ms with exogenously induced reversals.

We speculate as follows: The RP is a marker of a decision conflict arising with ambiguity at a certain stimulus-specific perceptual processing step. The concurrent alpha-band decrease may reflect two loops of recurrent activity in order to resolve the ambiguity within at most 60 ms.

The similarity of the subsequent EEG components indicates that after a certain step perceptual processing of endogenous reversals and exogenously induced reversals are very similar if not identical. The earliest and shortest temporal delay between EEG components to endogenous and exogenously induced reversals is in the same time range as the duration of the alpha-band decrease and thus provides a good estimation of 40–60 ms endogenous disambiguation time (Kornmeier and Bach, 2006). Disambiguation is completed at the latest 250 ms after stimulus onset.

Table 1 provides an overview of all here discussed EEG signatures found with perceptual reversals of ambiguous and unambiguous figures, their latencies, their locations and the stimuli used to induce them. Interestingly, Lumer et al. (1998) reported frontal and parietal fMRI activation during perceptual reversals of binocular rivalry stimuli. Further, Sterzer and Kleinschmidt (2007) found overlapping parietal and frontal brain structures with higher fMRI BOLD activity during endogenous reversals of the SAM stimulus and exogenously induced reversals of a disambiguated SAM version compared to related control conditions. This is in line with several fMRI studies report about a parietal–frontal network being activated during spontaneous perceptual reversals of ambiguous figures and binocular rivalry stimuli (Sterzer et al., 2009 for a review). Due to the much coarser temporal resolution of BOLD responses it is difficult to discern between primary processes directly related to the reversal event and secondary processes after the perceptual decision has taken place. Keeping this in mind, it may well be possible that the parietal and frontal fMRI activity may be related to the RN and the Parietal and Frontopolar Positivities, discussed above. According to our reasoning at least the latter three signatures are of secondary nature. A recent review discussing correlates of conscious perception indicates that perception related neural activity after 200 ms reflects the "ignition" of a large-scale prefronto-parietal network, necessary for conscious perception and that the P3b ERP component is a relevant part of the related neural activity (Dehaene and Changeux, 2011). The Parietal and Frontopolar Positivies are broad and temporally overlapping ERP occurring in the same time range as reported for the P3b. They are thus good candidates to reflect the recurrent activity of this network.

FOCUSING THE BOTTOM-UP VS. TOP-DOWN CONTROVERSY WITH EEG

The present results suggests as optimal starting point to probe the influence of bottom-up and top-down factors on the EEG in a critical time window (temporal ROI) between stimulus onset and the RN at 250 ms.

EEG CORRELATES OF TOP-DOWN INFLUENCE

One of the strongest top-down factor influencing the reversal dynamics of ambiguous figures is volitional control: Although perceptual reversals cannot be totally prevented, the rate of perceptual reversals can be doubled with the instruction to alternate the percept as fast as possible, and it can be halved by the instruction to prevent reversals (e.g., Liebert and Burk, 1985; van Ee et al., 2005; Kornmeier et al., 2009). To our knowledge only three EEG studies on volitional control about ambiguous figures perception have been conducted so far, two of them already published: Mathes et al. (2006) used the Manual Response Paradigm with the Necker cube and found increase in both a slow positive component (labeled as increase in delta band activity and probably identical to our Parietal Positivity) and in gamma-band power when participants tried to volitionally prevent reversals compared to trials when they tried to volitionally induce them. While the slow positivity is clearly outside our ROI before 250 ms, it is not possible to decide this

Table 1 | EEG correlates of endogenous and exogenously induced (parentheses) perceptual reversals and their temporal occurrences with reference to stimulus onset (onset paradigm) or to reaction times (manual response paradigm).

	Peak latency (ms)		Location	Stimuli
	Stimulus onset = 0	**Reaction time = 0**		
Reversal positivity (RP)	**130**[1–6]	−470	Occipital electrodes[1–3] Primary visual areas[6]	Necker cube[2], Necker lattice[1, 3], old/young woman[4], vase/face stimulus[5], Schroeders staircase[5], Binocular rivalry stimuli[6]
Alpha-power decrease (≈10 Hz)	−400 to +600 (−1400–+600)	−**1000** to **0**[8, 10, 20] **(−2000–0)**[8]	Parietally distributed[8]	Necker lattice[7], Necker cube[10, 19], SAM[8]
	130–200[7]	−470 to −400	Left-hemispheric, from occipital to frontopolar electrodes[7]	
Reversal negativity (RN)	**260**[1–6, 11–14] **(220)**[1, 11, 12, 14]	−340 (−380)	Occipital and parietal electrodes[1, 11–13] Lateral occipital and inferior temporal areas[6, 9]	Necker lattice[1, 3, 7, 12–14], Necker cube[9], face/vase[5], old/young woman[4], Schröder staircase[5], Binocular rivalry stimuli[6]
Late (incl. parietal and frontopolar) positivity	**340**[1, 4, 11–13] **(300)**[1, 11, 12]	−260 (−300)	Frontopolar electrode[1, 4, 12, 13]	Necker cube[9, 16–18], Necker lattice[7], old/young woman[4], SAM[8, 15], Binocular rivalry stimuli[6]
	470[1, 3, 4, 11–15] **(400)**[1, 11, 12, 15]	−130 (−200)	Parietal electrodes[1, 4, 12–14], inferior temporal, and superior parietal regions[9]	
	350	−**250**[8, 16–18]	Right parietal electrodes[15–18, 20]	
Beta power increase (14–26 Hz)	**340 (180)**[7]	−260 (−420)	Parietal and central electrodes[7]	Necker lattice[7]
Gamma power increase (≈30–70 Hz)	−400 to +600	−**1000** to **–0**[16, 17, 20, 21]	Right frontal electrode[20]	SAM[20, 21], Necker cube[16, 17], Necker lattice[7]
	−**200**[7]	−800	Right parietal/central electrodes[7]	
	300 (150)[7]	−300 (−450)	Left-central electrodes[7]	
Global field power effects	−**50**[3] −**300**[24]	−650 −900	Right inferior parietal lobe[3, 22]	Necker lattice[3], SAM[24], Binocular rivalry stimuli[22]

Bold indicates raw values, regular type indicates values are translated by a 600-ms reaction time[2, 8, 12].

[1] Kornmeier and Bach (2005), [2] Kornmeier et al. (2011), [3] Britz et al. (2009), [4] Kornmeier and Bach (2004a), [5] Pitts et al. (2007), [6] Britz and Pitts (2011), [7] Ehm et al. (2011), [8] Strüber and Herrmann (2002), [9] Pitts et al. (2009), [10] İşoğlu-Alkaç (2000), [11] Kornmeier et al. (2001), [12] Kornmeier and Bach (2004b), [13] Kornmeier et al. (2007), [14] Pitts et al. (2008), [15] Intaite et al. (2010), [16] Basar-Eroglu et al. (1993), [17] Strüber et al. (2001), [18] Mathes et al. (2006), [19] O'Donnell et al. (1988), [20] İşoğlu-Alkaç and Struber (2006), [21] Basar-Eroglu et al. (1996), [22] Strüber et al. (2000), [23] Britz et al. (2010), [24] Muller et al. (2005).

for the gamma modulation, occurring in a time window 500 ms before the late positivity peaks.

Pitts et al. (2008) used the Onset Paradigm with the Necker lattice and found an increased RN with a perceptual reversal when participants were instructed to reverse as often as possible compared to a passive viewing condition without volitional effort. No effects were found in the ROI before 250 ms.

In an EEG study from our lab with a slightly different variant of the Onset Paradigm (so far only published as diploma thesis, Hein, 2006) we found central and left temporal ERP components 370 ms after stimulus onset, which differed between an instruction to reverse condition and a passive condition as well as between the instruction to reverse condition and an instruction to prevent reversals condition. Again no effects were found in the ROI before 250 ms.

In summary, participants could successfully modulate their reversal rates if instructed to do so, but no EEG effects related to volitional control were found in the critical time window between stimulus onset and the RN at 250 ms.

EEG CORRELATES OF BOTTOM-UP INFLUENCE

Presentation mode is regarded as a bottom-up factor (Long and Toppino, 2004) strongly modulating the reversal dynamics of both, ambiguous figures and binocular rivalry stimuli (e.g., Orbach et al., 1963; Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003; Kanai et al., 2005, Noest et al., 2007; see **Figure 3**). The reversal rates of different ambiguous figures and also binocular rivalry stimuli can more than double or even brought to stand still as a function of ISI with discontinuous stimulus presentation (Orbach et al., 1963; Kornmeier et al., 2002; Leopold et al., 2002; Maier et al., 2003; Klink et al., 2008). In an EEG study with the Necker lattice we looked for modulations in the first 250 ms after onset as a function of ISI. All EEG modulations we found, however, occurred at and after 250 ms, no modulation within the critical ISI could be observed (Kornmeier et al., 2007).

SUMMARY

Neither the top-down factors nor the bottom-up factors tested so far, significantly modulated EEG data within the critical time window between stimulus onset and the occurrence of the RN at 250 ms. This raises some doubts about the expected importance of this time period for the perceptual reversal process and about our above interpretations of the EEG literature on multistable perception. However, maybe our interpretations are correct but our predictions concerning expected bottom-up and top-down modulations were wrong.

PROPOSAL OF AN INTEGRATIVE THEORY

In the following, we present a new perspective that can nicely integrate our and previous bottom-up and top-down results. It assumes two separate processes underlying spontaneous perceptual reversals, *destabilization* and *restabilization/disambiguation*, working on different time scales (seconds and milliseconds).

The following thoughts are based on accumulating evidence from psychophysical, EEG, and fMRI studies. All the so far used methods have advantages and limitations and none of the techniques allow a complete view on the processes at work during spontaneous perceptual alternations. It may thus well be possible that highly relevant neural activity is restricted to a small number of neurons and neither detectable with EEG nor with fMRI methods. The absence of detectable signatures in a specific paradigm can thus mean that no activity is present or that such activity is not measurable with the methods at hand. Having this in mind, we regard the following as a working hypothesis, allowing us to develop predictions that may be tested in future experiments.

The terminology from non-linear dynamics provides a helpful framework to describe the mechanisms underlying spontaneous perceptual reversals of ambiguous figures (Haken, 1983; Atmanspacher, 1992; Kruse et al., 1996; Kornmeier et al., 2004; Braun and Mattia, 2010). Brain states are regarded as points in a hypothetical state space. Representations of objects, e.g., a 3D cube, are modeled as attractors and their depth as a measure of the current representation's stability. Physiologically, the form of the attractor may depend on the connectivity matrix of neurons within a relevant assembly but also on the quality of the visual input. If the state of the perceptual system is located within an attractor, the related neural assembly is "activated" and the percept is (consciously) perceived (e.g., Kornmeier et al., 2004). Let us look at two extreme cases: If the visual stimulus is completely unambiguous we have a single unique and deep attractor and thus a stable conscious experience of the represented object. In the case of an ambiguous figure, two (or even more) representations fit with the visual information and thus two (or more) perhaps shallower attractors are in close vicinity with a relatively low barrier in between. For the ambiguous Necker cube, the two 3D interpretations would correspond to the two attractors (**Figure 12**). A perceptual reversal occurs if the system escapes from one attractor and jumps into the alternative one. The main question addressed by the research of the last 200 years on ambiguous figures could be translated to "what is the mechanism underlying the spontaneous state change from one attractor to the other?"

We here regard it as conceptually fruitful to subdivide the reversal event into two steps:

DESTABILIZATION

The observation of an ambiguous figure typically leads to a transiently stable percept, which destabilizes over time. This destabilization is relatively slow and takes on average 5–6 s if a Necker cube is passively observed (Orbach et al., 1963; Kornmeier et al., 2009). However, destabilization times (also known as stability durations or dwell times) are highly variable within and across participants (e.g., Borsellino et al., 1972) and also differ between different types of ambiguous figures (e.g., Strüber and Stadler, 1999); most of the bottom-up and top-down literature on ambiguous figures describes the variables that alter destabilization time. Often, passive adaptation of low-level neurons is discussed as the mechanism underlying a slow destabilization (e.g., Orbach et al., 1963; Toppino and Long, 1987). This can be modeled as a slow depth reduction of the attractor in which the state is located. Spontaneous fluctuations (e.g., synaptic fluctuations, variations in neurotransmitter concentrations, etc.) or exogenously induced neural fluctuations (e.g., by blinks and/or eye movements, visual transients, like short interruptions (Orbach et al., 1963) of stimulus

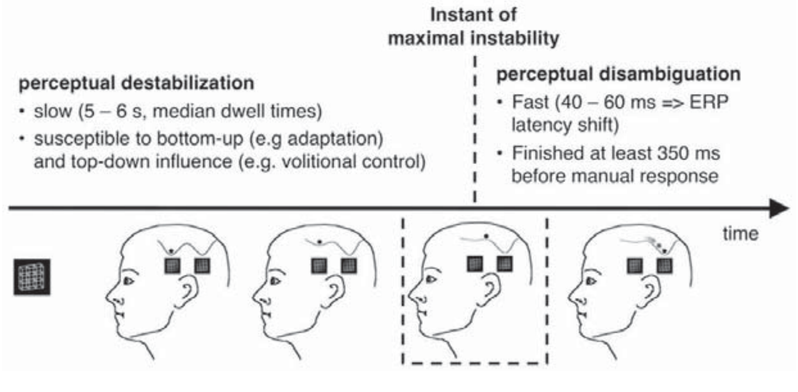

FIGURE 12 | Destabilization and disambiguation of ambiguous visual information. With prolonged observation of the ambiguous lattice stimulus a transiently stable percept gets destabilized slowly, symbolized as a depth reduction of the brain states current attractor. Both bottom-up and top-down factors can accelerate and decelerate this process. After transition of a state of maximal instability, fast (40–60 ms) disambiguation takes place, leading to a different stable percept. The brain state is now located in the alternative, deeper attractor.

presentation or light flashes (Kanai et al., 2005)) may also be relevant factors for a perceptual reversal and even more, the flatter the current attractor is. At least a part of the data from the Orbach group may thus be explained by an interaction between transients (fluctuations) and adaptation (influencing attractor depth). Moreno-Bote et al. (2007) recently provided a neurally plausible attractor model that assumes weak adaptation and noise underlying perceptual alternations. This model explains nicely several empirical findings like gamma distributed dwell times and more.

Effects of volitional control on reversal rates fit within the attractor model in the following way: The instruction to volitionally control the percept, typically given at the begin of an experimental block, may cause an *a priori* "top-down" change of depth of specific attractors in the sense of a global change of baseline activity or of a certain threshold, and thus prolong or shorten the destabilization time and increase or decrease the influence of fluctuations on the transition probability.

In summary a neural representation can be modeled as a brain state, located in an attractor within a state space. The depth of the attractor depends on the quality of the visual input (amongst others). The more ambiguous the input is, the shallower is the attractor, the more sensitive the representation is to spontaneous fluctuations and the more probable is a reversal between representations (attractors). It is reasonable to assume that in the case of ambiguous visual information the attractor, which is currently occupied, is initially shallow and slowly flattens over time. Different bottom-up (e.g., mode of stimulus presentation, Kanai et al., 2005) as well as top-down factors (like volitional control, Kornmeier et al., 2009) may be able to alter attractor depth and/or increase the noise level (Moreno-Bote et al., 2007) and thus influence the reversal dynamics, even simultaneously in an additive manner (Kornmeier et al., 2009). Bottom-up and top-down explanations are thus no longer mutually exclusive with this conception.

RESTABILIZATION/DISAMBIGUATION

Each reversal from one stable percept to another passes through a point of maximal instability when the perceptual state is on top of the barrier between the two related attractors (**Figure 12**).

The sensory information we receive is inherently incomplete and ambiguous. We have to disambiguate and interpret it in order to perceive it. Our perceptual system is optimized to disambiguate and interpret the visual information as fast as possible (e.g., we immediately perceive faces or objects in the formation of clouds in the sky or in the formation of country rocks). This indicates that due to evolutionary reasons our perceptual system tries to keep the inevitably instable brain states in between attractors as short as possible and thus to achieve a fast perceptual interpretation of whatever sensory information is available in order to be able to react immediately.

These considerations apply to ambiguous-figure perceptions in the following way: Leaving of an attractor (destabilization) and arriving at another attractor (disambiguation/restabilization) are different processes, working on different time scales (minutes and seconds vs. milliseconds): Given a brain state of maximal instability either at the onset of an ambiguous figure or as a result of the above described slow destabilization process during prolonged observation, our perceptual system tries to find as fast as possible a more stable state. The early RP dERP component and the Beta band deactivation may be related to the fast disambiguation of ambiguous visual input, taking place immediately after stimulus onset (within the Onset Paradigm) and being time-locked to it (±30 ms). Destabilization, on the other hand, may start immediately after the new percept has been established and is much slower. It can take from seconds to minutes and its dynamic can be changed in different ways and perhaps at different time points. Any EEG correlate of destabilization should thus occur before the onset of the stimulus that is perceived as reversed and it should indicate an upcoming reversal.

An EEG correlate of perceptual destabilization

Indeed, we recently found an increase in lower gamma-band activity (26–40 Hz) at the right-hemispheric central and parietal electrodes roughly 200 ms before onset of a Necker lattice that is perceived as reversed compared to a lattice that is perceived as stable (**Figures 9** and **10**, component U1) together with an occipital decrease of higher gamma-band activity (40–65 Hz; **Figures 9** and **10**, component U2). No such gamma modulations were observed with exogenously induced reversals of unambiguous lattice variants (Ehm et al., 2008, 2011). Britz et al. (2009) also used the Necker lattice with the Onset Paradigm. They compared dominant potential maps with temporally stable global field power (spatial SD of the potential field) and current source distributions for reversal and stability trials in a 50-ms pre-stimulus interval and also found significant differences in the right inferior parietal lobe. No unambiguous stimulus variants were used in their experiment.

A series of related studies underscore the importance of the above findings: Basar-Eroglu et al. (1996) reported a right anterior gamma power increase within 1000 ms before participants indicated an endogenous perceptual motion reversal of the SAM stimulus. We assume that their gamma modulation contains both, the pre-stimulus and post-stimulus gamma modulations indicated in our data (Ehm et al., 2011). Roeber et al. (2008) recently reported a right-hemispheric ERP correlate of perceptual reversals of binocular rivalrous sine wave gratings. Nakatani and van Leeuwen (2006) found EEG gamma-band synchronization between right-hemispheric parietal and right-hemispheric frontal electrode positions 800–600 ms before the manual indication of a Necker cube reversal. VanRullen et al. (2006) found higher gamma activity at right-hemispheric central locations with illusory motion direction reversals of the Wagon-Wheel Illusion compared to real motion reversals. Lumer et al. (1998) reported selective right-hemispheric BOLD (fMRI) activation during perceptual transitions of binocular rivalry stimuli, but no such activity with exogenous transitions of unambiguous stimulus variants. Sterzer and Kleinschmidt (2007) found increased fMRI response in the right inferior frontal cortex with endogenous motion reversals of the SAM stimulus compared to exogenously induced reversals of unambiguous SAM variants. Similarly, Ilg et al. (2008) found posterior right-hemispheric fMRI activity with spontaneous motion direction reversals of the spinning wheel illusion (Wertheimer, 1912), but no such activity with exogenously induced reversals. Müller et al. (2005) used the onset of the SAM stimulus immediately before a button press as the time reference for reversals of motion direction. They found changes in EEG activity about

300 ms before the reversal-related SAM flashes, i.e., temporally close to our pre-onset gamma modulation. Meenan and Miller (1994) reported about difficulties of patients with lesions in right frontal areas to recognize more than one interpretation of several ambiguous figures.

Further evidence for an important role of right-hemispheric areas comes from recent studies with transcranial magnetic stimulation (TMS). It was shown, that TMS stimulation of the parietal lobe can modulate dwell times of ambiguous structure-from-motion stimuli (Kanai et al., 2010, with bilateral stimulation) and binocular rivalrous moving gratings (Carmel et al., 2010; Kanai et al., 2011, with right-hemispheric stimulation). Stimulation of the posterior parts of the parietal lobe increased dwell times whereas stimulation of anterior parts decreased dwell times (Kanai et al., 2011). Zaretskaya et al. (2010) found during perceptual reversals of a rivalrous face/house stimulus a stronger BOLD response in the right intraparietal sulcus in nine participants and stronger BOLD response in the left intraparietal sulcus in 6 participants. TMS stimulation of the right intraparietal sulcus increased dwell times.

In summary, there is converging evidence that right-hemispheric brain areas play an important role during spontaneous perceptual reversals across stimulus types and categories (ambiguous figures and binocular rivalry stimuli) and experimental paradigms. More precisely, some studies, providing precise temporal information, indicate that this activity precedes perceptual reversals and may thus have predictive character, although this has to be demonstrated on a single trial level. Further, the reversal dynamics can be altered by right-hemispheric TMS stimulation. The spatial variability of the right-hemispheric signature across studies is so far unexplained.

So far we can only speculate about the function of this right-hemispheric pre-onset activity. A common feature across all stimulus types, stimulus categories, and paradigms is that perception changes spontaneously while the visual information stays unchanged. As a working hypothesis we suggest that the pre-onset gamma modulation indicates a transient brain state of maximal instability at the transition from one stable brain state to another or its recognition by some unconscious and so far unknown neural instance. Such an instable brain state in between two adjacent attractors is a necessary pre-condition for a perceptual reversal to occur and thus for a decision conflict preceding a reversal. Moments of instable brain states should thus be inherent in all types of perceptual reversal and related right-hemispheric modulations – perhaps in the EEG gamma band – should be observable. A sufficiently precise time reference for a reversal in the continuous case is necessary to test this

During continuous viewing of an ambiguous figure, state instability (or its recognition) and the subsequent decision conflict during (re)interpretation of the ambiguous visual information may be in close temporal vicinity. The short interruptions in the Onset Paradigm may act as a "temporal magnifier," slowing down the reversal process and thus temporally separating the two steps. According to these considerations a second working hypothesis, may thus be that the right-hemispheric central gamma modulation, which is pre-onset with the Onset Paradigm, may occur immediately before the occipital RP during a perceptual reversal of a continuously observed Necker cube. Again, a sufficiently precise time reference for a reversal in the continuous case is necessary to test this.

TWO (OF SEVERAL) MAJOR OPEN QUESTIONS IN THE CONTEXT OF MULTISTABLE PERCEPTION

WHAT DO NEURAL REPRESENTATIONS LOOK LIKE – AND WHY ARE THEY SOMETIMES UNSTABLE?

This is essentially the question about perceptual states and their destabilization over time with ambiguous visual input. One of the basic assumptions in the multistable perception literature is that each conscious interpretation of an ambiguous figure is based on the activity of a distinct neural assembly (e.g., Blake and Logothetis, 2002, for a review). Thus one central goal of the physiological studies of multistable perception was to find brain areas where neural activity fluctuates in correlation with the perceptual experience, in contrast to areas with unchanged neural activity, reflecting the unchanged visual input. Especially the border between sensory and percept-related activity was assumed to play a key role for the perceptual reversal process and consciousness in general (e.g., Blake and Logothetis, 2002).

Logothetis et al. (e.g., Logothetis, 1998; Leopold and Logothetis, 1999) recorded from primate single cells in different brain areas, while the animals reported their percepts of binocular rivalry stimuli. They found that the number of neurons with a percept-related firing pattern increased from V1 (striate cortex, 20%) over V2, V4, MT, medial superior temporal sulcus (MST, 80), the inferotemporal cortex (IT, 80%), and the superior temporal sulcus (STS, 80%; Logothetis, 1998; Leopold and Logothetis, 1999). A large number of V1 neurons remained active whether the stimulus was perceived or suppressed. Percept-related firing patterns were neither found in monocular V1 neurons (e.g., Leopold and Logothetis, 1999) nor in LGN neurons (Lehky and Maunsell, 1996). Several results from fMRI studies are in line with these single cell findings, indicating the importance of higher cortical areas for object representation. Tong et al. (1998) presented binocular rivalry stimuli containing the picture of a house and of a face and found reciprocal modulations in BOLD activity in the parahippocampal place area and the fusiform face area highly correlating with participants' reports of seeing a face or a house. Interestingly, this level of modulation was comparable to that with binocular house and face perceptions (non-rivalrous conditions). Similarly, Andrews et al. (2002) presented Rubin's ambiguous Face/Vase stimulus and found slightly increased BOLD activity in the fusiform face area during the perception of the faces compared to trials with house percepts. Recently Watanabe et al. (2011) found in V1 strong fMRI BOLD effects of attention but none of dominance vs. suppression intervals of binocular rivalry stimuli.

Other studies point to the importance of lower-level areas for object representations: Dodd et al. (2001) reported correlation between single cell activity in primate area MT and the perceived motion direction of an ambiguous structure-from-motion stimulus. Further, fMRI studies provided evidence for percept-related activity in V1 (e.g., Tong and Engel, 2001) and in the LGN (Haynes et al., 2005) during humans' observation of binocular rivalry stimuli.

Today there are potential explanations for the inconsistency between single cell and fMRI findings: fMRI BOLD activity is (like EEG activity) more related to local field potentials than to neural spiking activity (Logothetis et al., 2001). Thus percept-related modulation in early visual areas, as shown with fMRI, should be reflected in local field potentials rather than in spike modulation. This has been demonstrated recently in primates (Wilke et al., 2006; Maier et al., 2008). Further, information may be coded by temporal synchronization of neural activity (i.e., temporal coding), rather than amplitude modulations. Fries et al. (1997) presented binocular rivalry stimuli to cats and found precept-related synchronization of neural gamma-band oscillations in V1. Like surface EEG, the MEG is believed to reflect synchronous spiking activity of a large number of cortical neurons. MEG studies on binocular rivalry showed correlations between activity over a wide range of sensors (from occipital to frontal lobes) and observers dominance and suppression reports, indicating the involvement of the entire cortex in conscious object representation (e.g., Tononi et al., 1998; Dehaene and Changeux, 2011).

In summary, there is no isolated cortical area selectively correlating with the participant's current percept. The locus of the attractor and its specific neural realization is so far not understood (e.g., Moreno-Bote et al., 2007). Rather, object representations seem to result from a complex, probably reciprocal interplay between early visual and several higher brain areas across the cortex. Further, most of the physiological correlates are transient in nature and so far it is unclear how the maintenance of a stable conscious percept is neuronally realized (Ehm et al., 2011). This however, has to be understood in order to understand the destabilization of a given representation in the case of ambiguous figures and its susceptibility to bottom-up and top-down factors. There is some experimental and theoretical evidence that neural activity is somewhat weaker with ambiguous or rivalrous stimuli compared to disambiguated variants (e.g., Leopold and Logothetis, 1999; Kornmeier and Bach, 2006; Moreno-Bote et al., 2007; Pitts et al., 2010). This may indicate that the activated attractors are in general flatter and thus more susceptible to any type of fluctuation the more ambiguous the visual information is. In a recent study we analyzed this systematically with ambiguous figures from different categories: Slight low-level figural changes of an ambiguous figure disambiguate it and produce more sustained stable percepts. We found dramatic ERP differences between ambiguous figures and their disambiguated variants, independent of the reversal dynamics and across different types of figures (Necker cube, Old/Young Woman and SAM stimulus, as latest – unpublished-results from our lap indicate). This difference might (directly or indirectly) reflect the difference in depth of the respective attractors (Kornmeier and Bach, 2009).

WHO DECIDES ON THE PERCEPTUAL RESULT IF THE VISUAL INPUT IS AMBIGUOUS?

This is essentially the question about perceptual transitions. A large number of psychophysical studies about ambiguous figures aimed to find or understand "the one mechanism" that underlies spontaneous perceptual reversals – they looked for the deciding instance or mechanism. The major difference between bottom-up and top-down explanations thus pertains to the question whether this process is located at lower visual or at high-level cognitive processing units (e.g., Long and Toppino, 2004).

We suggest the reversal process can be subdivided into two separate steps, which need to be understood:

(1) How the current brain state gets out of its attractor and on top of the barrier in between this one and the alternative attractor. (2) How the "decision" takes place about whether the instable brain state returns to the old or the alternative attractor or perhaps whether it approaches another, so far less probable attractor.

Both steps depend on several factors like the energy distribution of the state space at this specific moment and thus the depth of the currently activated and the alternate attractors and the amount of energy fluctuations within the system (endogenous and/or exogenously introduced neural noise or background activity). Recent empirical evidence indicates that these factors depend at least in part on the perceptual history (on different time scales; e.g., Hesselmann et al., 2008; Pastukhov and Braun, 2008). Influence may be exerted at different steps and levels of complexity during visual perception (Blake and Logothetis, 2002; Kornmeier and Bach, 2006; Sterzer and Rees, 2008; Bartels and Logothetis, 2010), which is in line with the distributed object representation account discussed above. Nakatani and van Leeuwen (2006), e.g., provided evidence for different types of reversal of a Necker cube within and between participants, reflected by different patterns of synchrony in EEG oscillations. Blake and Logothetis (2002) summarized related evidence from the binocular rivalry literature and Bartels and Logothetis (2010) found recently with binocular rivalry stimuli, that perceptual reversals can be triggered at different levels of complexity during the perceptual process.

In summary, there is probably no unique neural switch area or "unique gate to conscious perception" within the brain that governs perceptual reversals. However, the EEG findings discussed above indeed indicate some generality aspects across types of reversals, types of stimuli (e.g., Necker cube or old/young woman) and even across categories (ambiguous figures and binocular rivalry stimuli). First, each endogenous perceptual reversal comes with a transient state of instability at the barrier between the two alternative attractors (**Figure 11**). The generality of the pre-reversal right-hemispheric activity (e.g., Britz et al., 2009; Britz et al., 2010; Ehm et al., 2011) may classify this modulation as a good candidate reflecting this instable brain state or its detection. What this would mean in terms of neural processing, however, is so far unclear. More research has to be done in order to determine more attributes of this right-hemispheric activity modulation in detail.

Second, a general finding across stimulus types (Necker cube, Old/Young woman) and categories (ambiguous figures and binocular rivalry stimuli) is the early occipital RP. It may be possible that after some central instance (perhaps general across types of reversals) has notified an instable perceptual brain state (reflected in the right-hemispheric activity modulation, described above), the "decision" about the perceptual outcome needs one (or two) top-down reactivation(s) of early visual areas for reinterpretation of the available visual information. It may also be possible that the surface EEG can only detect the strong activity of the "low-level receiver" (i.e., the RP) but not the potentially weaker activity of the "higher-level sender," wherever in the brain it may be located. This is highly speculative and further experiments are necessary, e.g., to describe the attributes of the RP in more detail. A step in this direction has been done recently by demonstrating the RP's independence of stimulus size (Kornmeier et al., 2011) and stimulus complexity (cubes or lattices Kornmeier and Bach, 2003).

SUMMARY AND CONCLUSION

Applying the Onset Paradigm to investigate spontaneous perceptual reversals of both ambiguous figures and binocular rivalry stimuli sizably improved the temporal resolution of the underlying processes. Since its first application several independent lines of evidence encouraged us to propose that spontaneous perceptual reversals are governed by two independent processes working on different time scales: (1) The transiently stable perceptual interpretation of the ambiguous information destabilizes over time until the perceptual system reaches a state of maximal instability. This destabilization is slow in the order of seconds to minutes and subject to multiple endogenous and exogenous influences. The result of this destabilization, a perceptual brain state of maximal instability seems to be correlated with a right-hemispheric modulation in EEG activity which occurs pre-onset in the case of discontinuous stimulus presentation. (2) Due to evolutionary pressure our brain is optimized to keep unavoidably instable brain states as brief as possible. Electrophysiological evidence indicates that the transition from maximal instability to a (potentially altered) stable brain state is very fast, in the order of 40–60 ms, and not susceptible to endogenous or exogenous manipulations. EEG data further indicates that perceptual processes within 350 ms before the manual indication of a perceptual reversal are post-decision and thus of secondary nature with respect to the reversal process. The (unconscious) decision about the perceptual outcome thus seems to be rather early.

Numerous psychophysical and physiological evidence indicates that neural representations are not restricted to circumscribed brain regions but involve almost the entire cortex. A clear border between sensory and perceptual processing is thus difficult to find and may depend on experimental and stimulus details.

The available evidence further suggests that, in contrary to previous expectations, no circumscribed neural unit exists that decides about the perceptual outcome. Rather, perceptual reversals can be induced at different locations and levels of complexity along the processing of visual information.

Recent evidence from our lab suggests the existence of a central evaluation instance that estimates the reliability of the perceptual outcome, given a certain quality of visual information. The outcome of this evaluation thus may indirectly reflect the depth of the activated attractor (e.g., Kornmeier and Bach, 2009; Hassberg, 2010). Understanding the mechanisms of such reliability estimation may be highly relevant for a better understanding of psychiatric perception disorders and ambiguous figure may be an interesting tool for this.

Ambiguous figure perception is an ideal model to investigate changes of brain states between already existing attractors in other domains. Already the Gestalt Psychologists regarded this phenomenon as interesting for the understanding of insight phenomena (Knoblich and Öllinger, 2006), where probably a transition from an existing attractor to an instantaneous newly built attractor takes place. Most interesting in this respect may be the transient states of maximal instability on top of the barrier between two attractors ("acategorial states," Feil and Atmanspacher, 2010). Thus ambiguous figure perception may also be an interesting tool for future research in insight processes. The gain in temporal resolution attained with the Onset Paradigm provided specific electrophysiological marker of critical processing steps underlying spontaneous perceptual reversals of ambiguous figures. The speculations above about their functional role encourage precise experimental hypotheses that may be tested in future experiments.

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Unmixing binocular signals

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Incompatible images presented to the two eyes lead to perceptual oscillations in which one image at a time is visible. Early models portrayed this binocular rivalry as involving reciprocal inhibition between monocular representations of images, occurring at an early visual stage prior to binocular mixing. However, psychophysical experiments found conditions where rivalry could also occur at a higher, more abstract level of representation. In those cases, the rivalry was between image representations dissociated from eye-of-origin information, rather than between monocular representations from the two eyes. Moreover, neurophysiological recordings found the strongest rivalry correlate in inferotemporal cortex, a high-level, predominantly binocular visual area involved in object recognition, rather than early visual structures. An unresolved issue is how can the separate identities of the two images be maintained after binocular mixing in order for rivalry to be possible at higher levels? Here we demonstrate that after the two images are mixed, they can be unmixed at any subsequent stage using a physiologically plausible non-linear signal-processing algorithm, non-negative matrix factorization, previously proposed for parsing object parts during object recognition. The possibility that unmixed left and right images can be regenerated at late stages within the visual system provides a mechanism for creating various binocular representations and interactions *de novo* in different cortical areas for different purposes, rather than inheriting then from early areas. This is a clear example how non-linear algorithms can lead to highly non-intuitive behavior in neural information processing.

Keywords: binocular rivalry, blind source separation, non-linear dynamical systems, non-negative matrix factorization, independent component analysis

When incompatible images are presented to the two eyes, the visual system is thrown into oscillations. First one image is visible and then the other, typically alternating with a period of a couple of seconds. This is known as binocular rivalry. A commonly used rivalrous stimulus is a pair of orthogonal gratings, one grating presented to each eye. However, non-matching stimuli in general will work, such as a face and a house. Seminal psychophysical work on rivalry was done by Levelt (1965), who studied how the time course of the oscillations depended on the nature of the stimuli. In recent years the study of rivalry has expanded from psychophysics to neurophysiology and functional MRI (fMRI) brain imaging, as described in various reviews (Leopold and Logothetis, 1999; Blake and Logothetis, 2002; Lee, 2004; Tong et al., 2006; Sterzer et al., 2009).

Early models portrayed binocular rivalry as involving reciprocal inhibition between monocular representations of the two images, occurring at an early visual stage prior to binocular mixing (Lehky, 1988; Blake, 1989). (See Wilson, 2007, for a more recent and elaborate version of this idea.) Low-level monocular representations postulated by such models would make the striate cortex or the lateral geniculate nucleus likely locations for rivalry.

However, psychophysical experiments found conditions where rivalry appeared to occur at a higher, more abstract level of representation. In those cases, the rivalry was between image representations dissociated from eye-of-origin information, rather than directly between monocular signals from the two eyes. Evidence for this higher-level "image rivalry" came from two types of experiments. One involved studies in which two rivalrous images were physically switched back and forth rapidly between the two eyes, typically at a rate of around three times per second (Logothetis et al., 1996; Lee and Blake, 1999). For particular stimulus configurations under those conditions, the rivalrous percept oscillated much more slowly than the physical switching of the stimuli, at a rate of around 1 cycle every 2 s. That suggested the rivalry was between representations of the images divorced or abstracted from the direct monocular representations coming from each eye. The second type of experiment involved rivalrous stimuli that were patchworks synthesized from two incompatible images. For example, the left eye stimulus might be composed of randomly intermixed patches of image A and image B. The right eye image would then be a complementary patchwork, having a patch of the image B where the other eye had a patch of image A. Using those stimuli, the rivalrous percept was not of oscillations between the two patchworks. Rather, what occurred was rivalry between a coherent image A and a coherent image B, showing that the patches had been grouped before rivalry (Dörrenhaus, 1975; Kovács et al., 1996; Ngo et al., 2000). Again this indicated that rivalry was occurring at a more abstract level of image representation than direct monocular signals from the two eyes.

Neurophysiological recordings in monkeys corroborated the psychophysical finding that in some situations rivalry could involve higher-level image representations. The strongest neurophysiological correlate of rivalry was found in inferotemporal cortex (Sheinberg and Logothetis, 1997), a high-level, binocularly driven visual area involved in object recognition. In contrast early visual areas, where large populations of monocular neurons exist, showed modest rivalry effects. Weak correlates of rivalry were reported for single-cell recordings in striate cortex (Leopold and Logothetis, 1996), and no rivalry related activity was reported for single-cell recordings in lateral geniculate nucleus (Lehky and Maunsell, 1996; Wilke et al., 2009). FMRI studies, on the other hand produced somewhat different results from single-cell physiology, showing vigorous rivalry correlates in striate cortex (Polonsky et al., 2000; Tong and Engel, 2001; Lee et al., 2007) and to some extent in lateral geniculate nucleus as well (Haynes et al., 2005; Wunderlich et al., 2005).

Overall, examining the psychophysical, neurophysiological, and fMRI data, there is evidence for rivalry occurring at a wide range of levels within the visual system. Faced with this body of results, a new class of "hierarchical" binocular rivalry models was created (Wilson, 2003; Freeman, 2005). Earlier models had postulated reciprocal inhibition between monocular representations of images tied to signals from left and right eyes. Hierarchical models augmented that with an additional stage (or stages) involving inhibition between higher-level, binocular representations of images, where eye-of-origin was lost. That allowed "eye rivalry" to occur at lower levels of the visual system and "image rivalry" to occur at higher levels.

An unresolved issue in hierarchical models is how can the separate identities of the two images be maintained after binocular mixing in order for rivalry to be possible at higher levels? We suggest that a way for left and right images to retain their separate identities after binocular mixing is to simply unmix them. Recently a new class of non-linear signal-processing algorithms has been developed that has the potential to do that, called blind source separation (BSS) algorithms (Choi et al., 2005; Cichocki et al., 2009; Comon and Jutten, 2010). BSS algorithms separate signal mixtures into component "sources." The algorithms are called "blind" because they are given little or no information about the nature of the underlying source signals they are trying to recover. Because they are blind, they fall into the category of unsupervised learning algorithms.

From amongst the various BSS algorithms we focus on one, non-negative matrix factorization (NMF; Lee and Seung, 1999). The non-negativity constraint in NMF is appealing for applications in neural processing as firing rates must be non-negative. However the ability to do binocular unmixing is not unique to NMF, and we shall also demonstrate it using a second, unrelated BSS algorithm called independent component analysis (ICA). Matlab code for NMF was obtained from Hoyer (2011) and for ICA from Hyvarinen (2011). We believe that this is the first suggestion that BSS algorithms may be dynamically operating within the brain for real-time visual processing.

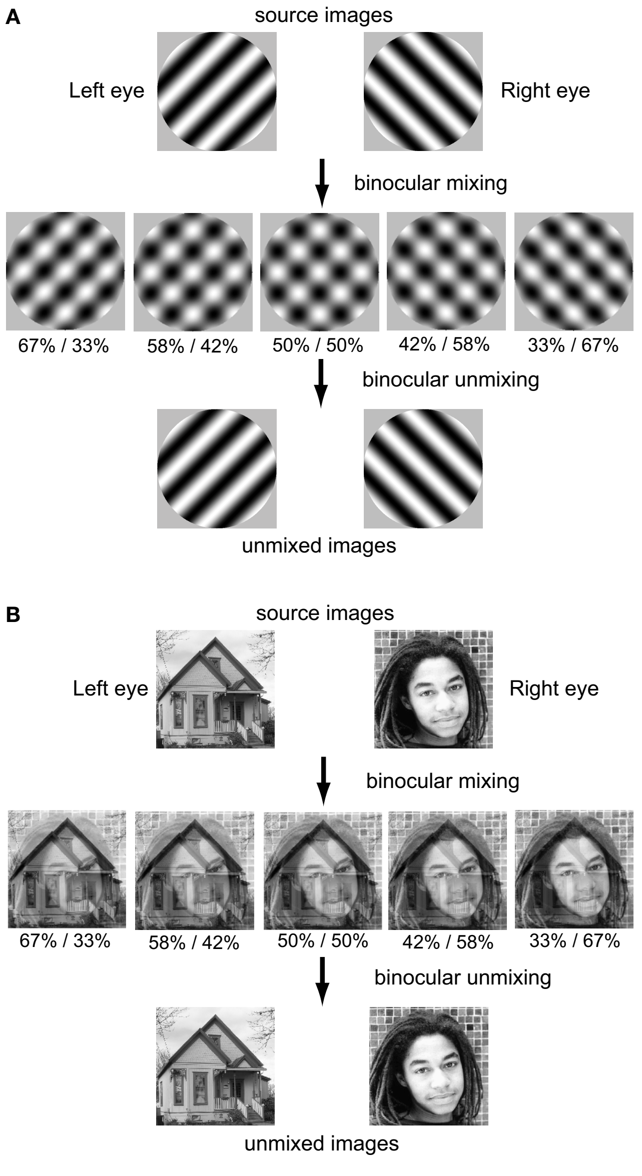

FIGURE 1 | Schematic of image mixing and unmixing process.

RESULTS

Two pairs of images were used to test the algorithms (**Figure 1**), a pair of orthogonal sinusoidal gratings and a face/house pair. Both stimulus classes are widely used in binocular rivalry studies. Each pair was linearly mixed in various proportions to form five mixed images. This variable mixing in the algorithm corresponds to physiological observations that binocular neurons in striate cortex of macaque monkey occur in various ocular dominance mixtures (Hubel and Wiesel, 1968). In the words of Hubel and Wiesel (1977), "Just why the two eyes should be brought together in this elaborate but incomplete way is not yet clear. What the ocular dominance columns appear to achieve is a partial mixing of influences from the two eyes, with all shades of ocular dominance throughout the entire binocular field of vision." Whatever the reason for this variable binocular mixing, it is precisely what is needed for BSS algorithms to work. The algorithms would not work if only a single binocular mixture were available. fMRI studies also show ocular dominance columns in humans (Cheng et al., 2001; Yacoub et al., 2007), suggesting variable binocular mixing may be similar in humans and macaque monkeys.

Variable ocular dominance also occurs in extrastriate visual cortex. Ocular dominances in extrastriate cortex are more narrowly spread than in striate cortex, as indicated by data from inferotemporal cortex (Uka et al., 2000) and area MT (Kiorpes et al., 1996). The unmixing results reported here were produced using left/right ocular dominance mixtures spread over the range 67%/33%–33%/67%, as shown in **Figure 1**. However, similar results were obtained using an even narrower spectrum of ocular dominances, going from 55/45 to 45%/55%, so it does not take a large range to allow the BSS algorithms to work. The variability of ocular dominances in extrastriate cortex appears sufficient to support the sort of binocular unmixing being proposed here.

The NMF algorithm was implemented in terms of matrix algebra (**Figure 2A**). The procedure was to factorize the binocular mixture matrix B into two matrices, $B = M \times A$, subject to the constraint M and A were non-negative. Each column in the binocular mixture matrix B corresponded to one mixed image (there

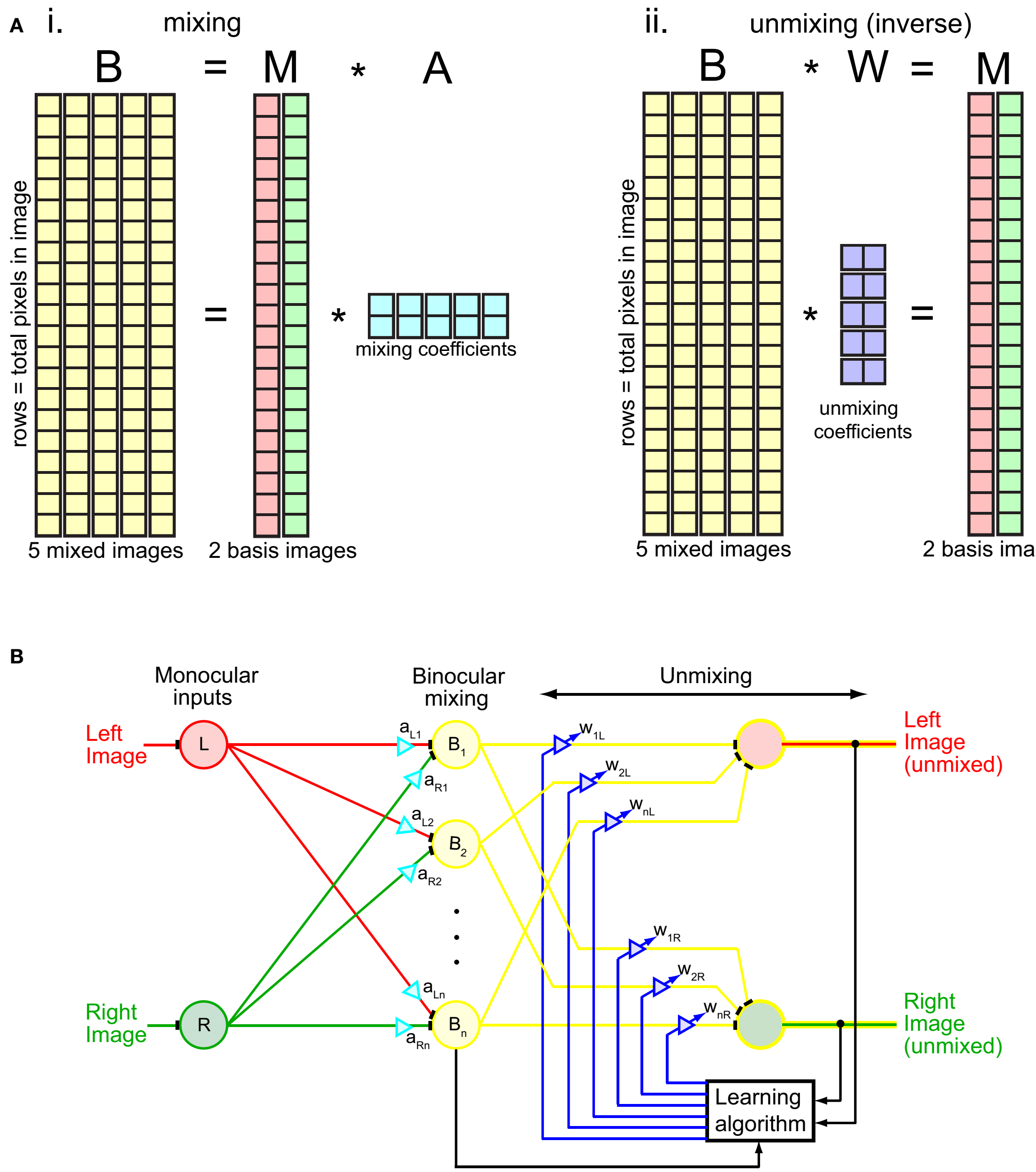

FIGURE 2 | Mechanics of the unmixing algorithm. (Ai) Matrix representation of binocular mixing. The binocular mixture matrix *B* had five columns, representing the five mixed images depicted in **Figure 1.** Each column had 40,000 rows, corresponding to 40,000 pixels in each image (200 × 200 pixels). Thus each image is "unfolded" from a 2D array to a 1D column of pixels. The binocular matrix *B* was factored into two non-negative matrices *M* and *A* such that $B = M \times A$. The factorization was done by iteratively updating *M* and *A* in accord with the NMF algorithm so as to gradually reduce error between *B* and $M \times A$, with error based on entropy divergence (Lee and Seung, 1999, 2001). The matrix *M* had two columns, containing left and right source images, and 40,000 rows. The matrix *A* contained mixing coefficients, which combined the two source images in *M* to form different binocular mixtures. Matrix *A* had five columns and two rows, corresponding to five pairs of mixing coefficients to produce five different binocular mixtures. **(Aii)** Matrix representation of binocular unmixing. The matrix *W* of unmixing coefficients is the Moore–Penrose generalized inverse of the mixing matrix *A*. **(B)** Neural network interpretation of the unmixing algorithm. Diagram adapted from Cichocki et al. (2009).

are five mixed images in this example). Each row corresponded to a different image pixel. Starting from random values of M and A, the algorithm iteratively updated their values so as to reduce error between $M \times A$ and B, following standard update rules for the algorithm using an error measure based on entropy divergence (Lee and Seung, 1999, 2001). (The error measure used is not critical for the algorithm.) Gradually the two images unmixed as $M \times A$ converged to B. The binocular mixture matrix B was now expressed in terms of the multiplication of M, a matrix containing the two unmixed monocular images, by A, a matrix containing mixing coefficients.

What we really want to solve, however, is the inverse problem to that described above. Rather than find the matrix A of mixing coefficients used to combine monocular images into binocular mixtures (**Figure 2Ai**), we want an unmixing matrix W that can decompose the binocular mixtures into component monocular images: $B \times W = M$ (**Figure 2Aii**). Fortunately there is a simple relationship between the mixing and unmixing matrices: they are inverses of each other: $W = A^{+}$. (In this case, because the mixing and unmixing matrices are not square, the Moore–Penrose generalized inverse A^{+} must be used rather than the regular matrix inverse A^{-1}). Although we applied the algorithm directly to image pixel values, the principle remains the same whether the numbers in matrices M and B represent pixel values or neural firing rates derived by convolving receptive fields with the image.

The unmixing algorithm can be given a more physiological interpretation by formulating it in terms of a neural network rather than matrix algebra (**Figure 2B**). The iterative nature of the algorithm is indicated by the feedback loop originating from the outputs. The gradual unmixing of the binocular signal as it cycles through the feedback loop may have a perceptual correlate in binocular rivalry. When orthogonal gratings are briefly flashed to the two eyes for less than 150 ms they appear mixed, in a checkerboard pattern (Wolfe, 1983). It is only after longer exposure that the mixture disappears and the image from one eye or the other starts to predominate.

Feedback was mathematically implemented here as discrete time updates on a set of matrices. It could equivalently be expressed within a network as a non-linear dynamical system operating in continuous time, expressed as a set of coupled differential equations. As the dynamical system evolves to a stable point (unmixed images at the output), it is not only neural activities that must change dynamically, but also the strengths of synaptic interactions. There is indeed evidence for rapid dynamic modulation of neural connectivity in a network (Vaadia et al., 1995), and rapid synaptic plasticity as a mechanism for implementing neural computations has been reviewed by Abbott and Regehr (2004).

Unmixing produced by the NMF algorithm was not perfect. There was residual crosstalk within the two unmixed images. This was apparent when an unmixed image was subtracted from the original source image (**Figure 3**). The crosstalk was small enough, however, that in most trials it was not apparent upon inspection of the unmixed images. However, in some trials (around 25% for the face/house pair), the NMF algorithm converged to a situation with visible crosstalk, possibly because lack of noise in the algorithm allowed it get stuck in a local error minimum. Details of the crosstalk pattern varied from trial to trial as the algorithm started from different random states.

In addition to NMF, we tried another BSS algorithm, ICA (Bell and Sejnowski, 1995; Hyvärinen and Oja, 2000; Stone, 2002). Instead of being constrained to finding non-negative factors of a matrix, this algorithm was constrained to find a set of unmixed images that were as statistically independent as possible from each other. FastICA (Hyvärinen and Oja, 2000) was the specific variant of the ICA algorithm used. ICA was able to unmix binocular images in a manner similar to NMF (compare **Figures 3Aii,B**). Unlike NMF, ICA never converged to produce visible crosstalk between unmixed images, although subliminal crosstalk remained. The ICA algorithm, on the other hand, did have the disadvantage that in 50% of unmixing trials the recovered images were contrast reversed, as ICA did not have a non-negativity constraint.

The NMF algorithm was able to unmix gratings with small orientation differences, down to the smallest difference tested of 1°. In contrast, the ICA algorithm had an increasing probability of finding an incorrect solution to the unmixing problem as the orientation difference dropped below 15°.

Although both BSS algorithms were capable of unmixing images, they differed in the details of their behavior. Presumably other BSS algorithms would each have their own mix of characteristics.

DISCUSSION

Binocular unmixing neatly solves the problem of how two images can retain their separate identities after binocular mixing, so that rivalry can occur between high-level binocular representations of incompatible images. Although unmixed images appear virtually identical to the original monocular images (**Figure 3**), they are binocularly driven (**Figure 2B**).

The ability of two unrelated algorithms, NMF and ICA, to unmix binocular signals suggests that there is a whole class of BSS algorithms having similar capabilities. This opens the opportunity for combined theoretical and experimental investigations to uncover the particular implementation that may be occurring biologically.

The binocular unmixing model does not consider how the oscillations of rivalry themselves are produced. The actual oscillations during rivalry would require further interactions between the two images after unmixing. Mechanisms to produce oscillations have already been extensively modeled (among them Lehky, 1988; Lumer, 1998; Laing and Chow, 2002; Wilson, 2003, 2007; Freeman, 2005; Grossberg et al., 2008; Gigante et al., 2009). Binocular unmixing augments those models of oscillations by creating conditions at higher visual levels that allow them to operate.

The binocular mixing model also does not consider mechanisms of perceptual grouping that occur under some rivalry conditions (Dörrenhaus, 1975; Kovács et al., 1996; Ngo et al., 2000). Grouping mechanisms in rivalry have received less theoretical attention than oscillatory mechanisms (although see Grossberg et al., 2008). Binocular unmixing again serves to create conditions at higher visual levels that would allow grouping algorithms to operate.

As signals pass through the unmixing circuitry, eye-of-origin labeling is lost in the recovered left and right images. There is no way to tell which image originated from the left eye and which

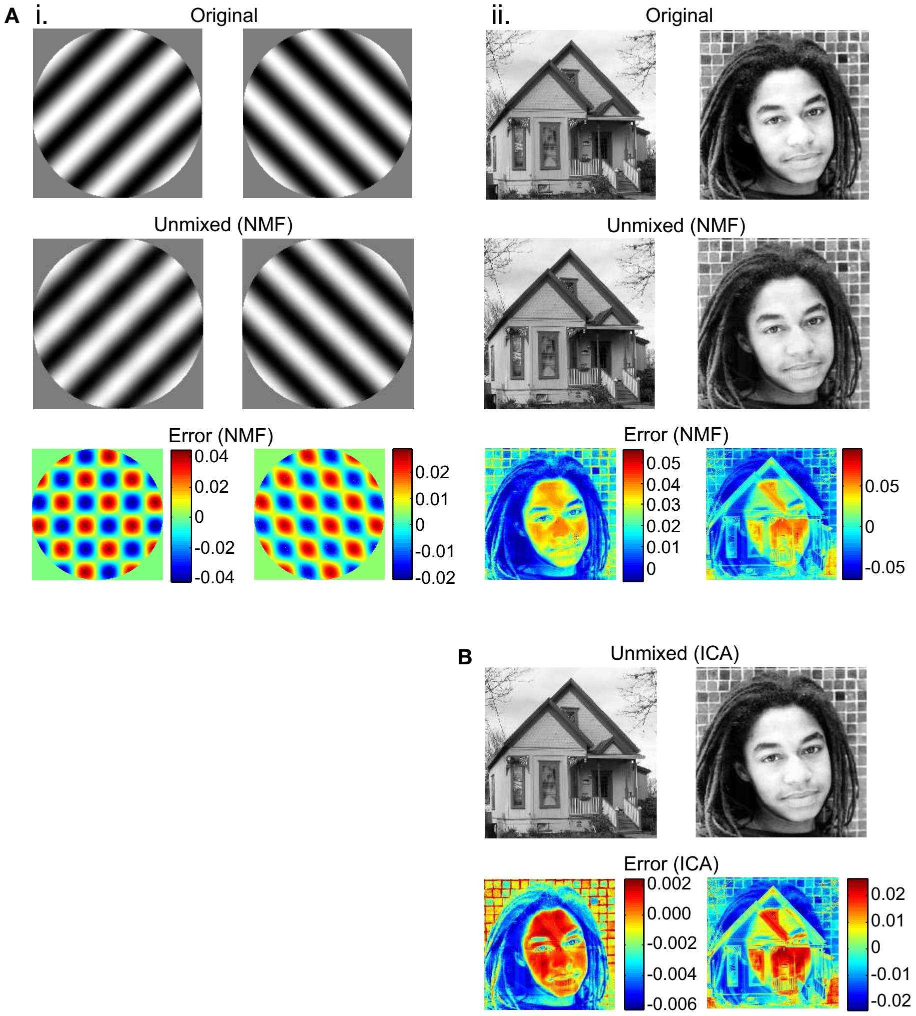

FIGURE 3 | Unmixing results and errors, for example runs of the NMF and ICA algorithms. Source images are shown, together with images recovered after the source images were binocularly mixed and then unmixed. Error indicates pixel subtraction (*original image*)–(*unmixed image*). Gray levels in source and unmixed images fell in the range 0.0–1.0. **(A)** Results for NMF unmixing algorithm. **(B)** Results for ICA unmixing algorithm.

originated from the right eye. This lose of eye-of-origin information is consistent with the psychophysical data outlined earlier, and is in fact a defining characteristic of high-level "image rivalry." The situation is different for stereopsis, where the preservation of disparity sign (near/far) indicates that eye-of-origin information is implicitly retained within the population of binocular cells. That was emphasized by Assee and Qian (2007) in a model of da Vinci stereopsis that extracted eye-of-origin information for occluded monocular regions using binocular cells. While the BSS algorithms used here lose eye-of-origin information, in the future it might be possible to devise binocular unmixing models that do retain such information, for applications other than rivalry.

We found a low level of crosstalk in the unmixed left and right images (**Figure 3**). Binocular crosstalk has not been a prediction of previous binocular models. In experimental observations under conditions of high-level "image rivalry," we would expect a strong level of crosstalk immediately following the initial presentation of rivalrous stimuli, with the crosstalk smoothly decaying over time to some non-zero value before the oscillations started. Subliminal crosstalk would remain during the oscillatory period.

Non-negative matrix factorization was introduced as a possible mechanism for parsing objects into parts for object recognition (Lee and Seung, 1999). We see that it may also be involved in binocular rivalry. At the single neuron level, neurophysiological correlates of binocular rivalry are strongest in inferotemporal cortex (Sheinberg and Logothetis, 1997), a ventral visual area associated with object recognition, and weaker in striate cortex (Leopold and Logothetis, 1996) or in the dorsal visual pathway (Logothetis and Schall, 1989). Although as a binocular phenomenon rivalry tends to be most associated with stereopsis, we suggest at higher levels it may also have connections with mechanisms of shape representation during object recognition.

Besides binocular rivalry in inferotemporal cortex, another example that might use binocular unmixing involves area MT, a cortical area believed to represent visual motion. There is evidence that area MT can support comparisons between velocities in left and right images for computation of 3D motion (Rokers et al., 2009, 2011), despite being binocularly driven. In this case, MT appears to be performing visual processing as if it had access to the original unmixed images.

Binocular unmixing thus raises the possibility that new binocular interactions between left and right images can be created in different cortical areas for different purposes, rather than being inherited from striate cortex.

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Awareness of central luminance edge is crucial for the Craik-O'Brien-Cornsweet effect

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The Craik-O'Brien-Cornsweet (COC) effect demonstrates that perceived lightness depends not only on the retinal input at corresponding visual areas but also on distal retinal inputs. In the COC effect, the central edge of an opposing pair of luminance gradients (COC edge) makes adjoining regions with identical luminance appear to be different. To investigate the underlying mechanisms of the effect, we examined whether the subjective awareness of the COC edge is necessary for the generation of the effect. We manipulated the visibility of the COC edge using visual backward masking and continuous flash suppression while monitoring subjective reports regarding online percepts and aftereffects of adaptation. Psychophysical results showed that the online percept of the COC effect nearly vanishes in conditions where the COC edge is rendered invisible. On the other hand, the results of adaptation experiments showed that the COC edge is still processed at the early stage even under the perceptual suppression. These results suggest that processing of the COC edge at the early stage is not sufficient for generating the COC effect, and that subjective awareness of the COC edge is necessary.

Keywords: Craik-O'Brien-Cornsweet effect, lightness perception, visual awareness, visual masking, binocular suppression, continuous flash suppression

INTRODUCTION

The perception of lightness is a fundamental aspect of vision, and it depends not only on the retinal input at the corresponding visual area but also on the distal retinal inputs (e.g., Gilchrist, 1977; Adelson, 1993). The Craik-O'Brien-Cornsweet (COC) effect (O'Brien, 1958; Craik, 1966; Cornsweet, 1970) has been studied to provide a clue as to the underlying mechanisms of lightness processing in the brain. In the COC effect, a central edge of an opposing pair of luminance gradients (COC edge) makes adjoining regions with identical luminance appear to be different. Recent brain imaging and physiological studies have shown that when the COC effect is observed, the early visual cortical areas, starting as early as the primary visual cortex (V1 or V2), are activated (e.g., Roe et al., 2005; Boyaci et al., 2007; Hung et al., 2007; for reviews von der Heydt et al., 2003; Komatsu, 2006). Furthermore, there is evidence suggesting that activity of higher cortical area, such as the lateral occipital (LO) sulcus, is correlated to the illusory lightness perception (Perna et al., 2005). On the other hand, regarding psychophysical studies, although it was suggested that the COC effect is influenced by higher-stage processing of planar surface attributes (Knill and Kersten, 1991), most of the studies have been performed only by modulating the physical features of the COC edge, such as luminance contrast, spatial frequency, and direction, which were assumed to be processed at the early stage of human visual system (Grossberg and Todorovic, 1988; Paradiso and Nakayama, 1991; Davey et al., 1998; Devinck et al., 2007; Perna and Morrone, 2007). Meanwhile involvement of subjective awareness, whose processing presumably includes the higher stages (for a review Rees et al., 2002), has not been studied directly. In this work, consequently, we examined whether the COC effect can be observed when subjective awareness of the COC edge is suppressed.

We used visual backward masking (BM; Breitmeyer and Ganz, 1976; Breitmeyer and Ogmen, 2000) and continuous flash suppression (CFS; Tsuchiya and Koch, 2005) to manipulate the visibility of the COC edge. In the BM experiment, the masking stimulus was presented immediately after the COC stimulus, which leads to failure to consciously perceive the corresponding area. The masking stimulus was presented in the area of the COC edge to selectively eliminate the visibility of the edge. In the CFS experiment, observer's visual percept was continuously suppressed by presenting a dynamic Mondrian stimulus and the COC stimulus to the dominant eye and the other eye, respectively. CFS could selectively render the COC edge invisible for a few 10 s in all trials. Our results demonstrate that the COC effect almost completely vanished in both conditions (BM and CFS) when the COC edge was invisible (The results in CFS experiment agree with the observation in Supplemental Data of Boyaci et al., 2007).

The BM and CFS experiments phenomenologically showed that when the subjective percept of the COC edge was suppressed, the lightness induction of the COC effect was not observed, but the visual processing associated with the subjective awareness is still unclear. If the neural processing at the early stage did not survive under BM and CFS conditions, loss of subjective awareness could not be regarded as the prime determinant of inhibition of lightness induction in those experiments. In the next experiment (adaptation experiment), we examined whether the COC edge was still processed at the early stage of the visual system, when the COC edge was rendered invisible. In the adaptation experiment, we examined the luminance aftereffect of the COC edge presented under the CFS condition, since the duration of perceptual suppression produced by the CFS enabled us to use the adaptation paradigm to assess the neural processing psychophysically. The results of adaptation experiments showed that the COC edge is still processed at the early stage even under the perceptual suppression of the COC edge. Together with the BM and CFS experiments, it can be suggested that the early-stage processing of the COC edge itself is not sufficient for generating the COC effect, and that subjective awareness of the COC edge is crucial.

MATERIALS AND METHODS

OBSERVERS

Five observers participated in all experiments, and the observers in each experiment included one or two of the authors. The rest of the observers were volunteers unaware of the purpose of the experiments. All observers had normal or corrected-to-normal vision. The dominant eye was determined for each observer by the Dolman method (Fink, 1938). Informed consent was obtained from the naïve participants before the experiment started. Recruitment of the participants and experimental procedures were conducted in accordance with the Declaration of Helsinki.

APPARATUS

Stimuli were generated with a PC/AT compatible personal computer using the Psychlops library (Maruya et al., 2010), and displayed on a 21-inch CRT monitor (TOTOKU Calix CDT2141A), with a refresh rate of 100 Hz. An 8-bit grayscale with gamma correction was provided by a video card (Aopen GeForce4Ti4200 with AGP8X). The observer viewed the monitor from a distance of 64 cm while sitting in a completely dark room with his/her head fixed on a chin rest. The spatial resolution of the monitor was 1280 × 1024 pixels, with each pixel subtending 1.6 arc minutes at the viewing distance of 64 cm. In the BM experiment, visual stimulus was presented at the center of the monitor, and the observers viewed the stimuli with two eyes. In the CFS and adaptation experiments, the display area of the monitor was horizontally divided into two areas and the observers viewed two stimuli presented in each area through a mirror stereoscope so that each eye could see its corresponding stimuli.

VISUAL STIMULI

Figure 1A shows the COC stimulus used in the BM and CFS experiments. The width and height of the stimulus were 9.4 and 5.3 arc degree, respectively. The size of the luminance gradient region was 2.4 × 5.3 arc degree. The observers compared the perceived lightness of left and right flanking regions. As shown in **Figure 1B**, the mean luminance of the flanking region was 24.0 cd/m^2. When the left and right flanking regions are physically equiluminant, they appear to be different in lightness due to the presence of the COC edge. The maximum and minimum luminances of the COC edge were 27.6 and 19.9 cd/m^2, respectively.

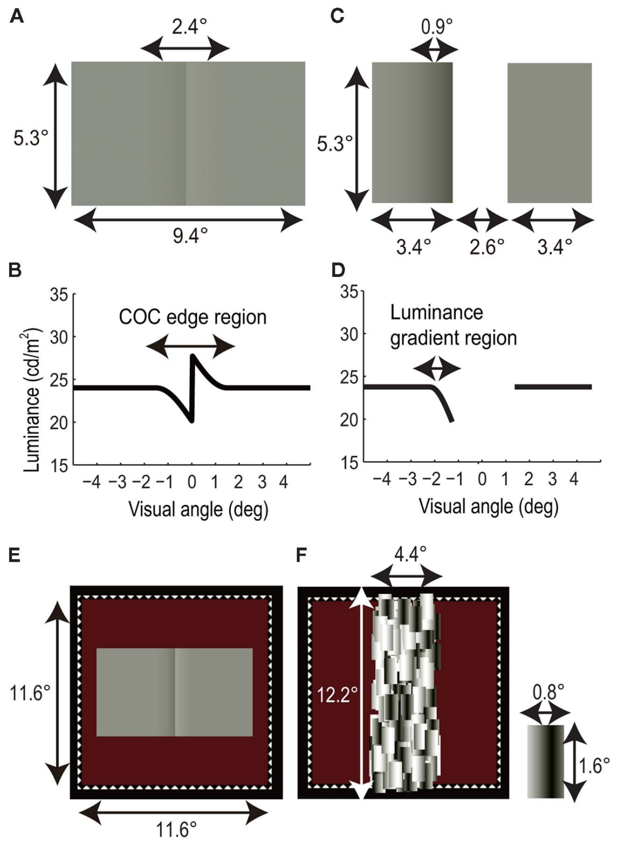

FIGURE 1 | Visual stimuli. (A) Craik-O'Brien-Cornsweet (COC) stimulus. **(B)** Luminance profile of COC stimulus. **(C)** Modified COC stimulus consists of two rectangles. **(D)** Luminance profile of modified COC stimulus. **(E)** COC stimulus with white dotted line and red background. **(F)** Mondrian stimulus and a rectangular patch of Mondrian stimulus.

Figure 1C shows a modified COC stimulus used in the adaptation experiment. The modified COC stimulus was composed of two rectangles 3.4 × 5.3 arc degree in size, arranged with 2.6 arc degree horizontal spatial interval. One of the rectangles had a luminance gradient 0.9 × 5.3 arc degree in size, which caused lightness induction into the whole rectangle area. The baseline and minimum luminances of the luminance gradient were 24.0 and 19.9 cd/m^2, respectively (**Figure 1D**). We used the modified COC stimuli instead of the original COC stimulus, since this enabled us to measure the aftereffect of the COC edge without influence on its lightness induction into adjacent areas.

As shown in **Figure 1E**, the COC stimulus and the modified COC stimulus were presented with a square frame (11.6 × 11.6 arc degree) drawn with white dotted lines ("fuse frame"). The background color was dark red (0.11 cd/m^2, (CIE1931); $x = 0.476$, $y = 0.523$) in the BM and CFS experiments, and it was red (3.73 cd/m^2, (CIE1931); $x = 0.494$, $y = 0.375$) in the adaptation experiment to optimize the adaptation effect (These values were decided on the basis of preliminary observations). Before the initiation of a trial in all experiments, fixation targets (white crosses 0.53 × 0.53 arc degree in size and 78 cd/m^2 in luminance) were presented for stable fixation at the center of the stimulus and 6.3

arc degree above and below it. The three fixation targets were presented to avoid misalignments caused by ocular torsion.

In the BM experiment, a static Mondrian stimulus was presented immediately after the COC stimulus. As shown in **Figure 1F**, the size of the Mondrian stimulus was 4.4 × 12.2 arc degree. The Mondrian stimulus was composed of patches of rectangles, subtended 0.8 × 1.6 arc degree and consisting of horizontal sinusoidal gratings. The spatial frequency of the sinusoidal gratings was 0.63 cycle/degree. The COC and masking stimuli were presented to both eyes. The central positions of the COC and Mondrian stimuli were aligned in the displayed area, and the area of the Mondrian stimulus totally covered the COC edge.

In the CFS experiment, a dynamic Mondrian stimulus and the COC stimulus were simultaneously presented to the dominant eye and the other eye, respectively. We used a dynamic Mondrian stimulus composed of drifting sinusoidal gratings instead of static rectangles, since it allowed us to render the COC edge invisible completely and continuously for several tens of seconds (Maruya et al., 2008). The size and position of the Mondrian stimulus were the same as those in the BM experiment. The rectangles of the Mondrian stimulus comprised dynamic horizontal sinusoidal gratings, which were individually moved horizontally at the speed of 5.33°/s. The direction of motion (left or right) was reversed with random timing to avoid motion adaptation by these gratings. The arrangement of these rectangles changed every 500 ms. The central positions of the COC and dynamic Mondrian stimuli were aligned. The Mondrian stimulus totally covered the COC edge during stimulus presentation and interocularly suppressed the awareness around the COC edge[1].

In the adaptation experiment, luminance aftereffects of the invisible COC edge were tested. In the adaptation phase, the dynamic Mondrian stimulus used in the CFS experiment and a modified COC stimulus were simultaneously presented to the dominant eye and the other eye, respectively. The positions of the Mondrian stimulus and modified COC stimulus were aligned. The Mondrian stimulus totally covered the luminance gradient region of one rectangle and interocularly suppressed the awareness around the luminance gradient region[1]. In the test phase, two uniform rectangles with 24.0 cd/m^2 of luminance were presented to the dominant eye or the other eye. The sizes, positions, and eye of the test rectangles were changed depending on the experimental conditions. In the standard test condition, the test rectangles were the same as the modified COC stimulus in size and position; in the flanking test condition, the test rectangles 1.8 × 5.3 arc degree in size arranged with a 5.8 arc degree horizontal spatial interval were used.

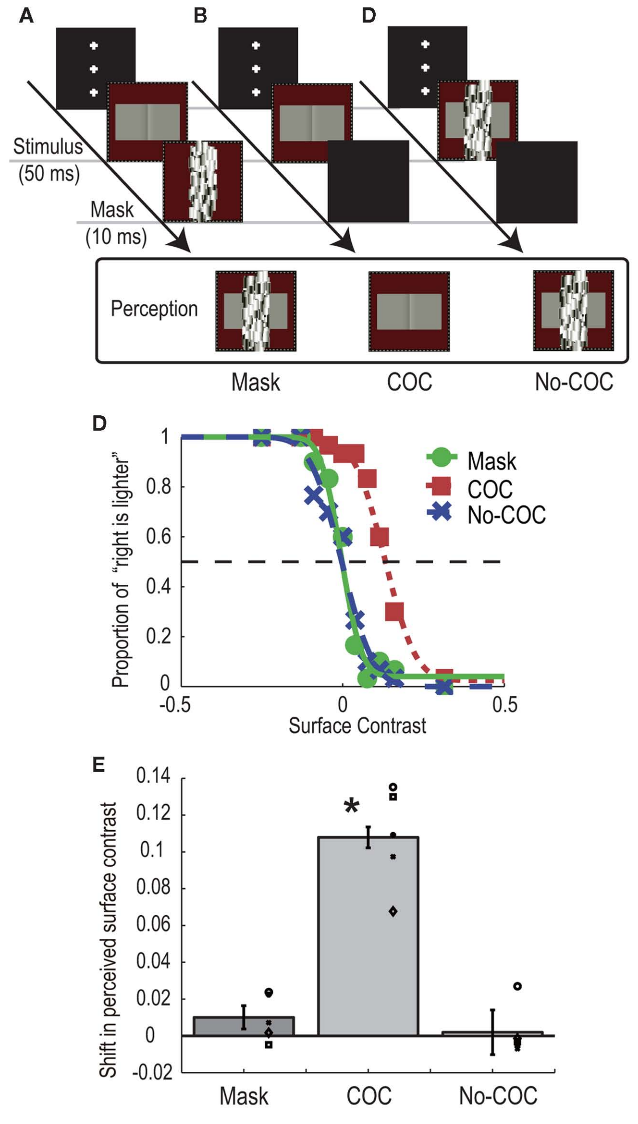

FIGURE 2 | Schematic illustrations of procedure and visual stimuli in the BM experiment: (A) Mask condition, (B) COC condition, and (C) No-COC condition. (D) Psychometric functions obtained with observer AM. **(E)** Shifts of PSEs in the three conditions. The bars indicate the averaged shift of PSE, with error bars showing ± SEs. Symbols indicate individual data points.

BM EXPERIMENT

Procedure

In the mask condition (**Figure 2A**), a COC stimulus was presented for 50 ms, and a Mondrian stimulus was presented for 10 ms immediately after the COC stimulus disappeared. Observers were asked to make a two-alternative forced choice about which surface region of the COC stimulus was perceived lighter (left or right). Prior to the experiment we confirmed that all observers could not perceive the COC edge in this condition. The luminance of left and right flanking regions were systematically changed from trial-to-trial, while the polarity of COC edge was fixed so that the right flanking region was perceived lighter when the flanking regions of both sides had the same luminance. The Michelson contrast of the flanking surface regions of the COC stimulus was varied in 10 steps: −0.24, −0.12, −0.08, −0.04, 0, 0.04, 0.08, 0.12, 0.16, and 0.32. Negative values mean that luminance of the right flanking region was high and vice versa. At the lowest contrast

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[1] It is known that interocular suppression is not strictly confined to the retinal area of rival stimulation, but spreads beyond the boundaries of those stimuli (e.g., Kaufman, 1963; Blake and Camisa, 1979; Liu and Schor, 1994). The spatial extent of suppression can spread across several degrees when the suppression is strong (Maruya and Blake, 2009). However, in this study, we adjusted the strength of suppression so that the suppression did not reach the area the observers used to judge the perceived lightness.

−0.24, the luminances of left and right flanking regions were 18.2 and 29.7 cd/m^2, respectively. At the highest contrast 0.32, the luminances of the left and right flanking regions were 31.4 and 16.1 cd/m^2, respectively. For the purpose of control, we performed experiments in which the Mondrian stimulus was not presented (COC condition, see **Figure 2B**) and in which the Mondrian stimulus superimposed on the COC stimulus was presented for 50 ms (No-COC condition, see **Figure 2C**). Thirty trials were performed for each contrast value (300 trials for one condition, 900 trials in total). Trials in the three conditions were performed in a randomized order.

Results

Figure 2D shows psychometric functions of an observer (AM) under the three conditions. In general, when the surface contrast was negative (the luminance of right region was high), the observers reported that they perceived the right region as being lighter, indicating that the observers could judge the surface lightness properly. Although both psychometric functions obtained in the Mask and No-COC conditions were non-biased, that in the COC condition was shifted in the direction of positive surface contrast (the luminance of left region was high). The apparent lightness was estimated for each condition by calculating the point of subjective equality (PSE) with the cumulative Gaussian function fitted to the psychometric function. The averaged PSEs across all observers with SEs are shown in **Figure 2E**. A positive value means that a typical COC effect occurred. A significant shift toward positive surface contrast from zero was observed in the COC condition [$t(4) = 8.87$, $p < 0.05$], indicating that the COC effect could occur even for very short stimulus duration. Conversely, no shift in the PSE was observed in the Mask condition [$t(4) = 1.78$, $p = 0.15$] and No-COC condition [$t(4) = 0.31$, $p = 0.77$]. A one-way repeated measures ANOVA revealed that there was a significant difference between conditions [$F(2,8) = 74.48$, $p < 0.01$]. The *post hoc* comparison (Ryan's method, significant level = 0.05) showed that the value in the COC condition was significantly higher than those in the Mask and No-COC condition, and that there was no significant difference between the Mask condition and No-COC conditions. These results demonstrated that when the percept of the COC edge was suppressed by a BM stimulus, the COC effect was reduced to the identical level where the COC edge was physically covered.

CFS EXPERIMENT

Procedure

A dynamic Mondrian stimulus and the COC stimulus were presented to the dominant eye and the other eye, respectively. The Mondrian stimulus interocularly suppressed the awareness of the COC edge (CFS condition, see **Figure 3A**). The observers were asked to make a two-alternative forced choice about which region was perceived lighter as the Michelson contrast of the flanking regions was systematically changed in the same manner as in the BM experiment. When observers detected the COC edge at any time during a trial, they were asked to report it by pressing a button to abort the trial, and the same trial condition was presented afterward. Such aborted trials were rare, occurring only one or two times for the whole experiment at most. For control, we performed two additional conditions, one in which the dynamic Mondrian stimulus was not presented (COC condition, see **Figure 3B**) and another in which the Mondrian stimulus superimposed on the COC stimulus was presented to the non-dominant eye (No-COC condition, see **Figure 3C**). The presentation duration of the COC stimulus was 50, 200, or 2000 ms. Trials with the three durations and three conditions were performed in a randomized order. Thirty trials were performed for each contrast value (900 trials for one condition, 2700 trials in total).

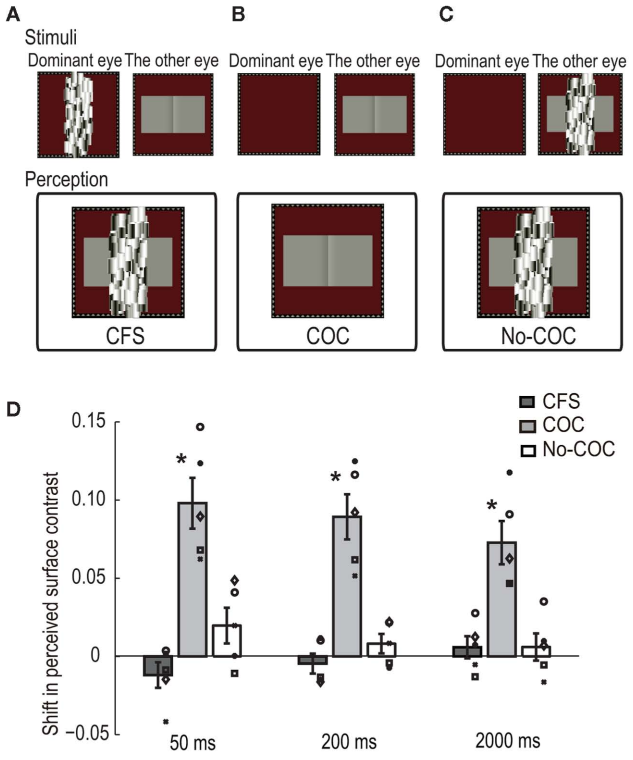

FIGURE 3 | Schematic illustration of visual stimuli in the CFS experiment: (A) CFS condition, (B) COC condition, and (C) No-COC condition. (D) PSE of surface contrast for 50-, 200-, and 2000-ms presentation duration in the three conditions. The bars indicate the averaged shift of PSE, with error bars showing ± SEs. Symbols indicate individual data points.

Results

We estimated PSEs to quantitatively evaluate apparent lightness under the presentation of CFS. **Figure 3D** shows results for all conditions with the three presentation durations. The vertical axis represents the shift of PSEs in the surface contrast. A positive value means that a typical COC effect occurred. The averaged PSEs across all observers with SEs are shown. The amounts of shift in the COC condition were significantly larger than zero for all durations [$t(4) = 6.03$, $p < 0.05$ for 50 ms, $t(4) = 6.18$, $p < 0.05$ for 200 ms, $t(4) = 5.27$, $p < 0.05$ for 2000 ms], although the magnitude of the COC effect slightly decreased as the presentation duration increased. On the other hand, the amounts of shift were not significantly different from zero in the CFS condition [$t(4) = 1.46$, $p = 0.22$ for 50 ms, $t(4) = 0.72$, $p = 0.51$ for 200 ms, $t(4) = 0.83$, $p = 0.46$ for 2000 ms] or No-COC conditions [$t(4) = 1.73$, $p = 0.16$ for 50 ms, $t(4) = 1.31$, $p = 0.26$ for 200 ms, $t(4) = 0.67$, $p = 0.54$ for 2000 ms].

In order to evaluate the statistical difference in the shifted PSE between conditions at each presentation duration, we first performed a two-way repeated measures ANOVA with condition and duration as factors, and the shift of PSE as the dependent variable. The results showed a significant difference between the conditions [$F(2,8) = 48.86$, $p < 0.01$] and a non-significant difference between the durations [$F(2,8) = 3.40$, $p = 0.09$]. The interaction between them was significant [$F(4,16) = 3.98$, $p < 0.05$]. Simple main effects were tested between conditions under each duration, and the results revealed that there were significant differences between the conditions under all durations [$F(2,24) = 45.92$, $p < 0.01$ for 50 ms, $F(2,24) = 37.20$, $p < 0.01$ for 200 ms, $F(2,24) = 21.38$, $p < 0.01$ for 2000 ms]. The *post hoc* multiple comparison (Ryan's method, significant level = 0.05) showed that the values in the COC condition were significantly higher than those in the CFS and No-COC conditions for all durations. These results demonstrated that in conditions where the visual awareness of the COC edge was suppressed by CFS, the COC effect was drastically reduced to the identical level where the COC edge was physically covered.

Simple main effects were also tested between durations for each condition, and a significant difference was only acquired in the COC condition [$F(2,24) = 3.14$, $p = 0.06$ for CFS condition, $F(2,24) = 6.42$, $p < 0.01$ for COC condition, $F(2,24) = 2.14$, $p = 0.13$ for No-COC condition]. The *post hoc* multiple comparisons (Ryan's method, significant level = 0.05) showed that the values for the 50- and 200-ms durations were not significantly different but were significantly higher than for the 2000-ms duration condition. This tendency for the strength of the COC effect to decrease with increasing presentation duration is consistent with the result of a previous study (Wachtler and Wehrhahn, 1997). Although we do not clearly know the reason behind this, it might reflect temporal dynamics of the lightness induction process, which might be composed of a fast process for generating an initial percept of surface lightness (Robinson and de Sa, 2008) and a slow process to fill the lightness information into the whole surface area (De Valois et al., 1986; Rossi and Paradiso, 1996).

ADAPTATION EXPERIMENT

Both the BM and CFS experiments phenomenologically demonstrated that when the subjective percept of the COC edge was suppressed, the COC effect was not observed. However, the processing stage of this phenomenon is still unclear. The results of the BM and CFS experiments lead to, at least, two possibilities: (i) the neural processing of the COC edge at the early stage was suppressed or (ii) the COC edge was still processed at the early stage, but the subsequent process of lightness induction was suppressed. Our next investigation used an adaptation paradigm to look into the processing stage of the COC edge. Specifically, we measured the luminance aftereffects of the COC stimulus under conditions where the COC edge was rendered invisible during the adaptation period.

Procedure

In the COC + CFS condition, as shown in **Figure 4A**, the dynamic Mondrian stimulus and the modified COC stimulus was presented to the dominant eye and the other eye, respectively, for 8000 ms during the adaptation phase. One rectangle of the modified COC stimulus had a luminance gradient region (gradient rectangle), in which lightness induction into the whole rectangle area was observed, and the other had uniform luminance (see **Figure 1C**).

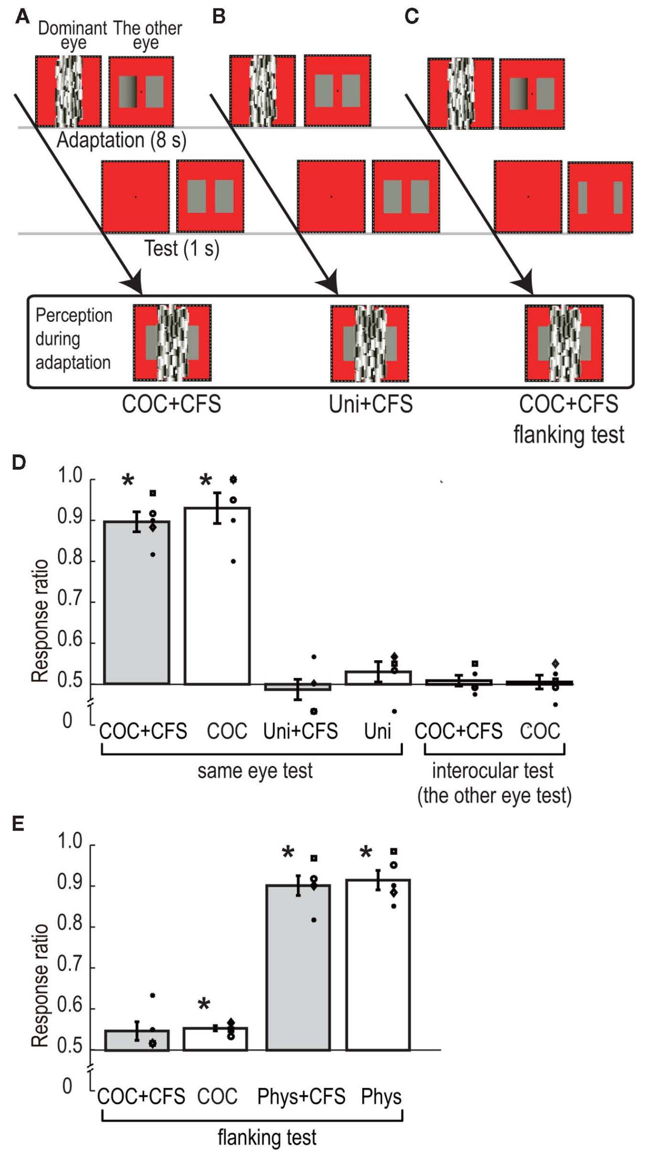

FIGURE 4 | Schematic illustration of procedure and visual stimuli in adaptation experiment: (A) CFS standard test condition, (B) CFS equiluminant adaptation condition, and (C) CFS flanking test condition. (D) Ratio of the rectangle at the side of luminance gradient reported as brighter in the six conditions of the adaptation experiment. The bars indicate the averaged rate, with error bars showing ± SEs. Symbols indicate individual data points. **(E)** Ratio of the rectangle at the side of luminance gradient reported as brighter in the four conditions of the subsidiary adaptation experiment.

In the test phase, two rectangles with uniform luminance (standard test rectangles) were presented to the non-dominant eye for 1000 ms, and observers reported which rectangle they perceived to be lighter (right or left). When observers detected the luminance gradient at any time during adaptation, they were asked to report it by pressing a button to abort the trial, and the same trial condition was presented afterward. As a control experiment, we tested a condition in which both the two rectangles for adaptation had uniform luminance (Uni + CFS condition, see **Figure 4B**). The luminance of the uniform rectangles was 24.0 cd/m^2, which was the same as the luminance of the flanking region of the modified COC stimulus. As reported in the CFS experiment, observers could not tell which rectangle had the luminance gradient in the COC + CFS condition. Therefore, the perceived stimuli during the adaptation were subjectively the same in the COC + CFS and Uni + CFS conditions.

To check the basic adaptation effects of the modified COC stimulus, we presented the modified COC stimulus or the equiluminant rectangles without the CFS stimulus for adaptation (COC, and Uni conditions). In addition, to examine the stage of adaptation, we also used conditions, in which the standard test rectangles were presented to the opposite eye to which the modified COC had been presented. After adapting to the modified COC stimulus to the non-dominant eye with CFS to the dominant eye (COC + CFS interocular test condition), or without CFS (COC interocular test condition), the standard test rectangles were presented to the dominant eye. The number of trials in which the gradient rectangle was presented at one side (right or left) was set to 30, and these 30 trials were blocked in the COC + CFS, COC, and the two interocular test conditions (60 trials in total for each condition). The number of trials in the Uni + CFS and Uni conditions was set to 30.

Results

The average ratios of observers' perceiving a test rectangle lighter at the location where the gradient rectangle was presented are shown in **Figure 4D**. In the COC + CFS, and COC conditions, the ratios were around 90%, and significantly higher than chance level [$t(4) = 11.15$, $p < 0.05$ for COC + CFS, and $t(4) = 6.42$, $p < 0.05$ for COC]. On the other hand, the ratios of the Uni + CFS and Uni conditions were not significantly different from chance level [$t(4) = 0.53$, $p = 0.62$ for Uni + CFS, and $t(4) = 1.20$, $p = 0.30$ for Uni]. We observed no statistically significant effect of interocular transfer both with CFS and without CFS, ratios of subjective report being not significant from chance level [$t(4) = 0.63$, $p = 0.56$ for COC + CFS interocular test, and $t(4) = 0.30$, $p = 0.78$ for COC interocular test].

To statistically analyze the relationship between the conditions, we performed a two-way repeated measures ANOVA with the type of CFS (with or without CFS) and stimulus combination of adaptation-test (COC-standard test, Uni-standard test, and COC-interocular test) as factors and the ratio as the dependent variable. The results showed non-significant difference for the type of CFS [$F(1,4) = 2.46$, $p = 0.19$] and a significant difference for the type of stimulus combination [$F(2,8) = 62.13$, $p < 0.01$]. The interaction between them was not significant [$F(2,8) = 2.58$, $p = 0.14$]. These statistical analyses showed that the ratio in the COC + CFS condition was equivalent to that in the COC condition, suggesting that the CFS did not interfere with the processing of luminance adaptation.

The *post hoc* comparison (Ryan's method, significant level = 0.05) showed that the values in COC-standard test stimulus combination were significantly higher than those for the Uni-standard test and COC-interocular test combination, and that there was no significant difference between the Uni-standard test and COC-interocular test combinations. These analyses indicate that, although the perceptions during adaptation were subjectively the same in the COC + CFS and Uni + CFS conditions, their ratios were significantly different, and this provided evidence that the adaptation effect in the COC + CFS condition was not an artifact due to observers' being able to see the side of the gradient rectangle. These results supported scenario (ii), indicating that the COC edge was still processed under the CFS, presumably at the early stage of monocular processing (see the results of interocular test conditions), and that the CFS stimulus disrupted subsequent process of lightness induction.

SUBSIDIARY ADAPTATION EXPERIMENT

Given the results of the above adaptation experiments suggesting that the neural processing of the COC edge seems to survive interocular suppression by CFS, we next attempted to test for the subsequent processing of lightness induction into the adjacent surface using a similar paradigm of adaptation. For this purpose, we presented the test stimulus only in retinotopic regions where the adaptation stimulus had no luminance gradient.

Procedure

The procedures were the same as the standard test conditions in the adaptation experiment except for the size of the test rectangles. The adaptation stimulus was the modified COC stimulus presented to the non-dominant eye with the CFS stimulus presented to the dominant eye (COC + CFS flanking test condition) or only the modified COC stimulus presented to the non-dominant eye (COC flanking test condition). As shown in **Figure 4C**, small uniform test rectangles, which did not cover the area of the luminance gradient, were presented in the test phase. The size of the test rectangle was chosen to avoid the spread of the adaptation effect of the luminance gradient region (see the details in the "Visual Stimuli" section). As a control, we tested a condition in which the two rectangles for adaptation had uniform but different luminance. The luminance of one rectangle for adaptation was 24.0 cd/m^2, which was the same as that used in the Uni conditions. The luminance of the other rectangle was adjusted from 18.0 to 20.2 cd/m^2 according to the observers so that the rectangle could be perceived as having the same lightness as illusory lightness of the gradient rectangle of the modified COC stimulus (lower luminance rectangle). During the adaptation phase, the two rectangles were presented to the non-dominant eye with or without the CFS stimulus presented to the dominant eye (Phys + CFS flanking test or Phys flanking test condition), and during the test phase, flanking test rectangles were presented. The number of trials in which the gradient rectangle or lower luminance rectangle was presented at one side (right or left) was set to 30, and these 30 trials were blocked (60 trials in total for each condition).

Results

The average ratios of observers' perceiving a test rectangle lighter at the location where the gradient rectangle was presented are shown in **Figure 4E**. The ratio for the COC + CFS flanking test condition was not significantly different from chance level [$t(4) = 2.05$, $p = 0.11$], and that for the COC flanking test condition was slightly higher than chance level and statistically significant [$t(4) = 8.52$, $p < 0.01$]. The ratios for the Phys + CFS flanking test and Phys flanking test conditions were significantly higher than chance level [$t(4) = 11.46$, $p < 0.01$ for Phys + CFS flanking test; $t(4) = 10.46$, $p < 0.01$ for Phys flanking test]. We performed a two-way repeated measures ANOVA with type of CFS (with or without CFS) and adaptation stimulus (COC adaptation and Physical adaptation) as factors and the ratio as the dependent variable. The results showed a non-significant difference in the CFS [$F(1,4) = 2.37$, $p = 0.20$], demonstrating again that the CFS did not interfere with the processing of luminance adaptation, and a significant difference in the type of adaptation stimulus [$F(1,4) = 63.13$, $p < 0.01$]. The interaction between them was not significant [$F(1,4) = 0.48$, $p = 0.53$]. These analyses show that when the test rectangles did not cover the region of the luminance gradient of the adapting stimulus (the modified COC stimulus), the effect of luminance adaptation was significantly reduced. This suggests that the induced lightness on the adjacent surface area itself causes a significantly smaller luminance adaptation effect compared to the physical luminance stimulus, which has subjectively the same lightness (see the COC flanking test and Phys flanking test conditions).

DISCUSSION

PRINCIPLE FINDINGS

Using visual masking and interocular suppression paradigm, we found that the online percept of the COC effect nearly vanishes when the COC edge is rendered invisible. The result of BM experiments, in which the subjective percept of the COC edge was suppressed by temporally adjacent stimulus, is a novel finding, but it is unclear whether the COC edge was processed, since the COC and the mask stimuli were presented at the same retinal location. On the other hand, it was guaranteed that the retinal inputs were preserved at the stage of monocular processing in the CFS experiment, since the COC and the Mondrian stimulus were presented to different eyes. The results of the CFS experiment agree with a previous observation (see Supplemental Data of Boyaci et al., 2007), and in our experiment the effect of presentation duration of the COC stimulus tested systematically. In addition, the results are further supported by a recent report that the binocular rivalry suppresses the COC effect (see Shevell et al., 2011).

More importantly, the results of the adaptation experiments performed to test the processing stage of the COC edge under the CFS demonstrated that the neural processing of the COC edge was intact, presumably at the stage of monocular processing, even when the COC edge was invisible. This suggests that the neural processing of the COC edge at the early stage is not sufficient for generating lightness induction in the COC effect, and rather indicates that subjective awareness of the COC edge is crucial. Additionally, a subsidiary adaptation experiment demonstrated that the induced lightness of the adjacent surface showed a weaker adaptation effect than that caused by a subjectively equivalent physical stimulus, which also indicates the involvement of higher processing for lightness induction in the COC effect.

MECHANISMS OF LIGHTNESS INDUCTION

It is known that simple lightness induction effects, such as simultaneous contrast effects and Mach bands, can be explained by spatial filtering, say, lateral inhibition among neurons in the retina. Although the COC effect differs from such effects in its region of induction (the COC edge affects the perception of entire large areas) and its direction of induction (the region adjacent to the lighter part of the COC edge appears lighter, the opposite of the usual contrast effects), one might consider that the mechanism of the COC effect is similar to that of low-level-filtering effects (Békésy, 1972; Heggelund and Krekling, 1976). It is likely that such simple lateral inhibitions may occur at the earliest processing stage on the retina, but recent studies indicated the involvement of cortical processing (e.g., Perna et al., 2005; Boyaci et al., 2007; Hung et al., 2007), and our results further support the involvement of higher processing related to subjective awareness in the COC effect.

The activities related to the lightness induction are found in the broader areas of visual cortex. Recent brain imaging and physiological studies have raised the possibility that the neural mechanisms underlying lightness induction could be operated at the earliest stages of cortical visual processing in V1 or V2 (Rossi et al., 1996; Rossi and Paradiso, 1999; Hung et al., 2001, 2007; Kinoshita and Komatsu, 2001; MacEvoy and Paradiso, 2001; Roe et al., 2005). Also, several psychophysical studies implied that the surface lightness is encoded by the cortical filling-in process (Grossberg and Todorovic, 1988; Neumann et al., 2001) or banks of spatial frequency filters (Dakin and Bex, 2003; Perna and Morrone, 2007). Furthermore, another brain imaging study (Perna et al., 2005) indicated that the COC effect activates higher cortical areas, such as LO, which has been considered to be responsible for amodal completion (Sasaki and Watanabe, 2004). Although the brain areas responsible for the neural processing of the lightness induction are still unspecified, our results suggest that conscious processing of the COC edge, not automatic or unconscious processing, is required in order to trigger the lightness induction into the adjacent surfaces in the COC effect (see also Harris et al., 2011 for simultaneous contrast effect and Kanizsa illusion).

The series of our experimental results lead us to hypothesize that two mechanisms are responsible for the COC effect: a feedback mechanism in a hierarchical system, which is associated with subjective awareness of the COC edge, and a mechanism for surface lightness, which may rely on lateral connectivity and be activated by the feedback signal (Lamme and Roelfsema, 2000; Lamme, 2006; see also Bair et al., 2003 for a physiological study that showed a fast feedback mechanism and slow low-level mechanism relying on lateral connectivity in the primary visual cortex). It might be speculated that the feedback mechanism was disrupted by the BM and CFS stimuli and that the second mechanism for lightness induction was not activated, resulting in a failure of observation of the COC effect. Our hypothesis remains highly speculative at the moment, but it might also explain the results of the subsidiary adaptation experiment that the negative aftereffect caused by the illusory lightness on the surfaces was very limited and much smaller compared to conditions where observers were adapted with luminance rectangles that mimicked the illusory COC percept (see **Figure 4E**). Under the hypothesis, no input was given to the first feedback mechanism in the test phase, since the test stimulus did not cover the area of the luminance gradient of the modified COC stimulus, and the second mechanism responsible for the lightness induction was not activated. In summary, our results imply that the COC effect is an outcome of synthetic processing including feedback mechanisms, not solely an outcome of either early-stage processing of lateral interactions or higher-stage processing associated awareness.

The COC effect has been explained by another line of view, which is based on the empirical notion that the percept is determined by a statistical consequence of an accumulation of past experience rather than a veridical representation of the objects in the environment (Purves et al., 1999, 2004). The results of the BM and CFS experiments might be concomitant with the empirical view, assuming that the invisible COC edge could not be embedded in the empirical strategy as the contextual information to infer lightness of the surface area. On the other hand, the interpretation of the adaptation results with the empirical view seems to be more complicated. Although, in the empirical view, the visible contents could be considered as an essential quality for the inference of the global scene, previous studies suggested that invisible contents could affect perception of subsequent visual features (Lehmkuhle and Fox, 1975; O'shea and Crassini, 1981; Blake et al., 2006; Maruya et al., 2008). Our results of the adaptation experiments showed that prolonged viewing of the invisible COC edge influenced subsequent lightness perception of the same retinal location (COC + CFS condition), but not that of adjacent flanking surface areas (COC + CFS flanking test condition). This suggests that invisible features could affect effective strength of subsequent inputs within spatially restricted areas, but could not play a role to infer subsequent global scenes in the lightness perception.

CONCLUSION

To investigate the underlying mechanisms of the COC effect, we examined whether the subjective awareness of the COC edge is necessary for the generation of the COC effect. We used visual BM and CFS to manipulate the visibility of the COC edge while obtaining subjective reports about the percepts and aftereffects of adaptation. Psychophysical results showed that the online percept of COC effect nearly vanishes in conditions where the COC edge is rendered invisible. On the other hand, the results of adaptation experiments showed that the COC edge is still processed at the stage of monocular processing. These results suggest that conscious processing of the COC edge is crucial for generating the COC effect and that automatic processing of the COC edge, presumably at the early stage of visual processing, is not sufficient.

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Attentional switching in humans and flies: rivalry in large and miniature brains

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Human perception, and consequently behavior, is driven by attention dynamics. In the special case of rivalry, where attention alternates between competing percepts, such dynamics can be measured and their determinants investigated. A recent study in the fruit fly, *Drosophila melanogaster*, now shows that the origins of attentional rivalry may be quite ancient. Furthermore, individual variation exists in the rate of attentional rivalry in both humans and flies, and in humans this is under substantial genetic influence. In the pathophysiological realm, slowing of rivalry rate is associated with the heritable psychiatric condition, bipolar disorder. Fly rivalry may therefore prove a powerful model to examine genetic and molecular influences on rivalry rate, and may even shed light on human cognitive and behavioral dysfunction.

Keywords: binocular rivalry, ambiguous figure, *Drosophila*, attention, switch rate, bipolar disorder, individual variation, endophenotype

INTRODUCTION

Perceptual rivalry amuses and intrigues those who experience it and those who study it. Though it has many faces, the phenomenon is defined fundamentally by conflicting or ambiguous sensory input that induces involuntary alternations in perception. Famous examples include ambiguous figure rivalry (AFR) such as the Necker cube (**Figure 1A**) and Rubin's vase-faces illusion (**Figure 1B**), which cause perspective reversals and figure–ground reversals, respectively, and are elicited under normal (dioptic) viewing conditions (Long and Toppino, 2004). Under dichoptic viewing conditions, in which stimuli are presented separately to each eye, perceptual alternations also arise if the stimulus features are sufficiently incongruent – a phenomenon known as binocular rivalry (BR; **Figure 1C**; Blake and Logothetis, 2002; Alais, 2012; Howard and Rogers, 2012; Miller, forthcoming).

For more than 100 years, AFR and BR have been characterized and probed in the hope of eventually understanding neurophysiological mechanisms underlying the perceptual alternations (e.g., McDougall, 1906). In the last 20 years, psychophysical methods have merged with modern neuroscientific methods and there is now widespread, concerted effort to reach the goal of this mechanistic understanding. Along the way, a multitude of new rivalry types have been described and incorporated into the pursuit, and promising new research directions have emerged.

CLINICAL, GENETIC, AND MOLECULAR APPROACHES TO PERCEPTUAL RIVALRY

One such new direction stems from recent reports that the *rate* of BR is slow in the psychiatric condition, bipolar disorder (BD; manic depression; Pettigrew and Miller, 1998; Miller et al., 2003). Factors affecting switch rate during perceptual rivalry have long been studied using both AFR and BR. Indeed, in both rivalry types, the similar effects on switch rate of varying such factors has been used to argue, along with a range of other evidence, that AFR and BR share at least some degree of common mechanism (e.g., Leopold and Logothetis, 1999; Ngo et al., 2008). In the case of BR, modifying the level of stimulus salience or "stimulus strength" is well known to affect the rate of alternation between the presented images. Thus, observers presented with stimuli that are moving, of high contrast, and of high spatial frequency, will switch faster than when presented with stationary, low contrast, low spatial frequency stimuli (Howard and Rogers, 2012). Similar findings regarding stimulus properties and switch rate have been shown with AFR (e.g., Long and Toppino, 2004).

Another feature both types of rivalry share is that switch rate between individuals exhibits wide variation, but within an individual is highly reliable (e.g., McDougall, 1906; Ewen, 1931; George, 1936; Enoksson, 1963; Aafjes et al., 1966; Borsellino et al., 1972; Pettigrew and Miller, 1998; Miller et al., 2010). Although individual variation in perceptual rivalry rate was a topic of interest in the early-mid twentieth century (e.g., Frederiksen and Guilford, 1934; Crain, 1961), the search for rivalry mechanisms in the late twentieth century led instead to individual differences being considered a distraction. However, just as the pendulum has swung historically between low- and high-level mechanistic explanations of rivalry (Blake, 2001), so too it appears to be swinging back toward the field's interest in individual differences. With psychophysicists having well characterized extrinsic (stimulus and presentation) features affecting rivalry rate, the search is now on to determine intrinsic (endogenous) determinants of individual variation in switch rate (Miller et al., 2010). This renewed interest in individual differences began with the serendipitous finding in the late 1990s that the rate of BR is slow in BD (Pettigrew and Miller, 1998). Not surprisingly however, given proposals for common mechanisms of BR and AFR, similar reports of slow AFR rate in BD had been published in the early twentieth century (Ewen, 1931; Hunt and Guilford, 1933).

Bipolar disorder is characterized by episodes of mania and depression, most often with periods of euthymia (normal mood) in between. The condition, when diagnosed accurately, is usually amenable to control with appropriate medication but can also be devastating to individuals who fail to take such medication or who become refractory to it. There are two main types of BD, the severe form (BD-I; diagnosis of which requires the individual having been admitted to hospital with a manic episode), and a less severe form (BD-II; which involves only hypomanic episodes, without hospital admission). Current psychiatric classification (American Psychiatric Association, 2000) also provides for additional related diagnoses such as cyclothymia and BD-not otherwise specified. In the initial report of slow BR in BD (Pettigrew and Miller, 1998), using high-strength stimuli (drifting gratings of high spatial frequency), control subjects showed perceptual switches on average every 1–2 s, whereas subjects with BD-I switched, on average, every 3–4 s, with some perceptual periods lasting as long as 7–10 s.

This finding was confirmed in a subsequent study, using lower strength stimuli (Miller et al., 2003), though group separation was less in this second study. Together however, the two studies suggested that slow BR rate could distinguish BD-I ($n = 50$) from controls ($n = 93$) with a sensitivity of approximately 80% (requiring confirmation with larger datasets). The second study also reported that (i) BR rate in BD-I ($n = 30$) was significantly slower than that in schizophrenia (SCZ; $n = 18$) and in major depressive disorder (MDD; $n = 18$), and (ii) BR rate in SCZ and MDD was not significantly different from that of controls ($n = 30$). The findings for SCZ and MDD, though preliminary, suggested that specificity of the slow BR rate trait for BD-I may also be of the order of 80% (again requiring confirmation with larger datasets).

There have since been two independent replication studies, one using an ambiguous structure-from-motion stimulus (Krug et al., 2008) and another using BR (Nagamine et al., 2009), with both confirming significantly slower perceptual rivalry rate in BD-I compared with controls. The study by Nagamine et al. (2009) also found that BR rate in BD-II was not significantly different from that in controls. Nagamine et al. (2009) used BR stimuli of intermediate strength, while Krug et al. (2008) used an ambiguous structure-from-motion stimulus that was of very low strength (inducing switches in BD subjects and controls of the order of tens of seconds). Although switch rate was significantly slower in BD-I subjects than in controls in both studies, the differences found between groups were less than in earlier work using high-strength BR stimuli (Pettigrew and Miller, 1998). One explanation for the group separation differences found between studies is that high-strength stimuli provide better discriminative separation of BD subjects from controls (and by extension, from other clinical groups; Miller et al., 2003; Ngo et al., 2011). However, further work varying stimulus strength parameters within the same control and clinical subjects is required to verify this proposal. The available BR rate data (with corresponding stimulus strengths indicated) are presented in **Figure 2**.

Bipolar disorder is highly heritable (Smoller and Finn, 2003; Lichtenstein et al., 2009) and reports of a slow BR rate associated with this condition have raised the prospect of using this trait as a biological marker (or "endophenotype") for the disorder. Misdiagnosis is common in clinical psychiatry, especially between (i) the psychosis of SCZ and that due to BD, and (ii) the depression of MDD and that due to BD (Joyce, 1984; Conus and McGorry, 2002). Such misdiagnosis has important implications because treatment decisions differ according to diagnosis. A biological marker that is sufficiently sensitive and specific to improve diagnosis in these contexts would have major treatment implications. Indeed, there are no diagnostic tests in clinical psychiatry. Slow BR rate is currently being explored regarding this potential diagnostic application (Ngo et al., 2011).

In addition to potential clinical diagnostic utility, biological markers can be explored as endophenotypes for heritable conditions, wherein the biomarker represents an "intermediate phenotype" that marks an underlying at-risk genotype. This marking occurs even though the clinical phenotype – the psychiatric disorder – may not have yet manifested (or indeed may never manifest). Such markers would have important preventive implications for relatives of individuals with BD, some of whom inherit the at-risk genotype, and some of whom do not. Indeed, the strategy of endophenotype identification is now acknowledged within psychiatric genetics (Gottesman and Gould, 2003) as an important approach to dealing with clinical heterogeneity of psychiatric disorders (the cause of the diagnostic difficulties). Because genome-wide association studies (GWAS) of psychiatric disorders (which aim to identify predisposing genes) depend on accurate clinical diagnosis, endophenotypes can thus be used in place of reliance

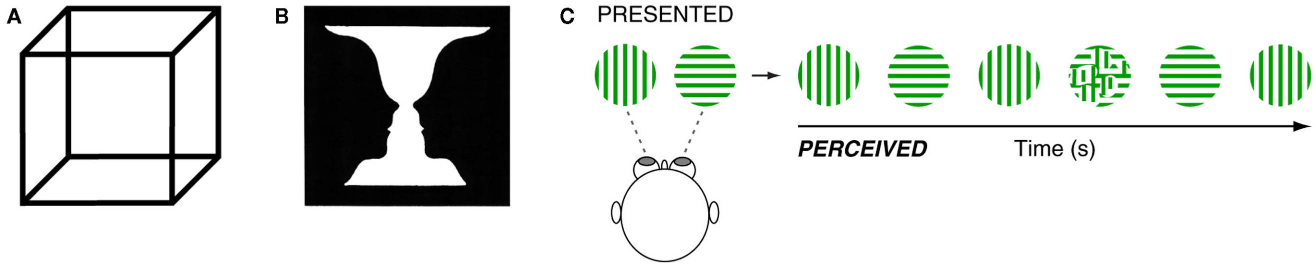

FIGURE 1 | (A) The Necker cube is a well known two-dimensional image that when viewed is perceived to alternate between two different depth perspectives. **(B)** Rubin's vase-faces illusion alternates between figure and ground. **(C)** To elicit binocular rivalry, two dissimilar images are presented, one to each eye. The observer alternates between perceiving one image for a few seconds, followed by the other image for a few seconds and so on (with occasional short periods of mixed percepts).

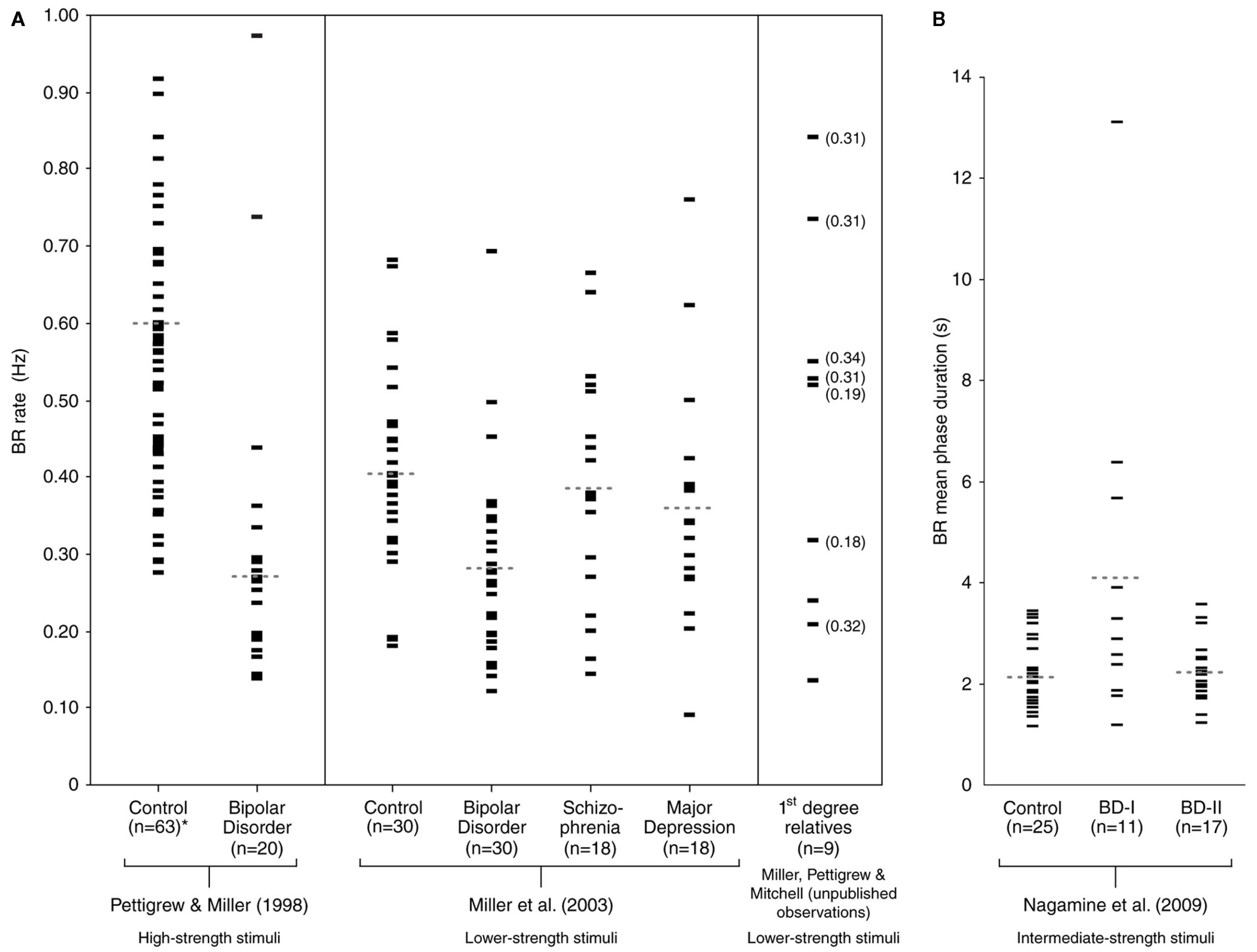

FIGURE 2 | Binocular rivalry in psychiatric groups. (A) In each subject group, the central tendency for BR rate (expressed in Hz) is indicated by the dotted line (medians in Pettigrew and Miller, 1998, and means in Miller et al., 2003; with *four control outliers in the former not shown: 1.11, 1.11, 1.19, and 1.48 Hz). BR rate in first-degree relatives are shown in the far right panel, with BD proband rates (where available) indicated in brackets. **(B)** The BR rate data from Nagamine et al. (2009) is expressed in mean phase duration, and each subject group's mean is indicated by the respective dotted line. Figure reprinted from Ngo et al. (2011).

on clinical diagnosis. This approach acts to increase the statistical power of such studies by more accurately classifying "affected" versus "unaffected" prior to genetic analyses. For this potential application too, slow BR rate is currently under investigation (Ngo et al., 2011).

The key criteria required for a trait to satisfy endophenotype status for heritable disorders (Gottesman and Gould, 2003; Kendler and Neale, 2010) include that it is: (i) associated with the condition (i.e., sensitive), (ii) heritable, (iii) reliable, (iv) unaffected by clinical state, (v) co-segregated with illness in families, and (vi) found in first-degree relatives more commonly than in the general population. Sensitivity of slow BR rate for BD has been discussed above. Heritability and reliability of BR rate were recently examined in a large-scale, 10-year study of normal monozygotic and dizygotic twins, aged 14 years ($n = 722$), 97 of whom were re-tested after 2 years (Miller et al., 2010; see **Figure 3**). Using high-strength stimuli, substantial genetic contribution to individual variation in BR rate was found, with the best-fitting model attributing 52% of the variance to additive genetic factors. The study also confirmed, with a large dataset, that BR rate is highly reliable within ($R = 0.93$) and between ($R = 0.70$) testing sessions. In a recent small twin heritability study, high monozygotic, but not dizygotic, twin concordance was confirmed for BR rate, and reported for Necker cube switch rate (Shannon et al., 2011).

With respect to the remaining endophenotype criteria, currently there are insufficient data on BR rate in relatives of BD probands to yet claim genetic correlation between slow BR rate and BD, but early data are promising (Ngo et al., 2011). Effects of clinical state in BD – i.e., mania, depression, euthymia – on BR rate remain to be clarified, however slow BR rate is evident in euthymic BD subjects (Ngo et al., 2011). Similarly, medication effects cannot yet be excluded, but do not appear to account for the trait (Ngo et al., 2011). Definitive assessment of state and medication effects requires BR rate measurement before and after state

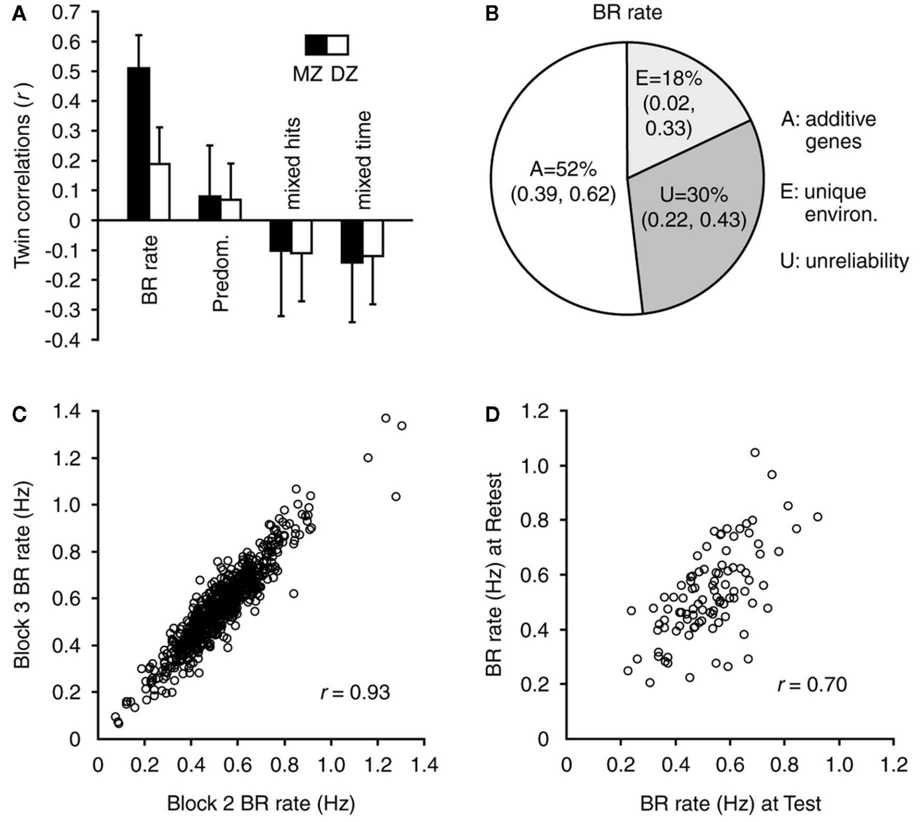

FIGURE 3 | Heritability and reliability of BR rate. These four panels show the population BR and genetic modeling data from a sample of 722 twins (Miller et al., 2010). **(A)** Twin correlations for BR measures in MZ and DZ twins (error bars indicate 95% confidence intervals). Correlations for BR rate were significant. Correlations for predominance (i.e., the amount of time spent perceiving one image relative to the other) and for mixed hits/time (i.e., number of, and time associated with, mixed percepts, or incorrect responses) were found to be not significant and therefore were not included in genetic modeling analyses. **(B)** The genetic modeling results indicate that the variance in BR rate was because of a substantial additive genetic component; plus unique environment and measurement unreliability over a period of 2 years. **(C)** Reliability of BR rate within a testing session was very high ($n = 722$). Note also the high degree of BR rate individual variation in this large dataset. **(D)** Reliability of BR rate was also high between testing sessions 2 years apart ($n = 97$). Figure reprinted from Miller et al. (2010).

and medication change in clinical subjects. Medication effects can also be addressed by way of pharmacological challenge studies in healthy controls (see below).

In addition, two factors that may affect BR rate and that are relevant in psychiatric populations are reaction time and eye movements. However, in the twin heritability study of BR rate (Miller et al., 2010), processing speed measures were not related to BR rate (additional publication in preparation), thereby eliminating reaction time differences as an explanation for individual variation in BR rate (see also Nagamine et al., 2009). Regarding eye movements, in the context of BR these are not thought to be the cause of perceptual switches, but do have an influence (with saccade frequency being positively correlated with BR rate; van Dam and van Ee, 2006). However, studies of eye-movement profiles in BD generally show no saccade frequency anomalies during smooth pursuit tasks (Martin et al., 2007). Hence, differences in eye-movement profiles are also considered unlikely to account for slow BR rate in BD. Nonetheless, a potential effect of eye movements on BR rate in clinical psychiatric groups cannot yet be excluded and remains to be directly assessed.

In pharmacological studies, alcohol and caffeine decrease and increase, respectively, both AFR and BR switch rate (George, 1936; Seedorff, 1956). These agents similarly affect AFR rate in subjects with SCZ or BD (Ewen, 1931). More recently, pharmacological studies have been applied in healthy controls, and have shown that BR rate decreases in the presence of serotonin agonists, with the serotonin receptor subtype 5-HT$_{1A}$ implicated in mediating this effect (Nagamine et al., 2008). However, 5-HT$_{2A}$ may also play a role (Carter et al., 2005) and it remains unclear at what site in the brain – from raphe nucleus in the brainstem, to limbic regions, to visual cortex – such effects are exerted (Nagamine et al., 2008). Noradrenergic pathways also appear to be involved in AFR and other rivalry types (Einhäuser et al., 2008). These reports suggest targets for candidate gene studies (in addition to GWAS) that could be undertaken to examine molecular mediators of individual variation in perceptual rivalry rate (e.g., Kondo et al., in press).

The findings of slow BR rate in BD and of substantial genetic contribution to individual variation in BR rate, suggest that the stage is now set for vigorous pursuit of genetic and molecular determinants of rivalry switch rate. Moreover, in light of this new direction in perceptual rivalry research, an animal model of the phenomenon that could readily enable genetic and pharmacological manipulation of switch rate would be highly advantageous. As it turns out, one such model has been recently reported for *Drosophila melanogaster* (Tang and Juusola, 2010). Moreover, the *Drosophila* model is also (i) amenable to direct mechanistic examination, and (ii) beginning to be understood at the level of attentional selection and suppression.

PERCEPTUAL RIVALRY AND ATTENTION

Attention can be as difficult to describe as it is easy to understand intuitively. Attention describes our ability to focus our perception on one stimulus (or group of related stimuli), while filtering out other simultaneous stimuli that are less relevant at any moment (Posner et al., 1980). The relevance of a stimulus is dependent on its salience, and salience itself clearly depends on the history of events as well as on the physical features of the stimulus. To better segregate these distinct contributions to salience, attention is often conveniently compartmentalized as "bottom up" (guided by the physical stimulus only, e.g., loudness or brightness), or "top down" (guided by past experience; Treisman and Gelade, 1980; Itti and Koch, 2000). However, a more fundamental feature of any attention process is that it involves suppression. Attention is often viewed as a "spotlight" (LaBerge, 1983; Eriksen and St James, 1986), perhaps because that is how the process feels to our conscious minds. However, to identify and measure attention-like processes in animals – any animal from flies to apes – requires some evidence of suppressed responsiveness to competing stimuli (Van Swinderen, 2005). Otherwise, an animal's choice can always be argued to be a simple reflex, much like bacteria swimming up a chemical gradient, rather than a cognitive process where most stimuli were *blocked* from having a behavioral consequence and only one or a few not blocked. The role of suppression mechanisms in the evolution of animals is evident: to make effective connections between stimuli – to learn – requires blocking out the contexts, or the multitude of stimuli that have less predictive value, regardless of how salient they may be. To understand how salient stimuli are *prevented* from producing a behavioral response in animals seems just as important for any study of attention as is the more anthropocentric notion of a spotlight.

How can stimulus suppression be identified and measured in simple animals such as flies? The simplest way to do this is by studying sleep, and the decreased behavioral responsiveness associated with this altered arousal state. The discovery a decade ago that flies sleep (Hendricks et al., 2000; Shaw et al., 2000) suggested a broader role for stimulus suppression mechanisms, perhaps also relevant to attention-like processes in these simple animals – which were identified soon thereafter (Van Swinderen and Greenspan, 2003; Van Swinderen, 2007a). The special case of perceptual rivalry presents exactly the kind of stimulus conditions that, if identified in a genetic model such as *Drosophila melanogaster*, would allow one to investigate how an animal suppresses responsiveness to one salient stimulus while responding to another. By reducing the attention problem in the *Drosophila* model to two equally salient choices, selection and suppression dynamics might be more easily studied and possible underlying mechanisms unraveled. Before putting forward the case for attention and rivalry in flies, we first review the connection between these related phenomena in humans.

Binocular rivalry has been long considered in terms of attention, with respect to notions of both voluntary and involuntary attention (Von Helmholtz, 1867; James, 1890; Sherrington, 1906). It is well known that BR and AFR predominance and switch rate are subject to some degree of voluntary control, though such modulation is modest (especially for BR) and the perceptual switches cannot be prevented (Wheatstone, 1852; Von Helmholtz, 1867; Breese, 1899; Lack, 1978). In support of high-level theories of the phenomenon, semantic content in presented stimuli can also influence percept dominance (Walker, 1978). Moreover, during BR and AFR, engaging in a concurrent attentional task has been shown to influence the rate of perceptual alternations (Wallace and Priebe, 1985; Paffen et al., 2006; Alais et al., 2010). Investigators have also previously highlighted the overlap between rivalry and selective attention in regard to both cortical areas and mechanisms involved (Logothetis, 1998; Lumer et al., 1998; Leopold and Logothetis, 1999; Stoner et al., 2005). Other psychophysical studies have shown that voluntary attention facilitates the induction and maintenance of perceptual dominance of a spatially cued target image (Ooi and He, 1999; Chong and Blake, 2006; Hancock and Andrews, 2007), while involuntary attention also facilitates induction of dominance in this selective attention paradigm (Mitchell et al., 2004; Chong and Blake, 2006; Hancock and Andrews, 2007; Kamphuisen et al., 2007). The psychophysical evidence therefore argues for a strong modulatory role of attentional selection in BR.

Just as notions of attentional selection have contributed to theorizing about rivalry, so too have notions of suppression. In contrast to the high-level attentional explanations of rivalry discussed above, an earlier body of work by Fox, Blake and colleagues favored a low-level explanation of the phenomenon. This view was based largely on the finding of reduced sensitivity to detection of test probes presented whilst a stimulus was suppressed compared with while the stimulus was visible, even though the probe's stimulus features were different to those of the suppressed stimulus (Fox and Check, 1968, 1972; Wales and Fox, 1970). This finding suggested perceptual suppression during BR was non-selective (i.e., not limited to particular features of the suppressed stimulus) and led to a low-level neural theory of BR (Blake, 1989). Other psychophysical and brain-imaging studies have also led theorists to suggest that the neural mechanisms underlying dominance (selection) during rivalry may be distinct from those underlying suppression (Logothetis, 1998; Blake, 2001; Blake and Logothetis, 2002). More recently, brain-imaging studies and new dichoptic presentation paradigms (continuous flash suppression; Tsuchiya and Koch, 2005) have been employed to further examine the neural basis of rivalrous perceptual suppression (Lin and He, 2009).

Around the time that notions of attention were applied to BR (Von Helmholtz, 1867), other scholars noted that perceptual rivalry could also occur in non-visual modalities, such as olfaction and audition (Valentin, 1844; Fechner, 1860). Recently, similarities and differences between rivalry in visual and non-visual domains have been examined. For example, perceptual switches in both auditory and visual rivalry types (including AFR) were found to be associated with pupil dilation (Einhäuser et al., 2008; cf. Hupé et al., 2009). Others have found a lack of correlation between the temporal properties of rivalry (including rate and predominance) in different modalities within individuals (Pressnitzer and Hupé, 2006; Carter et al., 2008), though Hupé et al. (2008) did show an association between auditory and visual rivalry rates within individuals. However, the temporal dynamics of simultaneous presentation of these rivalry types revealed limited crossmodal interactions (e.g., a brief effect of crossmodal congruence on perceptual dominance), which these investigators argued was evidence for a distributed processing account of perceptual disambiguation, over a central supramodal mechanism.

Several other studies though, have argued for multisensory and attentional processing in BR, based on the following findings: directional sound increases perceptual dominance of a directionally congruent motion stimulus (Conrad et al., 2010); tactile stimulation increases perceptual dominance and reduces suppression of a congruent grating orientation (Lunghi et al., 2010); increased perceptual dominance and reduced suppression of a moving stimulus that was congruent with an individual's hand movement direction (Maruya et al., 2007); voluntary attention to non-visual congruent stimuli (auditory and/or tactile) enhances attentional control of visual dominance (van Ee et al., 2009); and an olfactory stimulus increases dominance and decreases suppression of a visually congruent image (Zhou et al., 2010). These findings therefore raise the possibility of a supramodal attentional mechanism that resolves conflicting sensory input during rivalry.

Further evidence for the role of attention in BR comes from brain stimulation studies in which activation of attentional structures modulates predominance during BR and AFR (Miller et al., 2000; Ngo et al., 2007, 2008), and from recent EEG and fMRI studies (Watanabe et al., 2011; Zhang et al., 2011). In the next section, we maintain focus on the visual domain and examine the evidence for attention and rivalry in a miniature brain.

ATTENTIONAL SWITCHING AND PERCEPTUAL RIVALRY IN *DROSOPHILA MELANOGASTER*

It comes as a surprise for some people to learn that flies have a brain. Until quite recently, the fruit fly was not considered a useful model for investigating higher-order cognitive phenomena such as selective attention, let alone perceptual rivalry. Rather, a century of work had already proven that *Drosophila melanogaster* was an excellent model for unraveling fundamental biological processes, such as gene regulation or development (for an excellent recent review on *Drosophila* applications and relevance to neuroscience, see Bellen et al., 2010). Although the anatomy of human and fly brains is in many respects substantially different (e.g., 100 billion versus 200,000 neurons in each animal, respectively), there are some organizational similarities (e.g., the fly brain is also largely divided across the midline) and the neuronal processes and molecules involved are remarkably similar in each case. For example, dopamine and serotonin control arousal states in both flies and humans (Van Swinderen and Andretic, 2011). For a complex phenomenon such as rivalry, the difference in neuroanatomy between flies and humans can be turned to an advantage: if both creatures display perceptual alternations via a substantially different neuroanatomy, then mechanistic comparisons between both species should highlight the fundamental requirements for rivalry, rather than the structures that may have co-evolved with rivalry in one animal alone. Thus, fly-human comparisons are also extremely valuable for understanding common phenomena, such as sleep and attention. A brief overview of *Drosophila* behavior genetics will highlight how the vinegar fly was promoted from humble beginnings to its growing status alongside human psychiatric research (for a more extensive review on using *Drosophila* for neuropsychiatric research, see O'Kane, 2011).

Behavior can be genetically dissected, much like any physical phenotype. A revolutionary approach by Seymour Benzer and colleagues in the 1960s saw *Drosophila* genetic methods being applied to behavior (Hotta and Benzer, 1970). Indeed, researchers soon found *Drosophila* to be an ideal organism for dissecting the genetic underpinnings of various behaviors: one could screen for mutants, much like with viruses or bacteria, but in an animal endowed with a brain. The first behavioral screens were the simplest: responsiveness to light, seemingly a simple reflex, was found to be variable among populations of flies, and odd mutants such as *photophobia* (which ran away from light) were among the first genetic manipulations of behavior in flies (Benzer, 1967). Combined with parallel advances in molecular genetics, the genes *causing* the behavioral effects could be identified, and cellular/molecular pathways controlling these behaviors could be understood. Among the many triumphs resulting from this approach to dissecting behavior, two stand out: circadian rhythms and memory formation (for a review, see Vosshall, 2007). While we now know much about the cellular and molecular underpinnings of learning/memory and circadian rhythms in flies, we know far less about how the fly brain actually controls behavioral choices made by the animal. In part, this is because *Drosophila* studies have mostly measured behavior as a probabilistic variable, where the outcome of a population determines the phenotype that is being associated with gene effects. Indeed, when examined at a population level, flies behave probabilistically (Quinn et al., 1974). But any fly behaviorist will admit that, when examined individually, their flies display idiosyncrasies, much like humans do. Even Seymour Benzer, who pioneered population approaches to dissecting fly behavior, noted that "an individual fly will make its own decision." The highly successful strategy of studying fly behavior at a population level has been less useful for understanding decision-making in flies, or whether perceptual rivalry might exist in this simple animal. Another paradigm, the flight arena, would prove most insightful in this regard.

When humans are engaged in visual psychophysical experiments in a psychology laboratory, they are typically asked to sit still and fixate on a point on a screen while responding to queries about what they see. Responses are either verbal, or via button presses. The *Drosophila* flight arena presents a quite similar scenario for flies (**Figure 4A**): individual flies are tethered to a rod while they respond with flight torques to visual stimuli displayed on a rotating drum that surrounds them (Heisenberg and Wolf, 1984; see Brembs, 2008, for a visual explanation of the device). A torque meter attached to the tether measures ongoing behavioral choices (torque spikes to the left or to the right) made by the fly, and negative feedback from the torque meter (termed "closed-loop" mode) can be used for the fly to itself control the angular position of a visual scene displayed on the inside of the drum. More recent designs use wing-beat detectors and virtual displays on LED arenas

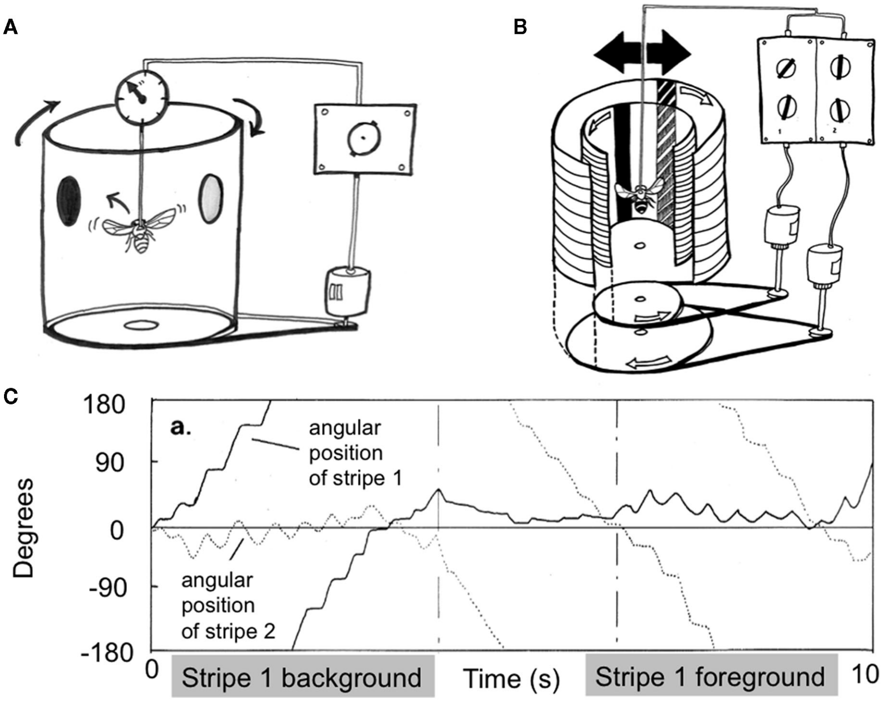

FIGURE 4 | *Drosophila* flight arena concept and first rivalry experiments. **(A)** Tethered flies respond to visual stimuli displayed on a drum surrounding them by modulating their flight dynamics. A torque meter measures the flies' left or right turn choices, and negative feedback can be used for the fly to control the angular position of displayed objects. Tethered flies will tend to fixate on objects, by modulating their torque behavior to keep attended objects in front of them. **(B)** Adding an extra visual layer, as well as a separate control system requiring a distinct behavioral response, allows the fly to fixate on one or the other object separately. **(C)** An early experiment showing alternating figure–ground selection in flies presented with two competing objects, as in **(B)**. Reprinted with permission, from Heisenberg and Wolf (1984, p. 274).

can be used to accomplish the same goal of measuring behavioral responses to visual stimuli in individual flies (Lehmann and Dickinson, 1997; Sareen et al., 2011). It may be somewhat surprising to note that there are few visual paradigms in any animal models that offer such a careful level of control as the *Drosophila* flight arena: since the animal is tethered, the fly only sees and responds to what is presented to it under a defined set of conditions. By minimizing any visual "contamination" (such as may be generated by the animal's own movement through space), the tethered flight paradigm provides exactly the kind of experimental conditions required for a study of perceptual rivalry. In contrast, a rat (for example) provided with visual choices while running around a cage is less amenable to studies of rivalry, because the experimenter can never be entirely certain of what the animal is seeing at any one time. However, restraining an animal often prevents any behavioral report, presenting a serious dilemma for rivalry studies in animals. Indeed, between head-restrained, lever-operating primates, and tethered flies, there are strikingly few visual perception paradigms conducive to the stringent conditions required for studying rivalry in awake animals.

In the flight arena, a tethered fly will respond to stimuli by turning in the same direction as perceived movement (Heisenberg and Wolf, 1984). This behavior is called an optomotor response, and like the optokinetic responses of humans (e.g., Masseck and Hoffmann, 2009), it is considered a simple reflex that is important for image stabilization and gaze control. Considerable work has been done to describe fly optomotor responses to a variety of visual parameters, and most were documented in the early 1980s by Martin Heisenberg and Reinhard Wolf in their "little green book" on vision in *Drosophila* (Heisenberg and Wolf, 1984). Careful reading of that seminal work will reveal the first experiments suggesting perceptual rivalry in flies (e.g., pp. 174–175). Instead of presenting flies with just one visual stimulus printed on one layer of the surrounding drum, they presented two objects on separate transparent layers, each moving with a fixed angular velocity relative to one another, and thus each requiring an opposing behavioral response for closed-loop stabilization (**Figure 4B**). Therefore, if the fly "fixated" on one object (by modulating its torque behavior accordingly), the other would spin wildly, and vice versa for the alternate object. Heisenberg and Wolf (1984) noticed that a fly would often select one object as a "foreground" and the alternate as the "background," by adjusting its optomotor balance to one while stabilizing the other by means of torque spikes. After a period of time, the fly would then switch its behavior and reverse the foreground-background contingency (**Figure 4C**). Optomotor theory (see Borst et al., 2010, for a review) would suggest that flies adjust their torque to the mean of the two values, resulting in the two objects moving with equal (reduced) speed in opposite directions. Although this outcome did occur too at times (much like the occasional mixed and grid percepts during human rivalry with orthogonal gratings), these first closed-loop experiments showed that flies could alternate their behavioral response between two competing percepts presented simultaneously.

Behavioral alternations between competing percepts were also demonstrated in open loop experiments (where the fly cannot control the angular position of objects). In these experiments (Heisenberg and Wolf, 1984, pp. 188–191), flies were presented with two competing vertical stripes, one to either eye (at 45° to the left or right of a forward-facing direction). The fly was found to be able to adjust its torque behavior to oscillatory movements of either object *independently*, alternating its behavior between two choices presented bilaterally (**Figure 5A**). In addition to suggesting that rivalry may also be partitioned between the two hemispheres of the fly brain, these experiments showed that the fly does not require closed-loop control to display perceptual alternations. In this way, behavior during these visual competition experiments resembled selective attention: flies alternately selected or suppressed responses to either object, and this occurred with a defined tempo that seemed variable among individuals. More dedicated follow-up experiments would likely have identified and quantified fly rivalry, and individual variation therein, but this line of research was not pursued at the time. The preparation was exploited instead over the following decades for two other challenges: visual learning (e.g., Wolf and Heisenberg, 1991; Brembs and Heisenberg, 2000) and flight control (e.g., Dickinson et al., 1999; Sherman and Dickinson, 2003).

Evidence for rivalry in flies was found again in a recent study, by combining tethered flight and electrophysiology in *Drosophila* (Tang and Juusola, 2010). The authors utilized a similar tethered set-up as in the paradigm described above, but instead placed the fly between two moving gratings – one presented to either eye (**Figure 5B**). Two tiny electrodes recorded local field potential (LFP) and spiking activity from either optic lobe while the fly responded in open loop (i.e., without being able to control the optic flow) to these competing visual stimuli (**Figure 5C**). The experiment presented a visual conflict similar to Heisenberg and Wolf's (1984) original experiment consisting of two opposing oscillating bars (discussed above). As in some of that original flight arena work, in the current paradigm flies were observed to alternate their flight direction choices between the right and the left moving grating. Again, this was not expected according to optomotor theory: equivalent optic flow presented to either eye should either (i) elicit a landing response (Tammero and Dickinson, 2002), or (ii) produce straight flight as a result of averaged optomotor responses from either eye (Srinivasan et al., 1999). Instead, flies displayed a number of behaviors that were more reminiscent of visual attention than optomotor reflexes: first, left or right flight choices were not made immediately following bilateral image motion, but was often delayed for up to a few seconds. Then, flight behavior was sustained in either direction rather than saccadic, as is more common for classical optomotor responses in a rotating drum (Heisenberg and Wolf, 1984). Third, flies

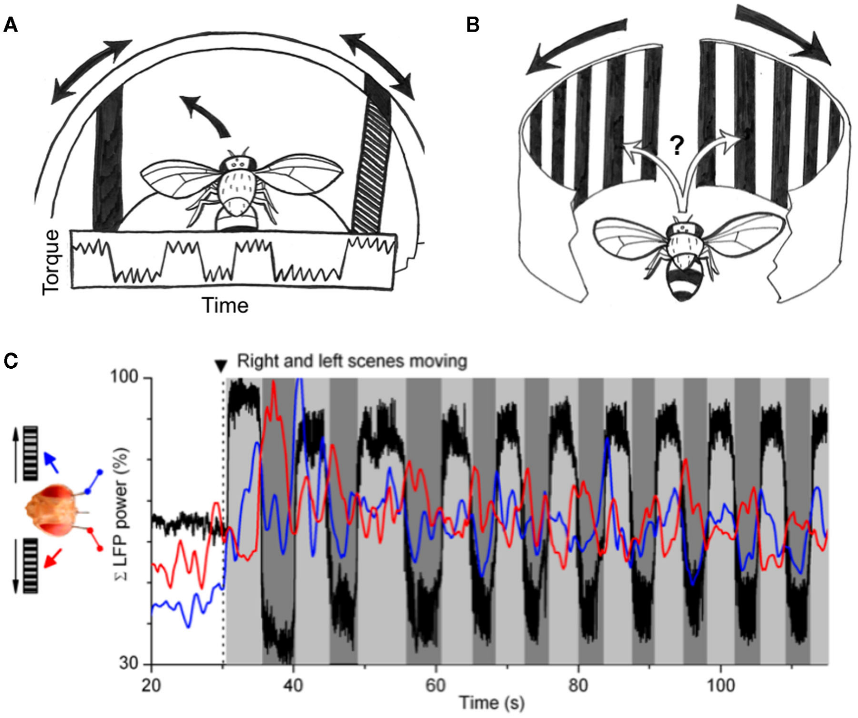

FIGURE 5 | Perceptual rivalry in *Drosophila*. (A) Original experiments by Heisenberg and Wolf (1984) showed that flies presented with two oscillating bars, one presented to either eye, would alternate their torque responses to either object (details in text). **(B)** Competing moving gratings presented to either eye of the fly also revealed alternating responses, rather than straight flight. **(C)** Recordings from the left and right brain of flies performing as in **(B)** revealed alternating local field potential (LFP) dynamics correlated with the behavioral switches. Black trace: torque behavior; red trace: left-brain LFP; blue trace: right-brain LFP. Figure reprinted from Tang and Juusola (2010).

completely ignored optomotor flow from the contralateral side for seconds at a time. Fourth, flies alternated between the stimuli, and finally, flies displayed individual variability in their alternation dynamics. The stage was thus set to question whether flies were indeed attending to the competing gratings, and whether brain recordings might exhibit alternating activity that correlated with the behavioral choices (**Figure 5C**).

Behavior alone increases brain responses in flies. This was shown recently in two different studies in which *Drosophila* brain responses to moving gratings were boosted when the animals were actively walking (Seelig et al., 2010) or flying (Maimon et al., 2010). Tang and Juusola's (2010) recording preparation probed this effect further to ask how such boosted activity might be partitioned in the fly brain when the animals were making active behavioral choices to follow one or another competing visual stimulus. Two measures of brain activity were examined, LFPs and spikes. LFPs are voltage differentials between recording electrodes (in this case, between either optic lobe and a reference in the central brain), usually sampled around 500 Hz. LFPs typically reveal oscillatory activity in brains, much like electroencephalograms taken from human scalps. Spikes, typically sampled above 25 KHz, represent single neuron firing. Typically, these are resolved as coming from single neurons (termed "units") by simultaneous recordings from multiple close wires (tetrodes). In Tang and Juusola's (2010) study, only one wire was implanted in each optic lobe, so spikes in that case most likely represent summed activity from multiple nearby action potentials. The study found that activity for both spikes and LFPs increased *unilaterally*, on the side associated with a behavioral choice (left or right). Although already a striking result, a closer examination of the LFP activity revealed even more interesting dynamics relevant to studies of rivalry. First, initial choices to fly left or right were *preceded* by a boosted LFP, sometimes by several hundred milliseconds. This effectively separated the behavior from brain activity, suggesting that the brain response might gate the behavior, and not vice versa. Second, when the fly alternated behavioral choices between the visual stimuli, LFP activity again predicted when a behavioral switch might happen. This was evidenced by calculating a ratio between LFP activity from either optic lobe, and plotting how LFP bias assigned to either hemisphere changed on average during a choice bout. Finally, the LFP frequencies found to be most increased during such alternating choice behavior were in the 20–50 Hz range, a frequency domain found previously in flies (Van Swinderen and Greenspan, 2003; Van Swinderen, 2007a; Van Swinderen et al., 2009) and other animals (e.g., Engel and Singer, 2001) to be involved in attention-like states.

The observation by Tang and Juusola (2010) that brain activity in the fly can precede and predict behavioral choices in a rivalry-like situation suggests that alternations in attention might exist independent of behavior, even in the small insect brain. Indeed, previous work in *Drosophila* has shown that 20–30 Hz LFP activity can be modulated by visual salience, even without associated behavioral responses, and that these LFP frequencies can be selected or suppressed in response to competing visual stimuli in classical conditioning or novelty paradigms (Van Swinderen and Greenspan, 2003; Van Swinderen, 2007a; Van Swinderen et al., 2009). In this slightly different recording preparation, tethered flies inside a drum of LEDs are exposed to moving stimuli rotating continuously around them (once every 3 s) while LFPs are recorded from their brain (**Figure 6A**). Competing stimuli presented 180˚ apart evoke 20–30 Hz responses when either object sweeps in front of the fly (**Figure 6B**); the objects are thus "tagged" by their timing on the rotating panorama. Interestingly, LFP responses to the competing stimuli are not stable through time when these are presented continuously to the fly for successive rotations. Instead, 20–30 Hz power assigned to one stimulus or the other may wax and wane during each successive presentation. Quantification of this process revealed 20–30 Hz alternation dynamics, where LFP activity would be increased for one object for multiple sweeps while activity was suppressed for the alternate object, and vice versa (**Figures 6C,D**). This dynamic appeared non-random in wild-type

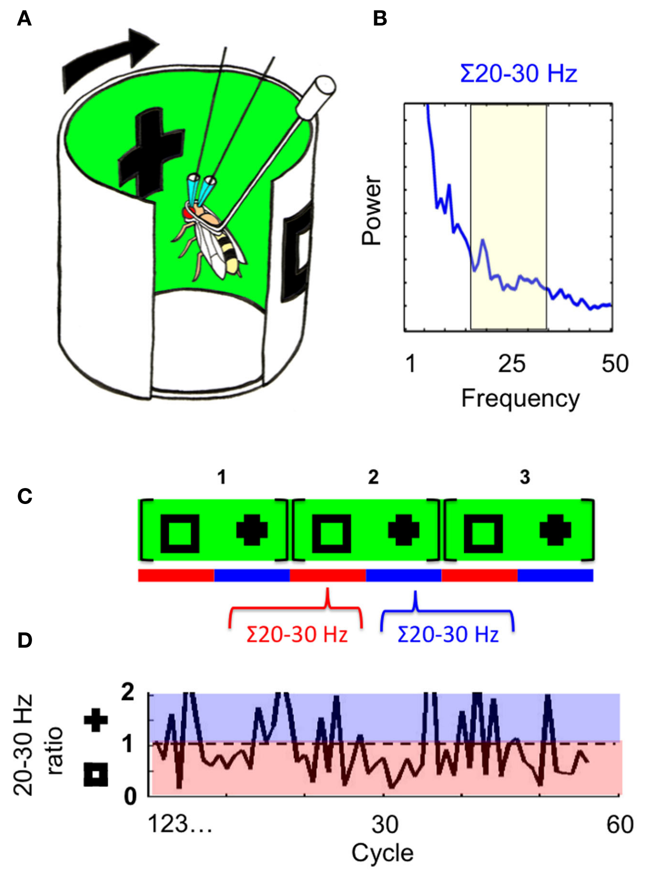

FIGURE 6 | Attention dynamics in the fly brain. (A) The recording arena. Flies are presented with moving visual stimuli displayed on a wrap-around LED screen. Two objects, a square and a cross, are displayed 180˚ apart. **(B)** A spectral analysis of the flies' LFP in response to the moving visual stimuli, from 1 to 50 Hz. The 20–30 Hz domain is selected for further analysis. **(C)** The cross and the square sweep recurrently in front of the fly every 3 s (every cycle). Twenty to 30 Hz responses are measured separately for each object sweep within a cycle (red and blue bars). **(D)** A ratio of the 20–30 Hz response evoked by either object is plotted, for each consecutive cycle. Ratios in the blue domain reveal increased responsiveness to the cross, and in the red domain show increased responsiveness to the square. Sixty cycles, or 180 s of data, are shown. Figures reprinted from Van Swinderen and Brembs (2010).

flies (when compared to temporal permutations of the same LFP data), suggesting a persistence of attention-like responses assigned to either competing object (Van Swinderen, 2007b; Van Swinderen and Brembs, 2010).

A critical feature of Tang and Juusola's (2010) findings was their demonstration of alternating unilateral LFP activity during visual rivalry. In relation to this, they note the possibility that the fly brain spontaneously generates "rivalry between its left and right optic lobes by interhemispheric switching of their activity states" (p. 13). Tang and Juusola (2010) suggest this on the basis of their own electrophysiological data and a similar mechanistic model of rivalry in humans (Miller et al., 2000). The brain stimulation evidence garnered in support of the human interhemispheric switch model of rivalry, and the model's basis in the context of attentional selection, has been reviewed in detail elsewhere (Miller, 2001; Pettigrew, 2001; Miller and Ngo, 2007; Ngo et al., 2007, forthcoming). We do not here discuss in detail the issue of rivalry mechanisms (see Miller, forthcoming). These remain the subject of intense investigation and ongoing debate. Although there is agreement within the field that multiple levels of the visual hierarchy are involved, exactly what is rivaling at the neuronal population level in humans and other primates is still unknown.

It is debatable just how much support is provided by fly interhemispheric switch activity during rivalry, for the proposal that human rivalry is an interhemispheric switch phenomenon. After all, fly brains and human brains are substantially different (despite their similarities, as discussed above), with human brains possessing massive interhemispheric connections and discrete cortical area functional specialization. These and other differences may suggest an entirely different mechanism of competition in human and fly brains during rivalry. While this is certainly a possibility, we consider it remarkable that miniature brains demonstrate apparently higher-order cognitive phenomena such as selective attention and indeed, perceptual rivalry. It would not be that surprising therefore, in our view, if the fly brain's method of perceptual conflict resolution, involving switching between unihemispheric attentional selection mechanisms (Tang and Juusola, 2010), turns out to be one which human brains also employ (Miller, 2001). If so, this also suggests avenues for deciphering both the molecular mechanisms of slow rivalry rate in BD and the underlying pathophysiology of BD (Pettigrew and Miller, 1998; see below). Either way, although interhemispheric switching as a biological mechanism has been reported to mediate phenomena as diverse as sleep and birdsong (reviewed in Ngo et al., forthcoming), the data of Tang and Juusola (2010) are the first electrophysiological evidence to demonstrate such a mechanism can mediate perceptual rivalry.

UTILIZING THE GENETIC WORKHORSE, *DROSOPHILA*

Thus far, we have discussed the clinical relevance of rivalry rate differences, the relationship between attention and rivalry, and behavioral and electrophysiological properties of attentional switching in flies. In this section, we describe how the *Drosophila* rivalry model might be utilized to probe the genetic and molecular basis of individual variation in switch rate, as well as other applications relevant to clinical psychiatry. First however, it might be argued that more work needs to be done to establish that *Drosophila* switching behavior in the tethered flight arena is indeed rivalry. Tang and Juusola (2010) point out that conventional BR involves conflicting visual stimuli occupying overlapping regions of the visual field, which is not the case with their presentation of non-overlapping monocular flow fields. Alternating torque responses might be reasonably considered evidence of alternating attentional selection (Heisenberg and Wolf, 1984; Maye et al., 2007), and indeed Tang and Juusola's (2010) recent electrophysiological work suggests further that this is in fact alternating unihemispheric attentional selection (interhemispheric switching). As discussed above, exactly such a process has been proposed to mediate rivalry in humans, although this is not yet conclusively established and it remains possible to question whether fly behavioral alternations indeed represent rivalry.

In our view however, we find it difficult to conceive of fly behavioral alternations as anything but rivalry, because the fundamental elements of rivalry phenomena are satisfied: the fly is presented with conflicting visual stimuli, albeit in non-overlapping visual field regions, and rather than respond in accordance with both sensory inputs (which it does however do some of the time, just as in human rivalry), it alternates between them with a period of seconds. The lack of overlapping visual fields with monocular flow stimuli in the tethered flight arena might indicate a difference from human BR, but human AFR similarly does not involve dichoptic presentation of field-overlapping stimuli, yet is quite clearly a form of perceptual rivalry. Indeed, AFR is a form of perceptual rivalry with many aspects in common with BR, including similar temporal properties, similar predominance modulation by activation of unilateral attentional structures, and similar slowing in BD. Perhaps not surprisingly therefore, fly behavioral switching has itself been reported in the context of visual figure–ground reversals (discussed above).

The path is open to now explore similarities and differences between fly and human visual rivalry. Most obvious would be exploration of temporal properties (alternation dynamics) of fly switching behavior, in terms of known human rivalry features, such as fit to a gamma distribution and other distributions (Brascamp et al., 2005), successive independence of phase durations (Fox and Herrmann, 1967), modulation of rate and predominance by stimulus strength parameters (Howard and Rogers, 2012), and within-subject rate reliability. Using more versatile LED arenas (**Figure 6A**), a host of other features of human rivalry could also be examined with respect to fly rivalry: selective versus non-selective suppression, involuntary attention effects, rapid eye-swap rivalry, interocular grouping (coherence) rivalry, perceptual and associative learning effects, priming and adaptation effects, onset rivalry, non-visual input and crossmodal effects on temporal dynamics, and perceptual stabilization with intermittent presentation. For all such phenomena to be examined, the fly model also enables assessment of individual variation therein (and its genetic basis), as well as their electrophysiological correlates. In addition, aspects of fly rivalry could be looked for in humans, including for example, neural activity that significantly precedes a perceptual switch. Indeed, such activity has recently been observed with human intracranial electrocorticogram recordings during rivalry (Tsuchiya et al., 2011). Brain-imaging and EEG in humans has also demonstrated with bistable motion rivalry and BR that right-sided cortical activation preceded transition-related activity, thus implicating these regions in the instigation of perceptual transitions (Sterzer and Kleinschmidt, 2007; Britz et al., 2011; cf. Knapen et al., 2011). Moreover, the fact that some degree of voluntary attention can be exerted on perception during human rivalry is also mirrored in the experiments by Tang and Juusola (2010), who consider that flies similarly have some degree of control over their torque switching behavior.

Most importantly however, *Drosophila's* propensity for genetic manipulation means it is an ideal animal model of human rivalry. Thus, not only can it be utilized to potentially progress understanding of the genetics of attention (Posner et al., 2007; Bellgrove and Mattingley, 2008), it also offers a unique opportunity to probe the genetic and molecular determinants of normal and pathophysiological variations of rivalry rate. That is, *Drosophila* mutants can be compared with wild-type flies to examine the effect of mutant genotypes on flight torque switch rate. Through understanding the molecular implications of *Drosophila* mutants that exhibit abnormal rivalry dynamics, the molecular basis of switch rate determination might be slowly unraveled. This approach in flies may further suggest candidate gene studies in humans, to again probe the molecular basis of rivalry rate variation. For studies of the genetic and molecular basis of BD, this approach too may shed light. Thus postulates for the genetic basis of BD (e.g., Ferreira et al., 2008; Craddock and Sklar, 2009) can be examined by development of relevant *Drosophila* strains.

Although the tethered flight arena for *Drosophila* has provided the best insight to date on the possibility of perceptual rivalry in flies, it is less ideal for screening of genetic variants potentially useful for comparative studies with humans. Flies are tested one at a time in the arena – which is not conducive to large-scale screens – and the insects must fly for extended periods in order to report their perceptual choice dynamics, which is not guaranteed in mutant strains potentially burdened with pleiotropic defects. Thus, a dilemma presents itself, should we consider a *Drosophila* strategy to understanding perceptual rivalry: tethered, single fly assays are most revealing about rivalry, but least efficient for *Drosophila* genetic strategies. What are some possible strategies around this stumbling block?

The simplest solution is a brute force approach. The tethered flight arena is still amenable to genetic dissection; several studies have been published using this paradigm to test mutant strains and to dissect visual perception, learning, and saliency circuits in the *Drosophila* brain (Liu et al., 2006; Rister et al., 2007; Zhang et al., 2007; Pan et al., 2009). Provided that the mutants can fly sufficiently well, and that the questions asked are sufficiently narrow, the preparation does allow for genetic analysis. One drawback from being constrained to a narrow reverse-genetic strategy, however, is that little genetic exploration is possible along the lines of Seymour Benzer's original idea of uncovering new genes or circuits in an unbiased way. For example, almost all of the insight on visual learning in *Drosophila* has been an offshoot from olfactory learning studies, where the same genes or systems that were uncovered in olfactory learning screens were tested for visual learning. There is no strong reason to believe why these different memory systems (visual and olfactory) should be subserved by the same molecules or circuits in the fly brain, and indeed the evidence points to the contrary (Liu et al., 2006; Pan et al., 2009; Ofstad et al., 2011).

To get around the problem that the genetic variants need to fly, one solution is to screen by electrophysiology correlates alone. As we have seen above, the tethered non-flying fly still reveals attention-like responses in brain activity (Van Swinderen and Greenspan, 2003; Van Swinderen, 2007b) and these were found to alternate non-randomly in wild-type flies (Van Swinderen, 2007b; Van Swinderen and Brembs, 2010). Brain response dynamics to competing visual stimuli were altered in key variants, such as *radish*, a mutant that affects visual attention (Van Swinderen and Brembs, 2010). One could imagine a high-throughput electrophysiology paradigm where a succession of mutants are skewered with a multi-channel probe (as in Van Swinderen and Greenspan, 2003) to determine brain LFP dynamics in response to competing visual stimuli in an LED arena.

A simpler solution would be to utilize an alternative behavioral paradigm as a first-pass screen for rivalry phenotypes. The rate at which an animal may be switching its focus of attention may be difficult to quantify outside of tethered paradigms, but relatively easy to screen in population assays because of associated behavioral effects. The *radish* mutant in *Drosophila* is a case study in this regard. In brain-recording paradigms, *radish* mutants display random alternation dynamics in LFP responsiveness to competing visual stimuli, as discussed above. The same mutant displays a 1–2 Hz oscillation in activity at the torque meter, but only when presented with the competing visual stimuli (Van Swinderen and Brembs, 2010). Although both of these phenotypes (random 20–30 Hz dynamics in the brain and torque oscillations) are consistent with a perceptual rivalry defect, these phenotypes were not used to originally identify *radish* as a potential rivalry mutant. Rather, a high-throughput optomotor maze paradigm was used (Van Swinderen, 2007a; Van Swinderen and Flores, 2007). In this paradigm, populations of flies walk through eight consecutive choice points while they are exposed to moving gratings displayed on a computer monitor. A tendency to follow motion (the optomotor response) produces a bias in the distribution of flies at the end of the maze. This distribution bias was compromised in *radish* mutants, and further experiments adding competing visual stimuli to this paradigm revealed that the mutants were more distractible than wild-type flies (Van Swinderen and Brembs, 2010). Therefore, a simple and efficient behavioral assay such as the optomotor maze can be used to screen for potential rivalry phenotypes, producing candidates to be then tested more thoroughly in the arena or by electrophysiology. An automated and multiplexed version of the maze design (Evans et al., 2011) should allow for high-throughput screening of mutant strains potentially relevant to perceptual rivalry. In addition to providing an efficient platform for screening perceptual phenotypes, the visual maze design is also easily adapted to testing pharmacological influences on behavioral alternations. For example, *radish* mutant behavior in the maze was rescued from random alternations to significant optomotor responses by feeding flies methylphenidate (Van Swinderen and Brembs, 2010). A large-scale pharmacological screen of compounds that may influence perceptual alternations (e.g., psychotropic medications) would be easy to implement on this simple behavioral platform. Follow-up pharmacological studies could then also occur in the tethered flight arena.

Armed with the three different paradigms available to start screening for rivalry in flies (visual mazes, tethered flight, and electrophysiology), which mutants might be the most interesting to start with? Certainly, learning and memory mutants have a good chance of also being afflicted with defects in perceptual alternation dynamics. Indeed, many *Drosophila* learning and memory mutants have been found to also be defective in visual attention (Van Swinderen et al., 2009), providing promising candidates for further study in rivalry paradigms. On a broader scale, a variety of psychiatric disorders have been shown, albeit with less evidence than BD, to exhibit switch rate anomalies, including attention deficit hyperactivity disorder (ADHD; fast with AFR; Gorenstein et al., 1989) and anxiety disorders (fast with AFR and BR; Meldman, 1965; Li et al., 2000; Nagamine et al., 2007). Genes associated with these disorders (and associated with BD, as mentioned above) in humans might be screened in *Drosophila* mutants, first via a high-throughput visual maze paradigm, followed by tethered paradigms in select strains displaying aberrant phenotypes. The proof-of-principle for this approach is the recent *radish* mutant study in flies, where ADHD-like symptoms were suggested in a behavioral screen, confirmed by single fly behavior and electrophysiology, and then rescued by drug treatment (Van Swinderen and Brembs, 2010). Notably, this ADHD-like *radish* mutant was observed to perceptually switch at a fast rate, much like its human ADHD counterpart appears to do with AFR.

Knowing that we can test for rivalry-like effects in flies, some genes are clearly at the front of the line. For example, neuromodulators such as dopamine have been shown to modulate attention-like processes and arousal in flies (reviewed in Van Swinderen and Andretic, 2011). A likely connection between attention, reward systems or mood (discussed above), and rivalry rate make dopamine an excellent starting point for a deeper mechanistic understanding of perceptual rivalry in small brains (with noradrenaline implicated in human rivalry also; Einhäuser et al., 2008). Similarly, serotonin has been implicated in human visual rivalry (see above), mood and mood disorders, and hence variants in this neurotransmitter system can additionally be explored in the fly brain. Moreover, in relation to BD, one particular *Drosophila* study that can be undertaken stems directly from Pettigrew and Miller's (1998) sticky switch model of this disorder. They proposed that the period of a seconds-long temporo-parietal interhemispheric switch (mediating BR) is genetically coupled to the period of a minutes-long prefrontal interhemispheric switch (related to cognitive style and mood), such that genetic slowing of one interhemispheric switch is, via pleiotropy, associated with slowing of the other. As a precedent for this proposed genetic coupling of different-period rhythms, it was noted that the same *period* gene mutation in *Drosophila* modulates both circadian rhythms (hours-long) and male courtship song cycles (minutes-long; Alt et al., 1998; Zordan et al., 2003). Thus the short *per* mutation is associated with short circadian and courtship cycles, and vice versa for the long *per* mutation. This line of reasoning can now be directly examined with respect to rivalry. A specific prediction can be made therefore, on the basis of the sticky switch model of BD, that the short *per* mutant fly will exhibit a fast rate of torque flight behavior (for example), while the long *per* mutant, on the other hand, will exhibit a slow switch rate.

ATTENTIONAL SELECTION AND NATURAL SELECTION

Thus far, we have explored notions of attentional selection, suppression, and rivalry in humans and flies and outlined directions for future research to compare these processes in the two species and to understand the genetic basis of individual variation in human rivalry rate (and clinical anomalies therein). In what follows, we make some remarks about evolutionary aspects of attentional rivalry. We ask why there is rivalry at all, to what extent it is a ubiquitous feature of perception, how it may benefit or disadvantage an organism, and upon what aspects of the process natural selection acts.

First however, we note that two philosophical concepts have been applied to, and have benefited from, the study of perceptual phenomena – consciousness and free will. Consciousness is now widely regarded as a phenomenon (or group of phenomena, depending on one's definition) amenable to scientific investigation (Crick and Koch, 1998). Indeed, rivalry has proven one of the most useful tools in the scientific study of consciousness because it induces neural activity correlated with stimulus presentation that can be distinguished from neural activity correlated with stimulus perception (Logothetis, 1998). As useful as this approach is, the phenomenon of consciousness, and especially phenomenal consciousness (the subjective or experiential aspect), presents its own set of hard problems for science (Miller, 2007, forthcoming). These include locating the phenomenon in phylogeny and understanding what adaptive benefit, if any, there may be in an organism experiencing, rather than just behaving (as an automaton might). For such reasons, borrowing from notions of consciousness probably will not be a fruitful approach to addressing evolutionary aspects of rivalry. Adopting a different sense of "consciousness," in which the focus is not on experiential aspects but rather on perceptual content, or processes determining such content, may be more suited to evolutionary considerations. However, on this sense of "consciousness," the evolutionary issues seem just as effectively discussed by referring to notions of selection and suppression.

It is not clear whether the issue of free will, though of great philosophical and scientific interest in its own right (as for consciousness), will be informative for understanding evolutionary aspects of rivalry (despite the fact that this issue has recently been subjected to analysis in the context of the fly brain; Heisenberg, 2009; Brembs, 2011). As discussed above, though rivalry might be under some influence of voluntary attention, it is fundamentally an involuntary phenomenon involving alternate selection/suppression of conflicting stimuli, irrespective of the wants of the organism. It is of course, the *needs* of the organism that should be the focus of any evolutionary discussion. Why does an organism need the capacity to rival between alternative perceptions in situations in which more than one possibility exists? And if free will were to be relevant, at least in the sense of some degree of voluntary control over rivaling possibilities, why would an organism also need that capacity?

In an evolutionary context, perceptual switching cannot be seen in isolation from its behavioral consequences. In some species, such as the sandlance with alternating oculomotor activity (Pettigrew et al., 1999), switching behavior appears to be a foraging and predator detection strategy to cover a wide region of space for potential food sources and potential predators, respectively. In species with binocular vision, rivalry may have evolved alongside the development of stereoscopic/depth perception, even though rivalry timing may reflect more fundamental processes already existing in simpler species requiring behavioral strategies for depth perception (e.g., saccadic "peering" in locusts and mantids; Kral and Poteser, 1997). Regarding perceptual rivalry (rather than oculomotor switching), it is not difficult to envisage that searching for food could benefit from rapid and flexible disambiguation of conflicting visual, auditory and olfactory stimuli (or from discriminating figure and ground, in the case of vision). Perceptual rivalry could similarly offer an efficient mechanism of predator detection in scenarios in which threats may be located in more than one region of space. Rivaling between existing or looming threat directions could maximize an organism's chances of successful escape, just as rivaling between existent or looming food sources could maximize chances of successful feeding.

Moreover, in both cases, some degree of voluntary control over the switching process (i.e., some degree of free will, though these phenomena are not necessarily equivalent – see Brembs, 2011) would be even more advantageous, by enabling further behavioral flexibility. On this account, it could be questioned why rivalry then is not an entirely voluntary phenomenon, as this could offer the most flexibility. However, an entirely voluntary strategy might also predispose an organism to taking too long to switch to an alternative threat or food source. This indeed raises the issue of rivalry timing, its genetic basis and the selective advantages or disadvantages of polymorphisms for these traits (fast versus slow switching, high versus low degree of voluntary control over the process). It is not difficult to grasp that switching too fast or too slowly could be disadvantageous in both food/prey and predator scenarios. Similarly, being unable to engage or disengage each alternative with appropriate flexibility could also be disadvantageous. The heritability of the degree of voluntary control over rivalry remains to be demonstrated, but as discussed above, heritability for individual variation in rivalry rate in humans has been established at around 50%. The genes underlying such variation may well be those (along with their phenotypes) upon which selection has acted if indeed visual rivalry rate is reflective of evolutionarily ancient foraging and predator detection (attentional) switching mechanisms. In humans in particular, pleiotropy may also play a role in conferring selection pressures. Thus, genetic coupling of attentional switch dynamics to longer-period cognitive style interhemispheric rhythms may, according to Pettigrew and Miller's (1998) BD model, predispose individuals to becoming stuck in the left-approach (manic) or right-withdrawal (depressed) state. These imbalanced states may in turn confer selective advantage (e.g., sexual disinhibition in mania, creativity in mania) or disadvantage (e.g., risk-taking in mania, social isolation in depression).

However, at the level of short-period attentional and perceptual switches, it is also possible that rivalry alternation dynamics – in humans or flies – may be tuned to the rate of change occurring in the environment, rather than to some intrinsic clock in the brain. This might make intuitive sense if rivalry were to have some adaptive function: one could imagine entirely different switch rates required for slow or fast-moving animals, or for animals in different environments. The concept of time for a fly must be completely different than that for a human, and perceptual alternation dynamics in the fly may be largely dependent on the rather artificial experimental set-up in tethered paradigms. An alternative view on the rivalry data would suggest that there does exist an endogenous switch in even simple brains that controls perceptual alternation dynamics. In flies, such switches have been identified for longer-term processes, such as those associated with circadian rhythms (as discussed above regarding the *period* gene), as well as for seconds-long processes in the fly brain (Rosay et al., 2001), so why not with shorter-term processes related to perception and attention? What experiments might one do in the fly to determine if an endogenous switch exists that controls perception in the seconds-long time scale?

To address whether flies make spontaneous decisions based upon an internal switch (rather than an external cue) is difficult, because one can never be entirely certain whether a cue was evident for the fly but not to the experimenter. An early paradigm tested *Drosophila* populations walking through a sequential choice maze, and found a reliable asymmetry in distributions of alternation behavior, inferred from their distributions at maze endpoints (Murphey, 1965). This suggested the presence of organismic bias in the direction of stereotypy: if flies turned right, they were more likely to turn right again at the following choice point, almost as if a left-right decision persisted across multiple choices, until an internally generated switch occurred. This observation of choice stereotypy was replicated several decades later in the eight-point visual choice maze (Van Swinderen and Flores, 2007), which was discussed in the previous section.

An even better paradigm for addressing spontaneous behavior in flies is again the tethered flight arena, but now in the absence of salient visual cues. As we have seen above, in the tethered paradigm, much like in a head-restrained monkey preparation, flies can still report choices while only seeing exactly what we want them to see – the ideal context for investigating rivalry. When placed in the context of an evenly illuminated white drum, the tethered fly presumably sees nothing but a field of white as it makes decisions on whether to fly straight or torque to the left or to the right. Even under these unchanging sensory conditions, choice behavior during long flights in the arena is highly variable (Maye et al., 2007). Rather than producing random distributions of torque behavior, flies display behaviors more resembling foraging behavior (Reynolds and Frye, 2007) such as fractal patterns or long-tailed Levy distributions. This suggests that non-random timing between choices is an intrinsic, adaptive trait even in the fly brain. Such endogenous control of alternations in animal brains might promote a level of perceptual exploration required for assigning salience to stimuli relevant to survival, when such an endogenous switch is directed to a succession of competing stimuli in the environment. In this sense, rivalry (choice alternation) mechanisms may shape behavior in much the same way that random mutations shape the evolution of a species.

Reinhard Wolf and Martin Heisenberg, who performed the first fly rivalry experiments, described above, already proposed decades ago some parallels between spontaneous behavior in the brain and mutations in the evolution of a species. They stated:

> As chance events, mutations and initiating acts have in common that the causes generating them often are biologically irrelevant, yet they become most important for the organism. The main point with initiation is not the existence of stochastic processes in the brain, but the existence of a type of stochastic process which is at the basis of behavioral adaptation in a manner quite analogous to Darwinian evolution. Thus, we expect initiation to be a highly organized affair.
>
> (Heisenberg and Wolf, 1984, p. 222)

CONCLUDING REMARKS

Like the phenomenon itself, the focus of rivalry research has historically alternated, not just in terms of low- versus high-level mechanistic models, but also in terms of the field's interest in individual differences in rivalry parameters. We have discussed recent studies of rivalry rate differences in clinical and control populations and the new direction in rivalry research these perspectives represent. Thus, in addition to rivalry research benefiting from a combination of psychophysical and neuroscientific imaging techniques, there is now reason to add to this interdisciplinary collaboration, clinical, genetic and molecular approaches. As well as having outlined various issues that are being examined currently and will require examination in the future, we have described in detail a model of perceptual rivalry in *Drosophila*, and its attentional basis, that may enable genetic and molecular dissection of (i) determinants of individual variation in rivalry rate, and (ii) clinically relevant rivalry variants. To this end, we have presented a specific research agenda utilizing this *Drosophila* model. Finally, we have begun discussion of evolutionary considerations relevant to attentional switch dynamics. Far from being just a source of amusement and intrigue, rivalry – and its examination in both large and miniature brains – may shed light on fundamental aspects of perception, attention, cognition and behavior, as well as human psychiatric disorders.

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Attentional modulation of binocular rivalry

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Ever since Wheatstone initiated the scientific study of binocular rivalry, it has been debated whether the phenomenon is under attentional control. In recent years, the issue of attentional modulation of binocular rivalry has seen a revival. Here we review the classical studies as well as recent advances in the study of attentional modulation of binocular rivalry. We show that (1) voluntary control over binocular rivalry is possible, yet limited, (2) both endogenous and exogenous attention influence perceptual dominance during rivalry, (3) diverting attention from rival displays does not arrest perceptual alternations, and that (4) rival targets by themselves can also attract attention. From a theoretical perspective, we suggest that attention affects binocular rivalry by modulating the effective contrast of the images in competition. This contrast enhancing effect of top-down attention is counteracted by a response attenuating effect of neural adaptation at early levels of visual processing, which weakens the response to the dominant image. Moreover, we conclude that although frontal and parietal brain areas involved in both binocular rivalry and visual attention overlap, an adapting reciprocal inhibition arrangement at early visual cortex is sufficient to trigger switches in perceptual dominance independently of a higher-level "selection" mechanisms. Both of these processes are reciprocal and therefore self-balancing, with the consequence that complete attentional control over binocular rivalry can never be realized.

Keywords: binocular rivalry, visual attention

HISTORICAL BACKGROUND

When Wheatstone (1838) developed his mirror stereoscope in the first half of the nineteenth century, it was possible for the first time to independently control the presentation of images to the two eyes. In reporting his new device (Wheatstone, 1838), the main focus was on his impressive demonstration that presenting a matched image to each eye, and adding a small lateral displacement in opposite directions, produced a vivid sense of three-dimensional depth. Wheatstone went on to discuss stereo-depth and its underlying geometry at length, however, with complete control over what was presented to each eye, Wheatstone's curiosity led him to try an obvious variation: what would happen if different images were presented to each eye? Toward the end of his paper, Wheatstone (1838) illustrates the kind of stereo-image he used to investigate this question. It consists of two different upper case letters, one for the left eye and one for the right, each letter presented within a matching fusion circle. He then describes what happens when such an image is viewed through a stereoscope, and in so doing provides the first systematic description of binocular rivalry:

> "If *a* and *b* (fig. 25.) are each presented at the same time to a different eye, the common border will remain constant, while the letter within it will change alternately from that which would be perceived by the right eye alone to that which would be perceived by the left eye alone. At the moment of change the letter which has just been seen breaks into fragments, while fragments of the letter which is about to appear mingle with them, and are immediately after replaced by the entire letter. ***It does not appear to be in the power of the will to determine the appearance of either of the letters,*** but the duration of the appearance seems to depend on causes which are under our control: thus if the two pictures be equally illuminated, the alternations appear in general of equal duration; but if one picture be more illuminated than the other, that which is less so will be perceived during a shorter time. I have generally made this experiment with the apparatus, fig. 6. When complex pictures are employed in the stereoscope, various parts of them alternate differently." (Wheatstone, 1838, p. 386, bold emphasis added)

Remarkably, Wheatstone's (1838) pioneering observations manage to capture all the main characteristics of binocular rivalry. He refers to the alternation of the monocular images, he mentioned the fragmented or "piecemeal" state that may occur during perceptual transitions, and he describes the changes in relative dominance associated with changes in stimulus strength. Importantly, he also claimed not to be able to determine which image dominates by an act of will. In so doing, Wheatstone (1838) made the first assertion in what was to be a long and vigorously contested debate: can binocular rivalry be controlled by voluntary attention? In Wheatstone's own time, this question engendered much discussion, with the great early scholars of perception voicing a variety of views on it (e.g., Hermann von Helmholtz, Ewald Hering, and William James). Indeed, arguments about the role of attention in binocular rivalry have continued to the present day and the issue remains central in contemporary rivalry research. One could argue that this question is central to the most recent major controversy in binocular rivalry: whether rivalry is eye-based or image-based (for a review of the controversy, see Blake and Logothetis, 2002), where an image-based view on binocular rivalry would allow more room for voluntary control.

As this historical background shows, the question of whether or not binocular rivalry is under voluntary (or attentional) control is as old as research into the fascinating phenomenon of rivalry itself. In this review, we will evaluate Wheatstone's (1838) claim that attention cannot determine rivalry dominance in light of research published since. In addition, we will review other studies which have sought to demonstrate a more moderate point, namely that attention can be used to modulate binocular rivalry, even if it cannot ultimately determine what is perceived when experiencing it. As well as reviewing the literature relating to rivalry and attention, we will also discuss recent findings suggesting that neural networks implicated in binocular rivalry and visual attention overlap. Overall, the review will focus as much as possible on studies of rivalry and attention. For more information about the many other aspects of binocular rivalry, the reader is referred to more general reviews (Blake and Logothetis, 2002; Alais and Blake, 2005; Tong et al., 2006; Blake and Wilson, 2011).

VOLUNTARY CONTROL OVER BINOCULAR RIVALRY

Among the first scholars to study binocular rivalry, it was Helmholtz (1925) who argued most forcefully that perception during rivalry was under volitional control. Indeed, Helmholtz claimed to have full control over what he perceived when viewing incompatible images, stating that "...I can retain the image of one pair or the other according to my fancy" (Helmholtz, 1925, pp. 497). On this view, where perceptual dominance is controlled by the observer's volition, the mechanism responsible for selecting the dominant image must be at a high-level of processing. If a lower-level mechanism were to determine perceptual dominance in rivalry, then it should *not* be under the observer's control. This led Helmholtz (1925) to conclude that binocular rivalry was indeed a high-level phenomenon, or as he labeled it: "a psychic act." In adopting this position, Helmholtz dismissed the "retinal view" taken by others such as Breese (1899) and Hering (1964) who emphasized the role of low-level factors in determining rivalry dominance.

Breese (1899) conducted his own experiments to test whether observers could control binocular rivalry. In his experiments, observers viewed a red and a green field presented separately to the eyes, and were instructed to try to hold one of them dominant. Breese (1899) found that observers could lengthen the dominance period of the nominated color field according to instruction, but that the average number of perceptual alternations did not change. He also noted that in trying to maintain dominance of one image, observers made vigorous eye movements. He suspected that eye movements exerted a substantial influence over which of the images was dominant and for how long, and he went on to conduct experiments on himself in which he kept his gaze tightly fixed while inspecting rival images. Under these conditions, he was not able to exert volitional control over rivalry dominance. This observation led Breese (1899) to conclude, as Hering (1964) had before him, that eye movements – rather than volitional control – were responsible for influencing perceptual dominance in binocular rivalry, and that the failure to control eye movements was the reason that Helmholtz was able to control perceptual dominance in rivalry.

In the ensuing decades, a number of other low-level and peripheral factors were studied for a possible confounding role in the apparent ability of attention to determine rivalry dominance. Simple fixational eye movements were further considered, as were the possible roles of eye blinks and other ocular motor acts such as the intrinsic eye muscle activity involved in pupillary constriction and accommodation. McDougall (1903) and George (1936), for example, paralyzed the eye muscles of a single eye and found that this decreased the amount of apparent voluntary control over rivalry dominance, but it did not eliminate it. Several other studies investigated the role of blinking in control over rivalry dominance (Washburn and Gillette, 1933; Bárány and Halldén, 1947; Meredith and Meredith, 1962), with each reporting that voluntary control over rivalry was still possible when accounting for blinking. Although these early studies addressing peripheral mechanisms and their possible confounding roles in volitional control over rivalry made strong claims, Lack (1978) surveyed the literature and noted that all these studies were poorly conducted. For example, McDougall (1903) and George (1936) used only one observer in their studies, and Meredith and Meredith (1962) did not actually measure blink rates in their investigation. Clearly, a properly controlled reinvestigation of these peripheral factors was needed.

In his dissertation "Selective attention and the control over binocular rivalry," Lack (1978) presents several carefully controlled experiments designed to address the limitations of these preceding studies of peripheral ocular factors in rivalry, whose claims had been lingering for almost a century. In a systematic series of experiments, he was able to exclude a role for eye movements, blinking, accommodation, and pupillary activity as potential confounds in the apparent ability to voluntarily control binocular rivalry. With these peripheral factors excluded, Lack then returned to the central question: can observers attentionally control binocular rivalry? Lack's (1978) studies first established that unpracticed observers were able to exert a modest degree of attentional control over binocular rivalry, and he went on to show that the extent of voluntary control could be increased with practice. Thus, Lack's (1978) important study demonstrated two significant points. First, the claim against attention's control over rivalry, which was based on uncontrolled peripheral factors, could be ruled out. Second, with peripheral factors controlled, Lack (1978) showed that perceptual dominance in binocular rivalry could be significantly influenced by an act of selective attention (we will return to this point later). In the history of binocular rivalry, Lack's (1978) study was a turning point that paved the way for a return to an examination of the role of attention in rivalry.

In recent years, studies by Meng and Tong (2004) and van Ee et al. (2005) have revived the issue of voluntary control and reach a similar conclusion to that of Lack (1978): control over binocular rivalry is possible. Meng and Tong (2004) compared the extent to which attentional control was possible for binocular rivalry and for the Necker cube. They instructed observers to try to hold one image dominant (or one perspective, in the case of the Necker cube) at the cost of the other, and compared this to a neutral baseline. They observed that a degree of attentional control was possible for both stimuli, but that there was less control over perception during binocular rivalry than for the Necker cube. However, when observers followed a different instruction – to try to attentionally modulate the *rate* of perceptual alternation in the displays – the effect of attention on alternation dynamics was considerably greater, and comparable control was observed for rivalry and the Necker cube. Thus, although attentional control over binocular rivalry was possible, the authors concluded that rivalry involved a more automatic, stimulus-driven form of perceptual bistability than did the Necker cube.

A paper by van Ee et al. (2005) also looked at attentional modulation of alternation dynamics in several bistable displays, comparing binocular rivalry, the Necker cube, and a bistable stereo-slant stimulus. Similar to Meng and Tong's (2004) observation, van Ee et al. (2005) also found that attentional control over binocular rivalry dynamics was less than was possible for other perceptually bistable displays. In related papers (van Dam and van Ee, 2006a,b), the role of eye movements in voluntary control over bistable stimuli was re-investigated, returning to the possible contribution of peripheral mechanisms to voluntary control. These studies analyzed the role of eye movements and found a positive correlation between saccades and perceptual alternations during binocular rivalry, implying that eye movements can be used actively to instigate a perceptual alternation. Interestingly, however, these authors found that the role of saccades was not different in voluntary control conditions. Thus, when trying to control perception during rivalry, observers did not use eye-movement strategies that were any different to those employed during passive viewing. This conclusion agrees with Lack's (1978) investigation nearly 30 years earlier and confirms that voluntary control over binocular rivalry is indeed possible and cannot be explained by eye movements.

Interestingly, a recent study showed that voluntary control over binocular rivalry can be increased when accompanied by congruent auditory information (van Ee et al., 2009). Observers viewed a rival display consisting of a looming and a rotating pattern. When instructed to try to hold the looming percept dominant, attentional control was greater when a correlated looming sound accompanied the visual stimulus. This result shows a cross-modal influence on binocular rivalry and therefore broadens the search for the attentional mechanisms underlying voluntary control over binocular rivalry. Moreover, this cross-modal effect on binocular rivalry was only observed when the stimuli were attended: the mere presence an auditory signal correlated with the visual stimulus that observers were instructed to maintain in dominance did not help them in their task. The auditory signal had to be actively attended if the sound signal were to help to maintain the looming percept dominant in binocular rivalry. The correlation between the auditory signal and the visual stimulus to be attended was also critical, as a looming sound with a different rate to the looming visual stimulus was ineffective at enhancing perceptual control. In a couple of interesting extensions of this work, the authors also report that a correlated tactile stimulus is equally effective as the correlated auditory signal at facilitating attentional control over visual rivalry, and that a combination of auditory and tactile stimuli is even more effective. In addition, control over a bistable auditory stimulus was found to be enhanced by adding a correlated visual stimulus.

ATTENTIONAL MODULATION OF BINOCULAR RIVALRY

The earliest debate surrounding the role of attention in binocular rivalry was primarily concerned with whether perception during rivalry could be controlled entirely by an act of will. The notion that attention and rivalry may be closely linked has a neat appeal. There is a clear analogy between attentional selection among competing objects and perceptual selection in rivalry between competing images. Although appealing, this notion – at least in its strongest form – is easily overturned by empirical experience as selecting an image for perceptual dominance is only partly under the control of an observer. This led to the role of attention in rivalry being ignored for a long period. Lack's (1978) careful experimenting on the topic, however, opened the door for a weaker form of the attention hypothesis by showing clearly that attention is at least a factor at work in binocular rivalry, even if it is not the primary or causative one. Not surprisingly, therefore, the last decade or so has seen a number of studies published that have revisited the issue of attention and rivalry and asked a more subtle question: how can the various forms of attention *modulate* (if not totally control) binocular rivalry?

A fundamental distinction is drawn in the attention literature between voluntary or endogenous attention and involuntary or exogenous attention (see Bundesen and Habekost, 2008; Wright and Ward, 2008). Both are acts of attentional selection, but endogenous attention is a voluntary choice to focus on an object, location, or feature (an act of will, or as Helmholtz called it: "immediate attention") whereas exogenous attention occurs when a stimulus onset or stimulus change captures attention and is automatically selected. This is an involuntary form of attention (or "mediate attention" in Helmholtz's terms). The first paper (Ooi and He, 1999) among the recent flurry of studies examining attention and rivalry investigated how both forms of attention – voluntary and involuntary – affect binocular rivalry. Ooi and He (1999) first investigated the ability of voluntary attention to sustain dominance of a selected rival target. To do this, they exploited a well-known effect that a transient change in the suppressed eye's stimulus is an effective way to trigger a perceptual switch to that eye (Grindley and Townsend, 1965; Walker and Powell, 1979). Ooi and He (1999) instructed observers to attend to one of four targets presented to the dominant eye, and a transient perturbation was made to the stimulus in the suppressed eye. They observed that when the transient was located at the location corresponding to the attended target in the dominant eye, dominance of that target was terminated less often than when the transient occurred at the location of one of the three unattended targets in the dominant eye. This result shows that voluntarily attending to a dominant image will help maintain the "selected" image in a state of perceptual dominance.

Ooi and He (1999) also investigated whether involuntary attention directed to a suppressed stimulus could break its suppression and cause the suppressed stimulus to become dominant. They tested this using a monocular pop-out cue (a pair of parallel lines) that flanked the location of one rival target in a circular array of six rivaling targets. A cue was added around all six targets (thereby controlling for stimulus onset) but five cues were horizontal line pairs and the critical sixth cue was a vertical pair and thereby popped out of the display as an effective exogenous cue.

The authors found that this salient monocular cue significantly enhanced the tendency of the cued target to achieve dominance, relative to the non-cued targets. This finding demonstrated an effect of involuntary attention on the suppressed image in that the suppressed image was more likely to return to dominance when attention was drawn to it automatically by a salient monocular pop-out cue. Together with their manipulation of endogenous attention, this study provided some of the first empirical evidence that both endogenous and exogenous attention can modulate the neural processes underlying binocular rivalry.

In a recent study by Paffen and Van der Stigchel (2010) it was shown that involuntary attention can also initiate a perceptual alternation: in their experiments, rival targets were presented both to the left and right of fixation. Observers were instructed to press either of two buttons corresponding to the two rival locations whenever an alternation was perceived at these locations. At random intervals, an exogenous cue surrounding the rival targets was presented at one of the two locations. The results showed that alternations occurred earlier as well as more frequently at the location where the cue was presented. These results suggest that the occurrence of perceptual alternations is related to the spatio-temporal properties of visual attention: moving attention to a spatial location increases the chance of perceiving a perceptual alternation at that location.

DOES RIVALRY OCCUR IN THE ABSENCE OF ATTENTION?

From the studies discussed so far, it is clear that attentional selection can be used to modulate binocular rivalry. Selecting one image from a pair of rivaling images, whether by exogenous or endogenous attentional selection, will suffice to reveal this. Endogenously attending to the dominant image will extend its dominance duration, and exogenously cueing attention to the rival images will increase the likelihood of a perceptual switch (Ooi and He, 1999; Paffen and Van der Stigchel, 2010). But what if attention is withdrawn from the rival images? This question was addressed in an influential early study by Ooi and He (1999). In the final experiment of that paper, observers were briefly presented with a pair of rival images, one of which was preceded by a surrounding cue. Observers had two tasks to do. The first was to report which of the two rival images became dominant first. The critical manipulation, however, involved presenting a Vernier target at a different spatial location and having the observer perform a second task: was the Vernier stimulus offset to the left or to the right? A preceding experiment had shown that cueing an image usually caused it to dominate first. The results of the dual-task experiment showed that this cueing effect was reduced: the cued image became dominant less often in the divided attention condition, compared to a focused condition with no Vernier task. This result nicely shows that dividing attention between two tasks weakens its ability to select a given stimulus at rivalry onset.

Ooi and He's (1999) experiment concerned dominance at rivalry onset. What about ongoing rivalry alternations? One of the hallmarks of binocular rivalry is that constant visual input leads to spontaneous and ongoing changes in perceptual dominance. What happens to these alternations when attention is divided? If withdrawing attention from the rivalry stimuli to a demanding competing task were to eliminate perceptual alternations, it would imply that attention is necessary for binocular rivalry to occur. This question was addressed by Paffen et al. (2006) in a dual-task paradigm. They had observers continually track their rivalry alternations while also performing a secondary task at a different spatial location. Surrounding the rivalry stimuli was an annulus containing incoherent random-dot motion. Occasional bursts of weakly coherent motion intermittently replaced the incoherent motion, and observers had to detect when these weak motion bursts occurred. With this dual-task paradigm, Paffen et al. (2006) found that the rate of rivalry alternations decreased when observers had to detect the motion bursts, compared to when the motion was ignored. Thus, withdrawing attentional resources from the rivalry stimuli slowed the rate at which rivalry alternations occurred, but did not abolish them. As attentional resources might still have been deployed to the rival images while detecting motion bursts, the authors went on to increase the difficulty of the motion detection task. Even when the motion detection task was difficult (d' were around 1), rival alternations were far from arrested: alternation rates were still around 0.35 alternations per second. Although these results show that rival alternations still occur when attentional resources are withdrawn, it is clear that attentional resources affect the rate at which rival alternations occur: when attentional resources are withdrawn, rival alternations become slower. A similar result was recently reported by Paffen and Hooge (2011). In this study, observers reported perceptual alternations in multiple rival images. The results showed that the number of alternations reported per rival pair went down when the number of rival images was increased. Their results imply that distributing spatial attention also slows the speed of binocular rivalry.

Notably, withdrawing attention does not only slow alternations during binocular rivalry, but affects other instances of bistable perception as well (e.g., Reisberg and O'Shaughnessy, 1984; Pastukhov and Braun, 2007). For example, Pastukhov and Braun (2007) performed experiments in which attention was withdrawn from a bistable plaid stimulus. Even when attentional deployment to the plaid was minimized, perceptual alternations still occurred. Interestingly, when attentional resources are deployed in another modality, rival alternations also become slower: Alais et al. (2010b) recently showed that attending to auditory signals also slows alternations in a visual rival display. In addition, it was reported that withdrawing attention had a bigger effect when rivalry was instigated between images of a house and a face, than when instigated between two gratings. This result corroborates with those reported by van Ee et al. (2005): in that study, observers had greater (voluntary) control when rivalry occurred between images of a house and a face then when between sinewave gratings. This seems to imply that the influence of attention on rival images increases as these images are analyzed higher up the visual processing stream.

To our knowledge, there is one neuro-imaging study investigating the withdrawal of attention on binocular rivalry. For this, Lee et al. (2007) used the phenomenon of traveling waves that occurs when rival images are of considerable size: a transition from one percept to the next often involves a local breakthrough of the suppressed image, followed by a traveling wave of emergent perceptual dominance of the other parts of the suppressed image (Wilson et al., 2001). When attention was directed to the rival images, traveling waves of activity in V1, V2, and V3 correlated both temporally (i.e., the speed of the waves in perception and neural tissue) and spatially (the location of the waves in the visual field and retinotopically in the neural tissue) with perceived traveling waves. When attention was diverted to monitoring letters at the center of the display activity in V1 still correlated with perception of the dominance wave, in V2 and V3, however, the correlation was abolished. Thus, when attention was diverted, rivalry-related activity was present in V1, but not in later areas.

DOES BINOCULAR RIVALRY POP-OUT?

To this point, we have demonstrated a number of ways by which attention can modulate binocular rivalry. A converse question can also be asked: is a rivaling stimulus able to automatically attract attention? In other words, is binocular rivalry (or more specifically, "interocular conflict") a pop-out attribute? The first investigation of this question (Wolfe and Franzel, 1988) involved a series of experiments in which observers searched for targets defined by interocular conflict among an array of distractors that were interocularly matched. The stimuli were square-wave grating patches, with the distractors being interocularly matched in orientation and the target being orthogonally oriented gratings. By measuring search times for such targets among various numbers of distractors, search efficiencies can be calculated (i.e., search time per item). The results showed that search for a target defined by interocular conflict was not parallel (or in contemporary terms, was not "efficient"), nor was it much faster than the converse relationship (searching for a target of fused orientations among rival distractors). From this investigation, Wolfe and Franzel (1988) concluded that targets defined by binocular rivalry do not "pop-out."

In a recent study, however, Paffen et al. (2011), showed that search for targets defined by interocular conflict *could* lead to a "near efficient" search (corresponding to search slopes of about 15 ms per item), depending on the stimulus conditions. These authors found that slow search times occurred when high-contrast stimuli were used, but that search times were faster and more efficient for lower contrasts. While this explains the discrepancy with Wolfe and Franzel's (1988) findings (they used a high-contrast display of white gratings on a black background), it does seem counterintuitive: lowering the contrast of a search target generally attenuates search performance (Pashler et al., 2004). However, when dissimilar images are presented dichoptically, it takes a while for binocular rivalry to occur: during the first 150 ms or so, images do not rival but instead undergo a "false fusion" (Wolfe, 1983). This is not normal fusion (as the monocular images are not matched) and observers can easily discriminate between fused images and images that are fused optically (Georgeson and Meese, 1997). Furthermore, it has been shown that the duration of the false fusion period (or "proto-rivalry," as it was labeled by Solomon et al., 2006) increases as the contrast of rival images *decreases* (Liu et al., 1992). Paffen et al. (2011) reasoned that this relationship was the cause of the higher search efficiency observed in low contrast displays. Indeed, when Paffen et al. (2011) presented the search displays for just 150 ms (thereby optimizing abnormal fusion), observers could easily detect the search target defined by interocular conflict.

HOW DO ATTENTION AND RIVALRY INTERACT?

As has been discussed above, the debate about the relationship between binocular rivalry and attention has been present since research into rivalry first began. For Helmholtz (1925), binocular rivalry was a psychic act: keeping an image dominant in perception during binocular rivalry was an act of both immediate (voluntary) and mediate (involuntary) attention. If it seemed keeping an image dominant in perception by mere voluntary attention was difficult, it was because the image would eventually cease to be new, and voluntary control would become more difficult. Helmholtz thought this tendency could be counteracted by keeping an image interesting, for example, by counting the number of lines in the display. The parallel with visual attention is obvious: selection of visual information can occur voluntarily, but can also occur when aspects of the stimulus can attract attention automatically. More recently, after reviewing several commonalities between attention and binocular rivalry, Leopold and Logothetis (1999) concluded that "mechanisms of selective attention and multistability might be closely related" (Leopold and Logothetis, 1999). This conclusion was based on two general observations. First, both visual attention and binocular rivalry involve competition in which some information is selected at the expense of other information. Second, neuroanatomical networks of visual attention and binocular rivalry show considerable overlap. We will discuss these two observations below.

The first observation, that visual attention and binocular rivalry are both acts of selecting information, was used in a study by Mitchell et al. (2004). In their experiments, observers binocularly viewed two counter-rotating fields of rotating dots that were superimposed in transparent motion. Attention was then cued to one of the surfaces by a brief translational motion pulse after which the viewing conditions quickly changed to dichoptic, with each surface presented to a separate eye to trigger binocular rivalry. The authors observed that the surface that was cued prior to the initiation of dichoptic viewing tended strongly to be the dominant image in the first period of rivalry. Based on these results, the authors concluded that "attention and rivalry rely on shared object-based selection mechanisms" and that both "engage common competitive mechanisms" (Mitchell et al., 2004). A related result has earlier been published by Ooi and He (1999), who showed that pre-cuing the location of one rival target among an array of six rival targets raised the likelihood that it would become dominant at rivalry onset. While both these two studies used exogenous cues, Chong and Blake (2006) went on to study the effect of an endogenous cue on initial phase of rivalry dominance. Observers were presented with binocularly viewed plaids whose component gratings underwent independent changes in orientation and spatial frequency. Observers were instructed to direct their attention to one of the component gratings. Similar to Mitchell et al.'s (2004) procedure, each of the gratings was then presented separately to the eyes and the same result was reported: initial dominance tended to favor the endogenously attended grating.

As the above discussion shows that attention and binocular rivalry do interact, the next question is *how* they interact. A few studies suggest that attention affects binocular rivalry by affecting the effective contrast of the rivaling images (Chong et al., 2005;

Chong and Blake, 2006; Paffen et al., 2006; Paffen and Hooge, 2011). This notion is motivated by two observations. First, changing the contrast of rival images has a profound impact on the temporal dynamics of rivalry: lowering the contrast of both images will lengthen the time that each image is dominant in perception (e.g., Levelt, 1965; Brascamp et al., 2006). Second, attending a stimulus is known to increase its perceived contrast (Carrasco et al., 2004), a finding that parallels the finding that attending a stimulus (contrasted with disattending the stimulus) affects neural responses in a manner similar to increasing the contrast of that stimulus (Reynolds and Chelazzi, 2004). Both Chong et al. (2005) and Paffen et al. (2006) used these two observations and reasoned that one influence of attending to the rival stimuli could be to increase their effective contrast. Chong et al. (2005) had observers track spatial frequency changes of one of two rival targets, or increased the contrast of one of the targets as soon as it became dominant. These authors reported that both attending to the grating and increasing its contrast were effective at increasing the perceptual dominance of that grating.

The relationship between attention and contrast in binocular rivalry was also examined in Paffen et al.'s (2006) study. It has already been noted above that observers tracked rivalry alternations in a central stimulus while at the same time detecting brief motion bursts in an annulus surrounding the rival targets. This attentional condition was compared with a passive viewing condition, and both were done at four levels of contrast. The results showed that diverting attention to the motion detection task had a quantitatively similar effect on slowing the alternation rate as halving the contrast of the rival targets. Together, these results and those of Chong et al. (2005), with the tight relationship between stimulus contrast and rivalry alternation rate, show that attention's influence on binocular rivalry can be modeled as a change in effective contrast. When rival targets are attended, the effective contrast of the targets increases, leading to an increase in alternation rate equivalent to that produced by increasing stimulus contrast by roughly a factor of two (Paffen et al., 2006).

The observation that attention affects rivalry by boosting its effective contrast predicts that attention and contrast should influence rivalry in the same way. Interestingly, Levelt (1965) noticed that changing the contrast of only one rival image actually affected the dominance duration of the other image, leaving its own dominance unaffected. This famous finding (formalized into Levelt's 2nd proposition) leads to the counterintuitive prediction that attending to one rival image will affect the dominance of the *other* image, and not the attended one. Several studies have addressed this issue. In the attention condition of Chong et al.'s (2005) study, the mean dominance duration of the attended grating was increased by as much as 50%, but the mean dominance duration of the unattended grating was no different from what was observed in the passive viewing condition. This result shows that attention only exerts its influence on the stimulus that is perceptually dominant, and not on the suppressed stimulus, thereby violating what would be expected from Levelt's 2nd proposition. However, as Chong et al. (2005) remark, this is not surprising because one can only attend to an image that it is perceptually present and available for selection; it is impossible to select an image that cannot be seen. Their results square with those on voluntary control mentioned above, where voluntary control generally increases the time the attended image is perceived. In contrast to these findings, Hancock and Andrews (2007) reported that attending one of two rival gratings decreased the mean dominance duration of the unattended grating, leaving that of the attended grating unaffected. The latter result *is* in correspondence with Levelt's 2nd proposition. At present it is unclear what exactly explains the discrepancy between the findings of Chong et al. (2005) and those of Hancock and Andrews (2007) but there is clearly more to discover about the role of attention on rivalry dominance durations.

The second important point that Leopold and Logothetis (1999) made was that a number of the brain areas involved in attention are also implicated in binocular rivalry. At the core of this is the observation that both attention and binocular rivalry involve a distributed fronto-parieto-occipito network that is crucial in attentional selection and mediating perceptual alternations during binocular rivalry. In the case of visual attention, the existence of such a network is relatively undisputed: many studies have shown fronto-parietal areas to be crucial in exerting top-down control over visual perception (Posner and Dehaene, 1994; Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Bisley, 2011). As an example, Zanto et al. (2011) recently targeted frontal areas with rTMS and found that this lead to diminished top-down modulation of visual processing in posterior (visual) areas. In binocular rivalry, perception-related activity has been found as early as the lateral geniculate nucleus (LGN: Haynes et al., 2005; Wunderlich et al., 2005), primary visual cortex: (Polonsky et al., 2000; Tong and Engel, 2001; Lee et al., 2005) and later processing areas such as fusiform face area (FFA) and the parahippocampal place area (PPA: Tong et al., 1998). Interestingly, one of the first imaging studies of binocular rivalry found transient activation related to perceptual alternations in parietal and prefrontal areas (Lumer et al., 1998). In this study, BOLD activity was contrasted between observers viewing rival displays and displays in which rivalry was mimicked (images were presented in alternation on the display). The results showed that right fronto-parietal regions showed greater activation during rival alternations than during simulated rivalry. The authors noted that these brain regions were also involved in spatial attention and suggested that both visual attention and binocular rivalry "may there for call upon a common neural machinery in fronto-parietal cortex, involved in the selection of neuronal events leading to visual awareness" (Lumer et al., 1998).

Subsequent to Lumer et al.'s (1998) study, several later studies also found this fronto-parietal network to be implicated in binocular rivalry (Lumer and Rees, 1999; Srinivasan et al., 1999; Miller et al., 2000; Cosmelli et al., 2004; Sterzer and Rees, 2008). The involvement of frontal and parietal regions in binocular rivalry, therefore, is not disputed. The question remains, however, whether perceptual alternations during rivalry arise in these areas and mediate earlier processing via feedback (as suggested, for example, by Leopold and Logothetis, 1999), or whether perceptual alternations arise at an earlier level of visual processing and then feed forward to fronto-parietal areas. The feedback possibility would more closely correspond to the notion of frontal areas exerting top-down control over visual perception, as in the case of selection by attention. The feedforward possibility would correspond more with a bottom-up component to perceptual alternations during rivalry with the competition between the monocular inputs resolved at early levels, where subsequent percept-related activity can be found higher up the processing stream. There is some evidence for the feedback possibility (Sterzer and Kleinschmidt, 2007; Britz et al., 2009), where frontal (Sterzer and Kleinschmidt, 2007) and parietal (Britz et al., 2009) activity precedes occipital activity associated with perceptual alternations. Importantly however, these results were obtained by using a complex Necker cube (Britz et al., 2009) and apparent motion (Sterzer and Kleinschmidt, 2007) stimuli which, although clearly bistable, lack the interocular mismatch that triggers rivalry. This difference might explain the apparent difference with a study by Kamphuisen et al. (2008), who used binocular rivalry stimuli and observed that while parietal and frontal activation were involved in mediating perceptual alternations, a phase analysis of this activity showed it was the result of occipital sources.

Recently, is has become evident that regions of parietal cortex are particularly important in mediating perceptual alternations. Carmel et al. (2010) applied TMS over right superior parietal cortex (SPL) and found that this shortened dominance durations during binocular rivalry. In addition, Kanai et al. (2010) found that cortical thickness of bilateral superior parietal cortex was negatively correlated with the speed of perceptual alternations triggered by a structure-from-motion stimulus. Interestingly, these authors went on to apply continuous theta-burst stimulation (cTBS) over right and left SPL and found that applying this kind of TMS increased percept durations. The apparent contradictions between the two studies was resolved in another study by Kanai et al. (2011). By applying a ROI analysis based on the relation between percept durations and cortical thickness reported by Kanai et al. (2010), different sub-regions of SPL were targeted with offline TMS. Disrupting right anterior SPL was found to shorten percept duration, while disrupting right posterior SPL increased percept durations. Importantly, these results apply both to perceptual alternations caused by binocular rivalry stimuli and a structure-from-motion stimulus, implicating that these areas are similarly involved in both kinds of bistability. Although this study resolved the conflicting results of Carmel et al. (2010) on the one hand and Kanai et al. (2010) on the other, they *are* in conflict with another study showing that online TMS over anterior SPL increases percept durations during binocular rivalry (Zaretskaya et al., 2010). The reason for this discrepancy is not clear, although one notable difference between the studies is that Zaretskaya et al. (2010) used online TMS, whereas Kanai et al. (2011) used offline TMS. This difference may be critical, as it is possible that the region targeted by offline TMS spreads during the offline period to affect non-targeted regions during testing. More research will be needed to resolve this discrepancy but for the moment these TMS studies show that parietal cortex, a crucial structure in (spatial) attention (e.g., Corbetta and Shulman, 2002), also has a critical role in determining binocular rivalry dynamics. It is less clear what these studies imply regarding feedforward versus feedback initiation of perceptual alternations because apart from affecting processing in parietal areas, TMS likely also affects the feedback/feedforward interplay between parietal and other processing areas at both lower and higher stages.

A specific involvement of frontal areas in bistable perception has recently been implicated by Windmann et al. (2006). This study used patients with prefrontal lesions who were given one of three instructions; to hold one of the two bistable percepts, to look passively at the stimulus, or to try to speed up the rate of alternations. Interestingly, the ability to hold a percept was not different between patients and controls, however, patients were less able to speed up the rate of perceptual alternations by will. Although binocular rivalry was not used in this study, it suggests that prefrontal cortex serves a specific role in attentional control over bistable stimuli. As the authors remark, damage to prefrontal cortex might have hampered the ability to intentionally switch between two images, leaving the ability to hold a percept unaffected.

CONCLUDING REMARKS

We noted in the introduction that it was Wheatstone (1838) who first posed the question of whether binocular rivalry can be controlled by will. More than 170 years later, and with the benefit of techniques and methodologies that were not even conceivable when he published his pioneering observations in 1838, we can now answer his question: voluntary control over binocular rivalry is possible, yet limited. Like many highly polarized debates, the answer has turned out to be a mixture of both positions. Carefully controlled studies have clearly shown that observers can use attention to modulate their perception during binocular rivalry, either lengthening the dominant percept's duration or changing the overall alternation rate (Lack, 1978; Meng and Tong, 2004; van Ee et al., 2005). Complementing this is the wealth of data showing that binocular rivalry depends strongly on low-level visual attributes such as orientation, spatial frequency, and contrast (Blake, 1989).

The conclusion that binocular rivalry can be partially controlled by voluntary attention is suggestive of an interplay between top-down and bottom-up factors. The fact that observers cannot voluntary take full control over their perception in rivalry suggests that bottom-up factors are important. It has long been theorized that binocular rivalry is initiated early in cortical processing, at a stage where monocular inputs are first combined, and that reciprocal inhibition exists between the monocular neural populations (Blake, 1989). The balance between left- and right-eye neurons varies over time because of adaptation, changing the balance, and causing perceptual switches (Alais et al., 2010a). Within this framework, the image that happens to be dominant at a particular point in time is available to be attentionally selected by top-down processes. As is now well established, this will boost the neural response to the selected image (Reynolds and Chelazzi, 2004) and raise its effective contrast, causing it to dominate more. However, this process cannot continue indefinitely as there is also adaptation taking place that will weaken the response to the dominant image and inevitably lead to a switch in perceptual state. Thus, just as there is a reciprocal relationship between the left- and right-eye's responses, there is also a reciprocity between, on one hand, the response-boosting effect on the early neurons from top-down selection (Reynolds and Chelazzi, 2004), and on the other hand, the response decrement effect due to neural adaptation in these early neurons. Because of this reciprocity, an observer's attempt to attentionally control their perception in rivalry is inevitably limited.

While the primary role proposed for early interocular interactions in binocular rivalry has been contrasted with results implying that binocular rivalry involves later processing stages (Kovács et al., 1996; Logothetis et al., 1996), these results can be integrated within the contemporary view that binocular rivalry involves a multitude of visual stages from early to late processing (Ooi and He, 1999; Blake and Logothetis, 2002; Wilson, 2003; Blake and Wilson, 2011). This "distributed network" view also provides the neural framework within which the top-down/bottom-up interplay that we are proposing can take place. From the literature reviewed above it is obvious that neuro-anatomical networks involved in attentional selection and binocular rivalry overlap. There is also evidence that other networks maybe involved in interocular suppression. A series of fMRI studies by He and colleagues (Fang and He, 2005; Jiang and He, 2006) showed that for some classes of stimuli, a cortical response was still elicited even when they were perceptually suppressed. This was found in dorsal areas for visual objects such as tools, and in FFA, and STS for faces, especially fearful faces. Further, it has been found that when erotic images are suppressed they are still able to influence the spatial allocation of attention (Jiang et al., 2006). Although these studies used continuous flash suppression (Tsuchiya and Koch, 2005) rather than conventional binocular rivalry, they do suggest interesting possibilities relevant to this review. One is that visual information could arrive in extrastriate visual cortex through subcortical pathways and bypass early suppression (Weiskrantz, 1997; Morris et al., 1999). A second possibility is that suppression is an attenuation process that leaves signals weakened but still able to activate subsequent areas, albeit without awareness. Broadly, these findings are consistent with other recent evidence suggesting a multistage rivalry process (Nguyen et al., 2003; Alais and Melcher, 2007) and that dorsal and ventral rivalry-processes may be independent (Alais and Parker, 2006).

Although it is tempting to conclude that the fronto-parietal areas involved in attentional selection (Duncan, 2001; Miller and Cohen, 2001) must also be involved in selecting and maintaining the dominant image during binocular rivalry, it is not clear that this conclusion follows. Although a role for these areas in selection may be evident in some circumstances, the involvement of these areas does not appear to be strictly necessary to select a "winner" from the competing rivalry stimuli. That is, it is clear that an adapting reciprocal inhibition model of rivalry can also explain perceptual switches (Alais et al., 2010a), and that such a model can be located early in visual processing (Tong and Engel, 2001; Lee et al., 2005, 2007). Indeed, the sufficiency of the early process to produce switches may explain the finding in several reports that while removing attention slows the rate of rivalry alternations, the alternations continue to occur in the near-absence of attention (Paffen et al., 2006; Pastukhov and Braun, 2007; Paffen and Hooge, 2011). In addition, this suggestion is in line with a very recent report by Knapen et al. (2011), who showed that frontal activation related to perceptual alternations was more likely reflecting a response to these alternations rather than being their cause.

Human frontal cortex has been implicated as the site responsible for maintaining conscious representations of the visual world (Crick and Koch, 1995; Rees, 2001). From these observations, it could be hypothesized that prefrontal cortex is involved in selecting one of two competing images during binocular rivalry. Nonetheless, it is still possible that a similar pattern of activity would be seen in prefrontal cortex without endogenous attention, simply as a consequence of maintaining a conscious representation of the current winner of the early reciprocal inhibition process. Indeed, this would be consistent with the results of Windmann et al. (2006) who found that the ability to hold a percept dominant in perception was unaffected in patients with prefrontal lesions (although this study did not use binocular rivalry displays).

In sum, binocular rivalry may be considerably modulated by voluntary attention, but it is not under complete attentional control. We propose that there are two important reasons for this. First, an adapting reciprocal inhibition arrangement between early monocular channels is sufficient to trigger switches in perceptual dominance independently of a high-level "selection" mechanism. Second, the contrast enhancing effect of top-down attentional selection is counteracted over time by a response attenuating effect of neural adaptation which weakens the response to the dominant image. Both of these processes can be thought of as reciprocal and therefore self-balancing processes, with the consequence that complete attentional control over binocular rivalry could never be realized.

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The effects of categorical and linguistic adaptation on binocular rivalry initial dominance

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Binocular rivalry (BR) is a phenomenon in which visual perception alternates between two different monocular stimuli. There has been a long debate regarding its nature, with a special emphasis on whether low- or high-level mechanisms are involved. Prior adaptation to one of the two monocular stimuli is known to affect initial dominance in the subsequent dichoptic presentation. In the present work, we have used three different types of adaptation in order to investigate how each one affects initial dominance during BR. In the first adaptation type, adapting to a stimulus identical to the one used during rivalry has led to its consequent suppression, verifying previous findings. The binocular presentation which we have used excludes the possibility of eye-adaptation, suggesting that it is the specific stimulus that the brain adapts to. In the second adaptation type, we find suppression effects following adaptation to stimuli belonging to the same category (face or house) but are different from the specific ones used in the following BR presentation. In the final adaptation type, in which the words "face" or "house" are used as adaptors, no statistically significant effect was found. These results suggest that perceptual selection can be directly influenced by the prior presentation of visual stimuli different to the ones used during BR, and thus support a higher-level, cognitive influence on the latter.

Keywords: binocular rivalry, high-level adaptation, embodied cognition, mental representations

INTRODUCTION

When two different visual stimuli are presented at corresponding retinal locations, one in each eye, perception alternates between them (or between parts of them – see below). This phenomenon is known as binocular rivalry (BR; e.g., Wheatstone, 1838; Blake, 1989). The unpredictable character of the perceptual alternations led Levelt (1965) to suggest that they are the result of a stochastic process following a gamma distribution, something that later became the "signature" of BR (Logothetis et al., 1996). In-between periods of complete dominance, perception has a piecemeal appearance (e.g., O'Shea et al., 1997) which, together with the dependence of perceptual alternations on low-level stimulus attributes (Breese, 1909) and the inability to control them by "the power of will" (Wheatstone, 1838, p. 386), have been taken by some as evidence toward an early, eye-competition mechanism, treating BR as the result of antagonism between opponent monocular neuronal populations (Levelt, 1965; Blake, 1989). Such a low-level account is also supported by studies showing that, during suppression, visual sensitivity is severely impaired in a way invariant to specific stimulus attributes, suggesting that suppression acts non-selectively upon the suppressed eye (e.g., Fox and Check, 1968; Fox and Rasche, 1969; Blake and Fox, 1974). Furthermore, when the two stimuli are interchanged between the eyes, observers perceive the previously suppressed stimulus (Blake et al., 1980). Such empirical findings support the notion of an early interocular competition, BR being the result of a continuous interplay of adaptation and recovery, mediated by reciprocal inhibition mechanisms (Blake, 1989). This notion, thus, predicts an early neuronal localization of the phenomenon, something partly confirmed by neuroimaging studies (e.g., Polonsky et al., 2000; Tong and Engel, 2001; Haynes et al., 2005).

Although piecemeal rivalry can be considered as indicating the existence of independent, local eye-zones of dominance, i.e., the footprint of a low-level mechanism (see Blake, 1989), it could also consist evidence for a higher-level control mechanism, combining inputs from the two eyes (Kovacs et al., 1996). Such an alternative, "stimulus-rivalry," theory treats BR as a high-level phenomenon, concerning central stimulus representations and thus permeable to top-down modulations (Walker, 1978; Logothetis, 1998). von Helmholtz was the first to suggest that rivalry is the result of attentional shifts and that, with practice, one can learn to prolong dominance of one of the stimuli (see Tong, 2001). Factors such as cultural background (Bagby, 1957), emotional content (Engel, 1956), and semantic meaning (Rommetveit et al., 1968) can modify the course of the effect, indicating an involvement of higher-level processes on perceptual dominance. This idea is further supported by more recent and rigorous studies (e.g., Sobel and Blake, 2002; Andrews and Lotto, 2004; Mitchell et al., 2004; Bannerman et al., 2008; Costello et al., 2009). Treating BR as a high-level process deals with issues that the low-level, monocular competition, view cannot deal with: for example, issues like the co-existence of rivalry and stereopsis (Ogle and Wakefield, 1967; Julesz and Miller, 1975; Harrad et al., 1994), the integration of motion signals during rivalry (Carney et al., 1987; Carlson and He, 2000) and aftereffects that survive rivalry suppression (Lehmkuhle and Fox, 1975; but see Blake et al., 2006). Accordingly, single-unit recordings have shown that many neurons in the visual cortex still respond to the perceptually suppressed stimulus (Logothetis and Schall, 1989; Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997). There is also evidence for interocular grouping in BR percepts that combine similar stimulus parts from the two eyes (Kovacs et al., 1996). Perceptual alternations can, under specific conditions, be totally unaffected by eye-swapping of the stimuli (Logothetis et al., 1996). Additionally, and opposed to Wheatstone's (1838, p. 386) view, several studies show effects of directed attention and/or "will" on perceptual alternations (van Ee et al., 2005; Klink et al., 2008; de Graaf et al., 2011). This second view, therefore, regards BR as a competition between alternative stimulus representations, in which perceptual alternations engage higher-level cognitive mechanisms (Logothetis et al., 1996; Leopold and Logothetis, 1999).

In recent years, there has been an effort for a holistic explanation of BR, using an integrative approach between the two theories. The fact that there is evidence supporting both sides (see above) does not make it necessary that the two views should exclude each other. Co-existence and interaction between the two different suggested (high- and low-level) mechanisms is also a possibility. The stimulus rivalry account, although challenged as a phenomenon taking place under very specific, limited circumstances (Lee and Blake, 1999), has refreshed the idea of a high-level, cognitive approach (Blake, 2001), endorsing a posterior neuronal localization of rivalry (Logothetis, 1998). The basic ideas of eye-rivalry had to be refined and restated (see Lee and Blake, 1999; Blake, 2001). The need for an integrative approach became necessary, and the hypothesis of eye-competition had to change into an "eye-and-percept-competition hypothesis" (Papathomas et al., 1999). A possible reconciliation is to assume that we have to do with two distinct phenomena (Lee and Blake, 1999; Tong, 2001; Blake and Wilson, 2011), arising from distributed neural events occurring at multiple stages of visual processing (Blake and Logothetis, 2002; Ooi and He, 2003). Perhaps different mechanisms support different aspects of rivalry, such as the generation of transitions during rivalry and the maintenance of dominance and suppression (Tong et al., 2006). The current tendency for most researches is to account for both the eye/low-level and stimulus/high-level factors (Bhardwaj et al., 2008; van Boxtel et al., 2008; Alais et al., 2010; Bartels and Logothetis, 2010; Keliris et al., 2010).

Visual adaptation, on the other hand, is a process by which one can alter the response of the perceptual system to a stimulus (test), by first exposing it to another stimulus (adaptor; e.g., Lin and He, 2009). In addition to aftereffects due to low-level adaptation, such as adaptation to orientation (Blakemore and Campbell, 1969), or to direction of motion (Wohlgemuth, 1911), there is also higher-level adaptation to elements such as natural images, artworks, or even eye gaze and natural facial attributes like gender, ethnicity, and facial expressions (e.g., Clifford et al., 2007; Carbon and Ditye, 2011). The virtue of adaptation to isolate specific neuronal populations by decreasing responsiveness to subsequent stimulus presentation has made it a powerful tool for dissecting the neural processes of the visual hierarchy underlying BR (van Boxtel et al., 2008). Adaptation aftereffects have been used to study the non-conscious visual processing during BR (Lin and He, 2009), the possible neural locus of suppression (Lehmkuhle and Fox, 1975; Blake et al., 2006), the crucial factors underlying perceptual selection (Alais and Melcher, 2007; Hancock et al., 2008; van Boxtel et al., 2008), the cause of perceptual switches (Lankheet, 2006; Alais et al., 2010; Bartels and Logothetis, 2010), as well as the nature of the phenomenon *per se* (Blake, 1989; Wilson et al., 2001).

A common question regarding adaptation is whether it can influence BR's initial dominance. Also termed as "onset rivalry," initial dominance is a basic characteristic of the neural processes involved in perceptual selection, and can be biased by even a small shift in the balance between the processing of the two images (Brascamp et al., 2007). A straightforward way to manipulate initial dominance is "flash suppression" (Wolfe, 1984), during which, prior presentation of one stimulus results in the dominance of the other. More recent studies (e.g., Holmes et al., 2006; Hancock et al., 2008) have confirmed that when one or both eyes view an (adaptor) grating stimulus of a particular orientation before the presentation of that grating to one eye and an orthogonal (non-adapted) grating to the other eye, the non-adapted one gains initial perceptual dominance during BR. van Boxtel et al. (2008) have used complex (faces/houses) stimuli to confirm that adaptation leads to the suppression of the adapted stimulus and to the dominance of the non-adapted one. Additionally, they have shown that the effects of adaptation to gratings are limited to retinotopically matched locations, while, for the complex stimuli, such effects are evident in both retinotopically and spatiotopically matched locations. Furthermore, Hancock et al. (2008) have shown that in order for a stimulus to produce adaptation aftereffects, it must be consciously perceived, suggesting that the initial selection during BR involves later stages of visual processing. In the present study, we use adaptation of varying levels of complexity in order to test the top-down influence of higher-level mechanisms in BR.

MATERIALS AND METHODS

General note on participants:

In both experiments, native Greek speakers, undergraduate students at the University of Athens, participated for course credit. All reported normal or corrected-to-normal vision and were naïve about the purpose of the study. All experiments were carried out in accordance to the national regulations and legislations of the University of Athens, and informed consent was obtained from all the participants.

EXPERIMENT 1

Participants

This experiment used 25 participants (17 females, mean age = 24.7, SD = 6.8).

Material

For the binocular presentation of stimuli, we have used a ScreenScope mirror stereoscope SA200, mounted in front of the stimulus-presentation monitor. Stimuli consisted of gray (33 cd/m^2) sketches of face and house images (two of each) as well as the words "Face" and "House" written in the Greek language. All stimuli were presented against a black (1 cd/m^2) background. All the BR-testing periods across conditions consisted of a particular face and a particular house image presented dichoptically, and thus competing for perceptual dominance. The rest of our stimuli were used as adaptors, depending on the condition (see *Design and Procedure*). In order to enable fusion and alignment, so that the two monocular stimuli would fall on corresponding retinal locations, a red (30 cd/m^2) square aperture (2.86° of visual angle) surrounding the stimuli and a fixation cross were also used. In order to secure fixation and eye-alignment in each trial, adaptation and BR periods were intermediated by the presentation of the aperture and the fixation cross alone. Stimuli were generated using Adobe Illustrator and presented on a 17-inch LCD HP monitor (1280 × 1024 pixels at 60 Hz) using DMDX software (Forster and Forster, 2003). Luminance was measured using a Gossen Mavolux 5032C photometer. Experiments were conducted in a dark room, and participants viewed the computer monitor through the stereoscope, resting on a custom-made chin holder at a distance of 40 cm.

Design and Procedure

Figure 1 shows a schematic example of the procedure. Across conditions, the BR-testing period was preceded by an adaptation period, in which a single stimulus (adaptor) was presented to both eyes. Adaptation duration was 10 s, except for the "Linguistic" (see below) conditions, in which it was 1 s. After the adaptation period, the adaptor stimulus was removed leaving only the aperture and fixation cross for 50 ms on the screen, accompanied by a beep (at 480 Hz) used to indicate that the testing period was about to begin. This was, in turn, followed by 5 s of dichoptic presentation of a face and a house, during which, participants had to give their response. Their task was to keep fixation and indicate their perceptual state (face or house) using continuous button presses. They were instructed to respond even when the suppression of the less-visible stimulus was not complete. Although we have included only initial dominance in our analysis, participants had to keep pressing the appropriate buttons during the whole 5-s period of dichoptic presentation.

We have used seven different experimental conditions, belonging to four different main types of adaptation sessions (control, same, categorical, and linguistic). In the Control condition, designed to provide baseline performance, BR was preceded by adaptation to the aperture and fixation cross alone. In the Same Face Adaptation ("SameF") and Same House Adaptation ("SameH") conditions, BR was preceded by adaptation to the standard face or house images (used also during BR) respectively. In the Categorical Face Adaptation ("CatF") and Categorical House Adaptation ("CatH") conditions, BR was preceded by adaptation to a face or a house image, different to the ones used during BR testing. This design let us examine whether high-level adaptation, i.e., adaptation to different tokens of the categories *faces*/*houses*, could result in the suppression of the adapted stimulus category and the dominance of the non-adapted one. Finally, in the Linguistic Face Adaptation ("LingF") condition, BR was preceded by the word "Face" and in the Linguistic House Adaptation ("LingH") by the word "House." The purpose of these two conditions was to examine whether the presentation of a single word referring to a stimulus category would be able to induce suppression effects similar to the ones produced by adaptation to images.

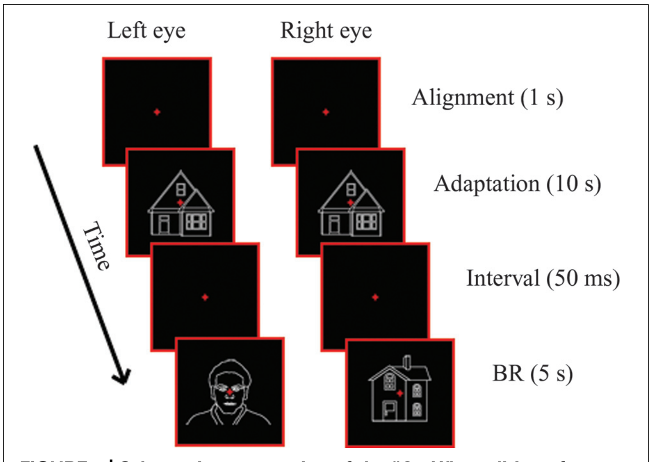

FIGURE 1 | Schematic presentation of the "CatH" condition of Experiment 1.

In order to keep a steady adaptation level, conditions were completed in separate blocks consisting of 30 trials each, apart from the "LingF" and "LingH" conditions which were presented within the same block in random order (60 trials: 30 with "Face" adaptor and 30 with "House" adaptor). To avoid any eye-of-origin effects, a counterbalanced design was used during all BR periods: in half the trials of each condition, the face image was presented to the left eye and the house image to the right, while in the other half, they were presented reciprocally. The blocks were attended in random order and participants made a break of up to 10 min between blocks. Before the experiment started, each participant attended a 20-trial practice block (with no adaptation) in half of which, the face was presented alone, and in the other half the house alone, always binocularly. The purpose of this was to familiarize participants with the appropriate button presses for each percept. During practice, the program provided feedback presenting the message "CORRECT," written in green, for correct answers and "WRONG," written in red, for wrong answers.

EXPERIMENT 2

Participants

This experiment used another 10 native Greek speakers (nine females, mean age = 27.2, SD = 7.3).

Design and procedure

A possible objection to the design of Experiment 1 would be that, in the categorical conditions, participants adapt to some low-level characteristics of the stimuli, which are different between faces and houses. In particular, although the two categories were equalized in terms of their average size, luminance, and contrast, one could argue that the houses contained more straight than curved lines, with the opposite being true for the faces. For this reason, we have conducted the present, control experiment using, as adaptors, scrambled versions of our stimuli, which were no longer recognizable as proper faces and houses. If the effects that we have observed in Experiment 1 (see Results) were due to low-level factors, such a manipulation should make no difference. On the other hand, if adaptation was of a higher-level categorical type, no significant effects should be observed with the scrambled adaptors. Additionally, in Experiment 1, the linguistic conditions were, contrary to the rest of the conditions, randomized within the same block, and the adaptation duration was only 1 s. In order to make sure that it was not because of these methodological differences that the linguistic conditions gave no significant effects (see Results), in Experiment 2, we have separated the two linguistic conditions into different blocks and have increased the time-course of adaptation to 10 s. Thus, the linguistic conditions here are similar and directly comparable to the categorical ones. In particular, this experiment consisted of the following conditions: “Control,” “CatF,” “CatH,” “LingF,” and “LingH.” Materials, testing stimuli, and the general procedure were identical to Experiment 1, apart from the following two differences: (1) the adaptors in “CatF” and “CatH” were turned upside down and their parts randomly scrambled, to the point that they did no more resemble face and house caricatures. (2) The two linguistic conditions were presented in separate blocks, with an adaptation duration of 10 s.

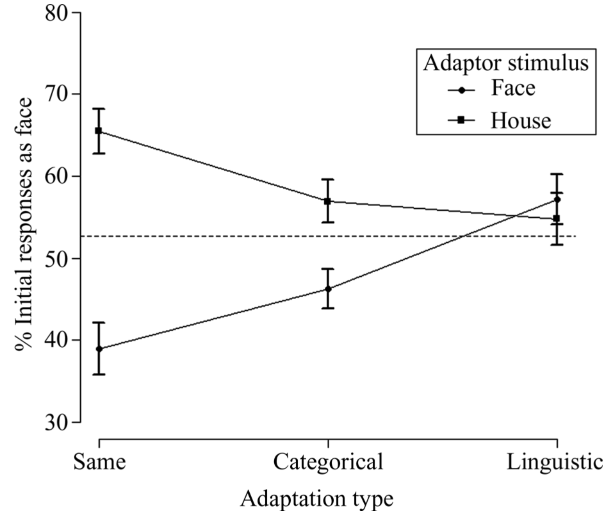

FIGURE 2 | Face initial dominance as a function of adaptation type and adaptor stimulus for Experiment 1. The dashed line represents the control condition-without adaptation (52.7%). Error bars represent ±1 standard error of the mean.

RESULTS

EXPERIMENT 1

Table 1 and **Figure 2** show the percentage of trials in which the initial percept was face, as a function of the condition, averaged across all 25 participants. In the control condition, used to reveal any biases in favor of the one percept or the other, the face stimulus dominated first in 52.7% of the trials ($p = 0.01$, binomial distribution). This suggests that, without any stimulus-adaptation, there was a slight but statistically significant preference for faces, which was used as a baseline in order to evaluate perceptual biases after adaptation to different types of stimuli.

A 3 (adaptation type: same/categorical/linguistic) × 2 (adaptor stimulus: face/house) repeated-measures ANOVA for the initial face dominance showed a non-significant main effect of adaptation type [same: $M = 52.2\%$, SE = 1.802; categorical: $M = 51.6\%$, SE = 2.049; linguistic: $M = 56\%$, SE = 2.339; $F(2,48) = 2.784$, MSE = 102.259, $p = 0.072$]. The lack of adaptation type main effect suggests that, on average, participants adopted similar response strategies, no matter whether they were adapted to same, categorical, or linguistic face/house stimuli. On the other hand, there was a significant main effect of adaptor stimulus on face initial dominance [face adaptors: $M = 47.5\%$, SE = 2.278; house adaptors: $M = 59.1\%$, SE = 2.151; $F(1,24) = 17.101$, MSE = 295.074, $p < 0.001$] showing that adaptation to a face stimulus resulted in a decrease of face initial dominance and in an increase of house initial dominance during BR, whereas the opposite was the case after adaptation to a house stimulus. Also, there was a significant interaction between adaptation type and adaptor stimulus, $F(2,48) = 17.212$, MSE = 152.463, $p < 0.001$, showing that not all types of adaptation were equally effective.

Table 1 | Summary statistics for face initial dominance across conditions, for Experiment 1.

Condition	*N*	*M* (SD)	SE
Control	25	52.7 (8.9)	1.8
SameF	25	38.9 (15.8)	3.2
SameH	25	65.5 (13.7)	2.7
CatF	25	46.3 (12.2)	2.4
CatH	25	56.9 (13.1)	2.6
LingF	25	57.2 (15.3)	3.1
LingH	25	54.8 (15.9)	3.2

SE = ±1 standard error of the mean, across participants.

In order to further investigate the interaction between the type of adaptation and adaptor stimulus, we conducted simple effects analyses: paired comparison analysis within adaptation type categories, showed that in significantly more BR trials face gained initial dominance after adapting to “SameH” ($M = 65.5\%$, SE = 2.747) compared to “SameF” ($M = 38.9\%$, SE = 3.160), $t(24) = 5.645$, $p = 0.003$. More interestingly, in significantly more BR trials face gained initial dominance after adapting to “CatH” ($M = 56.9\%$, SE = 2.617) compared to “CatF” ($M = 46.3\%$, SE = 2.436), $t(24) = 3.60$, $p = 0.003$. There was not a significant difference for the face initial dominance between “LingH” ($M = 54.8\%$, SE = 3.180) and “LingF” ($M = 57.2\%$, SE = 3.065), $t(24) = 0.580$, $p = 0.567$. (All p-values were adjusted for multiple comparisons). As shown in Figure 2, the strongest effect of adaptation on initial dominance was observed in the same adaptation type, followed by the categorical adaptation type, with no statistically significant differences observed in the linguistic type. In both the same and categorical, adapting to a face resulted in the suppression of the face in favor of the rivaling house stimulus during BR, whereas adapting to the corresponding house stimulus had the opposite effect. One-way repeated-measures ANOVA with different adaptation types to face stimuli as factors revealed a significant main effect of face-adaptation type: because the sphericity assumption was violated, we used Greenhouse–Geisser correction ($\epsilon = 0.76$): $F(1.522,36.525) = 17.335$, MSE = 160.142, $p < 0.001$. Pair-wise comparisons revealed a significant difference between “SameF” and “CatF” (face dominance was less in “SameF,”

$p = 0.007$), a significant difference between "SameF" and "LingF" (face dominance was less in "SameF," $p < 0.001$), and a significant difference between "CatF" and "LingF" (face dominance was less in "CatF," $p = 0.008$). Conversely, one-way repeated-measures ANOVA with different adaptation types to house stimuli as factors, also revealed a significant main effect of house-adaptation type: $F(2,48) = 5.994$, $\text{MSE} = 132.864$, $p = 0.005$. Pair-wise comparisons revealed a significant difference between "SameH" and "CatH" (face dominance was greater in "SameH," $p = 0.039$) and a significant difference between "SameH" and "LingH" (face dominance was greater in "SameH," $p = 0.007$). There was no significant difference between "CatH" and "LingH" ($p = 1$).

To evaluate the effect that each adaptation condition had, we investigated whether there were any differences in initial dominance between the control and the other conditions. Paired comparisons showed a statistically significant difference between Control and "SameF" ($p < 0.0001$), between Control and "SameH" ($p < 0.0001$), and between Control and "CatF" ($p = 0.037$). These results show that these three adaptation conditions significantly changed the balance of initial dominance in perception, compared to what it was without adaptation.

EXPERIMENT 2

No effect was found in either paired comparison analysis of the conditions ["CatF" vs "CatH" comparison: $t(9) = 1.208$, $p = 0.258$; "LingF" vs "LingH" comparison: $t(9) = 0$, $p = 1.0$; see also **Table 2**].

DISCUSSION

In the present study we have shown that adaptation to a visual stimulus results in its initial suppression in a subsequent dichoptic presentation. In the "same" adaptation type, the stimuli used during adaptation and BR were identical, confirming what Wolfe (1984) has previously termed as "flash suppression." A difference between the present result and that of Wolfe's is that we (as well as Holmes et al., 2006; Hancock et al., 2008) have presented the adaptor stimulus binocularly. In this way, the observed suppression cannot be accounted for by eye-specific adaptation, but rather reflects the adaptation of the system to the specific stimulus, indirectly supporting a higher-level view of the mechanisms underlying perceptual selection during dichoptic presentation (Walker, 1978; Logothetis, 1998). However, despite the exclusion of an eye-adaptation effect, the possibility that the brain adapts to low-level characteristics of the specific stimulus still remains. Interestingly, our data also showed perceptual suppression when the adaptor stimulus belonged to the same category as the test stimulus, but was not identical to it: adaptation to faces and houses different to the ones subsequently presented dichoptically, were found to bias perception in favor of the other category. By using scrambled versions of the adaptor stimuli, and thus resembling all the low-level characteristics, we have verified that the observed adaptation effects were indeed categorical, i.e., of a higher, more abstract level. The fact that the presentation of one type of images can affect the fate of other images of the same type is in agreement with higher-level, cognitive, mechanisms being responsible for perceptual selection, when a controversy between the information from the two eyes has to be dealt with.

Along this line of thought, we have assumed the possibility that adaptation to an even higher, semantic level could perhaps influence perceptual selection during BR as well. Embodied theories for language comprehension regard words as the cues enabling the neuronal reactivation of the perceptual experience of the words' referents (e.g., Glenberg, 1997; Barsalou, 1999; Fincher-Kiefer, 2001; Glenberg and Kaschak, 2002; Zwaan, 2004; Gallese and Lakoff, 2005). The idea that linguistic representations reside in perceptual representations is supported by several behavioral studies (e.g., Stanfield and Zwaan, 2001; Zwaan et al., 2002, 2004; Yaxley and Zwaan, 2007), whereas a direct influence of language on perceptual sensitivity has also been shown by Meteyard et al. (2007), and Pelekanos and Moutoussis (in press). Moreover, neuroimaging evidence suggests that linguistic stimuli (words or sentences) activate neuronal circuits which are also selectively active during actions or perceptions involving the linguistic stimuli's referents (e.g., Isenberg et al., 1999; Pulvermüller, 1999, 2005; Speer et al., 2009). Similar, and especially interesting brain-imaging results have also been obtained by a recent fMRI study, using linguistic material specifically related to faces and places: Aziz-Zadeh et al. (2008) showed that listening to sentences which are related to faces can modulate neuronal activity in the left hemisphere's fusiform face area (FFA), while listening to sentences related to places modulates neuronal activity in the left hemisphere's parahippocampal place area (PPA). FFA has been found to respond more strongly to the perception of faces compared to a great variety of other, non-face stimuli, and PPA has been found to respond strongly during the perception of place and house stimuli, but not of face stimuli (see below). Based on the studies reviewed above, in the linguistic conditions of the present study, we briefly presented the words "face" or "house" before the dichoptic presentation of face and house image stimuli, with the assumption that an imagery-like, perceptual representation of the linguistic face/house adaptor could be sufficient to evoke suppressive effects. On the other hand, facilitation following prior presentation of images has been also reported previously, especially when the adaptor/prime is presented briefly (e.g., Brascamp et al., 2007) as was the case with our linguistic adaptors in Experiment 1. Furthermore, the semantic meaning of words presented prior to dichoptic stimulation has been also shown to have facilitative-priming effects: the word "hell" was more likely to gain perceptual dominance during BR between that, and a typographically similar word like "tell," when the BR period was preceded by the binocular presentation

Table 2 | Summary statistics for face initial dominance across conditions, for Experiment 2.

Condition	*N*	*M* (SD)	SE
Control	10	49.7 (5.5)	1.8
CatF	10	42.0 (12.2)	3.9
CatH	10	47.7 (11.2)	3.5
LingF	10	47.3 (11.2)	3.5
LingH	10	47.3 (11.6)	3.7

SE = ±1 standard error of the mean, across participants.

of a context-related word like "devil" (Rommetveit et al., 1968). Similarly, semantically related words have been found to come out of suppression faster than unrelated words, when a prime-precedent word is presented (Costello et al., 2009). Taking everything into consideration, it would seem quite reasonable to assume that prior presentation of a word would affect, by any means, perceptual selection mechanisms during BR. However, no statistical significance effect of language on perceptual selection was found in our study.

Our main, novel finding remains that of the effect of a general type, categorical adaptation on the perceptual result of a subsequent dichoptic presentation. In the domain of BR, a somehow similar result has been reported by Wolfe (1984): by changing the spatial frequency and luminance of the gratings used, he showed that suppression is not dependent on a perfect match between the adaptor and the test stimuli. The fact that he used low-level stimuli, however, does not indicate any higher-level, categorical influence on BR—a general adaptation of early orientation-selective channels could easily account for his result. In fact, since monocular adaptation was used, Wolfe's result could also be accounted for by eye-specific adaptation. In the present experiments, we show that a general, categorical adaptation to complex, high-level stimuli such as faces and houses can affect the outcome of perceptual competition during BR. A similar adaptation effect on ambiguous images has been reported recently: when participants were first adapted to a face or a hand and then presented with a combination of both, they perceived the non-adapted stimulus (Cziraki et al., 2010). Interestingly, the ambiguous image used consisted of a face and a hand different from the adaptors, showing a more abstract, categorical adaptation aftereffect, as is the case in the present study. The fact that such a categorical adaptation had an influence in our experiments as well supports the notion of a higher-level nature of BR, in which top-down cognitive interactions play a role in perceptual selection (Walker, 1978; Logothetis, 1998). Furthermore, this influence is not only based on "simple," perceptual representations, but on cognitive, knowledge-based representations as well.

A well-known aftereffect caused by prolonged adaptation is the motion aftereffect (MAE): after adaptation to a motion of a particular direction, the subsequent viewing of a stationary scene will be perceived as moving to the opposite direction (e.g., Anstis et al., 1998). MAE was originally explained by Sutherland (1961) who suggested that the direction in which something is perceived to move may depend on the ratios of firing of cells sensitive to opposite directions of motion: after prolonged adaptation to a specific direction, a stationary scene "would produce less firing in the cells which had just been stimulated than normally, hence movement in the opposite direction would be seen to occur" (Sutherland, 1961, p. 227)[1]. This explanation was inspired by Hubel and Wiesel's (1959) observation of opponent populations of directionally selective neurons in cat's cortex. Would a similar account be possible for the aftereffects observed in our study? The complex stimuli that we and others (e.g., van Boxtel et al., 2008) have used are known to activate specific, "higher" brain regions: the human FFA, in the fusiform gyrus, which responds more strongly to the perception of faces compared to a great variety of other, non-face stimuli (e.g., Puce et al., 1996; Kanwisher et al., 1997, 1999; McCarthy et al., 1997), and the PPA, which responds strongly during the perception of place and house stimuli, but not of face stimuli (Aguirre et al., 1998; Epstein and Kanwisher, 1998). Furthermore, such specificity is also present during BR (Tong et al., 1998). Adaptation of these areas, following the presentation of various face and house adaptor stimuli, could perhaps, theoretically explain the subsequent result on perceptual selection. However, such a hypothesis, suggesting an opponent mechanism between FFA and PPA, remains highly speculative, since there is no known anatomical connection or activity "comparison" between the two areas.

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[1] We recognize that the explanation for MAE may require a lot more complex models (e.g., Stocker and Simoncelli, 2009) than the one suggested by Sutherland (1961).

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Insights from intermittent binocular rivalry and EEG

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Novel stimulation and analytical approaches employed in EEG studies of ambiguous figures have recently been applied to binocular rivalry. The combination of intermittent stimulus presentation and EEG source imaging has begun to shed new light on the neural underpinnings of binocular rivalry. Here, we review the basics of the intermittent paradigm and highlight methodological issues important for interpreting previous results and designing future experiments. We then outline current analytical approaches, including EEG microstates, event-related potentials, and statistically based source estimation, and propose a neural model of the sequence of brain events that may underlie different aspects of binocular rivalry. Finally, we discuss the advantages and limitations of using binocular rivalry as a tool to investigate the neural basis of perceptual awareness.

Keywords: binocular rivalry, perceptual reversals, EEG microstates, ERP, visual awareness

INTRODUCTION

Traditionally, binocular rivalry involves continuous (uninterrupted) presentation of different stimuli to the left and right eyes. Perception stochastically alternates between these two stimuli every few seconds (Tong et al., 2006; Sterzer et al., 2009) and is likely to involve competition between neural signals representing each stimulus and its associated percept. (Blake and Logothetis, 2002). fMRI studies in humans have identified activity in frontal and parietal areas in addition to early visual areas during binocular rivalry (Lumer et al., 1998; Lumer and Rees, 1999). Single-cell recordings in non-human primates have shown that firing rates of cells in higher-level visual areas (in the ventral stream) are correlated with the momentarily active percept (Leopold and Logothetis, 1996; Logothetis et al., 1996). These measures provide complementary spatial/temporal information: fMRI provides wide spatial coverage (i.e., the entire brain) but with low temporal resolution, whereas single-cell recordings provide high temporal resolution but measure activity at a limited number of spatial locations at any given time. Here, we review an approach that affords measures with concurrently high temporal resolution and whole brain spatial coverage: EEG source imaging (Michel et al., 2009). Studies that have used this analysis approach in combination with intermittent stimulation have begun to provide fresh insights into the sequence of neural events that contribute to different aspects of binocular rivalry (Pitts et al., 2010; Britz et al., 2011; Britz and Pitts, 2011).

THE INTERMITTENT PARADIGM

In all binocular rivalry paradigms subjective reports are required in order to relate measured brain activity to each percept or to transitions between percepts. The subjective reports (usually keypresses) are used to indicate the current percept and to index the time at which a perceptual transition has occurred. With continuous rivalry, the time intervals between the perceptual changes themselves and the reports of such changes are likely to vary from trial-to-trial by tens to hundreds of milliseconds. For fMRI, this temporal jitter between percept and report is unlikely to affect measurements of brain activity which are on the scale of several seconds. With EEG however, such trial-to-trial variation can obliterate event-related potentials (ERPs) and thus compromise the advantages offered by this temporally precise measure.

To alleviate this problem, stimuli can be presented intermittently (alternated with blank intervals) and EEG recordings can be time-locked to stimulus onset instead of subjects' reports. Influenced by previous work (Orbach et al., 1963, 1966; O'Donnell et al., 1988), Kornmeier and Bach (2004) were the first to detail the advantages of the intermittent paradigm for the measurement of ERPs during ambiguous figure perception. An ERP component dubbed the "reversal negativity" (RN) was found to be associated with perceptual changes reported by subjects while viewing the Necker cube (Kornmeier and Bach, 2004). The RN component, which is characterized by a negative amplitude shift for perceptual reversals at ∼200–300 ms post-stimulus onset over the posterior scalp, has subsequently been identified in a variety of studies using various types of bistable stimuli including binocular rivalry (Kornmeier and Bach, 2004, 2005; Kornmeier et al., 2007; Pitts et al., 2007, 2009; Britz et al., 2009; Intaite et al., 2010; Britz and Pitts, 2011). In addition to the RN, an earlier component, the "reversal positivity" (RP; ∼100–130 ms), and a later component, the "late positive complex" (LPC; ∼400–600 ms), have also been linked with perceptual reversals (Kornmeier and Bach, 2005; Pitts et al., 2007; Britz et al., 2009; Britz and Pitts, 2011).

Importantly, intermittent rivalry appears to closely resemble continuous rivalry with respect to perceptual dominance periods and reversal rates (Britz et al., 2009; Britz et al., 2011), although to achieve this consistency, the duration of the stimulus and the duration of the intervening blank interval must be fine-tuned. If the stimulus duration is too long, reversals may occur within a single presentation. If the intervening blank interval is too long, reversals can be prevented altogether (Leopold et al., 2002; Sterzer and Rees, 2008). Conversely, if the stimulus duration or blank interval is too brief, subjects will have trouble reporting their percepts during each trial and the resulting ERPs (including motor potentials) for a given trial will overlap and thus contaminate ERPs elicited in the subsequent trial. With these concerns in mind, most studies have presented stimuli for durations of 600–800 ms, with 400–600 ms blank intervals. Recently, Brascamp et al. (2009) showed that reversal rates during intermittent rivalry become substantially slower than continuous rivalry when the blank interval is extended beyond ~1.5 s. Kornmeier et al. (2007) systematically manipulated blank interval durations (ranging from ~15–400 ms) and found that reversal rates for the Necker cube were reduced for very short blank intervals (e.g., ~15 and ~50 ms). Taken together, previous findings suggest that a "sweet spot" may exist between long and short blank interval durations in which reversal rates for intermittent and continuous rivalry can be made equivalent. However, a systematic manipulation of blank interval durations ranging from very short (e.g., <100 ms) to very long (e.g., >2 s) has not yet been carried-out, and even though reversal rates can be made equivalent, it is not yet clear whether the neural systems supporting perceptual rivalry under each type of presentation paradigm are exactly the same.

Perhaps the most surprising feature of the intermittent paradigm is that perceptual reversals seem to be tightly time-locked to stimulus onset (Orbach et al., 1963). In other words, as the stimuli flash on-and-off, subjects perceive one of the two possible images for a few trials, and then suddenly they experience the alternative percept *on the next flash*. Subjectively, it is difficult to tell whether the change is perceptual or physical. In fact, subjects often express disbelief that the same stimulus is being flashed on-and-off, insisting that the experimenter must be physically alternating the images on the computer screen. At first glance, this feature of the intermittent paradigm may seem to imply that reversals are exogenously, rather than endogenously, controlled. However, the purpose of the intermittent design is to allow control over *when* reversals *can* occur but not *whether* they actually *do* occur. Whether a reversal occurs or not in the intermittent paradigm (at least for studies in which appropriately tailored blank interval durations are employed) is determined by the same statistical properties (log normal and gamma distributions) as in continuous rivalry.

WHAT CONDITIONS TO COMPARE AND WHY?

In the basic intermittent paradigm, subjects are instructed to report whether their perception has changed (or remained the same) on the current trial relative to the previous trial (Kornmeier and Bach, 2004). These reports allow comparisons between ERPs elicited during endogenous "reversals" versus "stability." This paradigm can be extended by adding a "physical alternation" or replay condition in which unambiguous (Kornmeier and Bach, 2004) or non-rivaling stimuli (Lumer et al., 1998; Pitts et al., 2010) are presented at rates that match those of endogenous reversals. This extended design allows additional comparisons between endogenously versus exogenously generated perceptual reversals.

By modifying how subjects report their percepts, a third (and fourth) type of comparison is possible. Instead of having subjects report perceptual changes, subjects can report whether they perceive image A or image B during each trial. This allows additional comparisons between brain activity associated with percept A versus percept B (Pitts et al., 2010). Notably, with this reporting method, the same data can be re-categorized to allow comparisons between reversals and stability. Thus, by instructing subjects to report their percepts (A or B) during binocular rivalry and physical alternation conditions, the same data can be used to make all four types of comparisons: endogenous percept A versus B; exogenous percept A versus B; endogenous reversal versus stability; exogenous reversal versus stability (see **Figure 1**).

With the goal of comparing ERPs associated with percept A versus B, it is important to choose stimuli that differ on at least one dimension that will produce measurable differences when these stimuli are presented in physical alternation. For example, if ERPs elicited by grating stimuli oriented at 45° versus 135° do not differ during physical alternation, it is unlikely that ERPs associated with percepts of these gratings will differ during binocular rivalry. To circumvent this issue, in a recent study we presented gratings of high versus low spatial frequencies (SF) during binocular rivalry and during physical alternation. ERPs were already known to differ considerably for high versus low SF stimuli, so the question was whether (and when) ERPs might differ based on *percepts* of high versus low SF during rivalry. We found that the amplitude of the C1 component (60–100 ms), which is known to be generated in early visual cortex (V1/V2/V3), differed between the two stimuli during physical alternation but not between the two percepts during rivalry, while subsequent ERPs (130–160 ms), with similar scalp distributions as the C1, differed according to the reported percept in both conditions (Pitts et al., 2010). This pattern of results suggested that the same anatomically early visual areas may play different roles in the rivalry process during different time windows. This strategy, i.e., rivaling stimuli that are known to produce reliable ERP differences when presented in physical alternation, is likely to work for face/house rivalry, upright/inverted face rivalry, as well as the ambiguous face/vase stimulus. Future studies may consider adopting this strategy to help determine the timing and brain regions involved in the resolution of different types of perceptual rivalry.

EEG MICROSTATES AND SOURCE ANALYSES

While analysis of post-stimulus ERPs under the intermittent paradigm has proven fruitful, EEG microstates can be used to compare brain activity during pre-stimulus as well as post-stimulus time periods. EEG microstates refer to brief (~80–120 ms) periods of quasi-stability of the scalp electrical field and provide a measure of the momentary global state of the brain (Lehmann et al., 1987, 2009). Recently, particular microstates have been linked to activity in large-scale functional networks at rest (Britz et al., 2010; Van De Ville et al., 2010), indicating that they represent functionally different states of the mind. Also, the treatment of physically identical stimuli has been shown to vary as a function of the pre-stimulus EEG microstate (Kondakor et al., 1995; Mohr et al., 2005).

Using this analysis approach along with the intermittent paradigm, recent studies have identified two microstates during a pre-stimulus period (−50 to 0 ms) that doubly dissociate perceptual reversals from perceptual stability in the upcoming trial for both the Necker cube (Britz et al., 2009) and binocular rivalry (Britz et al., 2011). The analysis of pre-stimulus EEG microstates in this type of paradigm follows the notion that the different treatment (e.g., reversal versus stability) of physically identical stimuli arises from differences in the microstate immediately preceding

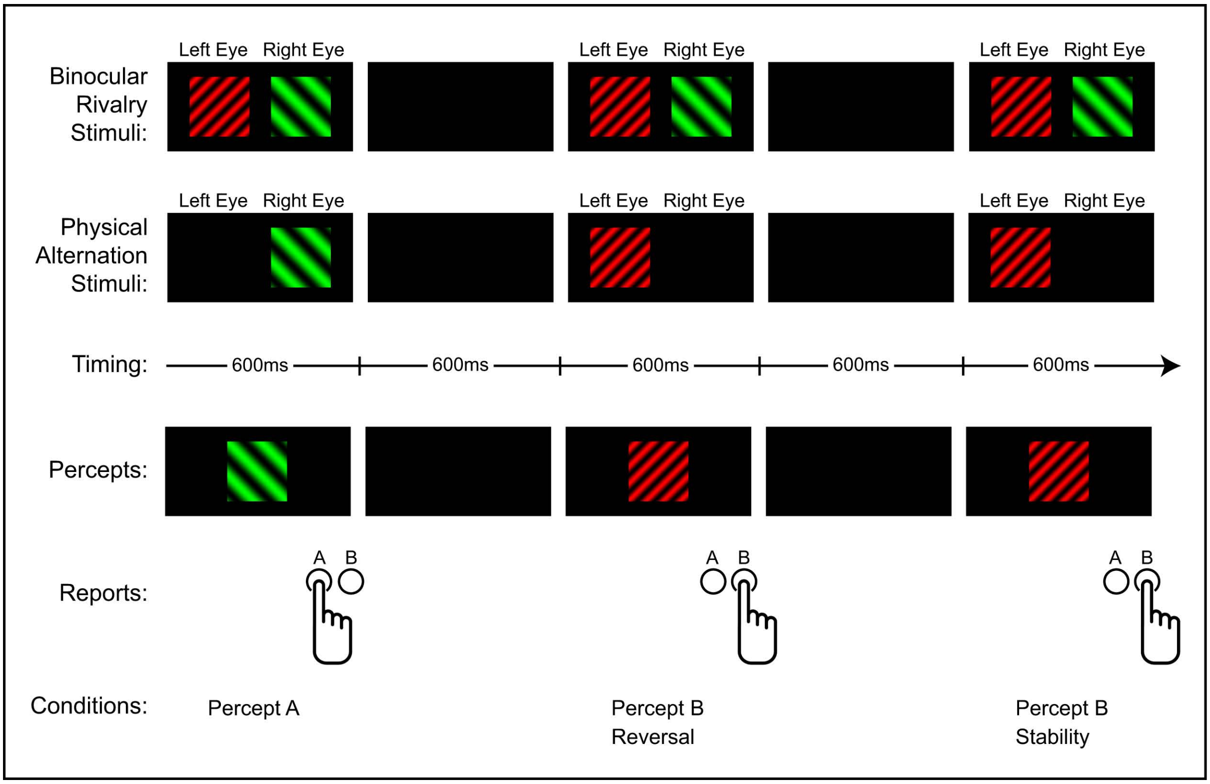

FIGURE 1 | Example of the intermittent paradigm. By presenting stimuli under binocular rivalry and physical alternation conditions and instructing subjects to report their percepts on each trial, all four types of comparisons are made possible: endogenous percept A versus B; exogenous percept A versus B; endogenous reversal versus stability; exogenous reversal versus stability.

stimulus onset. During the brief periods of quasi-stability, only the strength (i.e., the global field power, GFP), but not the configuration of the scalp electrical field can vary. Because the average duration of a microstate is ∼100 ms and it is not disrupted by the arrival of a stimulus, the GFP maximum in the 50-ms time window prior to stimulus onset reflects the best representative sample in terms of signal-to-noise-ratio of the pre-stimulus state. In a first step, the microstates that dissociate two conditions (e.g., reversals versus stability) are identified *within* each subject by means of a cluster analysis. In a second step, those microstates that dissociate the conditions *between* subjects are likewise identified by cluster analysis.

By applying distributed source localization methods to these data, we found that the pre-stimulus activity occurring prior to perceptual reversals is likely generated in the right inferior parietal cortex (Britz et al., 2009; Britz et al., 2011). The pre-stimulus microstate associated with perceptual stability was estimated to have generators in bilateral inferior temporal (IT) areas (Britz et al., 2011). These results are in accordance with previous fMRI studies (e.g., Lumer et al., 1998) that found the right inferior parietal cortex to be involved in multistable perception, and single-cell recordings (e.g., Leopold and Logothetis, 1996) that found correlations between IT activity and the dominant percept. It is important to note however that Britz et al. (2011) found IT activity to be stronger for perceptual stability regardless of the specific percept, whereas Leopold and Logothetis (1996) correlated IT activity in distinct subsets of cells with each specific percept. Nevertheless, the combination of spatial and temporal information offered by the Electrical Neuroimaging approach allowed us to determine that these neuronal events occurred *prior to* perceptual reversals, thus narrowing down the possibilities for their functional contribution to binocular rivalry. Like all EEG and MEG source localization methods, distributed inverse solutions are non-unique and depend on the implemented constraints and regularization parameters. However, there is ample evidence from experimental and clinical studies showing that the constraints introduced in these distributed linear inverse solutions yield reasonable results and a spatial precision comparable to fMRI (Schulz et al., 2008; Vulliemoz et al., 2010; Grouiller et al., 2011; Laganaro et al., 2011).

Importantly, EEG microstates identified within post-stimulus time periods are consistent with traditional ERP components while eliminating potential biases inherent in choosing time windows and electrode locations for statistical tests (Michel et al., 2009). For example, we identified the RN component in a binocular rivalry experiment using both traditional ERP measures and the EEG microstate approach (Britz and Pitts, 2011). Statistical analyses in source space suggested that the RN is generated in inferior occipital–temporal cortex and that the scalp field during the RN time window is stronger for perceptual stability than reversals, corroborating the notion of percept stabilization in those areas (Sterzer and Rees, 2008). Similarly, the RP component was evident in both ERP and microstate analyses, and was estimated to have generators in extra-striate visual areas, while the LPC component appeared to be generated in superior and middle temporal as well as inferior frontal areas (Britz and Pitts, 2011).

A SEQUENCE OF NEURAL EVENTS

Based on our recent binocular rivalry experiments as well as previous ambiguous figure experiments, we can begin to map out the spatio-temporal profile of the brain events associated with bistable perception. The following model of the sequence of neural events mediating perceptual rivalry is intended to serve as an initial foundation for future investigations and is expected to be modified if warranted by additional data. **Figure 2** depicts the approximate spatial locations and temporal windows in which various brain areas have been shown to be differentially activated during bistable perception. Along with the location and timing information, we have listed hypothesized functional properties as well as the names of associated ERP components (where applicable).

It is important to note that these proposed functions are based on the types of comparisons made (e.g., reversal versus stable; percept A versus B), the timing of the measured brain activity, and logical assumptions related to the temporal sequence of events. These functional accounts are intended to serve as preliminary hypotheses that are testable in future studies. For example, if the RN reflects the establishment of a new perceptual representation and the LPC a post-perceptual appraisal of this change, the RN should be insensitive to manipulations of task while the LPC may vary according to task demands. Similarly, it is currently unknown whether the percept A versus B effect (from 130 to 160 ms) is associated with feedback from higher to lower level visual areas and whether the timing of this effect depends on the particular type of perceptual competition involved.

Overall, work spanning the past 5–10 years has produced converging evidence regarding the timing and spatial locations of the neural events involved in bistable perception. Now that the temporal dynamics of these components and their intracranial sources have been identified and have been shown to be robust and reliable, more fine-tuned manipulations are necessary to reveal the precise functional significance of each component. It is our hope that this model will serve as a decent starting point.

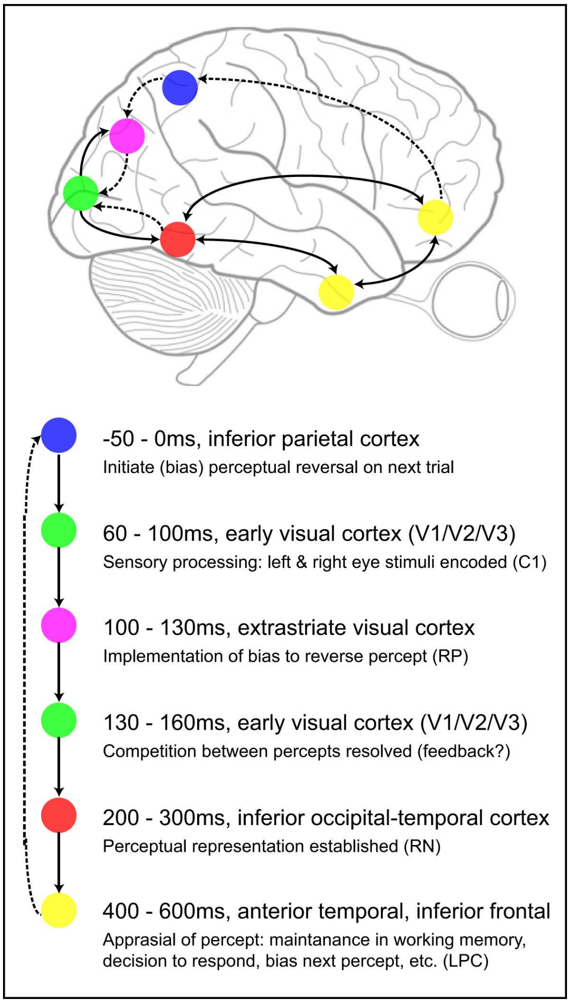

FIGURE 2 | Neural model of the sequence of brain events in which EEG differences have been found during binocular rivalry. Solid one-way arrows indicate hypothesized feed-forward pathways, dashed one-way arrows denote feedback connections, and double-sided arrows indicate possible wide-spread recurrent interactions between distant brain regions. Timing information, estimated neural generators locations, and proposed functional contributions are listed in order of occurrence. Names of associated ERP components are provided after each hypothesized function (where applicable).

BINOCULAR RIVALRY AND PERCEPTUAL AWARENESS

In our spatio-temporal model (**Figure 2**) we assume that the pre-stimulus inferior parietal activity as well as the post-stimulus extra-striate activity (RP) are not directly linked with perceptual awareness. To become aware of a stimulus, the stimulus must be present, so activity preceding stimulus onset may influence but is unlikely to directly reflect perceptual awareness. The timing of the RP (100–130 ms) was found to precede the signal that diverged according to the reported percept (130–160 ms), and is thus similarly unlikely to index awareness. The delayed activity in anatomically early visual areas (130–160 ms), however, varied according to perception during rivalry and is therefore a candidate neural correlate of perceptual awareness. Alternatively, this delayed activity might index a non-conscious (or preconscious) stage of processing in which the competition between percepts is resolved but requires an interaction with higher-level visual areas to enable the formation of a stable perceptual representation. In this latter view, the RN component (at ∼200 to 300 ms, with generators in inferior occipital–temporal cortex) would become the primary candidate for a neural correlate of awareness. Finally, while unlikely, the RN might index the perceptual change preconsciously while the LPC (with its wide-spread cortical sources) might reflect conscious processing of the perceptual information or maintenance of the percept in working memory. Alternatively, the occipital–temporal activity reflected by the RN may be more closely associated with what some theorists (e.g., Block, 2005) have dubbed "phenomenal consciousness," while the wide-spread activity indexed by the LPC may represent "access consciousness."

A notable finding with implications for perceptual awareness has been the striking similarity between ERPs/microstates identified for binocular rivalry and those identified for ambiguous figures (Britz et al., 2009; Britz and Pitts, 2011). It is often assumed that while perceptual alternations exhibit similar characteristics (e.g., reversal rates) in both cases, the underlying neural mechanisms, especially those contributing to perceptual competition and resolution, must be different. However, as suggested more than 10 years ago (Leopold and Logothetis, 1999), at least some of the neural networks involved may be similar across all types of bistable perception and these networks may reside in non-visual areas. The pre-stimulus (microstates from −50 to 0 ms) and post-perceptual (LPC) effects described above are consistent with this hypothesis in that their estimated generators are located in frontal–parietal areas. Recently, transcranial magnetic stimulation (TMS) has been employed to test the causal role of frontal–parietal areas in initiating perceptual reversals (Kanai et al., 2010; Zaretskaya et al., 2010). Interestingly, disruption of activity via TMS in different subregions of the parietal cortex appears to result in opposite effects (increasing or decreasing reversal rates), thus suggesting that a more complex network of parietal regions is involved in bistable perception (Kanai et al., 2011). Inferior frontal regions have also been implicated as playing a role in the initiation of perceptual reversals (Sterzer and Kleinschmidt, 2007). In a recent study, TMS applied over frontal areas was found to slow perceptual reversals, but only when reversals were under voluntary control (de Graaf et al., 2011). This finding is consistent with an earlier study that found reversal rates in frontal lesion patients to be normal during passive viewing, but impaired during a voluntary reversal condition (Windmann et al., 2006). Clearly frontal–parietal areas are involved in the initiation of perceptual reversals, but the precise contribution of each region (and possibly different subregions) appears to be complex and warrants further investigation.

Interestingly, the RN component also appears to be invariant with respect to the type of bistability involved. One possibility is that the neural mechanisms supporting the initiation and appraisal of perceptual reversals are common for all types of bistable figures, while the intermediate stages supporting stimulus/percept competition and resolution vary according to the particular stimuli involved. In this view, the RN would reflect a post-perceptual stage of processing, while earlier activity (e.g., the delayed response in V1/V2/V3) would index the perceptual representation. Future experiments may be able to test this hypothesis by systematically varying the competing features of the stimuli (e.g., orientation, color, motion, shape, etc.) to determine which ERP/microstate varies according to the specific features of the stimuli and thus most closely reflect the contents of perceptual awareness.

While binocular rivalry (and ambiguous figures) are undoubtedly powerful vehicles for dissociating sensory input from perceptual experience, their potential for helping determine the neural basis of perceptual awareness may be truncated by more direct manipulations of awareness. For each type of comparison outlined above (e.g., percept A versus B, reversals versus stability) subjects are always aware of one of the two stimuli/percepts. Thus, a straight-forward comparison between "aware" and "unaware" conditions is not possible. Other types of paradigms, such as the attentional blink (Sergent et al., 2005), inattentional blindness (Pitts et al., 2011), and backward masking (Koivisto and Revonsuo, 2010) may be more appropriate when the goal is to identify neural events linked with conscious perception. Nevertheless, binocular rivalry has proven to be largely successful in separating sensory input from subjective perception and will undoubtedly continue to be a valuable tool as our methodological techniques are further refined.

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Binocular rivalry alternations and their relation to visual adaptation

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When different stimuli are presented dichoptically, perception alternates between the two in a stochastic manner. After a long-lasting and rigorous debate, there is growing consensus that this phenomenon, known as binocular rivalry (BR), is the result of a dynamic competition occurring at multiple levels of the visual hierarchy. The role of low- and high-level adaptation mechanisms in controlling these perceptual alternations has been a key issue in the rivalry literature. Both types of adaptation are dispersed throughout the visual system and have an equally influential, or even causal, role in determining perception. Such an explanation of BR is also in accordance with the relationship between the latter and attention. However, an overall explanation of this intriguing perceptual phenomenon needs to also include noise as an equally fundamental process involved in the stochastic resonance of perceptual bistability.

Keywords: binocular rivalry, adaptation, perceptual alternations

INTRODUCTION

Binocular Rivalry (BR) is the perceptual competition resulting when two different images are presented simultaneously to corresponding retinal locations (Wheatstone, 1838). A “race” between the two monocular images leads to continuous perceptual alternations, with successive periods of dominance and suppression. The spontaneous character of these alternations (Levelt, 1965) is the hallmark of rivalry, and a rigorous debate regarding its origin is whether it is based on competition between the two eyes or between the two stimuli (Blake and Logothetis, 2002). The traditional version of this debate has been challenged by compelling evidence supporting that rivalry involves a cascade of neuronal events spanning through multiple levels of the visual hierarchy, thus, favoring an integrative approach (see Sterzer et al., 2009; Blake and Wilson, 2011). However, the interplay between low-level and high-level visual processing as well as their exact role in the instigation of rivalry remains to be clarified. Several attempts to shed light on this question focus on adaptation as a crucial variable (Alais et al., 2010; Kang and Blake, 2010; Theodoni et al., 2011a).

Adaptation is a ubiquitous property of the visual system (Clifford et al., 2007) and has been used as a powerful tool for dissecting the involvement of high-level, feature-based, and lower-level, eye-based factors in BR (e.g., Blake et al., 2006; van Boxtel et al., 2008; Lin and He, 2009; Bartels and Logothetis, 2010). It has in this way contributed in establishing a multi-level localization of rivalry (Wilson, 2003). Furthermore, adaptation *per se* could be the driving force behind spontaneous perceptual alternations (e.g., Kang and Blake, 2010). The present review aims to bring together evidence supporting the idea that adaptation is a key constituent process in generating perceptual switches which, together with other important constraints such as noise and voluntary control (Kim et al., 2006; van Ee, 2009; Paffen and Alais, 2011), could lead to a complete and successful explanation of this intriguing perceptual phenomenon.

THE POTENTIAL ROLE OF ADAPTATION IN TRIGGERING PERCEPTUAL ALTERNATIONS

LOCAL VERSUS GLOBAL ADAPTATION

An adaptation-based explanation of BR was firstly introduced in early, interocular-competition theories, which assigned a causal role to early, local inhibitory mechanisms (Blake, 1989). Stimulus-competition theories, on the other hand, have treated perceptual alternations as the result of a perceptual inference process, which controls these early mechanisms via feedback from higher visual areas (Logothetis, 1998; Leopold and Logothetis, 1999). Both views thus accept a crucial role for adaptation, making pertinent the need to clarify the stage at which adaptation-based interactions trigger bistability. Could adaptation provide a causal explanation for BR? If so, is it local or global adaptation processes that enjoy a primary role in triggering these perceptual switches? With the term local adaptation, we refer to adaptation occurring at an early, perhaps monocular level that is governed by local, eye-based processes. Global adaptation, on the other hand, refers mostly to feature/pattern-based processing at later processing stages of the visual system, with neurons having more complex receptive field properties (Alais and Blake, 1998). Such a distinction is consistent with the fact that suppression-depth is stronger for complex stimuli (Alais and Melcher, 2007), the former also probably increasing as one ascends the stages of visual hierarchy (Nguyen et al., 2003). Besides, it is well-established that low- and high-level rivalry are differentially affected by attention (Meng and Tong, 2004; van Ee et al., 2005) or noise (van Ee, 2009) and, despite the fact that they might share a common computational mechanism (Klink et al., 2008b), seem to take place at different processing stages (Wilson, 2003).

Given the multi-stage localization of both rivalry and adaptation (Clifford et al., 2007), the crucial question concerns how adaptation mechanisms at different levels interact in order to produce a perceptual change. It has been suggested that perceptual switches arise from adaptation of the currently dominant neuronal representation, the latter being gradually weakened via competing inhibition from the antagonistic representation, eventually succumbing to suppression that leads to a perceptual switch (Kang and Blake, 2010). These interactions are thought to occur at an early processing level (Blake, 1989; Wilson, 2003) even though mutual inhibition may rise from multiple cortical areas as well (Seely and Chow, 2011). Accordingly, initial dominance biases at specific locations of the visual field can be broken down by preceding spatiotopic adaptation, indicating that periods of adaptation can induce local perceptual switches (Carter and Cavanagh, 2007). Furthermore, the longer the duration of adaptation, the later the first breakout from suppression (van Ee, 2011), supporting a model of competing neuronal populations which encode the two alternative stimulus interpretations (Wilson, 2003). The spatial "profile" of this escape from suppression takes place in an inhomogeneous manner, arising from local random differences in adaptation at the monocular processing level, which might determine local perceptual switches (van Ee, 2011). A similar conclusion about the primacy of local adaptation comes from a study by Alais and Melcher (2007), focusing on the coherence of rivalry alternations (vs. piecemeal rivalry) and the suppression-depth of complex (faces) and simple (gratings) stimuli. They have shown that global adaptation processes are unable to overcome the stochastic character of rivalry alternations in local zones, even when a complex stimulus is rivaling with a simple one. These findings suggest that global processes fail to exert a stabilizing influence in rivalry alternations, thus assigning a primary role to local adaptation processes (but see van Boxtel et al., 2008). Along the same lines, Carlson and He (2004) have also shown that, unless there are local incompatibilities between rivaling stimuli, global differences *alone* fail to produce rivalry. Results like these do reject a role of global, top-down influences in rivalry, but rather suggest that it is *local conflict* that counts more. Contrary to these findings, other studies suggest that perceptual differences *can* induce rivalry despite physical similarities: physically identical random-dot displays, which are phenomenally different due to adaptation, can engage in rivalry (Blake et al., 1998), and BR can be induced by identical stimuli within a different chromatic surround (Andrews and Lotto, 2004). Thus, the emerging question concerns the conditions which are sufficient for bistability to be triggered: could perceptual differences account for the perceptual alternations or is the eye-of-origin information the driving force?

By interrupting rivalry at various time points after a period of dominance, Bartels and Logothetis (2010) have found a strong eye-of-origin stabilizing effect, which declines over time and a higher-level image/perceptual contribution which initially exhibits a small stabilizing effect, but later strongly destabilizes perception. This complementary variation over time underlines the need to include both eye-based and stimulus-based processes in a rivalry account, with the latter influencing eye-based processes possibly via feedback signals. Along these lines, recent findings show a weak modulation of early visual cortex activity by perception (Keliris et al., 2010), which becomes stronger in higher areas, as reported previously (Leopold and Logothetis, 1996). In a similar vein, Stuit et al. (2011) have examined the differential contribution of eye- and stimulus-factors as potential grouping cues in synchronizing the dominance of spatially segregated visual targets (Kovacs et al., 1996). They have shown that, even though both kind of cues act independently to promote grouping, the eye-of-origin information has a superior value as a grouping-cue. Taken together, these findings suggest that both levels of processing should be included in an adaptation-based explanation of BR. Nevertheless, it is rather difficult to separate the contribution of eye-based and feature-based processes in BR even at the earliest stage of the competition since, in addition to eye-of-origin signals, single cells in V1 also contain feature-related information (see Keliris et al., 2010) and top-down processing can influence the very early stage of rivalry onset (Klink et al., 2008a).

LOCATING CAUSALITY WITHIN THE CORTEX

It is obvious that unraveling the contribution of eye- and stimulus-related factors is still of high importance in rivalry literature (see Paffen and Alais, 2011), with serious implications regarding the neural localization of the triggering point of alternations. Accepting the primacy of image-content information, results in treating alternations as the outcome of inferential processes that concern perceptual interpretations (Sterzer et al., 2009). In this context, perceptual changes could be an expression of the frequent re-evaluation of the interpretations of the sensory input (Leopold and Logothetis, 1999). Rivalry starts because perceptual conflict about meaning is maximized (Sterzer et al., 2009), rather than just because fusion fails (Wolfe, 1986; Blake, 1989). The idea is further supported by imaging data, showing prefrontal and parietal activation during perceptual rivalry transitions (Lumer et al., 1998; Zaretskaya et al., 2010). Activation of right inferior frontal cortex is shown to have a temporal precedence, thus suggesting a causal role to these areas in the initiation of perceptual changes (Sterzer and Kleinschmidt, 2007). Whether these findings also indicate that top-down processes initiate the reorganization of activity in early visual cortex (Sterzer et al., 2009), remains speculative. If so, the adaptation of early, local inhibitory processes could play a role in destabilizing the activity underpinning the currently dominant percept, thus driving higher-order evaluative processes to initiate a perceptual reorganization (Sterzer and Kleinschmidt, 2007). Although such a scenario would give primacy to global adaptation mechanisms, this "trigger hypothesis" has been recently challenged by evidence toward the opposite direction (Knapen et al., 2011). By using more realistic rivalry simulations in the rivalry-mimicking condition,[1] no difference was found in frontoparietal activation between endogenous (actual rivalry) and exogenous (replay) transitions, with a difference observed in occipital cortex alone (see figure 3 in Knapen et al., 2011). This pattern of results implies that changes observed in frontoparietal activity may be the *consequence* of alternations rather than their cause, possibly reflecting

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[1] As opposed to earlier studies, using instantaneous replays that badly mimic the gradual perceptual changes observed in rivalry (e.g., Lumer et al., 1998; Polonsky et al., 2000).

changes in sensory experience, attentional state or task demand processes (Knapen et al., 2011). The existence of a broad network involved causally in BR transitions has been challenged by Kamphuisen et al. (2008). Using an MEG frequency tagging method in order to track how stimulus-based activity relates to perception, they have located the source of rivalry alternations mainly in early visual areas of the occipital lobe. In accordance, Pearson et al. (2007) have provided evidence for a causal role of early visual cortex activity in BR: they have found that TMS applied over V1/V2 during conventional and swap/stimulus rivalry can induce perceptual changes in the former but not in the latter case. On the other hand, TMS applied in parietal cortex during BR results in disrupting alternations rhythm by lengthening dominance durations, implying that causality could be located in higher areas as well (Zaretskaya et al., 2010; see also Paffen and Alais, 2011 for a review on the controversial role frontoparietal areas in BR).

THE ROLE OF ATTENTION

Although a possible causal role of frontoparietal cortex in BR alternations has not been yet firmly established, the findings mentioned above suggest a tight link between BR and attention, since there seems to be a major topographical overlap between the cortical networks mediating both phenomena (Paffen and Alais, 2011). The susceptibility of the alternation rate to attentional manipulations has been widely used as an indicator of top-down influences in BR, even though its sensitivity as a measure has been doubted (Meng and Tong, 2004). Alternations are enhanced once attention is driven to the stimuli and attenuated when it is withdrawn (Meng and Tong, 2004; van Ee et al., 2005; Paffen et al., 2006), or even eliminated by the total absence of attention (Zhang et al., 2011—but see Roeber et al., 2011). Attentional changes have been long suggested as the cause of alternations, a core-issue on the rivalry debate since its rediscovery by Wheatstone (1838; see also Blake and Logothetis, 2002). Nevertheless, though well-established, the role of voluntary control in BR is clearly limited (Paffen and Alais, 2011), especially when it comes to rivalry between low-level stimuli which, compared to ambiguous figures and rivalry between more complex stimuli, seems to be less subjective to (endogenous) attention (Meng and Tong, 2004; van Ee et al., 2005) and more prone to noisy variations (see van Ee, 2009).

The dependency of BR on bottom-up factors such as stimulus strength on the one hand and attention on the other, might seem contradictory, but could perhaps be explained by evidence for the apparent but quantifiable effects of attention on low-level stimulus characteristics (van Ee et al., 2005; Paffen et al., 2006; Klink et al., 2008b). Attention seems to boost the effective contrast of the attended stimulus (Carrasco et al., 2004; Chong and Blake, 2006), which in turn affects both the alternation rate and the dominance durations, following Levelt's predictions (see Paffen et al., 2006; Klink et al., 2008b). Within this framework, attention may be the counterpart of adaptation, attenuating the build-up of the latter by preventing its effects from developing fully, similar to the way in which stimulus strength's manipulations directly affect the time course of the recovery from adaptation (Wilson, 2003). In order to directly address the influence of adaptation on perceptual switches, Kang and Blake (2010) have created a novel "on-line" adaptation paradigm by physically removing and later reintroducing the suppressed stimulus, so that brief periods of monocular adaptation are interspersed during the actual duration of BR. They have shown that dominance duration decreases with increasing adaptation duration (see also van Ee, 2011). Furthermore, Blake et al. (2003) have found that when the conflicting stimuli are made to move continuously across the retina, alternations slow down significantly—a result also attributed to the removal of local adaptation. The similarity between attentional and adaptational manipulations, suggests that attention is another important variable that has to be incorporated in models explaining rivalry dynamics. Such an account must also take into consideration new experimental evidence showing that such an effect can also be multimodal (e.g., van Ee et al., 2009; Zhou et al., 2010; Chen et al., 2011). It is perhaps worth mentioning here that perceptual stabilization caused by intermittent presentation of rivalrous stimuli (Leopold et al., 2002), an extreme version of lengthening dominance durations (van Ee et al., 2005), has also been explained as the result of the insufficient development of the inhibitory-adaptational interactions eventually leading to a perceptual transition (Chen and He, 2004)[2]. However, it has been come evident by psychophysical and computational studies that local adaptation (or its absence) cannot account for stabilization caused by intermittent presentation (see Pearson and Clifford, 2005; Brascamp et al., 2007, 2009; Noest et al., 2007; also Pearson and Brascamp, 2008 for a detailed review).

CAN ADAPTATION FULLY EXPLAIN PERCEPTUAL SWITCHES? THE ROLE OF NOISE

The studies reviewed above make an adaptation-based explanation of rivalry highly plausible. Still, there are predictions of the adaptation-cross inhibition model that a solely adaptation-based account cannot explain (Alais et al., 2010; Kang and Blake, 2010). For example, according to this model, visual sensitivity should change over time in a way that reflects the reciprocal changes in the adaptation level of the antagonistic neuronal populations (Noest et al., 2007). Although earlier studies have failed to support this idea (e.g., Fox and Check, 1972), Alais et al. (2010) have used a novel probe-method to show that sensitivity during both rivalry states is not stable: performance during dominance declines over time, while the opposite is true during suppression. This complementary variation in dominance and suppression sensitivity over time corresponds exactly with the gradual reciprocal changes predicted by the adaptation-inhibition model. This finding, for the first time experimentally confirmed by Alais et al., overcomes what was previously thought an inconsistency between theory and observed data, supporting further the idea of adaptation as a crucial mechanism in BR (Alais et al., 2010).

Another intriguing aspect of BR is the irregular and unpredictable character of dominance shifts observed in other multistable perceptual phenomena as well (Leopold and Logothetis, 1999; Gigante et al., 2009). This random nature of perceptual

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[2] Instead of assuming a perceptual memory as it was originally suggested (Leopold et al., 2002).

fluctuations, thought to stem from stochastic variation (Lehky, 1995; Kim et al., 2006), contradicts the fairly regular character of alternations that should be observed if transitions were mediated *solely* by deterministic processes such as adaptation and cross inhibition (Shpiro et al., 2009; van Ee, 2009; Kang and Blake, 2010). Therefore, noise has also been incorporated in computational models of adaptation-inhibition based perceptual decisions, in order to account for the irregular character of perceptual alternations (e.g., Wilson, 2003, 2007; Noest et al., 2007; Shpiro et al., 2009). It has been suggested that it exerts a crucial, perhaps dominating role (Brascamp et al., 2006; Lankheet, 2006). Stochastic resonance is a noisy-driven process with the virtue of allowing for deterministic (adaptational) influences to take place as well, as in the case of rivalry (van Ee, 2009). It seems to be the key-process emerging from the coupling between adaptation, inhibition, and noise, controlling perceptual transitions (Kim et al., 2006). It has been suggested that it is noise in the adaptation of percept-related neurons, not noise in the cross-inhibition neurons, which accounts for transitions (Kim et al., 2006; van Ee, 2009; Theodoni et al., 2011a). This seems to be also true for the serial correlations observed between successive dominance durations, once experimental impurities are controlled for (van Ee, 2009; see also Kang and Blake, 2010). In support of this notion, recent computational studies of the relative contribution of noisy-driven or adaptation-driven models in generating bistability, have shown that noise is a crucial variable that needs to operate in balance with adaptation in generating perceptual alternations (Shpiro et al., 2009; Theodoni et al., 2011a). Other computational models examining the occurrence of alternations during intermittent viewing, go further and incorporate higher-order variables such as perceptual memory of the type Leopold et al. (2002) have suggested (Wilson, 2007; Brascamp et al., 2009), as well as voluntary control (Klink et al., 2008a). A recent computational model simulating perceptual decisions regarding higher-order, ambiguous visual stimuli (face/hand) has suggested that adaptation-driven transitions due to afterhyperpolarization currents, can explain oscillatory perceptual alternations better than noise-driven transitions, which are due to the probabilistic spike times of neurons (Theodoni et al., 2011b). It becomes clear that none of these factors should be excluded from a complete explanation of rivalry alternations. When it comes to causality, however, adaptation and noise seem to offer the most plausible explanation.

CONCLUDING REMARKS

After almost two centuries of rigorous debate about the contribution of eye- and stimulus-factors in rivalry dynamics, there is now growing consensus in incorporating both levels of processing in a successful explanation of the phenomenon (Blake and Wilson, 2011). Adaptation, conceived as a property of both early and late stages of visual processing (Clifford et al., 2007), clearly has an important role in this interaction as a key-point process behind perceptual alternations. Local adaptation is assigned a primary or even causal role in determining rivalry transitions (e.g., Blake, 1989; Pearson et al., 2007; Kang and Blake, 2010). However, this does not rule out the possibility that global adaptation plays an executive role as well, exerting a feedback influence on local inhibitory interactions, thus initiating a perceptual change (e.g., Sterzer et al., 2009; Zhang et al., 2011). Therefore, a model including dynamic interactions between local and global adaptation mechanisms, as well as the dynamics of noise in the observed stochastic variability (Brascamp et al., 2006; van Ee, 2009; Theodoni et al., 2011a), seems to be the ideal substrate for explaining perceptual transitions during BR.

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Onset rivalry: the initial dominance phase is independent of ongoing perceptual alternations

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Binocular rivalry has been used to study a wide range of visual processes, from the integration of low-level features to the selection of signals that reach awareness. However, many of these studies do not distinguish between early and late phases of rivalry. There is clear evidence that the "onset" stage of rivalry is characterized by stable, yet idiosyncratic biases that are not evident in the average dominance of sustained rivalry viewing. Low-level stimulus features also have robust effects in the onset phase that are not seen in sustained rivalry, suggesting these phases may be driven at least partly by different neural mechanisms. The effects of high-level cognitive and affective factors at onset are less clear but also show differences from their effects in sustained viewing. These findings have important implications for the interpretation of any rivalry experiments using brief presentation paradigms and for understanding how the brain copes with binocular discrepancies in natural viewing conditions in which our eyes constantly move around an ever-changing environment. This review will summarize current research and explore the factors influencing this "onset" stage.

Keywords: binocular rivalry, perceptual bias, vision, awareness, ambiguity, visual field, suppression, bistable stimuli

When dissimilar images are presented respectively to the two eyes, an initial fusion of the two scenes (Wolfe, 1983) is rapidly replaced by the perception of only one of the two images. If the observer continues to view these images, conscious perception will alternate between the two monocular percepts indefinitely (Wheatstone, 1838; Blake and Logothetis, 2002). Such "binocular rivalry" occurs without any change to the stimuli themselves. This disparity between unchanging stimuli and fluctuating conscious perception has provided an important tool for studying a vast range of neural processes, from early visual features such as luminance (Kaplan and Metlay, 1964), contrast (Mueller and Blake, 1989), and motion (Blake et al., 2003), to visual processing in psychiatric populations (Miller et al., 2003; Nagamine et al., 2007), and the neural correlates of conscious awareness (Logothetis, 1998; Lin and He, 2009). While binocular rivalry is a psychophysical paradigm, it has been used in conjunction with a variety of brain imaging (Tong and Engel, 2001; Haynes et al., 2005; Lee et al., 2005) and electrophysiological measures (Leopold and Logothetis, 1996) that have all contributed to providing considerable information about the associated brain mechanisms involved in visual processing and awareness.

Until recently, it was assumed that, subsequent to fusion, all rivalry was guided by a common process (or set of processes). Recent studies have now demonstrated that the initial properties of rivalry differ significantly from those seen over extended periods and may, in fact, be determined by distinct mechanisms. Most notable is the striking degree of stability and predictability in perceptual dominance at rivalry onset, which stands in complete contrast to the stochastic nature of perceptual switches that is often considered a fundamental property of sustained perceptual rivalry viewing (Fox and Herrmann, 1967; Kim et al., 2006; van Ee, 2009). This paper will review recent results concerning the different factors that affect onset rivalry and the differences between this onset phase and sustained rivalry. This review will also briefly consider the implications for current perceptual rivalry research.

ONSET BIASES ACROSS THE VISUAL FIELD

One of the most striking characteristics of onset rivalry is the existence of strong and stable localized biases that vary across the visual field both within and between subjects (Carter and Cavanagh, 2007; Stanley et al., 2011; see **Figure 1**). For example, one area of the visual field may have a strong onset rivalry bias, so that the same target is seen first on almost every trial. In another area of the visual field, however, the opposite target might be almost exclusively dominant at onset. This onset bias can only be partly explained by monocular dominance, and despite the idiosyncratic nature of the pattern of onset bias across the visual field, it is found to be stable across weeks within an individual. Such biases toward dominance of a given target were not seen during subsequent alternations in sustained rivalry (Carter and Cavanagh, 2007).

Onset rivalry also differs from sustained rivalry dominance periods in respect to the effects of equating stimulus strength. It is well established that changing the contrast, luminance, or spatial frequency of one rivaling target will reliably increase the

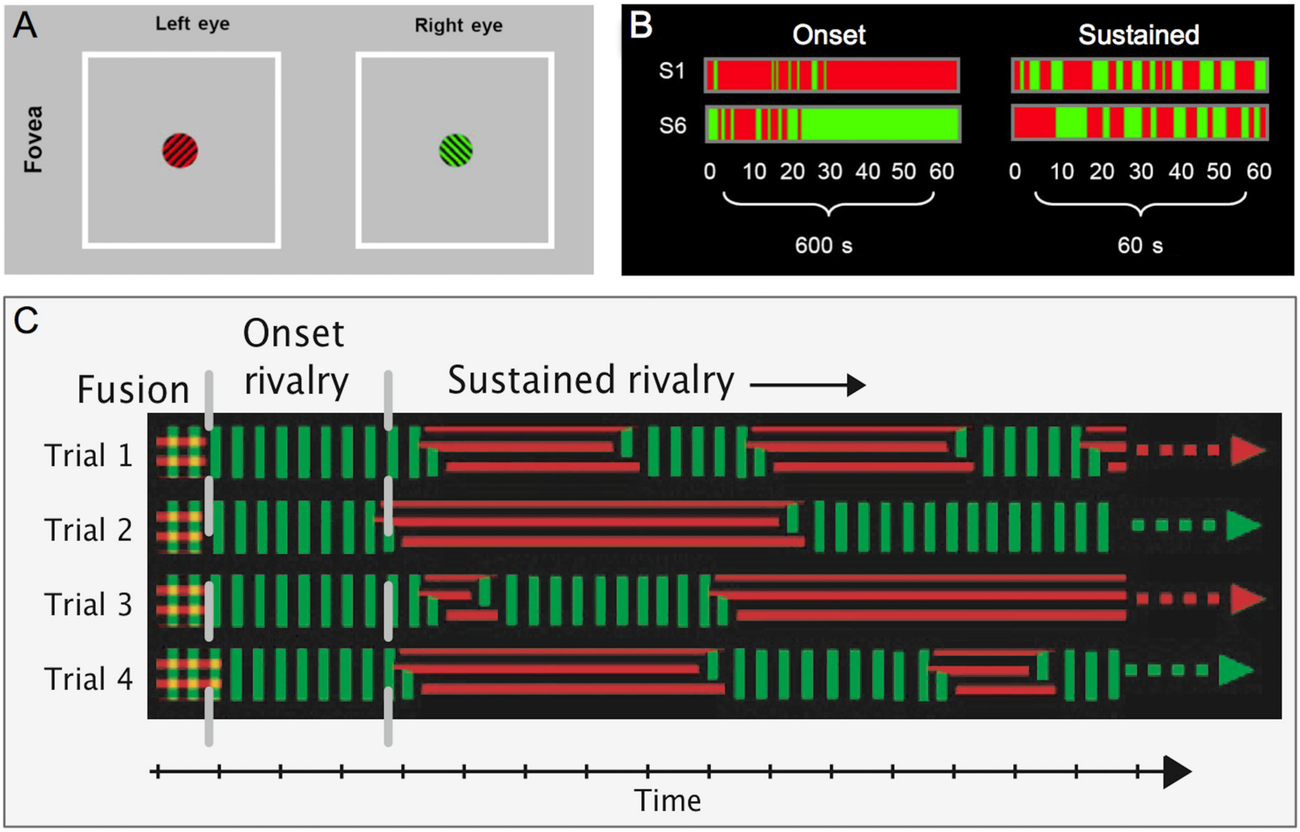

FIGURE 1 | Onset biases: (A) Examples of stimuli used to assess onset rivalry in the fovea. Orthogonal green and black, and red and black gratings were presented to the fovea for 60 presentations of 1 sec (with 9 sec of stimulus removal), or 60 sec of continuous presentation. **(B)** Data from two subjects show consistent, but opposite onset biases during the 60 intermittent 1 sec presentations (over 600 sec). In the sustained 60 sec presentation, however, average dominance durations show no bias (modified from Carter and Cavanagh, 2007). **(C)** A schematic illustrating the time course of rivalry over four trials depicts a consistent bias toward one target at onset, while dominance at a given time during the rest of the sustained viewing period is random.

proportion of dominance of that target over a sustained viewing period, and conversely, equating the stimuli will reduce these biases (Levelt, 1967). Onset rivalry is also strongly biased toward a target with greater stimulus strength (Chong and Blake, 2006; Song and Yao, 2009). Unlike sustained rivalry, however, the initial presentation of balanced stimuli will not necessarily result in an equal likelihood of either target gaining dominance at onset. At the onset of rivalry, strong and consistent onset biases remain after minimizing the luminance and contrast differences by calibrating the stimuli separately for each individual and in each location of the visual field (Stanley et al., 2011; see **Figures 2A–C**). The persistence of the localized onset bias suggests that other endogenous factors determine onset dominance. For example, the fact that swapping the eye of presentation of the calibrated images has led to complete reversal of perceived color in some areas, suggests that regions of monocular dominance may also have an influence on onset rivalry (Stanley et al., 2011).

LOW-LEVEL EFFECTS ON ONSET DOMINANCE

The influence of monocular dominance on the initial dominance phase in rivalry has been reported previously. In an early study on color rivalry, Crovitz and Lipscomb (1963) presented split and full color red and green fields for 100 ms in rivaling conditions. They found that observers most commonly reported a percept corresponding to the colors presented in the temporal visual fields (Crovitz and Lipscomb, 1963). Similarly, Leat and Woodhouse (1984) showed that flashed stimuli, which engage only the onset phase of rivalry, showed a dominance bias as great as approximately 5–95% in some individuals compared to continuous presentations, which were generally quite balanced with approximately 50% dominance. Although dominance biases for flashed and continuous presentations were correlated, the authors concluded that the difference in the range of bias indicated that flashed stimuli were more sensitive to ocular dominance by a factor of 10–20. Some observers showed enhanced dominance of the nasal retinas and others of the temporal retinas, but either pattern of dominance tended to be consistent within one-half of the visual field (Leat and Woodhouse, 1984). Although there was very little evidence of dominance bias during sustained viewing, more recent studies have shown that visual field location can affect the overall rate of switching in sustained rivalry (Chen and He, 2003). As these onset studies show, initial dominance is particularly sensitive to zones of monocular dominance that exist across the visual field. However, the substantial individual difference in the pattern of

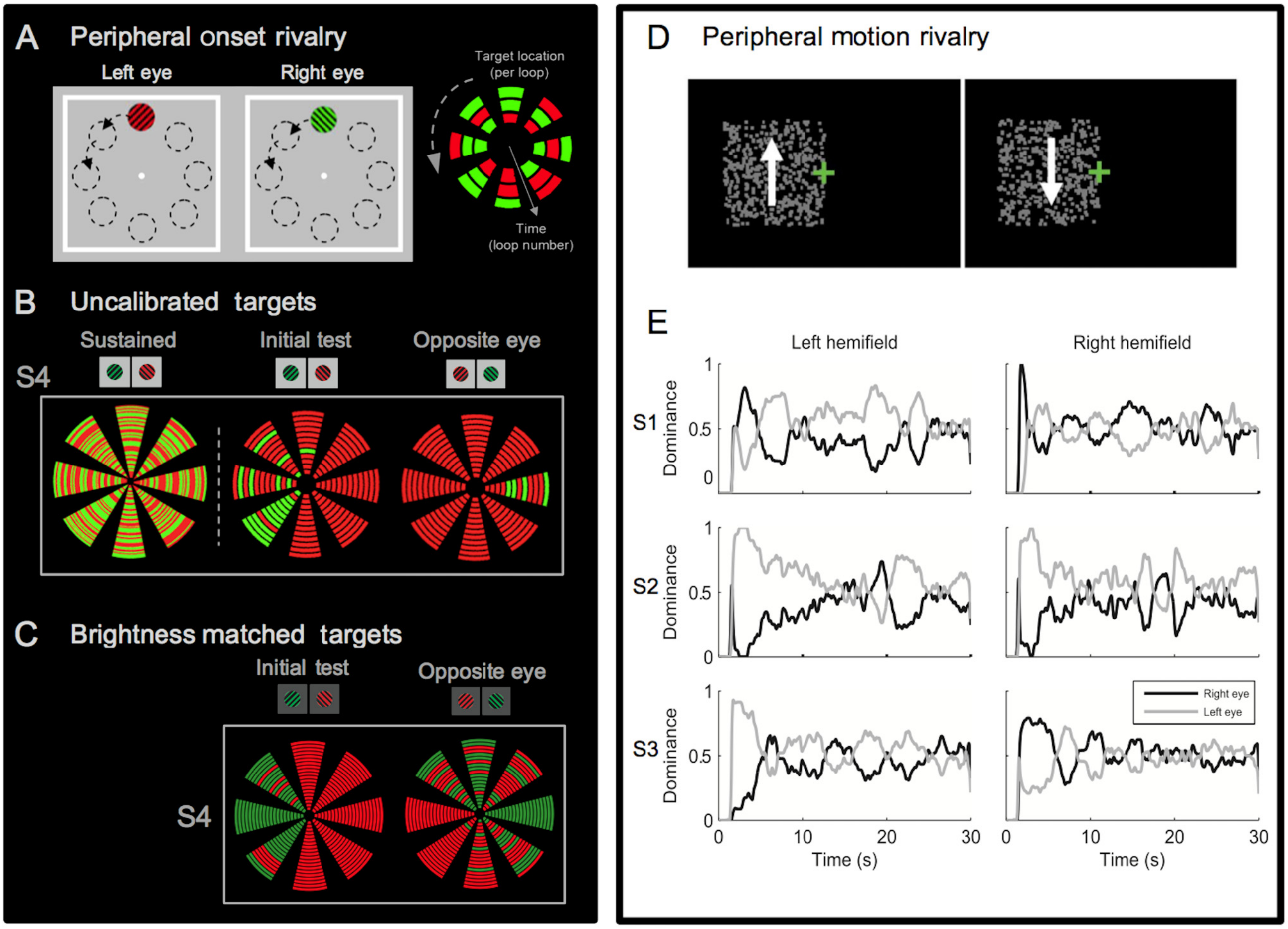

FIGURE 2 | Idiosyncrasies of onset rivalry across the visual field. (A) Peripheral stimuli used to test location specific onset biases within an individual. Orthogonal gratings were presented to the left and right eye, in eight locations of the visual field. The black dotted outlines of these locations are for illustration only and were not part of the experimental display. To the right is a schematic of the data presentation used in **(B,C)**. Each block of color represents the reported perceptual dominance at an individual stimulus onset (the eight wedges represent the eight locations and time is illustrated with the inner and outer locations representing the first and last presentations respectively. **(B)** On the left, data from sustained rivalry presentation in the periphery shows no dominance bias of either target (each loop represents 1 sec of presentation during 60 sec of sustained rivalry). In contrast the two right panels show that during onset rivalry the pattern of biases within a single person vary depending on the location of the visual field and the eye of presentation (individual data from S4 in Carter and Cavanagh, 2007). **(C)** Data from the same observer shows that when brightness is matched in each location onset biases remain, which is representative of the results seen across participants. Though there are still clear biases, some change in the pattern is evident after balancing the targets. For example, some locations have an exaggerated bias while others have less complete bias, and in some cases the preferred color has switched. With the calibrated rivalry targets, some locations show a complete reversal of onset bias when targets are presented to the opposite eyes, suggesting influence of monocular dominance (individual data from S4 in Experiment 1 of Stanley et al., 2011). **(D)** Ambiguous opponent motion stimuli presented to the right or left of fixation induces similar idiosyncratic onset biases (modified from Figure 1 in Kalisvaart et al., 2011). **(E)** At the onset of sustained presentation, S1 and S2 showed right and left eye bias, respectively, and S3 showed temporal field bias. However, subjects displayed no dominance bias during later periods of the presentation (modified from Figure 3 in Kalisvaart et al., 2011).

ocular dominance seen with a range of rivalry stimuli (Kalisvaart et al., 2011; Stanley et al., 2011), and the fact that hemifield effects are not always seen if the rivaling targets are not carefully calibrated (Carter and Cavanagh, 2007) shows that monocular dominance cannot fully explain the biases in onset rivalry (see **Figure 2**).

The finding that visual field effects are revealed after individually equating brightness in each eye suggests that there is an interaction between endogenous biases and influences that originate from the stimuli themselves. For example, influences from ocular dominance appear to interact with hypersensitivity at onset to differences in stimuli strength. With respect to stimulus strength, onset dominance appears to be particularly sensitive to small imbalances in luminance contrast (Chong and Blake, 2006; Song and Yao, 2009; see **Figure 3**). Onset dominance may be so sensitive to contrast differences that variability in spectral sensitivity between individuals and across the retina (Albrecht et al., 2002) may be sufficient to influence the pattern of onset bias (Stanley et al., 2011). Other studies have shown that both exogenous (Mitchell et al., 2004; Chong and Blake, 2006) and endogenous (Chong and Blake, 2006) attention have a greater influence at onset than on average dominance during sustained presentation. While attention is often thought of as a high-level

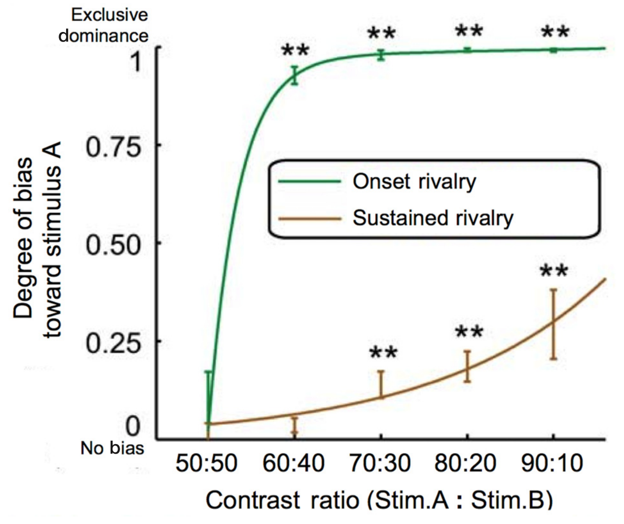

FIGURE 3 | Onset dominance is more sensitive to contrast imbalances than sustained dominance. By comparing stimuli with varying contrast imbalances (ranging in contrast ratios of 50:50 to 90:10), it was found that small imbalances are sufficient to cause exclusive dominance of the higher-contrast image at onset. In the case of sustained rivalry, however, exclusive dominance was never achieved even at the greatest contrast imbalance of 90:10 (modified from Figure 2B in Song and Yao, 2009).

effect, the authors suggest that their observed effect of attention may have, in fact, been mediated by an increase in apparent contrast (Chong and Blake, 2006). This interpretation was based on the finding that directing attention to a grating has been claimed to boost the apparent contrast between 30 and 70% (Carrasco et al., 2004).

The degree of location specificity observed across the visual field at rivalry onset suggests the endogenous biases are closely tied to the position of the image on the retina. Consistent with this view, it was shown that when rivaling images were displaced on the retina—through saccades or through shifting the stimulus itself—the dominant percept after the shift was systematically related to the initial onset bias displayed by each subject (Kalisvaart et al., 2011). These findings suggest that engaging new areas of the retina will again recruit onset processes. Interestingly, although this result was observed after both a saccade and a stimulus jump, the relationship between percept dominance and onset bias was weaker after a saccade. Despite both conditions engaging new areas of the retina, an active saccade appeared to diminish the effects of onset rivalry bias. There are currently no data available to determine the basis of this attenuation of the onset bias, however, possible causes could range from other relatively low-level effects beyond retinal signals to such high-level influences as saccadic remapping (Bays and Husain, 2007; Cavanagh et al., 2010).

HIGH-LEVEL EFFECTS ON ONSET DOMINANCE

Although most studies of the onset stage of rivalry have used features that are processed by the early visual system, there are a few studies that have investigated high-level, cognitive influences at rivalry onset. A recent study has shown that the utility of a particular percept can bias initial dominance in rivalry. When perception of one orientation of rivaling Gabor patches allowed observers to complete a search task more efficiently, observers were more likely to perceive that orientation as the initial percept, even though they were unaware of its utility. This bias continued even when the grating no longer provided any advantage to the task. Surprisingly, the influence of the learned utility of the grating orientation was limited exclusively to the onset phase and had no effect on subsequent dominance durations (Chopin and Mamassian, 2010). Denison et al. (in press) have shown that when rivalry of dichoptic orthogonal gratings is preceded by the predictive context of non-rivaling gratings in perceived rotation, there is a bias at the onset of rivalry toward the orientation that would match the next presentation in the rotation sequence.

Two other studies have investigated differences between images that influence psychological attributes like emotional saliency and show intriguing and somewhat contradictory effects with respect to initial dominance. The first study by Sheth and Pham (2008) used emotionally arousing images. These images showed no effect at the onset of rivalry, though the emotional content of the images affected overall percentage of dominance during sustained rivalry (Sheth and Pham, 2008). This finding suggests limited involvement at onset from higher areas where visual signals are coupled with emotional cues. However, a second study by Gray et al. (2009) found that an observer's anxiety level had a strong effect on initial dominance of emotional faces, and was associated with an increased tendency to perceive angry faces and decreased tendency to perceive happy faces. Such results suggest that the relatively high-level factors of an observer's emotional state and the emotional saliency of a rivaling target can affect rivalry during the onset stage. As this study only examined effects at the onset of rivalry, it is unclear whether heightened anxiety would continue to modulate an average dominance bias toward emotional stimuli over longer stimulus durations. Further research is needed to clarify the role of emotion and arousal in onset rivalry as distinct from their role in sustained rivalry.

ONSET BIASES USING OTHER AMBIGUOUS STIMULI

Although the onset stage of perceptual rivalry has been studied predominately using binocular rivalry stimuli, it is also important to note that disparate effects and biases at onset are also present when viewing other types of ambiguous stimuli. Dobbins and Grossmann (2010) presented rotating Necker cubes at various areas of the visual field and found that a cube rotating around a vertical axis was seen as viewed from above at onset more than 90% of the time, while a cube rotating around a horizontal axis was more likely to be interpreted as being viewed from the right side if it was placed on the left side of the screen. The authors suggest real-world asymmetries (e.g., boxes are more likely to be seen from above) are encoded in the visual system and this inherent expectation is particularly influential at onset (Dobbins and Grossmann, 2010).

The bistable auditory streaming paradigm (Pressnitzer and Hupé, 2006; Snyder et al., 2009) and plaid motion rivalry (Hupé and Rubin, 2003) have also been shown to have strong onset biases. In both cases the "coherent" percept of the visual

Table 1 | Studies investigating onset dominance in binocular rivalry.

Study	Onset effect	Sustained effect*
Visual field location	Dominance of the temporal hemifields demonstrated using full-field color stimuli (Crovitz and Lipscomb, 1963)	Not assessed in Crovitz and Lipscomb (1963)
	Hemifield dominance shown using gratings presented along horizontal midline, however, the dominant hemifield (temporal/nasal) varied between observers (Leat and Woodhouse, 1984)	No dominance bias in hemifields observed (Leat and Woodhouse, 1984)
	Colored grating patches presented in the periphery caused strong onset biases that varied between individuals and across locations within an individual (Carter and Cavanagh, 2007). Areas of temporal hemifield dominance only became evident after matching each location for perceived brightness (Stanley et al., 2011)	No localized bias observed when brightness was not matched (Carter and Cavanagh, 2007). Not assessed in Stanley et al. (2011) after brightness matching
	Onset bias shown for motion, house/face, and grating binocular rivalry. Individual observers exhibited right eye, left eye, or temporal hemifield bias, but no nasal hemifield bias (Kalisvaart et al., 2011)	No bias observed after 10 sec of sustained viewing (Kalisvaart et al., 2011)
Eye movements	Retinal image shift renewed onset bias, but more so for stimulus shifts than saccades (Kalisvaart et al., 2011)	Not assessed as part of image shift experiment (Kalisvaart et al., 2011)
Contrast	Small imbalances in contrast caused exclusive dominance of higher-contrast image (Song and Yao, 2009)	Average dominance of a target increased gradually with larger contrast imbalances up to maximum imbalance ratio of 90:10 but exclusive dominance was not achieved (Song and Yao, 2009)
	Minimizing contrast differences by matching brightness in each location for each observer unmasked other endogenous biases (Stanley et al., 2011)	Not assessed in Stanley et al. (2011)
Attention	Both exogenous (Mitchell et al., 2004; Chong and Blake, 2006) and endogenous (Chong and Blake, 2006) attention increased onset dominance of attended grating	Not assessed in Mitchell et al. (2004) or Chong and Blake (2006)
	Effect of attention counteracted by reducing contrast of attention-boosted target 0.3 log-units (Chong and Blake, 2006)	Not assessed in Chong and Blake (2006)
Task relevance	Onset bias toward task-relevant grating; bias persisted even when grating was no longer task-relevant (Chopin and Mamassian, 2010)	No increase in average dominance of task-relevant grating (Chopin and Mamassian, 2010)
	A spinning Necker cube was more likely to be seen as viewed from above when rotating on a vertical axis, and from the right when rotating on a horizontal axis on the left side of the screen. Authors suggest encoding of ecological relevance (Dobbins and Grossmann, 2010)	Some observers exhibited average dominance bias during 15-s presentation, though slow switch from biased dominance at onset may account for this result (Dobbins and Grossmann, 2010)
Context	Onset bias toward grating orientation that would match the next presentation in a preceding perceived rotation sequence (Denison et al., in press)	Not assessed in Denison et al. (in press)
Emotional salience	No significant bias toward emotionally arousing images (Sheth and Pham, 2008)	Greater average dominance of emotionally arousing images after 15 sec of viewing (Sheth and Pham, 2008)
	Observer's anxiety level influences onset dominance of emotional faces: greater tendency to perceive angry faces and less tendency to perceive happy faces (Gray et al., 2009)	Not assessed in Gray et al. (2009)

**Sustained effects reported here only refer to results obtained in the corresponding onset studies listed. Countless studies have been conducted using sustained rivalry, many of which show effects from the factors listed in this table, however, it is sometimes difficult to compare across paradigms, as multiple stimulus and procedural properties are likely to vary between studies. A number of detailed reviews of sustained rivalry have been published previously (Blake and Logothetis, 2002; Long and Toppino, 2004; Tong et al., 2006; Blake and Wilson, 2011). Also not listed in the table are studies that use an intermittent presentation paradigm. For a review of these studies see Pearson and Brascamp (2008).*

plaid or single auditory stream is almost exclusively found to dominate at stimulus onset (Hupé and Rubin, 2003; Pressnitzer and Hupé, 2006; Snyder et al., 2009). While we are not aware of any study that has specifically investigated onset dominance during tactile rivalry, it has been reported that proprioceptive and tactile stimuli known to induce illusory motion reversals show exclusive dominance of the veridical motion direction at stimulus onset and will only alternate in a more balanced fashion after sustained stimulus presentation (Holcombe and Seizova-Cajic, 2008). A summary of current literature investigating the distinct onset phase of rivalry can be found in **Table 1**.

ONSET DOMINANCE DISTINCT FROM PERCEPTUAL MEMORY

As the focus of this review is the factors influencing perceptual dominance at stimulus onset, it is important to also clarify how onset dominance relates to the influence of perceptual memory demonstrated by intermittent stimulus paradigms (for review see Pearson and Brascamp, 2008). When rivaling images are presented and removed every few seconds, percept switching slows and dominance can appear to stabilize, with each new presentation of rivalry more likely to display the same dominant percept as the one last seen (Leopold et al., 2002). Importantly, while dominance periods lengthen considerably under these conditions, perceptual dominance does continue to alternate, maintaining approximately equal average dominance between the two possible percepts (Brascamp et al., 2009).

This pattern of dominance is quite distinct from the localized onset biases that are the focus of the current review. When stimuli are presented intermittently in the same location of the visual field, the initial dominance at each *repeated* presentation is most likely to be consistent with the perceptual state during the last presentation (Pearson and Brascamp, 2008). This "perceptual memory trace" appears to build up and disappear over each stimulus presentation and removal period such that it takes multiple presentation cycles for a perceptual reversal to be triggered (Brascamp et al., 2008; Pastukhov and Braun, 2008). In contrast, in the absence of perceptual memory—with greater than 10-s intervals between stimulus presentations (Carter and Cavanagh, 2007) or after stimulus shifts (Kalisvaart et al., 2011; Stanley et al., 2011)—onset biases for an individual are stable across weeks. Furthermore, in the relatively rare event that onset dominance does switch to the "non-predominant" target, the switch does not stabilize consistent with a "memory" of the new target, but quickly reverts back to the target that is most typically dominant in that area on subsequent presentations (Carter and Cavanagh, 2007; Stanley et al., 2011).

Based on the current literature, therefore, there is little doubt that onset rivalry and perceptual memory are clearly distinct phenomena. It is less clear however, whether the two are completely independent. One alternative is that perceptual history is simply one factor, like monocular dominance, that can sometimes have a powerful effect at rivalry onset. Given that onset rivalry is evident with a 1 sec on, 9 sec off paradigm (Carter and Cavanagh, 2007; Stanley et al., 2011) and perceptual memory is typically observed when stimuli are on for 3 sec and off for 5 sec (Leopold et al., 2002), one would expect that the relative distinction between the two phenomena would be reduced by decreasing or increasing the interval between stimulus onsets respectively. While it is clear that perceptual memory cannot account for the onset biases observed after longer interstimulus intervals, more research is needed to tease apart these two paradigms. At least one study has demonstrated a degree of interaction between endogenous onset biases and non-local perceptual memory. Knapen et al. (2009) has shown that the degree to which perceptual memory can transfer to peripheral locations can be increased if the stimulus is adjusted to account for local onset biases. Future research into onset rivalry or perceptual memory should therefore guard against confounding of the two paradigms—repeated trials intended to examine onset rivalry may begin to engage perceptual memory, and onset biases may also interact to weaken the influence of perceptual memory during intermittent presentations.

MODELS OF RIVALRY

A few models of binocular rivalry have been extended to include the role of perceptual memory when stimuli are first presented after a blank period (Noest et al., 2007; Wilson, 2007). So far, however, these models have only focused on the initial dominance in an intermittent presentation paradigm as described above, and do not yet account for the endogenous biases and sensitivity that are apparent when stimuli are first presented to the retina and no perceptual history is available. These models do predict that even very small input imbalances can dictate dominance in intermittent presentation (Noest et al., 2007; Klink et al., 2008). However, whether this aspect of the model will be able to fully explain the sensitivities of onset dominance has yet to be explicitly explored. Other commonly cited models of rivalry focus primarily on the stochastic alternation of percepts during sustained viewing, and describe mutual inhibition and adaptation at several levels of the visual hierarchy (Tong et al., 2006; Sterzer and Rees, 2008), or refer to Bayesian (Sundareswara and Schrater, 2008), predictive coding (Hohwy et al., 2008), or random and noise effects (Brascamp et al., 2006; Kim et al., 2006; Moreno-Bote et al., 2007). Such models of traditional rivalry do not yet distinguish between the mechanisms underlying the onset phase and those that drive subsequent switching. They also do not attempt to explain the consistency of the strong biases seen at onset, or the variation in these biases observed across the visual field. Such findings suggest that models of rivalry may need to take into account the particular physiology of an individual observer as well as perceptual history.

A formal model of onset rivalry is yet to be proposed. However, the biases and heightened sensitivities at the onset of rivalry might be partly explained by a model in which slight differences in signal strength result in latency differences between information coming from the same area of each eye. These disparities may allow one percept to "win the race," either by reaching a relevant anatomical destination earlier or by attaining a required activation threshold more quickly. In such a race model, the winning signal will then become the exclusive conscious percept until the competing neural representation is similarly established. It is frequently proposed that rivalry depends on a degree of mutual inhibition that builds up over time between competing neural representations (for review see Blake and Logothetis, 2002). It would follow, therefore, that a perceptual switch could not begin until both neural representations had indeed become established. If this model were true, any small imbalances in the speed of the incoming signals would only be relevant at the point of stimulus onset, and would cease to be relevant once the competitive processes dictating sustained rivalry switching had begun. Of course, more focused research is needed to determine the neural areas or physiological processes that govern the initial processing of ambiguous visual input, such as pinpointing the "destination" or mechanisms within the brain that allow such conscious perception to first be decided. Further research is also required to determine how the mechanisms associated with onset rivalry relate to those involved in the initial fusion period reported with very brief (100 ms) presentations or to those associated with sustained rivalry paradigms.

It may turn out that onset and sustained rivalry involve identical mechanisms that differ in the degree to which they are influenced by certain factors. An extreme alternative that should also be considered, however, is that onset rivalry is closer to other forms of visual suppression such as "masking" (Breitmeyer, 1984). For example, the extent to which the suppressed image is represented in visual cortical regions might either be considerably reduced or completely distinct from the neural representations of suppression during sustained rivalry conditions. Although electroencephalography studies have been conducted using intermittent paradigms (for review see Pitts and Britz, 2011), no brain imaging or electrophysiological study of onset rivalry has been conducted to date. However, intracranial recording from early visual cortex shows the representations of suppressed stimuli which are seen during sustained rivalry presentation are not observable during the initial period of perceptual suppression after stimulus onset (personal communication with Tsuchiya—see also Tsuchiya et al., 2011). If the level of suppression seen at stimulus onset is indeed greater than the suppression associated with sustained rivalry, this may have implications for studies using continuous flash suppression (CFS). In CFS the image in one eye can be suppressed for minutes at a time by presenting the other eye with constantly changing, contour rich, and high contrast stimulation (Tsuchiya and Koch, 2005). The non-dominant image in CFS is also suppressed more deeply than in conventional rivalry (Tsuchiya et al., 2006). If the perceptual stability seen in CFS is effectively caused by the continual updating of the "onset state" due to the successive presentation of a new image to one of the two eyes, it is possible that the level of activation achieved by the suppressed image at onset will be overestimated or underestimated relative to that which might have been seen with a sustained rivalry paradigm. This concept of refreshing was raised by Tsuchiya and Koch (2005—supplementary material), however, at the time no distinction had been made between onset rivalry and sustained rivalry. Within this context, the persisting dominance period was conceptualized as a prolongation of a normal sustained rivalry state being repeatedly "refreshed," rather than resetting of the distinct state characteristic of onset rivalry. Further investigation is required to determine how onset rivalry, in which rivaling targets are presented simultaneously, is related to paradigms such as flash suppression and masking, in which stimuli are presented asynchronously.

CONSEQUENCES FOR PAST MODELS AND FUTURE RESEARCH

Although there is much more research required to determine how various individual differences and stimulus conditions interact at the onset of rivalry, it is clear that the initial period of dominance must be distinguished from subsequent periods in rivalry. This distinction has implications for both past and future research into perceptual rivalry. Firstly, as the normal visual environment is constantly changing due to the dynamic nature of the external scenery and rapid and continuous natural saccadic eye movements (Henderson and Hollingworth, 1998), the mechanisms underlying the first interpretation of an ambiguous visual scene are likely to be most relevant for understanding conscious visual perception in a natural environment. The observation that dominance in rivalry after a saccade appears to be heavily related to the onset bias (Kalisvaart et al., 2011) further suggests that onset rivalry paradigms are likely to provide the greatest insight into how the brain deals with ambiguity in natural viewing conditions.

In contrast, brief presentation paradigms may be less suitable for investigating the alternating periods of dominance that characterize sustained rivalry. As this review has shown, endogenous factors and stimulus features affect dominance differently at onset than during sustained rivalry. Experimental conditions intending to investigate rivalry switching may exhibit different effects depending on the period of rivalry that is examined. Even paradigms that last for several seconds may still be influenced by onset biases, particularly for observers with naturally slower switch rates (Dobbins and Grossmann, 2010). With this caveat in mind, one might consider the possibility that it is the first switch, rather than the first conscious dominant percept, that marks the commencement of traditional, sustained rivalry. Indeed, the underlying mechanisms governing onset dominance appear to be unrelated to the initiation of transitional "suppression waves" that typically characterize a change in dominance (van Ee, 2011).

As a final caution, the literature reviewed here suggests that care is needed when interpreting data using intermittent presentations involving multiple repeated stimulus onsets—such as perceptual memory paradigms or CFS. It is likely that factors specific to onset rivalry may interfere with intermittent presentations aimed at investigating longer-term aspects of perceptual competition. Similarly, effects of past stimulus history are likely to influence onset dominance if testing involves multiple repeated trials.

CONCLUSION

Perceptual rivalry is a valuable tool for investigating the neural processes underlying perceptual awareness. The complexity in the time course of rivalry can also shed light on the brain's mechanism for dealing with ambiguity in everyday environments. As the average fixation period in natural viewing is approximately 300 ms (Henderson and Hollingworth, 1998), an individual's initial perceptual experience is likely to be the most relevant in everyday encounters with rivaling visual input. Current data cannot distinguish whether onset and sustained rivalry are determined by completely distinct mechanisms or share mechanisms that are nevertheless influenced by a range of factors in quite distinct ways. For example, dominance at onset appears to be particularly sensitive to early visual factors such as contrast and ocular dominance, while the role of higher cognitive factors is less clear. Additional work is needed to explore the interaction between onset and sustained rivalry in hybrid paradigms like intermittent presentation and continuous flash suppression, which involve repeated onset presentations in rapid succession.

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Breaking continuous flash suppression: a new measure of unconscious processing during interocular suppression?

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Until recently, it has been thought that under interocular suppression high-level visual processing is strongly inhibited if not abolished. With the development of continuous flash suppression (CFS), a variant of binocular rivalry, this notion has now been challenged by a number of reports showing that even high-level aspects of visual stimuli, such as familiarity, affect the time stimuli need to overcome CFS and emerge into awareness. In this "breaking continuous flash suppression" (b-CFS) paradigm, differential unconscious processing during suppression is inferred when (a) speeded detection responses to initially invisible stimuli differ, and (b) no comparable differences are found in non-rivalrous control conditions supposed to measure non-specific threshold differences between stimuli. The aim of the present study was to critically evaluate these assumptions. In six experiments we compared the detection of upright and inverted faces. We found that not only under CFS, but also in control conditions upright faces were detected faster and more accurately than inverted faces, although the effect was larger during CFS. However, reaction time (RT) distributions indicated critical differences between the CFS and the control condition. When RT distributions were matched, similar effect sizes were obtained in both conditions. Moreover, subjective ratings revealed that CFS and control conditions are not perceptually comparable. These findings cast doubt on the usefulness of non-rivalrous control conditions to rule out non-specific threshold differences as a cause of shorter detection latencies during CFS. Thus, at least in its present form, the b-CFS paradigm cannot provide unequivocal evidence for unconscious processing under interocular suppression. Nevertheless, our findings also demonstrate that the b-CFS paradigm can be fruitfully applied as a highly sensitive device to probe differences between stimuli in their potency to gain access to awareness.

Keywords: continuous flash suppression, interocular suppression, binocular rivalry, unconscious processing, visual awareness, face inversion

INTRODUCTION

The degree to which stimuli are processed without conscious awareness is of fundamental importance to our understanding of the visual system. An answer to this question requires both a psychophysical method to render stimuli invisible and a measure sensitive to unconscious processing. Binocular rivalry (BR) offers a particularly elegant way to erase a visual stimulus from awareness, because during BR perception spontaneously fluctuates between two dissimilar images presented concurrently to the two eyes (e.g., Kim and Blake, 2005; Tong et al., 2006; Sterzer et al., 2009b). Recently, Jiang et al. (2007) introduced a promising new method aimed at uncovering preserved processing of stimuli rendered invisible by such interocular suppression. A rapidly growing number of studies applying this "breaking continuous flash suppression" (b-CFS) technique now suggest that many high-level stimulus properties can be processed without visual awareness, something traditionally thought not to be possible under interocular suppression. The b-CFS method uses a direct measure of conscious perception to infer unconscious processing, namely the time it takes a stimulus to be detected.

THE DISSOCIATION PARADIGM FOR MEASURING UNCONSCIOUS PROCESSING

In the majority of studies on unconscious visual processing, a direct measure of conscious awareness of a stimulus (e.g., detection performance) is compared to an indirect measure of unconscious processing of the same stimulus (e.g., priming effect). Unconscious processing is commonly inferred when the indirect measure exhibits some sensitivity to the same stimulus information to which the direct measure is insensitive. Applying this dissociation logic (Erdelyi, 1986), many studies found that basic stimulus properties such as orientation, spatial frequency, color, or translational motion are still encoded when rendered invisible by interocular suppression (for a comprehensive review, see Lin and He, 2009). While such low-level stimulus properties can be processed unconsciously during suppression, it has remained unclear to what extent higher-level aspects of visual stimuli, such as familiarity or category membership, can be extracted without awareness under such viewing conditions. Evidence from indirect measures such as priming effects or high-level aftereffects suggests that only certain stimulus attributes related to emotional facial expressions (Adams et al., 2010; Yang et al., 2011; but see Yang et al., 2010), highly arousing stimuli (Jiang et al., 2006; Yan et al., 2009), manipulable objects (Almeida et al., 2008, 2010; also see Roseboom and Arnold, 2011), and numerical information (Bahrami et al., 2010) can escape suppression and transpire in subcortical areas (Pasley et al., 2004; Williams et al., 2004; Jiang and He, 2006) and along the dorsal cortical pathway (Fang and He, 2005; but see Hesselmann and Malach, 2011), respectively.

By contrast, priming effects triggered by stimuli known to be processed in ventral cortical areas, such as words (Zimba and Blake, 1983), line drawings of objects (Cave et al., 1998), and images of vehicles and animals (Almeida et al., 2008, 2010) are eliminated by interocular suppression. Similarly, invisible faces fail to induce facial identity, gender, race, and face shape aftereffects (Moradi et al., 2005; Amihai et al., 2011; Stein and Sterzer, 2011). These psychophysical findings dovetail with neural responses in the ventral stream being virtually eliminated under suppression (Sheinberg and Logothetis, 1997; Tong et al., 1998; Pasley et al., 2004; Williams et al., 2004; Fang and He, 2005; Hesselmann and Malach, 2011). Only recently, signatures of preserved processing differences between suppressed faces and houses have been detected in distributed activation patterns in category-selective areas of the ventral stream and in magnetoencephalographic markers related to face processing (Sterzer et al., 2008, 2009a). However, it is currently unknown whether such residual traces of activity can influence overt behavior or whether they are purely "epiphenomenal," i.e., unrelated to task performance (cf. Williams et al., 2007).

All of these studies examined unconscious processing during interocular suppression using some implementation of the dissociation paradigm. While intuitively appealing, it is important to note that the dissociation logic has faced repeated theoretical and methodological challenges. For example, there is little consensus on the nature of a direct measure that validly indexes conscious awareness (Cheesman and Merikle, 1986; Draine and Greenwald, 1998; Seth et al., 2008). Even more, it has been questioned whether it is possible at all to devise a direct measure which is sensitive to all aspects of conscious information that might influence performance on the indirect task (Reingold and Merikle, 1988). Conversely, because objective measures of stimulus awareness such as detectability are (at least partly) mediated by unconscious processes, display parameters that yield chance performance in the direct measure may eliminate not only conscious, but also unconscious information (Merikle and Reingold, 1992). Therefore, the dissociation paradigm may underestimate the extent of unconscious processing. In light of these potential problems, it is important to consider alternative approaches to unconscious processing.

BREAKING CONTINUOUS FLASH SUPPRESSION

A fundamentally different strategy exploits the temporal dynamics of perceptual fluctuations during BR. Research on the influence of higher-level stimulus aspects on the dynamics of BR has a long tradition (for a review of earlier findings, see Walker, 1978). In most of these studies, observers continuously tracked periods of perceptual dominance of the two stimuli presented concurrently to the two eyes. Such measures of subjective dominance have revealed that familiar, meaningful, or emotional stimuli predominate more than do unfamiliar, less meaningful, or non-emotional stimuli (e.g., Engel, 1956; Yu and Blake, 1992; Alpers and Gerdes, 2007). However, with regard to unconscious processing these findings remain inconclusive, as increased predominance could be due to perceptual enhancement during dominance and does not necessarily imply enhanced unconscious processing during suppression.

By directly measuring the duration of perceptual suppression for familiar and unfamiliar stimuli, Jiang et al. (2007) broke new grounds in addressing the question of whether high-level stimulus properties can remain effective during interocular suppression. To reliably suppress stimuli at the beginning of a trial, Jiang et al. (2007) made use of continuous flash suppression (CFS), a variant of BR in which dynamic Mondrian-like masks flashed to one eye render stimuli presented to the other eye invisible for extended periods of time (Tsuchiya and Koch, 2005)[1]. For example, in their first experiment, Jiang et al. (2007) presented an upright or inverted face to one eye, while CFS masks were flashed to the other eye. Observers indicated as fast as possible on which side of fixation any part of the face emerged from suppression. Results revealed a face inversion effect (FIE), i.e., longer response times (RTs) for inverted than for upright faces. Since upright and inverted faces consist of identical features, the FIE was interpreted as reflecting preserved higher-level processing differences under rivalry suppression.

Following this interpretation, results from recent studies could be taken as evidence that this breaking continuous flash suppression (b-CFS) paradigm is extremely sensitive to unconscious processes. Suppression durations are not only modulated by face inversion (Jiang et al., 2007; Zhou et al., 2010a) or word familiarity (Jiang et al., 2007), but also by emotional facial expressions (Yang et al., 2007; Tsuchiya et al., 2009; Sterzer et al., 2011), eye gaze (Stein et al., 2011), emotional words (Yang and Yeh, 2011), semantic priming (Costello et al., 2009), natural scene content (Mudrik et al., 2011), and even by concurrently presented odors (Zhou et al., 2010b). Clearly, these b-CFS findings challenge the previous notion that higher-level influences on the dynamics of BR are restricted to dominance periods alone (Blake and Logothetis, 2002).

ISOLATING CFS-SPECIFIC UNCONSCIOUS PROCESSING

Most b-CFS studies have attributed differences in suppression durations to differential unconscious processing during rivalry suppression, i.e., to *CFS-specific* unconscious processing differences. CFS-specific unconscious processing means that unconscious processing is present *because* CFS is applied to selectively

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[1] In fact, it is not yet clear whether CFS should be regarded as a variant of BR that induces particularly strong suppression (Shimaoka and Kaneko, 2011), or whether CFS is supported by mechanisms distinct from BR (Tsuchiya et al., 2006). For the purpose of the present article, we follow the currently common practice (e.g., Lin and He, 2009) and use CFS and rivalry suppression interchangeably.

interrupt conscious processing while leaving some unconscious processing intact. However, shorter suppression durations, for example for more familiar stimuli, could also be caused by generally lower thresholds for conscious detection independent of CFS-specific unconscious processing. Under normal viewing conditions the threshold for conscious detection is determined primarily by the speed of visual processing, which is typically very fast, but slowed under difficult viewing conditions, for example in cluttered displays. To isolate the effect of CFS-specific unconscious processing it is necessary to exclude such non-specific threshold differences as a cause for differences in suppression durations. In addition, because b-CFS studies used RTs to record suppression durations, variable response criteria could also distort the results, especially in states of partial awareness around threshold.

Jiang et al. (2007) were aware of these alternative explanations and designed a non-rivalrous binocular control condition intended to perceptually resemble the CFS condition, assuming that non-specific threshold differences should equally unfold in this control condition (**Figure 1**). In the control condition, participants detected the same stimuli as in the CFS condition, but no interocular suppression was induced as the stimuli were gradually blended in binocularly on top of the CFS masks (see **Figure 2**). Following the logic of comparing the CFS condition to such a control condition, the absence of RT differences in the control condition would imply that only CFS-specific unconscious processing differences could have caused RT differences in the CFS condition. Thus, the interpretation of any b-CFS study depends critically on the outcome of the control condition (**Figure 1**). To illustrate, in Experiment 1 by Jiang et al. (2007), no FIE was found in the control condition. This was interpreted as demonstrating that the FIE in the CFS condition could not have been due to a non-specific detection advantage for upright faces, but was caused by CFS-specific unconscious processing differences. Had the control condition yielded an FIE of comparable size, the conclusion would have been that both the CFS and the control condition reflect a detection advantage for upright relative to inverted faces.

Taken together, the b-CFS paradigm represents a fundamentally new approach to the measure of unconscious processing. Unlike the classic dissociation paradigm, the b-CFS paradigm does not compare a direct measure of conscious perception to an indirect measure of unconscious processing. Instead, two direct measures of differences in detection performance are compared, obtained during CFS and during a binocular control condition, to draw conclusions about CFS-specific unconscious processing.

If an effect is observed in the CFS condition only, this is attributed to CFS-specific unconscious processing. For this reasoning to be valid, the logic behind b-CFS presupposes that the control condition captures or "emulates" all processes that are not CFS-specific, but were involved in mediating a difference in stimulus detection in the CFS condition (**Figure 1**).

In light of the importance of the control condition for interpreting b-CFS results, it is of note that all previous b-CFS studies demonstrated a null effect in this control condition (Jiang et al., 2007; Costello et al., 2009; Zhou et al., 2010a; Mudrik et al., 2011; Stein et al., 2011; Yang and Yeh, 2011). We found the consistently observed absence of RT differences in the control condition surprising, as most b-CFS studies compared suppression durations for stimuli (e.g., upright vs. inverted faces, fearful vs. neutral faces, emotional vs. non-emotional words, or direct vs. averted gaze) that have frequently been found to differ in their detectability in a range of paradigms not involving BR, such as visual search, backward masking, or the attentional blink.

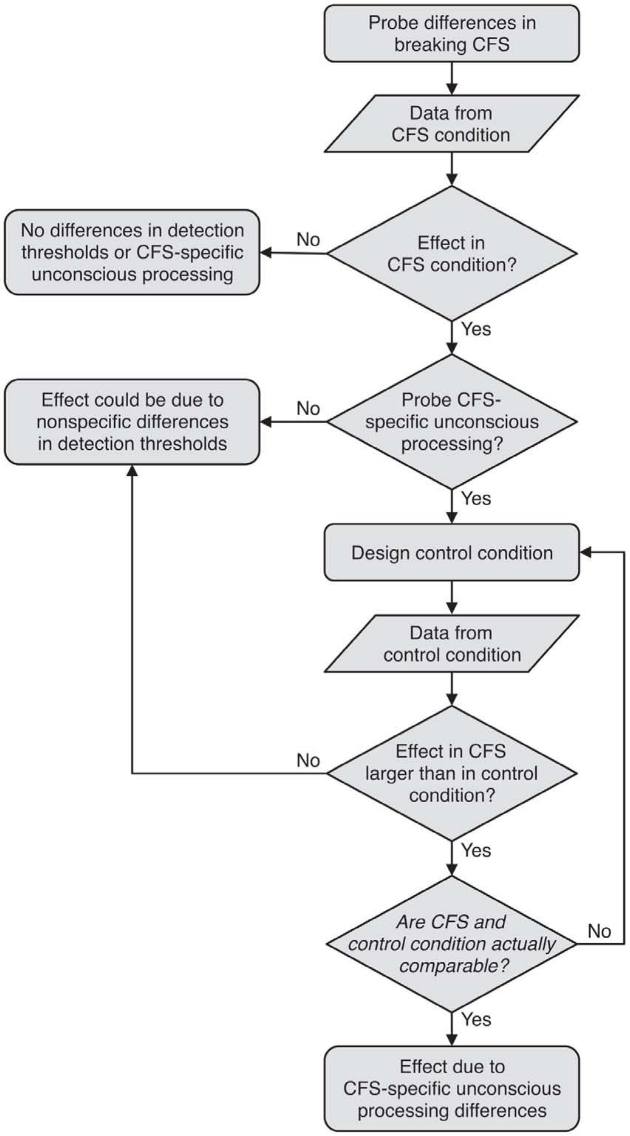

FIGURE 1 | Flowchart illustrating the logic underlying the b-CFS paradigm. If no control condition is included, no conclusions about CFS-specific unconscious processing differences can be drawn, as the effect obtained under CFS could be due to non-specific differences in detection thresholds. From the comparison of the effect obtained under CFS to the effect obtained in the control condition, CFS-specific unconscious processing can only be inferred if (a) the effect in the CFS condition is larger than the effect in the control condition, and, critically, (b) the CFS and the control condition are actually comparable in the sense that the control condition emulates all processes that are not CFS-specific, but were involved in mediating a difference in stimulus detection in the CFS condition.

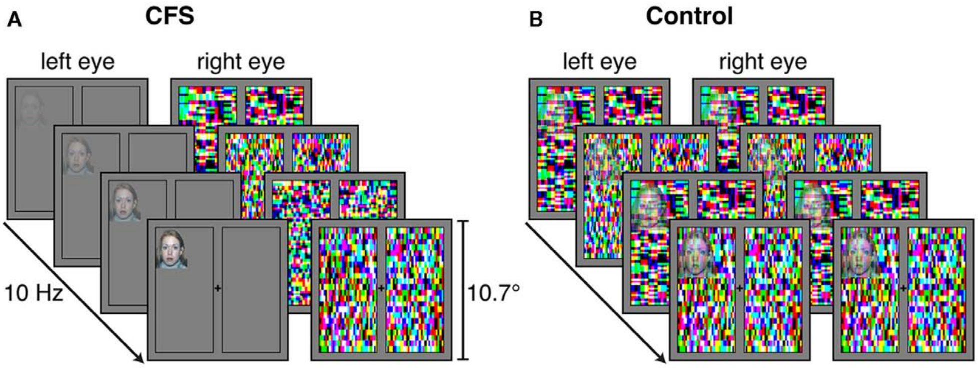

FIGURE 2 | Schematics of example trials from (A) the CFS condition and (B) the control condition in Experiments 1–3. (A) In the CFS condition, high-contrast Mondrian-like masks flashing at 10 Hz were presented to one eye, while a face stimulus was gradually introduced to the other eye. **(B)** In the control condition, the masks and the face stimulus were presented binocularly and the face was blended in transparently on top of the masks. In Experiments 1 and 2, participants were asked to indicate as fast and accurately as possible on which side of fixation the face or any part of the face became visible. In Experiment 3, presentation durations were fixed and subjects were required to indicate as accurately as possible, without speed pressure, on which side of fixation the face was shown.

THE PRESENT STUDY

We focused on the advantage of upright over inverted faces in overcoming CFS as an exemplary and consistent b-CFS finding (Jiang et al., 2007; Yang et al., 2007; Zhou et al., 2010a; Stein et al., 2011). The absence of an FIE in the control condition (Jiang et al., 2007; Zhou et al., 2010a) appears at odds with the well-established presence of an FIE in a variety of other detection paradigms under normal binocular viewing conditions (Purcell and Stewart, 1988; Aguirre et al., 1999; Lewis and Edmonds, 2003, 2005; Rousselet et al., 2003; Latinus and Taylor, 2006; Tyler and Chen, 2006; VanRullen, 2006; Chen et al., 2008; Garrido et al., 2008; for a review, see Lewis and Ellis, 2003). Intrigued by this discrepancy, we started off trying to replicate the results reported in the seminal b-CFS study by Jiang et al. (2007). Building up on this, we carried out a series of additional experiments intended to test the validity of the b-CFS paradigm. In particular, we examined whether the comparison between the CFS and the control condition can indeed be relied upon to isolate CFS-specific unconscious processing. We use face inversion only as an example, but the conclusions we draw are relevant for and extend to all applications of the b-CFS paradigm.

EXPERIMENT 1

In Experiment 1, we set out to replicate the results obtained by Jiang et al. (2007). Accordingly, visual stimuli, stimulus size, and experimental setup of Experiment 1 followed the description of their research. To increase sensitivity for detecting an FIE in the control condition we examined a larger sample of subjects and tested all participants both in the CFS and in the control condition. We expected upright faces to be detected faster than inverted faces. The critical question was whether this FIE would be restricted to the CFS condition, as reported by Jiang et al. (2007), or whether an FIE would also be present in the control condition.

In addition, we asked whether both conditions were actually comparable in the sense that the control condition emulated all critical factors that could have contributed to a detection advantage for upright faces in the CFS condition. As a first approach to this question, we explored differences between the RT distributions from the two conditions. Most RT analyses, including all previous b-CFS studies, evaluate a measure of central tendency of the RT distribution only, such as mean RT. Following Jiang et al. (2007), we sought to obtain roughly equal mean RTs in the CFS and in the control condition. However, limiting data analysis to a measure of central tendency can conceal important differences between conditions that can only be revealed by an analysis of the full RT distribution (e.g., Ratcliff, 1979; Hockley, 1984; Heathcote et al., 1991).

MATERIALS AND METHODS

Participants

Twenty-four observers (15 female, mean age 28.7 years) participated in Experiment 1. In all experiments, participants were paid, had normal or corrected-to-normal vision and were naïve to the purpose of the study. The study was approved by the Charité ethics committee and informed consent was obtained from all participants.

Apparatus

In Experiment 1 and in all further experiments, visual displays were presented on a 19-in Samsung CRT monitor (1024 × 768 pixels resolution, 60 Hz frame rate). Observers viewed a pair of dichoptic displays through a custom-built mirror stereoscope, with the subjects' heads stabilized by a chin-and-head rest. The effective viewing distance was 50 cm. To promote stable binocular alignment, the mirrors were adjusted for each observer. Visual stimuli were presented with Matlab (The MathWorks, Natick, MA, USA), using the Cogent 2000 toolbox (www.vislab.ucl.ak.uk/cogent.php).

Stimuli and procedure

Stimuli were displayed against a gray background. During the whole experiment two black frames (10.9° × 10.9°) were presented side by side on the screen, such that one frame was visible to each eye. In the center of each frame a black central fixation cross (0.7° × 0.7°) was displayed. Observers were asked to maintain stable fixation throughout each experimental block. In all experiments, face stimuli were 10 photographs (five female, 2.1° × 2.6°) and their vertical inversions derived from the NimStim face stimulus set (Tottenham et al., 2009).

Each trial started with a 1-s presentation of the fixation cross and the black frame only. In the CFS condition, colored high-contrast Mondrian-like CFS masks (similar to those used by Jiang et al., 2007; cf. Sterzer et al., 2008, 2009a) measuring 10° × 10° were flashed to one eye at a frequency of 10 Hz, while a face stimulus was introduced to the other eye (see **Figure 2**). The face was presented either to the left or to the right of the fixation cross, at a random location within the area corresponding to the location of the CFS masks. The contrast of the face stimulus was ramped up linearly from 0 to 100% (i.e., to its original contrast) within a period of 1 s from the beginning of the trial and then remained constant until the participant had made a response. In the control condition, CFS masks and face stimuli were presented binocularly. Face stimuli were gradually blended into the masks by reducing their transparency linearly from 100 to 0% within a period of 2.5 s from the trial's beginning.

We informed participants that both upright and inverted faces would be presented and asked them to press the left or the right arrow key on the keyboard to indicate as fast and accurately as possible on which side of fixation a face or any part of it appeared[2].

Design

Observers viewed one block containing 120 CFS trials and one block of 120 control trials. Within each block all possible combinations of face orientation (upright, inverted), two eyes for face presentation (only for the CFS condition, in the control condition face stimuli were always presented binocularly) and ten face exemplars were presented equally often and trial order was randomized. Block order was counterbalanced across participants.

Analysis

Trials with erroneous responses or RTs longer than 10 s were discarded (cf. Jiang et al., 2007). In total, less than 2% of all trials for each subject were excluded from the analysis.

RESULTS AND DISCUSSION

Upright vs. inverted faces

Mean RTs were analyzed by a repeated measures ANOVA with the factors condition (CFS, control) and face orientation (upright, inverted). There was a trend for a main effect of condition, $F(1, 23) = 3.50$, $p = 0.074$, and a significant main effect of face orientation, $F(1, 23) = 27.49$, $p < 0.001$, which was qualified by a significant interaction between condition and face orientation, $F(1, 23) = 13.13$, $p = 0.001$, indicating a larger FIE in the CFS than in the control condition (see **Figure 3A**). Importantly, however, the FIE was not only significant in the CFS condition, $t(23) = 4.53$, $p < 0.001$, but also in the control condition, $t(23) = 4.33$, $p < 0.001$.

The reliable FIE in the control condition indicates that different detection thresholds or criteria for upright and inverted faces that are not specific to CFS do exist in the b-CFS paradigm. Still, the FIE was larger in the CFS condition. One possibility is that this increase in FIE size reflected CFS-specific unconscious processing differences between upright and inverted faces. Alternatively, there might have been other factors that differed between the CFS and the control condition and that could have caused the increased FIE in the CFS condition.

CFS vs. control condition

Kolmogorov–Smirnov tests (KS-tests) demonstrated significant differences between the RT distributions from the CFS and the control condition for each individual subject (all $ps < 0.001$). To visualize these differences in the shape of RT distributions, we plotted group cumulative RT distributions comparing the two conditions (**Figure 4A**). For each subject and each condition, we computed the RTs corresponding to the 5th to 95th percentiles at 5% intervals which were then averaged across subjects. This method preserves the shape of the individual RT distributions (e.g., Thomas and Ross, 1980; Mordkoff and Yantis, 1991). **Figure 4A** shows that the CFS distribution had more spread and a considerably longer right tail, reflecting increased RT variability and a larger number of trials with particularly long RTs. This enhanced RT variability was also reflected in a significantly larger mean coefficient of variation (CV, SD divided by the mean) in the CFS condition compared to the control condition, $t(23) = 13.88$, $p < 0.001$ (**Figure 3B**).

To examine which aspects of the distributions were influenced by face inversion and whether face inversion affected the CFS and the control distributions differently, we again used the

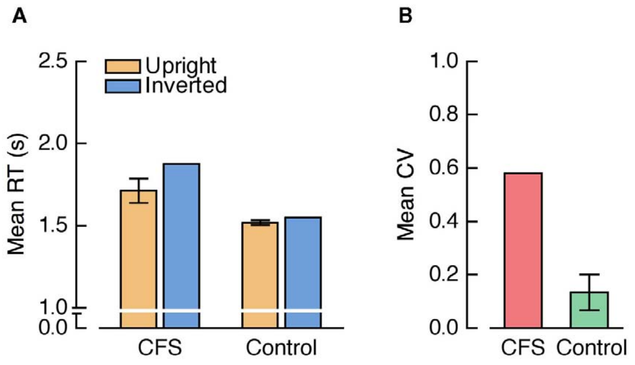

FIGURE 3 | (A) Mean RTs from Experiment 1. In this and all further graphs depicting mean RTs, positive and negative error bars represent 95% confidence intervals for the paired comparison between upright and inverted faces within each condition. **(B)** Mean coefficients of variation (CV; SD divided by the mean) from Experiment 1. In this and all further graphs depicting CVs, positive and negative error bars denote 95% confidence intervals for the paired comparison between the CFS and the control condition.

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[2] It is possible that this instruction slightly deviated from the study by Jiang et al. (2007) who instructed observers to "respond to the appearance of any part of the *test image* [emphasis added]." We informed participants about the presentation of faces as test images, because we found it difficult to instruct naïve participants to discriminate a "test image" from the CFS masks without further specifying what that test image distinguishes from the random shapes constituting the mask. Moreover, even when instructed to detect a test image, participants would realize after a few trials that the test image set consisted only of upright and inverted faces. We therefore do not believe that this possible difference to the study by Jiang et al. (2007) could have affected our results.

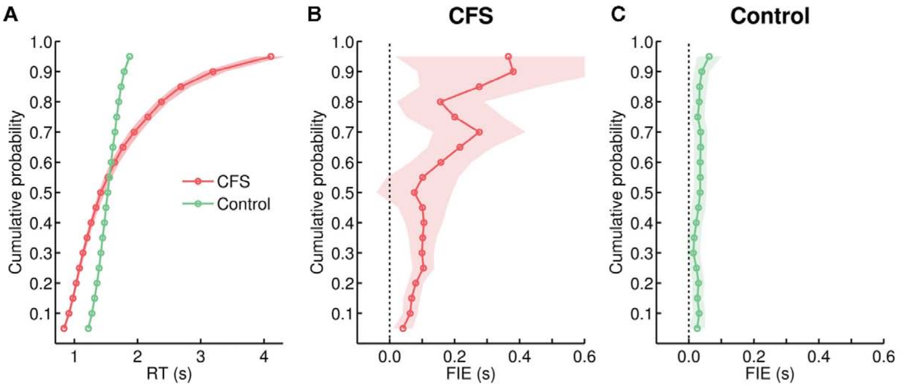

FIGURE 4 | (A) Cumulative group distributions of RTs from the CFS and the control condition in Experiment 1. We obtained the RTs corresponding to the 5th to 95th percentiles at 5% intervals from each subject's individual cumulative RT distributions. These percentile estimates were then averaged across subjects to create group average RT distributions (Thomas and Ross, 1980; Mordkoff and Yantis, 1991). In this and all further graphs depicting cumulative group distributions, the shaded areas represent 95% confidence intervals generated by bootstrapping (Mack et al., 2009). **(B,C)** Size of the FIE as a function of percentiles, plotted separately for the **(B)** CFS and the **(C)** control condition. Within each condition, we first created separate group average RT distributions for trials with upright and inverted faces and then computed the FIE (RT inverted–RT upright) at each percentile. In this and all further graphs depicting the FIE at separate percentiles, the shaded areas depict the 95% confidence intervals for the FIE at each percentile.

percentile averaging method to compare RTs to upright and inverted faces at each of the 5th to 95th percentile (spaced at 5% intervals; **Figures 4A,C**). Over the bulk of the distributions from both conditions, RTs were shorter for upright faces. However, in the control condition the FIE had a similar size across the full distribution (**Figure 4C**). By contrast, in the CFS condition, the size of the FIE increased toward the right tail of the distribution (**Figure 4B**). Correspondingly, linear regression analyses demonstrated that the slope for the CFS condition was significantly more positive than for the control condition, $F(1, 34) = 44.73$, $p < 0.001$. Thus, trials with exceptionally long RTs (which were virtually absent in the control condition, see **Figure 4A**) strongly contributed to the increased FIE in the CFS condition.

Interpretation of distributional differences

Although differences in RT distributions cannot unequivocally be related to specific underlying perceptual or cognitive processes, it is widely accepted that differences in distributional parameters other than the mean can reflect important differences between experimental conditions (e.g., Luce, 1986; Heathcote et al., 1991). Thus, the striking differences in distribution shape may indicate that the control condition failed to emulate all perceptual and cognitive factors (other than CFS-specific unconscious processing) that were involved in the CFS condition. If true, it would be problematic to rely on the results from the control condition to draw conclusions about the processes underlying the effects obtained in the CFS condition.

The most prominent difference between both conditions was the greatly increased RT variability in the CFS condition. One possibility is that this increased RT variability was driven by stochastic variations in the dynamics of BR (e.g., Levelt, 1965; Fox and Herrmann, 1967; Kim et al., 2006). This variability in perceptual dominance of the face stimulus would inevitably introduce temporal uncertainty with regard to the time of face appearance during CFS. By contrast, in the control block the appearance of the face could easily be anticipated, since the face stimuli were faded in at a constant rate. One concern is that different uncertainties with regard to face appearance could have led subjects to adopt different strategies for detecting faces in both conditions. Different strategies could then, for example, have shifted response criteria in a way that yielded different FIE sizes.

In the following two experiments, we examined whether the increased FIE in the CFS condition resulted from unconscious processing or from other differences between the CFS and the control condition, such as different strategies (Experiment 2) or response criteria (Experiment 3).

EXPERIMENT 2

In Experiment 2, we mixed CFS and control trials within the same blocks, instead of separating them into distinct pure blocks as done in previous b-CFS studies on the FIE (Jiang et al., 2007; Zhou et al., 2010a). This simple change in experimental design was introduced to attenuate any difference in temporal uncertainty regarding face appearance. We were concerned that differences in temporal uncertainty would lead subjects to adopt different strategies in CFS and control blocks. The impact of different strategies associated with different experimental conditions is known to be amplified when experimental conditions are separated into distinct pure blocks, even in simple perceptual tasks (e.g., Sperling and Dosher, 1986; Los, 1996). Therefore, if strategic differences contributed to the difference in FIE size, this influence should be reduced in a mixed design.

MATERIALS AND METHODS

Participants

A new set of 24 observers (20 female, mean age 23.4 years) participated in Experiment 2.

Design

Participants completed 320 trials separated by four breaks: each combination of two conditions, two face orientations, two eyes for face presentation, and ten face identities occurred equally often and trial order was randomized.

Analysis

Incorrect trials and RTs longer than 10 s were discarded (less than 2% of all trials for each subject).

RESULTS AND DISCUSSION

Upright vs. inverted faces

A repeated measures ANOVA on mean RTs revealed a trend for a main effect of condition, $F(1, 23) = 3.92$, $p = 0.060$, and a significant main effect of face orientation, $F(1, 23) = 24.98$, $p < 0.001$, with longer RTs for inverted than for upright faces. Crucially, the interaction between condition and face orientation was not significant, $F(1, 23) < 1$ (**Figure 5A**). Thus, the FIE was significant both for the CFS condition, $t(23) = 2.69$, $p = 0.013$, and for the control condition, $t(23) = 3.29$, $p = 0.003$, and the size of the FIE did not differ significantly between both conditions.

Hence, when CFS and control trials were mixed within the same blocks, both conditions yielded comparable FIE sizes. As the FIE in the CFS condition was not larger than the FIE in a condition intended to control for differences in detection thresholds or criteria for upright and inverted faces, one would have to conclude that in both conditions the FIE was mediated by a non-specific detection advantage for upright faces. Thus, following the logic of the b-CFS paradigm, the results from Experiment 2 provide no evidence for CFS-specific unconscious processing differences between upright and inverted faces.

CFS vs. control condition

The increased FIE in the control condition was accompanied by a change in the underlying RT distribution that now better approximated the shape of the CFS distribution (**Figure 6B**). KS-tests showed significant differences (at the 10% level) between both distributions in only nine out of 24 subjects. In comparison to Experiment 1, the control distribution had more spread and a longer right tail and now closely overlapped with the CFS distribution (**Figure 6A**). While the mean CV was still significantly larger in the CFS condition, $t(23) = 6.41$, $p < 0.001$ (**Figure 5B**), compared to Experiment 1 the difference between the two conditions was much reduced (compare **Figure 5B** to **Figure 3B**). Accordingly, a mixed ANOVA with the between subjects factor experiment (1, 2) and condition (CFS, Control) on the mean CVs yielded a significant experiment-by-condition interaction, $F(1, 46) = 93.88$, $p < 0.001$.

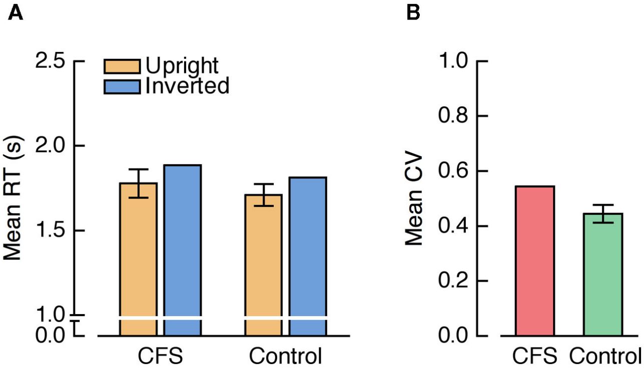

FIGURE 5 | (A) Mean RTs and **(B)** mean CVs from Experiment 2.

Furthermore, in Experiment 2 face inversion did not only shift the distribution from the control condition rightwards, but also increased the size of its right tail, thereby mimicking the effect of face inversion on the CFS distribution (**Figures 6B,C**). This impression was supported by linear regression analyses showing that the slopes were positive for both the CFS and the control condition, $F(1, 17) = 31.50$, $p < 0.001$, and $F(1, 17) = 15.56$, $p < 0.001$, respectively, while – in contrast to Experiment 1 – there was no statistically significant difference between the slopes, $F(1, 34) < 1$. Thus, both in the CFS and in the control condition the FIE was now particularly pronounced for trials with slow RTs.

Interpretation

We had hypothesized that a mixed design would reduce potential differences between conditions with regard to temporal uncertainty or subjects' strategies. Following this reasoning, the convergence of the distributions may reflect a reduction of factors that differed between the two conditions, such as temporal uncertainty or subjects' strategies. We would expect uncertainty and strategies to influence primarily (although not exclusively) "postperceptual" factors related to decision making, response selection, or response initiation. Clearly, the choice RT procedure employed in the b-CFS paradigm is susceptible to influences from postperceptual factors, such as different response criteria for upright and inverted faces. It is important to note that the possible impact of such non-perceptual factors may be limited to the comparison of upright and inverted faces and does not necessarily apply to other b-CFS studies using different stimuli. For example, it is difficult to imagine that observers would have different response criteria for images of complex scenes that differed only in their semantic content (Mudrik et al., 2011). By contrast, the greater familiarity of upright faces could be associated with a more liberal response criterion.

EXPERIMENT 3

To test this possibility, in Experiment 3 we again used a mixed design but ruled out the potential influence of differential response criteria. To that end, we fixed display durations and measured response accuracies instead of RTs, using a spatial two-alternative forced-choice (2AFC) task without speed pressure. If the increased FIE in the CFS condition reflected CFS-specific unconscious processing differences while the increased FIE in the mixed design control condition reflected postperceptual factors, in Experiment 3 we would expect a larger FIE in the CFS than in the control condition. Alternatively, if both FIEs were caused by a non-specific detection advantage for upright faces, we would expect FIEs of similar size.

MATERIALS AND METHODS

Participants

Twenty observers (16 female, mean age 27.4 years) participated in Experiment 3.

Procedure

Each trial started with a 1-s presentation of the fixation cross and the black frame only, followed by the face stimulus and the CFS masks displayed for 500, 700, 1000, or 1500 ms. In the CFS condition face contrast reached 50% in 500-ms displays, 70% in 700-ms displays, and 100% in 1000 and 1500-ms displays. In the control condition, face transparency was 80% in 500-ms displays, 72% in 700-ms displays, 60% in 1000-ms displays, and 40% in 1500-ms displays. In both conditions, face stimulus presentation was followed by three trailing masks, each presented for 100 ms binocularly to prevent afterimages.

At the end of the stimulus sequence, observers were prompted to press the left or the right arrow key on the keyboard to indicate as accurately as possible on which side of fixation the face image had been shown. No feedback was given. Participants were encouraged to take as much time as they needed to make their responses. Instructions informed observers that upright and inverted faces would be presented during each trial and that in some trials only parts of the faces might become visible.

Design

All participants were tested in two sessions separated by 1–3 days. A single session consisted of 640 trials separated by nine breaks. Within a session each combination of two conditions, two face orientations, two eyes for face presentation, four presentation durations, and ten face exemplars occurred with equal probability and trial order was randomized.

RESULTS AND DISCUSSION

Proportions of correct responses were analyzed by a repeated measures ANOVA with the factors condition, face orientation, and presentation duration (500, 700, 1000, 1500 ms). Face detection accuracy increased with longer presentation durations, $F(3, 57) = 193.64$, $p < 0.001$. More importantly, there was a significant main effect of face orientation, $F(1, 19) = 11.33$, $p = 0.003$, with higher accuracy for upright faces than for inverted faces (see **Figure 7**). Neither the main effect of condition, $F(1, 19) = 1.37$, $p = 0.257$, nor the interaction between condition and presentation

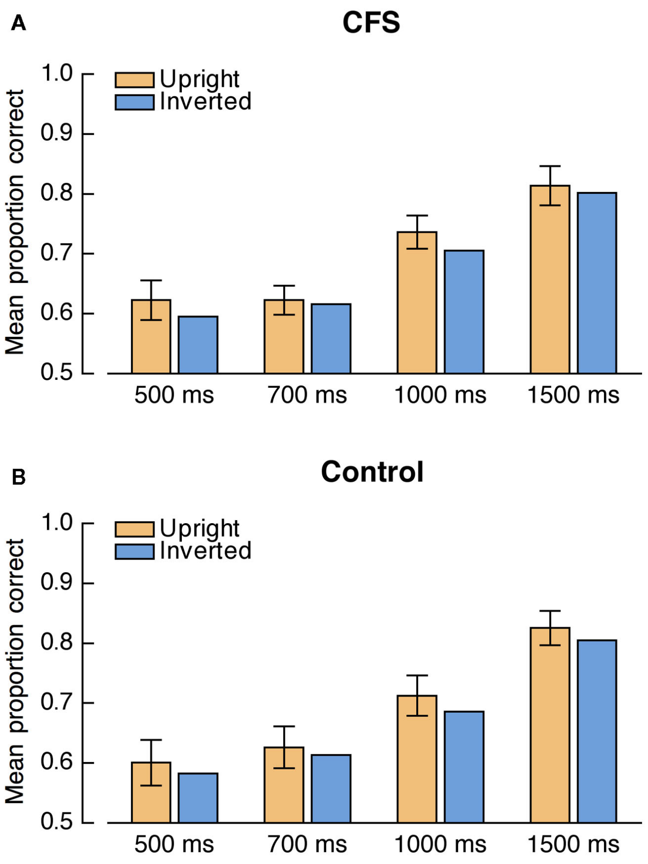

FIGURE 7 | Results from Experiment 3. Mean accuracies for upright and inverted faces, presented separately for **(A)** the CFS condition and **(B)** the control condition at each presentation duration. Error bars denote the 95% confidence interval for the paired comparison of upright and inverted faces at the respective presentation duration.

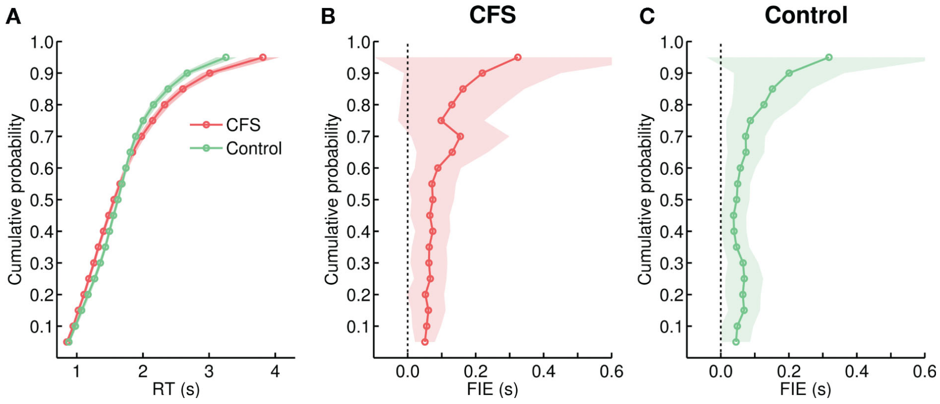

FIGURE 6 | (A) Cumulative group distributions of RTs from the CFS and from the control condition in Experiment 2. **(B,C)** Size of the FIE as a function of percentiles, plotted separately for the CFS and the control condition.

duration, $F(3, 57) = 1.59$, $p = 0.202$, were significant. Crucially, no other interaction, including the condition-by-face orientation interaction, approached significance, all Fs < 1.

Thus, when the putative influence of differential response criteria was eliminated we found a detection advantage for upright faces that was independent of condition. Accordingly, the FIE in the control condition reflected a lower detection threshold for upright faces and cannot be ascribed simply to the influence of differential response criteria or to other postperceptual factors. As the FIE was not enlarged in the CFS condition, the results from Experiment 3 suggest that shorter suppression durations for upright faces reflected the same non-specific detection advantage in both conditions and thus, consistent with the results of Experiment 2, fail to provide evidence for CFS-specific unconscious processing differences between upright and inverted faces.

In summary, the results from Experiments 1–3 demonstrate a detection advantage for upright faces that is not specific to CFS. In all three experiments we found an upright face advantage in the control condition. Still, in Experiment 1 the FIE in the control condition was smaller than the FIE in the CFS condition, allowing the possibility that CFS-specific unconscious processing could have contributed to the increased FIE. However, when CFS and control trials were mixed within the same block (Experiment 2) and when we measured detection accuracies instead of RTs (Experiment 3), the FIE was similarly large in both conditions. Thus, to account for different suppression durations in these experiments, it suffices to assume non-specific detection differences for upright and inverted faces, and it is not necessary to postulate CFS-specific unconscious processing differences.

EXPERIMENT 4

Taking the results of the previous experiments together, we found no evidence for additional CFS-specific unconscious processing under b-CFS compared to the control condition when RT distributions of both conditions were matched (Experiment 2) and when we controlled for effects of response criteria by using a 2AFC task (Experiment 3). Before throwing the baby out with the bathwater, we were interested whether it might nevertheless be possible to find evidence for CFS-specific unconscious processing.

The previous experiments were designed to closely resemble the experimental protocol and visual displays employed by Jiang et al. (2007) and to yield similar overall suppression durations as previous b-CFS studies on the FIE (Jiang et al., 2007; Zhou et al., 2010a). Still, it is possible that CFS-specific unconscious effects are indeed present, but cannot be increased beyond the size of non-specific effects with such short suppression durations. As results from other studies conducted in our laboratory (e.g., Stein et al., 2011) indicated that longer overall suppression durations might yield larger effects in the CFS condition, in the following experiments we adjusted the display parameters to induce longer periods of perceptual suppression. We asked whether longer suppression durations would result in a larger FIE and whether this FIE would be larger than the effect obtained in the control condition, despite the use of a mixed design.

Furthermore, these additional experiments allowed us to test whether mixing the CFS and the control condition would invariantly result in similar RT distributions for both conditions, as suggested by Experiment 2. In addition to the comparison of RT distributions, in Experiment 4 we tested whether the control condition actually mimicked the perceptual experience during CFS, as assumed by all previous b-CFS studies that relied on the comparison with a control condition to infer CFS-specific unconscious processing. To that end, we had participants judge their subjective impression of face appearance after each trial.

MATERIALS AND METHODS

Participants

Fourteen observers (nine female, mean age 24.5 years) participated in Experiment 4.

Apparatus and stimuli

For Experiments 4 (as well as for Experiments 5 and 6), the visual displays were slightly modified (**Figure 8**). To further facilitate stable binocular fusion, fusion contours (width 0.5°) consisting of randomly arranged black and white pixels were drawn within the frames (10.9° × 10.9°) presented to each eye. In order to induce longer periods of perceptual suppression, we generated another variant of Mondrian-like CFS masks (10.4° × 10.4°) consisting of colored, randomly arranged circles (diameter 0.4°–1.8°; similar to the masks used by Tsuchiya et al., 2009). During pilot testing, these masks suppressed stimuli for longer periods than those employed in the previous experiments.

Procedure

The face stimuli were always centered at a horizontal distance of 3.9° either to the left or to the right of the fixation cross, at a random vertical position relative to the fixation cross (maximum vertical center-to-center distance 2.9°). We now included three different control conditions that differed with regard to the length of the transparency ramp. In the 8.5-s ramp control condition, face transparency was reduced from 100 to 0% within 8.5 s. In the 2.5-s ramp control condition, this transparency ramp lasted 2.5 s. Finally, we also included a no-ramp control condition in which the face was displayed binocularly at full contrast at a randomly selected time point (0.5, 1.0, 2.0, 3.5, or 5.0 s after trial onset; cf. Sterzer et al., 2011).

As in Experiments 1 and 2, participants' primary task was to indicate as fast and as accurately as possible the side of fixation on which the face stimulus or any part of the face appeared, using the left or the right arrow key on the keyboard. In addition, participants judged their subjective impression of face appearance at the end of each trial. After indicating face location, participants were prompted to judge how abrupt the face had appeared by pressing a key from 1 to 4, with 1 meaning abrupt and 4 meaning gradual face appearance. Instructions emphasized that this "abruptness rating" represented a secondary task and that localization responses should under no circumstances be decelerated or withheld in order to better judge the abruptness of face appearance. Participants were encouraged to follow their spontaneous impressions when judging abruptness and to guess if necessary.

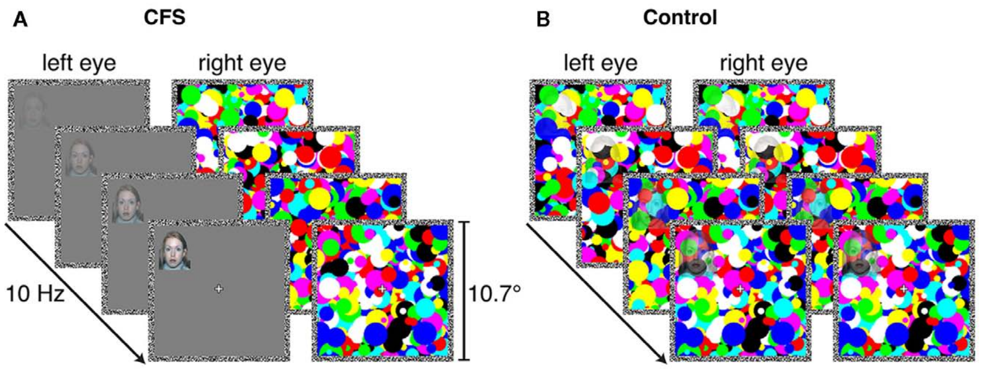

FIGURE 8 | Schematics of example trials from (A) the CFS condition and (B) the control condition in Experiments 4–6 in which we employed a new set of masks that induced longer periods of perceptual suppression in the CFS condition. In Experiments 4 and 5, we used a speeded localization task as in Experiments 1 and 2. In Experiment 6, display presentation durations were fixed and the localization task was unspeeded, as in Experiment 3.

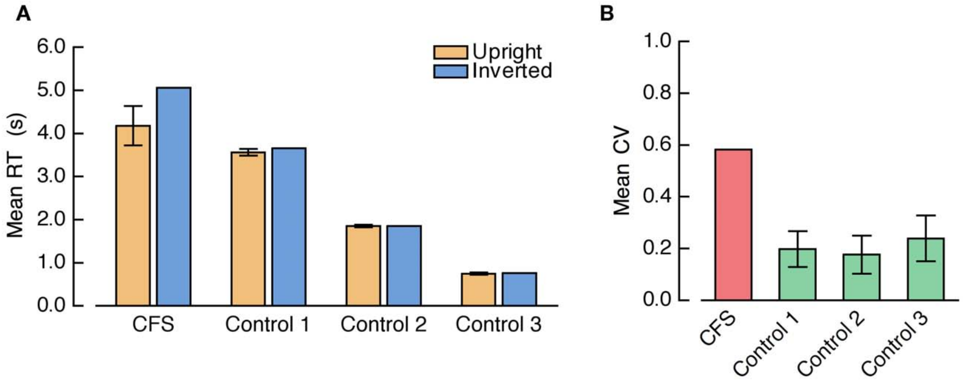

FIGURE 9 | (A) Mean RTs and **(B)** mean CVs from Experiment 4. "Control 1" refers to the 8.5-s ramp, "Control 2" refers to the 2.5-s ramp, and "Control 3" refers to the no-ramp control condition.

Design

Experiment 4 consisted of 320 trials (separated by three breaks). Each combination of four conditions (CFS, three control conditions), two face orientations, two eyes for face presentation, and ten face exemplars was presented equally often and trial order was randomized.

Analysis

Trials with incorrect responses (less than 4% of all trials for each subject) and CFS trials with RTs longer than 15 s (compared to Experiments 1 and 2 we extended the cut-off by 5 s to account for the prolonged overall suppression durations) as well as CFS trials in which the face went undetected (13.8%) were discarded. Overall, 95.5% of all trials were included in the analyses.

RESULTS AND DISCUSSION

Upright vs. inverted faces

A repeated measures ANOVA on mean RTs with the factors condition (CFS, three control conditions) and face orientation yielded a significant main effect of condition, $F(3, 39) = 41.80$, $p < 0.001$, a significant main effect of face orientation, $F(1, 13) = 19.78$, $p < 0.001$, and, importantly, a significant interaction between condition and face orientation, $F(3, 39) = 13.94$, $p < 0.001$. The FIE was significant in the CFS condition, $t(13) = 4.01$, $p = 0.001$, and in the 8.5-s ramp control condition, $t(13) = 2.46$, $p = 0.029$, but neither in the 2.5-s ramp control condition nor in the no-ramp control condition, both $t(13) < 1$ (see **Figure 9A**). Crucially, the FIE was significantly larger in the CFS condition than in the 8.5-s ramp control condition, $F(1, 13) = 14.18$, $p = 0.002$.

Thus, longer overall suppression duration resulted in a larger FIE compared to the CFS conditions in the previous experiments (compare **Figure 9A** to **Figures 3A** and **5A**) and this FIE exceeded the effect obtained in the control condition, despite the use of a mixed design. According to the b-CFS logic, the increased FIE in the CFS condition in Experiment 4 would provide evidence for CFS-specific unconscious processing differences between upright and inverted faces, contrary to the results of Experiments 2 and 3.

CFS vs. control condition

We next tested whether the mixed design used in Experiment 4 attenuated differences between the RT distributions from the CFS and the control condition, as in Experiment 2, or whether the increased FIE in the CFS condition was accompanied by marked differences between the RT distributions from both conditions, as in the blocked design in Experiment 1. KS-tests yielded significant differences between the CFS distribution and the 8.5-s ramp control distribution for each individual subject (all $p < 0.01$). As in Experiment 1, the CFS distribution had more spread and a longer right tail (**Figure 10A**), the mean CV was greatly enhanced in the CFS condition, $t(13) = 11.99, p < 0.001$ (**Figure 9B**), and the effect of face inversion strongly increased toward the right tail of the CFS distribution (compare **Figures 10B,C**).

Thus, using a mixed design as in Experiment 2 is not sufficient to eliminate differences between experimental and control condition in RT distributions. As discussed for Experiment 1, these considerable distributional differences could indicate that the control condition did not reproduce all relevant factors that might have played a role in the CFS condition.

Subjective face appearance

The concern that the control condition did not represent a good analog of the CFS condition was borne out by participants' ratings of subjective face appearance. Mean abruptness ratings significantly differed between the four presentation conditions, $F(3, 39) = 104.25$, $p < 0.001$ (see **Figure 11**). To test whether one of the control conditions yielded a subjective impression of face appearance comparable to the CFS condition, we compared the mean ratings between the CFS condition and the three control conditions. Face appearance in the 8.5-s ramp control condition was judged to be more gradual than in the CFS condition, $t(13) = -7.15$, $p < 0.001$. Even the 2.5-s ramp control condition that yielded much shorter overall RTs (see **Figure 9**) generated a more gradual impression of face appearance than the CFS condition, $t(13) = -2.39$, $p = 0.033$. Conversely, face appearance in the no-ramp control condition was rated as being more abrupt than in the CFS condition, $t(13) = 8.74$, $p < 0.001$.

Thus, none of the control conditions included in Experiment 4 could match the CFS condition in the subjective abruptness of face experience. Progressive fading-in of the face stimulus as in most previous b-CFS studies (Jiang et al., 2007; Costello et al., 2009; Zhou et al., 2010a; Mudrik et al., 2011; Stein et al., 2011; Yang and Yeh, 2011) led to the impression of a more gradual face appearance. Furthermore, the comparison to the no-ramp control condition revealed that breakthrough from suppression was not "all-or-none," i.e., it was not experienced as the sudden presence of a previously fully absent percept. This may reflect the perception of extended transition periods in which neither the mask nor the face achieved full dominance. Indeed, during conventional BR, observers frequently experience transition periods in which a compound of both stimuli is perceived, either piecemeal or superimposed (e.g., Blake et al., 1992; Yang et al., 1992), and these transition periods can be in the order of seconds (Brascamp et al., 2006). Mimicking the subjective perception during such transition periods in a binocular control condition appears difficult if not impossible (an issue we will return to in the General Discussion).

Interpretation

In summary, inducing longer periods of perceptual suppression led to a large FIE in the CFS condition that exceeded the effect obtained in the control condition. We can only speculate about

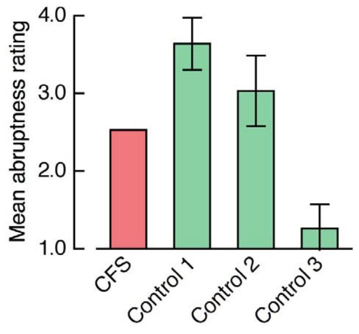

FIGURE 11 | Rating of subjective face appearance in Experiment 4. Bar plots denote participants' mean ratings of the abruptness of face appearance (from 1 abrupt to 4 gradual). "Control 1" refers to the 8.5-s ramp, "Control 2" refers to the 2.5-s ramp, and "Control 3" refers to the no-ramp control condition. Positive and negative error bars represent 95% confidence intervals for the paired comparison between the CFS condition and the respective control condition.

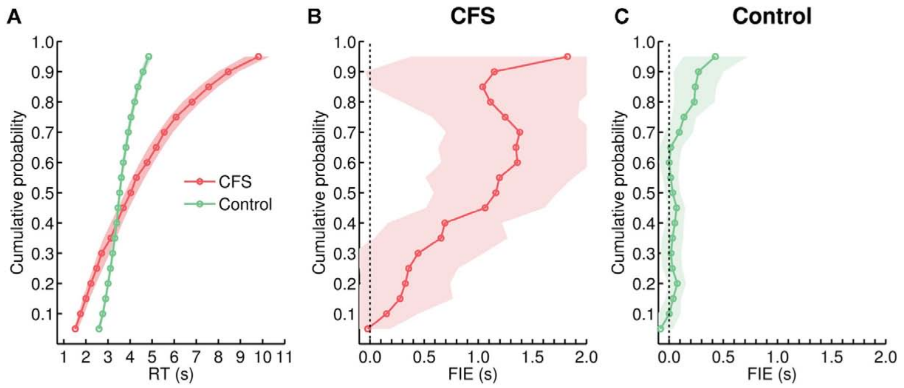

FIGURE 10 | (A) Cumulative group distributions of RTs from the CFS and from the 8.5-s ramp control condition in Experiment 4. **(B,C)** Size of the FIE as a function of percentiles, plotted separately for the CFS and the 8.5-s ramp control condition.

the cause of the apparent relationship between overall suppression durations and FIE size, one possible reason being unconscious processing differences unfolding successively over longer periods of invisibility. However, a caveat to this interpretation is that both the analysis of RT distributions as well as the subjective rating of face appearance revealed marked differences between the CFS and the control condition, as in Experiment 1. Therefore, the comparison of both conditions does not necessarily isolate CFS-specific unconscious processing, but could reflect any other process differentially engaged by the CFS and the control condition.

In contrast to Experiment 2, implementing a mixed design did not lead to a convergence of the RT distributions from the two conditions. In Experiment 4, longer overall durations of perceptual suppression resulted in a proportional increase in RT variability, whereas in the transparency ramp control conditions RT variability tended to be even lower than in Experiment 2 (compare **Figures 5B** and **9B**). We had hypothesized that the similarity of RT distributions seen in Experiment 2 could have reflected a reduction of differences between conditions, perhaps related to face predictability, subjects' strategies or response criteria. Following this reasoning, the divergence of RT distributions in Experiment 4 suggests that a mixed design is not always successful in reducing such differences. We can only speculate about this discrepancy, one possibility being that the overall prolonged duration of the CFS trials in Experiment 4 left sufficient time for subjects to consciously adjust their response strategy.

In the final two experiments, we addressed these concerns. In Experiment 5, we again tried to match RT distributions of the CFS and control condition as in Experiment 2 and made face appearance in the control condition less predictable by implementing a wide range of different transparency ramps. In Experiment 6, we used an unspeeded spatial 2AFC task similar to Experiment 3 to rule out the potential impact of different response criteria.

EXPERIMENT 5

MATERIALS AND METHODS

Participants

A new group of 14 observers (nine female, mean age 25.2 years) participated in Experiment 5. One subject was excluded from the analysis due to data loss (computer error in recording the log file).

Apparatus, stimuli, and procedure

While the CFS condition was identical to Experiment 4, in the control condition we now implemented a range of different transparency ramps. To increase variability in face appearance, for each subject 40 different ramp durations were randomly drawn from an ex-Gaussian distribution which typically provides an excellent fit to RT data from a wide range of experiments (e.g., Hockley, 1984; Heathcote et al., 1991). The parameters for this ex-Gaussian distribution ($\mu = 4.9$ s, $\sigma = 7.3$ s, $\tau = 12.2$ s) were selected based on pilot testing. Ramp durations shorter than 250 ms were set to 250 ms to replace negative values. The 10 face exemplars were then randomly assigned to the 40 different ramps, such that both the upright and the inverted version of a given face exemplar were presented using the same ramp durations.

Design

There were 160 trials (separated by one break): each combination of two conditions, two face orientations, two eyes for face presentation, and ten face exemplars occurred equally often and trial order was randomized.

Analysis

Trials with incorrect responses (less than 3% of all trials for each subject) and CFS trials with RTs longer than 15 s as well as CFS trials in which the face went undetected (10.9%) were discarded. In total, 92.3% of all trials were included in the analyses.

RESULTS AND DISCUSSION

Upright vs. inverted faces

A repeated measures ANOVA with the factors condition and face orientation yielded a significant main effect of condition, $F(1, 12) = 5.93$, $p = 0.031$, with somewhat shorter RTs in the control condition, and a significant main effect of face orientation, $F(1, 12) = 20.67$, $p < 0.001$, as well as a significant interaction between condition and face orientation, $F(1, 12) = 14.45$, $p < 0.001$. While the FIE was significant not only in the CFS condition, $t(12) = 4.91$, $p = 0.001$, but also in the control condition, $t(12) = 2.40$, $p = 0.033$, the FIE was again significantly larger in the CFS condition (see **Figure 12A**).

CFS vs. control condition

Before turning to the comparison of the RT distributions, it should be noted that in contrast to the previous experiments in which stimuli were presented in the same manner in each trial from a given condition, in Experiment 5 RTs in the control condition were artificially spread by the different ramp durations that varied from trial to trial. KS-tests revealed significant differences between the CFS and the control distributions for all but one subject (all $p < 0.05$). While the implementation of variable ramps increased RT variability in the control condition to a level close to the variability in the CFS condition (**Figures 12B** and **13A**), the mean CV was still significantly larger in the CFS condition, $t(12) = 2.75$, $p = 0.018$. Finally, as in the previous experiments the effect of face inversion increased toward the right tail of the CFS distribution, while no clear trend was seen in the control condition (**Figures 13B,C**). Correspondingly, linear regression analyses revealed that while the slopes were positive for both the CFS, $F(1, 17) = 282.70$, $p < 0.001$, and the control condition, $F(1, 17) = 15.49$, $p = 0.001$, there was a significant difference between the slopes, $F(1, 34) = 81.85$, $p < 0.001$.

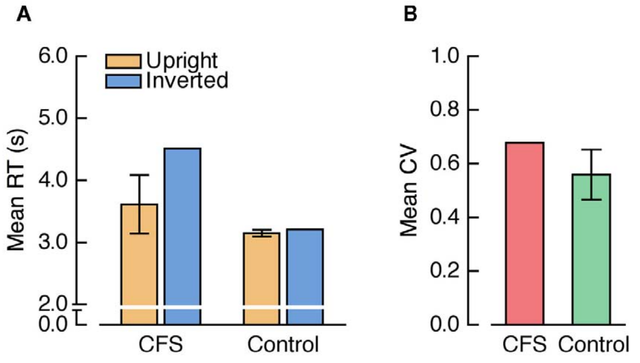

FIGURE 12 | (A) Mean RTs and **(B)** mean CVs from Experiment 5.

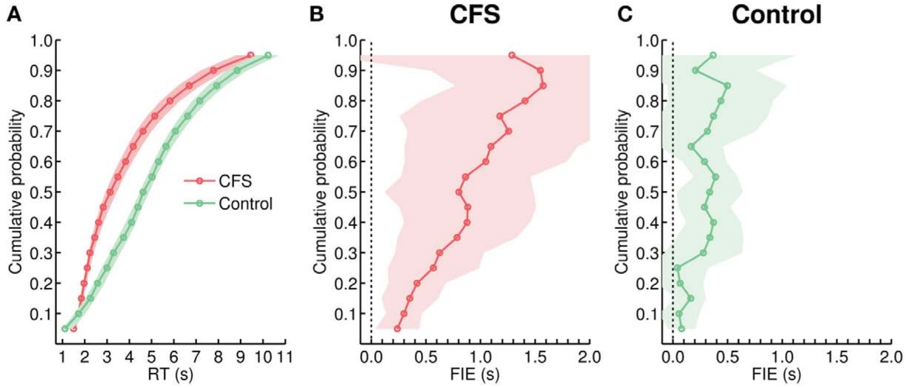

FIGURE 13 | (A) Cumulative group distributions of RTs from the CFS and from the control condition in Experiment 5. **(B,C)** Size of the FIE as a function of percentiles, plotted separately for the CFS, and the control condition.

In summary, although we failed to fully match both conditions in RT distributions, compared to the previous experiments RT variability was greatly enhanced in the control condition of Experiment 5, thus reducing predictability of face appearance. Nevertheless, the FIE was still considerably larger in the CFS condition, suggesting that stimulus predictability may not be the critical factor underlying the enhanced effect under CFS.

EXPERIMENT 6

PARTICIPANTS

Thirteen new participants (eight female, mean age 23.7 years) took part in Experiment 6.

Apparatus, stimuli, and procedure

In Experiment 6, we fixed presentation durations to measure face localization accuracies using an unspeeded 2AFC task (which was identical to Experiment 3). Apart from this, Experiment 6 was identical to Experiment 4, except that for the control condition we used the settings from the 8.5-s ramp control condition only. In the CFS condition, face stimuli were always presented to the subjects' dominant eye (to reduce the length of the experiment by shortening overall suppression durations), as determined by the Miles (1930) test.

For each of the four conditions (CFS upright, CFS inverted, Control upright, Control inverted) presentation durations were adjusted continuously by adaptive staircases using 1 up 3 down rules with fixed step sizes of 500 ms, with the constraint that presentation duration was not allowed to fall below 500 ms or to exceed 15 s. To prevent afterimages, each face presentation sequence was followed by six trailing CFS masks consisting of slightly smaller and differently colored circles.

At the beginning of each session participants completed a short RT block identical to Experiment 4 but containing 24 trials (12 CFS, 12 Control trials) only. The mean RTs (rounded to the next 500 ms) from the CFS and the control condition were then taken as initial values for the CFS and the control staircases, respectively.

Design

Participants completed 480 trials (separated by five breaks) in which each combination of two conditions, two face orientations, and ten face exemplars occurred equally often. Trial order was randomized, meaning that the four staircases were randomly interleaved.

Analysis

For each of the four staircases, we determined a threshold estimate by averaging all trials on which a reversal of the presentation duration occurred (other methods for calculating the threshold yielded virtually identical results). One extreme outlying subject (threshold estimates in the CFS condition: 3.48 s for upright faces, 8.66 s for inverted faces) was excluded from the analysis.

RESULTS AND DISCUSSION

A repeated measures ANOVA on the threshold estimates revealed a trend toward a significant main effect of condition, $F(1, 11) = 4.79$, $p = 0.051$, a significant main effect of face orientation, $F(1, 11) = 7.13$, $p = 0.022$, and a significant interaction between condition and face orientation, $F(1, 11) = 18.64$, $p = 0.001$. **Figure 14** shows that in the CFS condition thresholds were significantly lower for upright than for inverted faces, $t(11) = -4.58$, $p = 0.001$, while there was no significant threshold difference in the control condition, $t(11) = 1.19$, $p = 0.260$.

These results show that the large FIE observed in Experiments 4 and 5 cannot be explained solely by different response criteria for upright and inverted faces. However, in contrast to the previous experiments, in Experiment 6 we for the first time obtained no significant FIE in the control condition. Possibly, the relatively large fixed step size of the staircases was suboptimal for detecting threshold differences in the control condition. For example, it is conceivable that performance at a given presentation duration was at ceiling for both upright and inverted faces (i.e., face transparency was too low), whereas a 500-ms decrement in the presentation duration might have yielded floor effects (i.e., face transparency was too high).

GENERAL DISCUSSION

In the present study, we evaluated the validity of the b-CFS paradigm for studying unconscious processing during interocular suppression, using the effect of face inversion as an example. Initially invisible upright faces were detected faster under CFS than

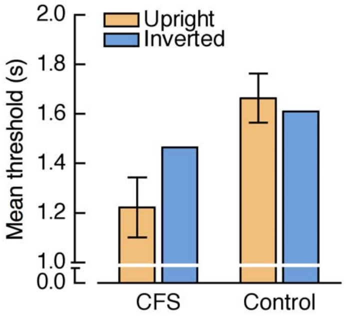

FIGURE 14 | Results from Experiment 6. Mean threshold estimates for upright and inverted faces. Positive and negative error bars denote the 95% confidence intervals for the paired comparisons between upright and inverted faces within each condition.

inverted faces (Experiments 1, 2, 4, and 5), replicating previous reports. Also in accuracy-based measures using unspeeded 2AFC tasks (Experiments 3 and 6) we found an advantage for upright faces in overcoming CFS, meaning that differential response criteria for upright and inverted faces cannot account for the effect. However, detection differences under CFS do not necessarily have to reflect unconscious effects *under* suppression, or differential *CFS-specific* unconscious processing, but could also be due to more general differences not specific to the method of CFS (**Figure 1**).

To infer CFS-specific unconscious processing, it is necessary to rely on the comparison of the CFS condition to the results from the binocular control condition which is supposed to index non-specific threshold differences. We found an FIE in the control condition in five out of the six experiments, but in all but one experiment this effect was smaller than in the CFS condition. Assuming that the comparison between detection differences measured in both conditions isolated CFS-specific unconscious processing, the increased FIE under CFS would provide evidence for CFS-specific unconscious processing differences. However, this conclusion depends entirely on the premise that the comparison between the CFS and the control condition does indeed isolate CFS-specific unconscious processing and does not reflect any other factors that might differ between conditions.

ARE THE CFS AND THE CONTROL CONDITION COMPARABLE?

As no previous b-CFS study actually considered the truth of this premise, here we made a first attempt to explore whether there might be other differences rather than CFS-specific unconscious processing between the CFS and the control condition. In three out of the four RT experiments we found a larger FIE in the CFS condition, but also marked differences between the RT distributions from both conditions, with much greater RT variability and a larger proportion of trials with very long RTs in the CFS condition. Only in Experiment 2 where RT distributions were more comparable, we found an FIE of the same size in both conditions. The distinct characteristics of the CFS and the control distributions may point to differences in the underlying perceptual and cognitive processes, for example reflecting reduced predictability of stimulus appearance and greater uncertainty in the CFS condition.

Are we suggesting that we only need (approximately) matched RT distributions in order to draw valid conclusions from the comparison between the CFS and the control condition? Certainly this would not be sufficient. In fact, previous b-CFS studies used the method of blending stimuli binocularly into the CFS masks as the control condition in order to *mimic the perceptual experience* (cf. Jiang et al., 2007) induced by the CFS condition. However, whether both conditions are indeed perceptually matched or at least perceptually similar had never been tested. The results from Experiment 4 speak against this assumption, revealing that gradual stimulus fade-in is subjectively considerably different than emergence from CFS. It is important to note that this "abruptness rating" measured only one particular aspect of an indefinite number of possible perceptual experiences. Further (unpublished) observations from our laboratory revealed even larger differences in rating scores when subjects were asked to judge their subjective impression of a stimulus feature that physically differed between both condition, such as the faces' transparency.

Ideally, one would want to show that both conditions are matched perceptually in all aspects of perceptual experience, which seems virtually impossible to achieve in practice, given that the factors governing the perceptual differences between both conditions are unknown. A less rigorous but more practical alternative for future b-CFS studies would be to demonstrate that subjects cannot distinguish between the CFS and the control condition, for example using a two-interval forced-choice task, asking subjects which of both instances was the CFS condition. Unfortunately, from our experimental experience it appears difficult if not impossible to design a control condition that mimics the perceptual experience under CFS in the sense that it cannot be discriminated from the b-CFS condition. In particular, it would be very challenging to accurately model the perceptual transitions associated with breakthrough from CFS.

To conclude, the present findings of striking differences between CFS and control – not only with respect to FIE, but also regarding a number of other factors – seriously challenge the fundamental premise of the b-CFS paradigm, namely that the two conditions differ only with regard to CFS-specific unconscious processing, and hence cast doubt on the notion that b-CFS can provide unequivocal evidence for CFS-specific unconscious processing.

DO LARGE B-CFS EFFECTS PROVE CFS-SPECIFIC UNCONSCIOUS PROCESSING?

It should be noted that our concerns relate only to the validity of the conclusions drawn from the b-CFS paradigm, while they do not categorically rule out the possibility that CFS-specific unconscious processing differences did play a role in mediating the advantage of upright faces in overcoming CFS. The size of the FIE varied enormously depending on the strength of suppression induced by the CFS masks, ranging from about 150 ms for short overall suppression durations (Experiments 1 and 2) to more than 850 ms for longer overall periods of suppression, far exceeding the FIE obtained in the control condition (Experiments 4 and 5). On the face of it, it may appear straightforward to explain the sheer size of the difference between the effects in the CFS and the control condition with CFS-specific unconscious processing above and beyond the "normal" stream of visual processing.

However, because the CFS and the control condition are not truly comparable, the mere difference in FIE size is not sufficient to infer CFS-specific unconscious processing. From other paradigms, it is well-known that apparently small changes in the experimental protocol or visual displays yield dramatically different effects. For example, the effect of inversion on detecting a face in visual search displays ranges from about 20 ms (Lewis and Edmonds, 2005) to nearly 1000 ms (Garrido et al., 2008), depending on target–distractor similarity. Similarly, large effect size differences between the CFS and the control condition could be due to a variety of differences between the two conditions other than unconscious processing during interocular suppression. To illustrate, consider a control condition in which stimuli at full contrast are popped in on top of the CFS masks at various points in time, as in the no-ramp control condition of Experiment 4. In principle, this could also be considered a condition that controls for non-specific threshold differences between the two conditions (e.g., upright and inverted faces). Yet, most previous b-CFS studies did not implement such a no-ramp control condition, presumably because it is more obvious that this condition does not perceptually resemble the CFS condition and, when comparing RTs to different stimuli, most likely produces floor effects.

That being said, we are not aware of any *a priori* reason to suppose that gradual blending stimuli into the masks would avoid floor effects or constitute a better perceptual analog of the CFS condition. In fact, the rating results from Experiment 4 indicate that both the no-ramp and the transparency ramp control condition fail to mimic the subjective impression of breakthrough from suppression. Thus, just as the transparency ramp control condition is a more sensitive measure of differences in stimulus detectability than the no-ramp control condition (Experiment 4), the CFS condition could be regarded as an even more sensitive measure of non-specific differences in stimulus detectability.

We can only speculate about potential reasons for these differences between conditions in their sensitivity to detection threshold differences. Again, the comparison of the no-ramp and the transparency ramp control condition may serve as an illustration. When popping in stimuli on top of the masks, the time window in which sensory evidence is sufficiently weak or ambiguous to allow detection threshold differences between stimuli to unfold is very short. Presumably, transparency ramps were implemented in previous b-CFS control conditions not only in an attempt to perceptually approximate the CFS condition, but also to avoid floor effects by widening this temporal window. However, gradual blending stimuli into the masks also yields only a narrow time window in which the transparency ramp reaches values that are appropriate for measuring threshold differences. While this may explain the weak or even absent effects in the control conditions, an important question for future research will be to pinpoint the perceptual mechanisms underlying the heightened sensitivity of the CFS condition, considering CFS-specific unconscious processing as only one possible explanation.

CONCLUSION AND FUTURE DIRECTIONS

To summarize, our study demonstrates that the b-CFS paradigm in its current form cannot provide unequivocal evidence for unconscious processing during interocular suppression. While our findings do not categorically exclude the possibility that CFS-specific unconscious processing might be involved in mediating breakthrough from suppression, the striking differences between the CFS and the control condition preclude definite conclusions based on the comparison of the two conditions. Although we focused on the effect of face inversion as an example, these concerns equally apply to b-CFS experiments that inferred differential unconscious processing during interocular suppression for other sets of stimuli. As these conclusions rested on the untested (and most likely unwarranted) premise that the CFS and the control condition differed with regard to CFS-specific unconscious processing only, differences between stimuli in overcoming suppression revealed by previous b-CFS studies should be reconsidered, taking into account that non-specific differences in detection thresholds rather than CFS-specific unconscious processing might have caused these effects.

Future b-CFS studies aimed at uncovering unconscious processing under interocular suppression should take great care in ensuring that the control condition does indeed represent an appropriate analog of the CFS condition and that the two conditions differ only with regard to CFS-specific unconscious processing. If the CFS and the control condition cannot be matched, one can only speculate about a potential role of CFS-specific unconscious processing, but no definite conclusions can be drawn.

However, for researchers primarily interested in measuring differences in the detectability of visual stimuli, regardless of unconscious processing differences specifically tied to interocular suppression, b-CFS clearly is a technique that offers unique sensitivity for measuring detection threshold differences. In the tradition of the New Look school of perception (Bruner, 1957), such threshold differences were considered as a measure of unconscious processing, because faster detection can only happen when the visual system discriminates stimuli *before* detection, i.e., unconsciously. Recently, this approach has been revived, for example in research on perceptual defense vs. vigilance for emotional words (Dijksterhuis and Aarts, 2003), and has been proposed to have greater sensitivity to unconscious processing than the dissociation paradigm (Gaillard et al., 2006). Applying b-CFS in this way obviates the need for creating a tediously designed control condition (see **Figure 1**), and equips researchers with a powerful and highly sensitive device to probe potency of visual stimuli to gain access to awareness.

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Fear modulates visual awareness similarly for facial and bodily expressions

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Background: Social interaction depends on a multitude of signals carrying information about the emotional state of others. But the relative importance of facial and bodily signals is still poorly understood. Past research has focused on the perception of facial expressions while perception of whole body signals has only been studied recently. In order to better understand the relative contribution of affective signals from the face only or from the whole body we performed two experiments using binocular rivalry. This method seems to be perfectly suitable to contrast two classes of stimuli to test our processing sensitivity to either stimulus and to address the question how emotion modulates this sensitivity. **Method:** In the first experiment we directly contrasted fearful, angry, and neutral bodies and faces. We always presented bodies in one eye and faces in the other simultaneously for 60 s and asked participants to report what they perceived. In the second experiment we focused specifically on the role of fearful expressions of faces and bodies. **Results:** Taken together the two experiments show that there is no clear bias toward either the face or body when the expression of the body and face are neutral or angry. However, the perceptual dominance in favor of either the face of the body is a function of the stimulus class expressing fear.

Keywords: binocular rivalry, emotion, face, body, expression, consciousness

INTRODUCTION

Social interaction relies on a multitude of signals carrying information about the emotional state of others. Facial and bodily expressions are among the most salient of these social signals. But the relative importance of facial and bodily signals is still poorly understood. Past research has focused on the perception of facial expressions while perception of whole body signals has only been studied recently. Many studies now provide direct and indirect evidence for visual discriminations of facial expressions in the absence of visual awareness of the stimulus (e.g., Esteves et al., 1994; de Gelder et al., 1999; Dimberg et al., 2000; Jolij and Lamme, 2005; Tamietto et al., 2009). For bodily expressions this is shown in healthy participants (Stienen and de Gelder, 2011) and hemianopic patients (Tamietto et al., 2009). Unattended bodily expressions can influence the judgment of the emotion of facial expressions (Meeren et al., 2005; Van den Stock et al., 2007) and the emotion of crowds is determined by a relative proportion expressing the emotion (McHugh et al., 2011) and influences the recognition of the individual bodily expressions (Kret and de Gelder, 2010). However, the relative importance of facial and bodily signals and its relation to visual awareness is still poorly understood.

In this study we investigate directly the contribution of both signals in a binocular rivalry (BR) experiment. BR forces perceptual alternation when two incompatible stimuli are presented to the fovea of each eye separately. This perceptual alternation can be biased by factors such as differences in contrast, brightness, movement, and density of contours (Blake and Logothetis, 2002). In addition visual attendance is necessary for rivalry to occur (Zhang et al., 2011). Given certain parameters the two stimuli compete with each other for perceptual dominance rather creating a percept that is a fusion of both. This method seems to be perfectly suitable to contrast two classes of stimuli to test our processing sensitivity to either stimulus and to address the question how emotion modulates this sensitivity.

Previous BR studies have shown that meaning of the stimulus influences the rivalry pattern as well (e.g., Yu and Blake, 1992). Subsequent studies have used BR to investigate dominance between faces expressing different emotions (Alpers and Gerdes, 2007; Yoon et al., 2009) and found that emotional faces dominate over neutral faces. In an fMRI study Tong et al. (1998) showed that the fusiform face area (FFA), a category specific brain area for processing faces (Haxby et al., 1994), is activated with the same strength as when the faces were presented in a non-rivalrous condition.

fMRI studies using BR in which emotional faces were contrasted showed that suppressed images of fearful faces still activated the amygdala (Pasley et al., 2004; Williams et al., 2004). When visual signals are prevented to be processed by the cortical mechanisms via the striate cortex the colliculo-thalamo-amygdala pathway could still process the stimulus (de Gelder et al., 1999; Van den Stock et al., 2011). This is in line with recent functional magnetic resonance imaging studies that have suggested differential amygdala responses to fear faces as compared to neutral faces when the participants were not aware (Morris et al., 1998b; Whalen et al., 1998). However, to date no BR experiments have been conducted using bodily expressions or comparing body and face stimuli.

We performed two behavioral experiments addressing relative processing sensitivity to facial and bodily expressions and investigated how specific emotions modulate this sensitivity. First, we performed an experiment involving the rivaling of bodies and faces with fearful, angry, and neutral expressions. We always presented bodies in one eye and faces in the other and asked participants to report what they perceived while stimuli were presented simultaneously for 60 s. In line with BR studies using facial expressions (Pasley et al., 2004; Williams et al., 2004; Alpers and Gerdes, 2007; Yoon et al., 2009) we expected that emotional bodily expressions would dominate over neutral expressions. The first experiment showed a special role of fearful expressions and therefore we isolated this condition in a second, more sensitive, experiment. In this second experiment we used the rivalry pattern resulting from the contrasting of neutral facial and bodily expressions as baseline performance and created two conditions in which fearful bodily expressions were contrasted with neutral facial expressions and fearful facial expressions with neutral bodily expressions. We expected that the perceptual dominance of the stimulus would be a function of the stimulus expressing fear.

EXPERIMENT 1

In this first experiment we contrasted bodily and facial expressions directly in a BR design in which the emotion of the faces and bodies were fearful, angry, or neutral.

MATERIALS AND METHODS

Participants

Twenty-two undergraduate students of Tilburg University participated in exchange of course credits or a monetary reward (19 women, 3 men, *M* age = 19.8 years, SD = 1.2). All participants had normal or corrected-to-normal vision and gave informed consent according to the declaration of Helsinki. The protocol was approved by the local Ethics Committee Faculteit Sociale Wetenschappen of Tilburg University.

Stimuli and procedure

Photos of two male actors expressing fear and anger the same actors performing a neutral action (hair combing) were selected from a well validated photoset as body stimuli (for details see Stienen and de Gelder, 2011). All body pictures had the face covered with an opaque oval patch to prevent that the facial expression would influence the rivalry process. The color of the patch was the average gray value of the neutral and emotional faces within the same actor. The face stimuli of two actors expressing fear and anger and the same actors showing a neutral expression were taken from the McArthur set (http://www.macbrain.org/resources.htm). A total of six pictures of bodily expressions and six pictures of facial expressions were selected for use in the present study.

All stimuli were fitted into an area with a white background of 3.00 × 4.83° enclosed by a black frame of with a border thickness of.29°. The function of the black frame was to enhance a stable fusion. A white fixation dot was pasted on each of the stimuli. Because we used a method which is comparable with the mirror stereoscope the faces and bodies were pasted 11.89° left and right from the center. Pairing the face and body stimuli resulted in 18 unique displays (3 bodily expressions × 3 facial expressions × 2 identities).

One experimental run consisted of 36 trials because the displays were counterbalanced to control for eye dominance. The trials were randomly presented. The stimuli were presented on a 19″ PC screen with the refresh rate set to 60 Hz. We used Presentation 11.0 to run the experiment.

The heads of the participants were stabilized using a chin and head rest. The fMRI compatible BR method we used is described in detail by Schurger (2009) but was here adapted for use out-side of the scanner. A black 70 cm wooden divider was placed between the screen and the middle of the eyes. The total distance between the screen and eyes was 77 cm. Participants wore glasses in which two wedge-shaped prism lenses of six DVA were fitted using gum. The prisms adjusted the viewing angle from which light from the screen enters each eye ensuring that the laterally presented stimuli would fall close to the participants' fovea. The wooden divider was placed between the eyes to keep the visual signals separated. Besides the fact that this is a low-cost method and it can be used in- and out-side the MRI scanner there is no crosstalk between the eyes (Schurger, 2009) as is the case with for example red–green filter glasses. See **Figure 1** for a picture of the experimental setup.

Before each trial two empty frames were shown with a black fixation dot in the middle. The participants were instructed to push and hold a button labeled "M" (Dutch for *mixture* = *mengsel*) on a response box with the middle finger to initiate a trial, but only if they saw one dot and one frame. This ensured that the participants fused the two black frames throughout the experiment. Subsequently, a facial expression and a bodily expression were presented for 60 s. For an example display see **Figure 1**. Whenever they saw a face or a body in isolation they were instructed to release the "M" button and push and hold the button corresponding to their percept; the "G" (Dutch for *face* = *gezicht*) if they saw a face or the "L" (Dutch for *body* = *lichaam*) if they saw a body with either their index or ring finger. The "G" and "L" button was counterbalanced across participants and they always used their right hand. When seeing both stimuli they were told to push and hold the button labeled "M" again. The program registered the time

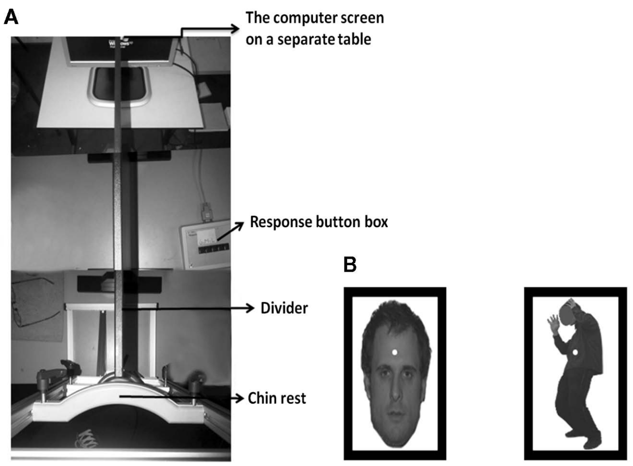

FIGURE 1 | Experimental setup (A). Example of a stimulus display. We always presented bodies in one eye and faces in the other **(B)**.

the button was pressed and released. The participants were naïve regarding the presentation techniques and during the experiment no reference to the emotions was made.

Prior to the experimental sessions the participants performed one practice session consisting of two trials. This session used different male identities taken from the same stimulus sets than the ones used in the main experiment. When the participants reported full understanding of the procedures the main experiment started. A total of two runs were presented adding up to a total of 72 trials. After each 10 trials there was a short break. Finally a short validation was performed in a separate session after a 5 min break. All stimuli were presented two times for 2 s adding up to a total of 24 trials (2 identities × 3 expressions × 2 face/body × 2 runs). Participants were instructed to categorize the bodies and faces in fearful, angry, or neutral bodily or facial expressions using three buttons labeled "A" for fearful (Dutch = *angst*), "B" for angry (Dutch = *boos*), and "N" for neutral (Dutch = *neutraal*).

RESULTS AND DISCUSSION

Cumulative viewing time for faces, bodies, and mixed perceptions were calculated per participant irrespective of experimental condition. Two participants indicating having seen mixed percepts more often than two SD below the group average (group mean = 104 s, SD = 34 s) were identified as outliers and excluded from analysis. See **Figure 2** for the individual data.

Wilcoxon Signed Ranks Tests revealed that the cumulative viewing time of faces ($M = 51$ s, SD = 24 s) and bodies ($M = 52$ s, SD = 17 s) was equal ($Z = -0.075$, $p = 0.940$) while the cumulative viewing time was longer for mixed perceptions ($M = 111$ s, SD = 34 s) in comparison to bodies and faces (respectively $Z = -3.696$, $p < 0.001$ and $Z = -3.696$, $p < 0.001$).

Following Levelt (1965) predominance ratios were calculated. The total time participants indicated seeing the face was subtracted from the total time participants indicated seeing the body. This value was divided by the total amount of time the body and the face was seen. If this predominance ratio has a value of zero it would mean they equally perceived the body and the face in time. A positive value means that the conscious percept of the body predominated over face while a negative value means that the conscious percept of the face dominated over body.

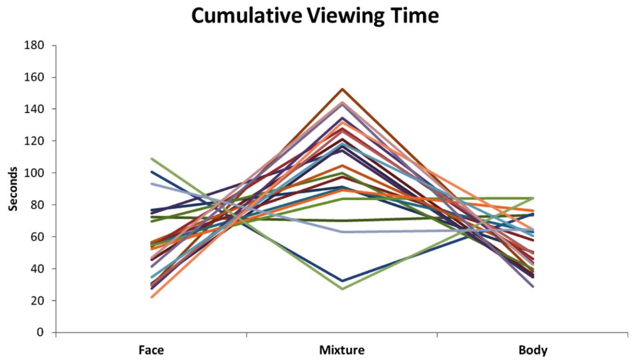

FIGURE 2 | Cumulative viewing time per face, body, and mixture. The two subjects with the lowest cumulative viewing time of mixtures were removed from analysis.

A 3 (bodily expressions) × 3 (facial expressions) GLM repeated measurements revealed a significant interaction between the bodily expressions and the facial expressions on the predominance ratios [$F(4,76) = 3.877$, $p = 0.006$] as well as a main effect of facial expressions [$F(2,38) = 24.718$, $p < 0.001$]. **Figure 3** shows the predominance ratios when the bodily or the facial expression was emotional and the other was neutral (**Figure 3A**), when the facial and bodily expressions were the same (**Figure 3B**), and when the facial and bodily expressions both differed (**Figure 3C**). A difference was deemed significant when the *p*-value was lower than 0.005 (Bonferroni correction: α level divided by 10 comparisons).

Figure 3A shows that when the body expressed fear and the face was neutral the participants reported more often seeing the body than when the face was fearful and the body was neutral [$t(19) = 2.903$, $p = 0.009$], but this effect did not survive the Bonferroni correction. The predominance ratios were equal when the bodily or facial expression was angry. **Figure 3B** shows that when both stimulus classes express fear the face dominates over the body compared when they are both neutral [$t(19) = 3.471$, $p = 0.003$]. **Figure 3C** shows that when the expressions were both emotional but different (fearful and angry) the fearful body triggered a stronger conscious percept of the body when the rivaling face was angry compared to when the face was fearful and the rivaling bodily expression was angry in which case the conscious percept of the face predominated [$t(19) = 4.586$, $p < 0.001$]. None of the conditions differed from zero.

To test the main effect of facial expressions pairwise Bonferroni corrected comparisons were performed between the predominance ratios irrespective of bodily expressions. When the facial expression was fearful the face dominated over the body more than when the facial expression was angry or neutral ($p < 0.001$).

A 2 (face/body) × 3 (fear/angry/neutral) GLM repeated measurements on the correct categorizations in the validation task revealed a main effect of stimulus class [$F(1,17) = 14.806$, $p = 0.001$]. It appeared that the facial expressions were categorized better in general regardless of expression. Because the results in the main experiment are specific for fearful expressions a general effect on the recognition of faces alone cannot explain the specific effect. See **Figure 4A** for the validation results.

In line with previous reports on the special role of fearful expressions (Öhman, 2002, 2005; Stienen and de Gelder, 2011) the main finding of this first experiment is that the stimulus class carrying the fearful expression suppresses the percept of the competing stimulus more than angry and neutral expressions do. In addition, participants seemed to be equally sensitive in perceiving the face and the body when the emotional expression was neutral or angry.

Past research has focused on for example the perception of facial or bodily expressions in isolation, but never compared these two important social signals together in one display. Although Meeren et al. (2005) and Van den Stock et al. (2007) showed the influence of unattended bodily expressions on the task relevant facial expressions, this study revealed how the two stimuli compete for visual awareness when they are both task relevant as it the case in natural situations.

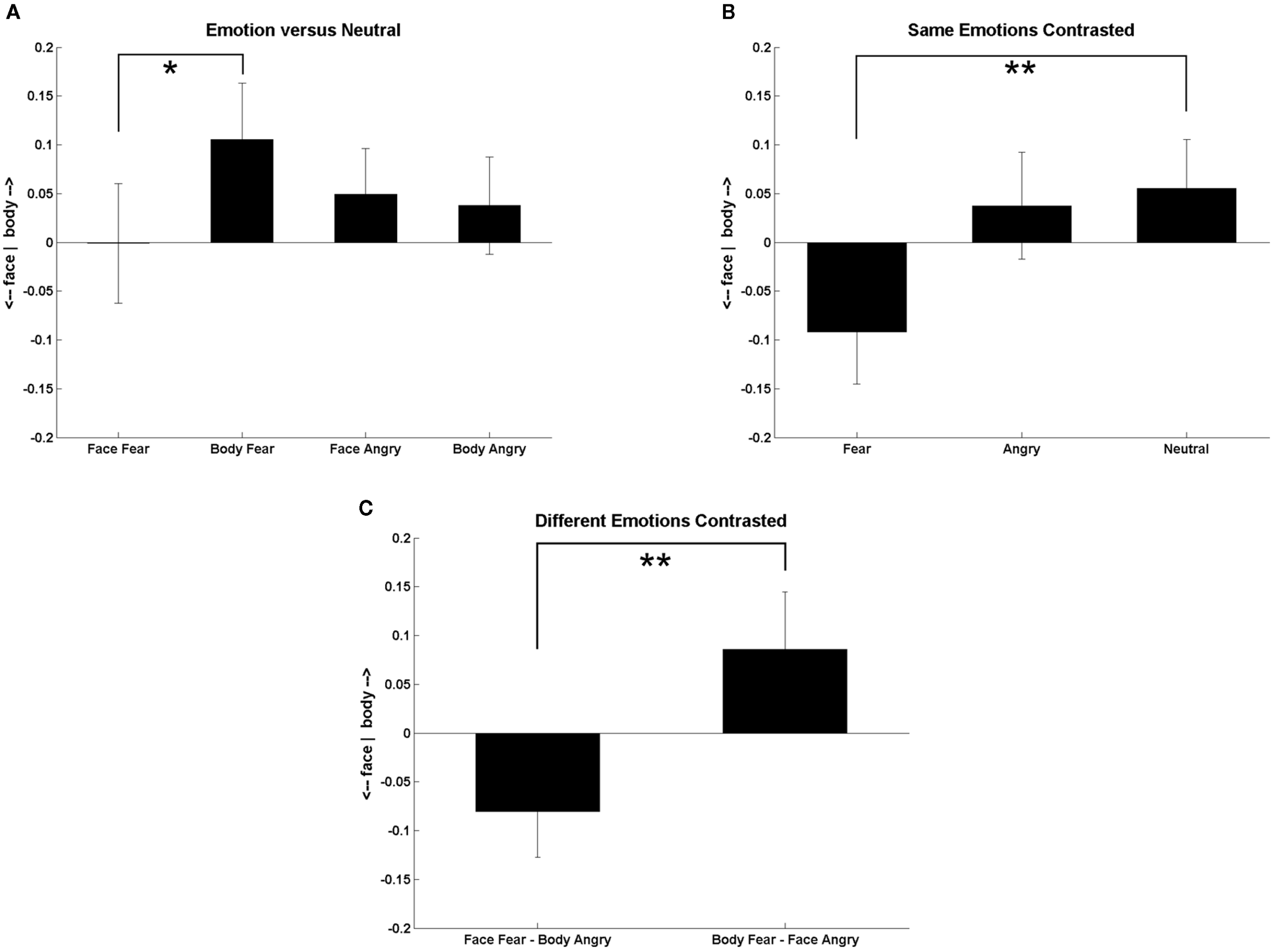

FIGURE 3 | A positive value means that the body predominates over the face and a negative value that the face predominated over the body. (A) Predominance ratios when the bodily or facial expression was emotional and the other was neutral. **(B)** Predominance ratios when the facial and bodily expressions were the same. **(C)** Predominance ratios when the facial and bodily expressions both differed. Error bars represent SEM. One asterisk = $p < 0.01$, double asterisks = $p < 0.005$.

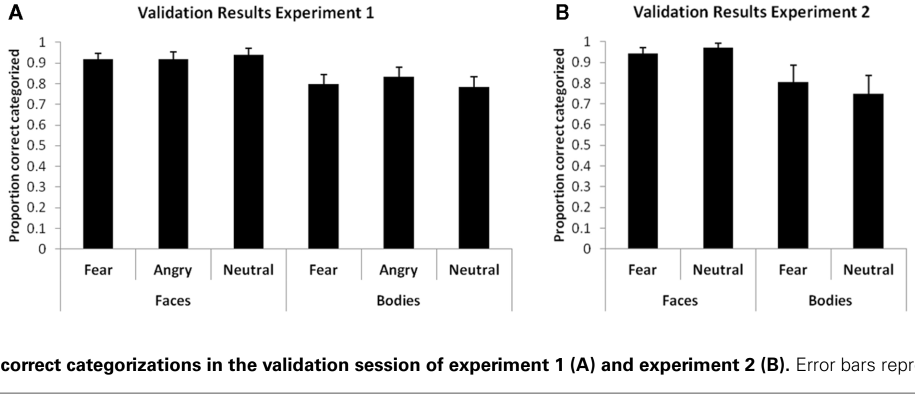

FIGURE 4 | Proportion correct categorizations in the validation session of experiment 1 (A) and experiment 2 (B). Error bars represent SEM.

There was no indication in this experiment that neutral or angry expressions modulated the rivalry pattern but there were clues indicating that fearful expressions modulated the resulting dominant percept. However, none of the conditions explicitly deviated from the value zero. The value zero meant an equal ratio between reporting the face or the body. To create a more sensitive design we repeated the first experiment but this time with only three conditions; one baseline condition in which neutral facial and bodily expressions were contrasted and two experimental conditions in which either the face or the body was expressing fear. By lowering the amount of conditions we could increase the number of trials.

EXPERIMENT 2

In this experiment a baseline was created by contrasting a neutral facial expression with a neutral bodily expression. The resulting perceptual alternation was compared when either the bodily or the facial expression was fearful while the other was neutral. Although these conditions were present in the first experiment as well we wanted to test these conditions in isolation. We hypothesized that based on our first experiment either the body or the face will dominate depending on which is expressing fear.

MATERIALS AND METHODS

Participants

Nineteen new undergraduate students of Tilburg University who had not taken part in the first experiment participated in exchange of course credits or a monetary reward (15 women, 4 men, *M* age = 19.9 years, SD = 1.6). All participants had normal or corrected-to-normal vision and gave informed consent according to the declaration of Helsinki. The protocol was approved by the local Ethics Committee Faculteit Sociale Wetenschappen of Tilburg University.

Stimuli and procedure

The stimuli were the same as in the first experiment, but this time only the bodily and facial neutral and fearful expressions were used. There were three conditions: a neutral body and face (baseline), a fearful body and a neutral face (fearful body), and a neutral body and a fearful face (fearful face). In total there were 12 different displays (2 body/face × 3 baseline/fearful body/fearful face × 2 identities). One complete run consisted of 24 trials because the displays were counterbalanced to control for eye dominance. A total of two runs were presented adding up to a total of 48 trials. The rest of the procedure remained the same as in Experiment 1.

RESULTS AND DISCUSSION

Wilcoxon Signed Ranks Tests revealed that the cumulative viewing time of faces ($M = 11$ s, SD = 6 s) was longer than for bodies ($M = 7$ s, SD = 3 s), $Z = -3.622$, $p < 0.001$. The cumulative viewing time was longer for mixed perceptions ($M = 23$ s, SD = 8 s) in comparison to bodies and faces (respectively $Z = -3.702$, $p < 0.001$ and $Z = -2.696$, $p = 0.007$).

Predominance ratios for all three conditions (baseline, fearful body, and fearful face) were calculated in the same manner as the predominance ratios in the first experiment were calculated. The ratio when the baseline trials were presented was subtracted from the predominance ratios of the fearful body condition and the fearful face conditions.

Figure 5A shows the baseline condition where neutral bodies were contrasted with neutral faces. A one sample t-test showed that the predominance ratio was not significantly different from zero which means that participants equally perceived the body or the face when the expressions were neutral [$t(18) = 0.085$, $p = 0.933$]. **Figure 5B** shows the modulation of the fearful expression when either the neutral body or the neutral face was substituted by respectively a fearful body or a fearful face. As indicated by a paired t-test a fearful body triggered a more dominant body percept and a fearful face triggered a more dominant face percept [$t(18) = -4.60$, $p < 0.001$]. When comparing directly to the baseline only fearful faces triggered a more dominant face percept [$t(18) = 3.975$, $p = 0.001$].

A different way of analyzing the results is by considering the participants' initial percept per condition (Berry, 1969; Long and Olszweski, 1999; Yoon et al., 2009). The frequency of reporting a face or a body as initial percept when a trial started was indexed. Subsequently the data was treated the same way as the predominance ratios.

As **Figure 6** shows these results follow approximately the same pattern. When both the bodily and facial expressions were neutral the reported initial percept was equally bodies and faces [$t(18) = -0.042$, $p = 0.967$]. **Figure 5B** shows that as an initial percept fearful body triggered more a body percept and a fearful face triggered more a face percept [$t(18) = -4.60$, $p < 0.001$]. Neither a fearful body nor a fearful face triggered more initial

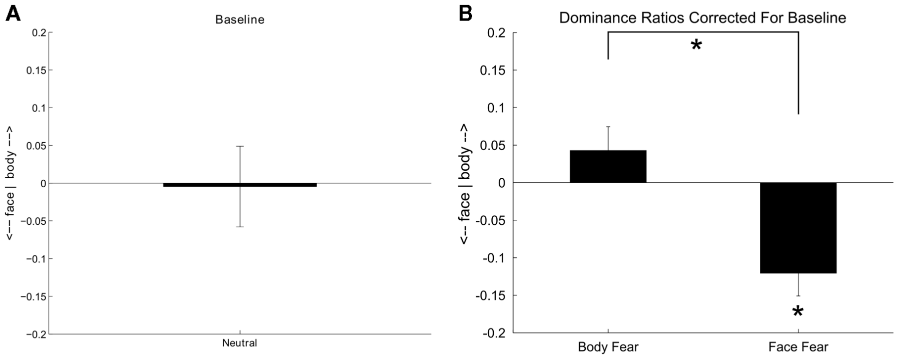

FIGURE 5 | A positive value indicates that the body predominated over the face and a negative value that the face predominated over the body. (A) Predominance ratio when a neutral bodily expression is contrasted with a neutral facial expression. **(B)** Predominance ratios when a fearful body is contrasted with a neutral face and when a fearful face is contrasted with a neutral body. Error bars represent SEM. Asterisk = $p < 0.01$.

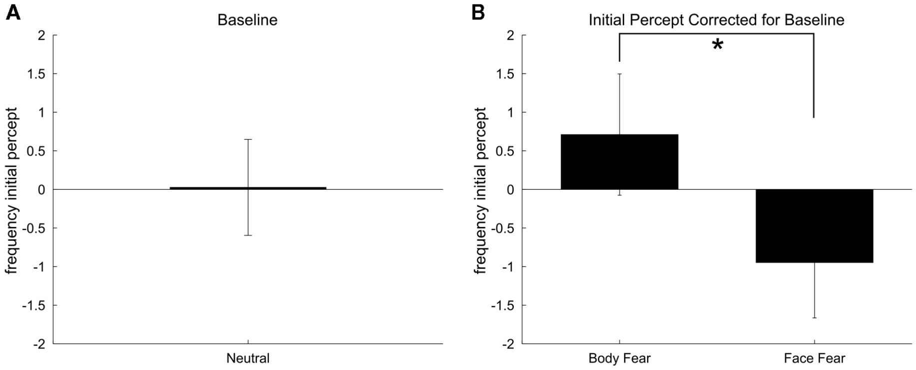

FIGURE 6 | A positive value means that the body is reported as the initial percept more often than the face, a negative value that the face is reported as the initial percept more often than the body. (A) Initial percept ratio when a neutral bodily expression is contrasted with a neutral facial expression. **(B)** Initial percept ratios when a fearful body is contrasted with a neutral face and when a fearful face is contrasted with a neutral body. Error bars represent SEM. Asterisk = $p < 0.05$.

percepts of their own stimulus class when directly compared to baseline performance.

See **Figure 4B** for the validation results. A 2 (face/body) × 2 (fear/neutral) GLM repeated measurements revealed a main effect of stimulus class on the validation scores [$F(1,17) = 11.311$, $p = 0.004$]. It appeared that facial expression was categorized again better in general regardless of emotional expression.

This second experiment shows that indeed the stimulus class expressing fear leads to perceptual dominance of the stimulus class carrying this information, although the effect seems stronger for the fearful faces.

GENERAL DISCUSSION

Taken together our experiments show that there is no clear bias toward either the face or body when both have either a neutral or an angry expression. When both the face and the body were expressing fear participants perceived more the face compared to when both categories were neutral. As especially the results of the more sensitive second experiment showed, the perceptual dominance in favor of either the face of the body is a function of the stimulus class expressing fear while the effect was stronger for fearful faces. In the second experiment the faces were perceived longer than bodies. Finally, the validation results of both experiments show that facial expressions were recognized better.

When there is no emotion expressed, the reported conscious percept of the body and face was equal indicating that in this case we have equal processing sensitivity to either stimulus class. Only when signals of fear are transferred by the stimulus the perceptual alternation is influenced by suppressing non-fearful expressions. This is in line with Öhman (2002, 2005) suggesting that fear stimuli automatically activate fear responses and captures the attention as shown in visual search tasks where participants had to detect spiders, snakes, or schematic faces among neutral distracters (Öhman et al., 2001a,b), and real faces when the emotion was not task relevant as in our study (Hodsoll et al., 2011) although this is not always found in other studies (e.g., Calvo and Nummenmaa, 2008). It is known that voluntary endogenous involuntary exogenous attention can modulate the rivalry pattern (Blake and Logothetis, 2002; Tong et al., 2006). However, the relative dominance of perceiving bodies when the body is fearful and the face is neutral in contrast when the face is fearful and the body is neutral is also consistent with a recent study of Pichon et al. (2011) showing that threatening bodily actions evoked a constant activity in a network underlying preparation of automatic reflexive defensive behavior (periaqueductal gray, hypothalamus and premotor cortex) that was independent of the level of attention and was not influenced by the task the subjects were fully engaged in. The fact that bodies expressing fear dominate the visual percept is in line with our recent finding that the detection of fearful bodies is independent on visual awareness (Stienen and de Gelder, 2011).

The dominant perception of the faces and bodies expressing fear was mostly relative but there was one case, in the second experiment, in which the conscious percept of the fearful face dominated in absolute terms. Although the recognition of faces was better regardless of expression in both experiments; this alone cannot explain the specific effect of fearful faces on the rivalry pattern. The fearful face deviated from zero in the second experiment and not in the first probably because of two reasons. Firstly, there were fewer conditions and more trials increasing the signal-to-noise ration. Secondly, the fearful expressions are likely to pop-out more when among neutral expressions without the angry expressions being present within the same experiment. Although, as already mentioned, this pop-out effect for fearful stimuli is not always found in visual search tasks using real faces.

Furthermore, it is possible that the relative proximity to the viewer of the faces in contrast with bodies could explain why the face was more dominantly perceived than baseline and bodies were not. As suggested earlier (de Gelder, 2006, 2009; Van den Stock et al., 2007) the preferential processing of affective signals from the body and/or face may depend on a number of factors and one may be the distance at which the observer finds himself from the stimulus.

The special status of fear stimuli is still a matter of debate, specifically in relation to the role of the amygdala (Pessoa, 2005; Duncan and Barrett, 2007). Theoretical models have been advanced arguing that partly separate and specialized pathways may sustain conscious and non-conscious emotional perception (LeDoux, 1996; Morris et al., 1998a,b; Panksepp, 2004; Tamietto et al., 2009; Tamietto and de Gelder, 2010). Our results are in line with Pasley et al. (2004) and Williams et al. (2004) showing amygdala activity for suppressed emotional faces. This hints at the possibility that the suppressed fearful faces are being processed through the colliculo-thalamo-amygdala pathway.

The underlying process may play an important role in everyday vision by providing us with information about important affective signals in our surroundings. Further research using neurological measures will give us insight whether the relevant pathways are indeed mediating detection of fearful signals independently of visual awareness. In addition, future studies using a different stimulus set or broadening the set to include other emotions would be of great value for the matter of validation and to investigate the generalization of the present findings to other emotions.

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What is grouping during binocular rivalry?

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During binocular rivalry, perception alternates between dissimilar images presented dichoptically. Although perception during rivalry is believed to originate from competition at a local level, different rivalry zones are not independent: rival targets that are spaced apart but have similar features tend to be dominant at the same time. We investigated grouping of spatially separated rival targets presented to the same or to different eyes and presented in the same or in different hemifields. We found eye-of-origin to be the strongest cue for grouping during binocular rivalry. Grouping was additionally affected by orientation: identical orientations were grouped longer than dissimilar orientations, even when presented to different eyes. Our results suggest that eye-based and orientation-based grouping is independent and additive in nature. Grouping effects were further modulated by the distribution of the targets across the visual field. That is, grouping within the same hemifield can be stronger or weaker than between hemifields, depending on the eye-of-origin of the grouped targets. We also quantified the contribution of the previous cues to grouping of two images during binocular rivalry. These quantifications can be successfully used to predict the dominance durations of different studies. Incorporating the relative contribution of different cues to grouping, and the dependency on hemifield, into future models of binocular rivalry will prove useful in our understanding of the functional and anatomical basis of the phenomenon of binocular rivalry.

Keywords: binocular rivalry, grouping, joint predominance, interocular grouping

INTRODUCTION

During binocular rivalry, dissimilar images presented dichoptically compete for awareness. As a result, perception varies over time (e.g., Wheatstone, 1838). When large images are engaged in rivalry, perception often consists of a patchwork combination of the competing images. That is, different locations have different perceptual outcomes (e.g., Meenes, 1930), implying that the dominant percept contains parts of both the left and the right eye's image. This patchwork or piecemeal rivalry does not occur when the images are rather small (estimated at 5–7 min of visual angle in the fovea; Blake et al., 1992). These observations reveal an important characteristic of rivalry, namely that it is a local phenomenon. Investigations into this local nature of rivalry revealed that the size of local rivalry zones scales with eccentricity and may correspond to the size of the receptive fields in the hypercolumns of early visual cortex (Blake et al., 1992).

Although perception during rivalry seems to be determined at a local level, different rivalry zones are not necessarily independent: similar (parts of) images tend to be dominant in perception together. That is, adjacent rivalry zones tend to produce the same dominant percept when neighboring zones share similar features like motion or color, even when this information is distributed across the two eyes (e.g., Whittle et al., 1968; Kovács et al., 1997; Alais and Blake, 1998). For instance, Kovács and her colleagues created rival targets consisting of patchwork combinations of two complex images. Each eye received only part of the originals when they were presented dichoptically. The perceptual outcome during rivalry often consisted of a coherent reconstruction of the original images (Kovács et al., 1997; also see Diaz-Caneja, 1928, translated by Alais et al., 2000). Interestingly, this reconstruction required simultaneous dominance of rivalry zones across both eyes; an effect known as interocular grouping. Similar effects have been found for grouping of spatially separated items (e.g., Whittle et al., 1968). Alais and Blake (1999) demonstrated that similar rival targets that were separated spatially also tend to be dominant at the same time, an effect referred to as *joint predominance*. They showed that Gestalt grouping cues were effective in increasing the joint predominance of rival targets: joint predominance was larger for parallel and collinear grating-pairs compared to that of orthogonal gratings. Also, correlated contrast modulations of the gratings increased joint predominance in comparison to uncorrelated contrast modulations. These results show how the dominant percept originating from a local rivalry zone is affected by the dominant percept of neighboring rivalry zones. Furthermore, since the effect of joint predominance decreased with angular separation between the rivaling targets, Alais and Blake argued that interactions between lateral connections of the cortical hypercolumns were responsible for their effect.

Together, the above results suggest that the perceptual outcome of two rivaling images is primarily determined at a local level, but that grouping[1] cues (such as good continuation) affect the local competition: when two adjacent regions contain similar image-content, the images tend to be dominant in perception at the same

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[1] In this study, grouping refers to the simultaneous dominance of two rival targets. When referring to grouping effects found in other studies, we will use the terminology of the original authors (i.e., interocular grouping or joint predominance).

time, even when the image-content is distributed across the two eyes.

The current study has two aims. First, we aim to assess the strength of grouping when rival images are presented to the same versus different eyes and presented in the same versus different hemifields. This allows us to link grouping strength to known aspects of functional visual pathways. As Alais and Blake (1999) suggested, grouping during binocular rivalry might be related to connections at the level of the primary visual cortex. Estimating the grouping strength between targets that have very different cortical representation loci (i.e., represented in different ocular dominance columns and different hemispheres) will provide more insight in the effective connectivity that drives grouping during rivalry.

Our second aim is to elucidate the relative contributions of stimulus-based versus eye-based rivalry during simultaneous dominance of spatially separated targets. Interocular grouping and stimulus-based rivalry both emphasize competition based on image-content over competition based on the eye-of-origin of the images. Theories suggesting that rivalry competition is resolved at "later stages" of visual processing rely on examples of stimulus-based rivalry, such as Flicker-and-Swap-rivalry (Logothetis et al., 1996). These "later stages" are meant as relatively later to those put forward in the many studies emphasizing the low-level nature of binocular rivalry. For example, Blake (1989) argued that monocular neurons are crucial for the initiation of binocular rivalry. The necessity of monocular neurons thus limits rivalry competition to be initiated early in the visual processing hierarchy. Both early and late theories have gained support from psychophysical as well as imaging studies (Polonsky et al., 2000; Tong and Engel, 2001; Silver and Logothetis, 2007). In recent years, these different views have started to converge to the idea that rivalry is resolved at multiple stages along the visual hierarchy (Blake and Logothetis, 2002; Nguyen et al., 2003; Wilson, 2003; Lee, 2004; Freeman, 2005; Silver and Logothetis, 2007). In accordance with this idea, stimulus-based rivalry has been suggested to have a synergetic effect on eye-based dominance periods (Kovács et al., 1997; Lee and Blake, 2004). Determining perceptual dominance durations for different percepts of separate rival targets, presented either to the same or to different eyes, allows us to investigate this in more detail.

Since we know that collinear and parallel gratings tend to group during rivalry, we presented such targets under various spatial arrangements. In our experiments, we presented identical, spatially separated, rival targets (1) to the same or different eyes, and (2) in the same or different hemifields. Estimating the relative strength of grouping two images under these different arrangements allowed us to dissociate low-level, eye-based contributions to perceptual grouping from high-level, pattern-based contributions. Next, we implemented their relative contributions in a simple descriptive model based on the known functional anatomy of primary visual cortex.

MATERIALS AND METHODS

OBSERVERS

A total of 12 observers, including one of the authors (Sjoerd M. Stuit) participated in the study. Eight observers participated in the main experiment and seven, including four observers from the main experiment, participated in a separate version of the experiment (see below). All had normal or corrected to normal vision and all but Sjoerd M. Stuit were naïve as to the purpose of the study. All observers were experienced psychophysical observers and passed a test for stereo vision (TNO test for stereoscopic vision). All observers gave informed consent before participating.

APPARATUS

Stimuli were created on an Apple Mac Pro computer running system OS-X and Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22″ at 75 Hz. Observers viewed the stimuli through a mirror stereoscope. The length of the optical path was 57 cm.

STIMULI

The rival stimuli were two pairs of half-images each consisting of two sine-wave gratings. To initiate rivalry, each interocular pair had orthogonal orientations (**Figure 1**). The gratings were presented at maximum contrast (98% Michelson Contrast, space-average luminance: 24.83 cd/m^2). The rivaling gratings (spatial frequency 4.1 cpd, diameter 1.65°) appeared in circular apertures of which the edges were softened by a cosine ramp of 0.2° of visual angle, and were presented on a random pixel noise background of 98% (Michelson) contrast (mean luminance 24.83 cd/m^2) that was identical in both eyes. The half-images were presented within a white square. We used four basic grating arrangements in our experiment (**Figure 1**): same orientations in the same hemifield – for the same eye: (**Figure 1A**), same orientations in different hemifields – for the same eye: (**Figure 1B**), same orientations in the same hemifield – for different eyes: (**Figure 1C**), and same orientations in different hemifields – for different eyes: (**Figure 1D**). All presentation conditions were counterbalanced for eye and hemifield. This resulted in each orientation being presented to each eye and in each hemifield equally often. The distance from the fixation point to the center of the target was identical for all targets in all conditions (2.1° of visual angle). Two versions of the grating-pairs were used. In the main experiment we used horizontal and vertical grating-pairs. Such gratings have been shown to result in perceptual grouping by Alais and Blake (1999). In a second version of the experiment we used oblique gratings, two of which were tilted 45° clockwise and two that were tilted 45° counterclockwise from vertical. Comparing the results of two versions of the experiment can provide insight into whether having identical image-content is sufficient for grouping during rivalry.

PROCEDURE

Observers performed the experiment in a darkened room with their heads stabilized by a chin rest. Before the onset of each trial, observers were presented with two identical pixel noise half-images surrounded by white frames. At the center of each half-image was a fixation point. When ready, an observer initiated a trial by pressing the space bar. Next, two pairs of orthogonal gratings were presented in one of four possible spatial arrangements. Observers performed a 2AFC perceptual tracking task where they indicated via a key press, whether they perceived two identically oriented gratings (right arrow key), or two orthogonal gratings (left arrow

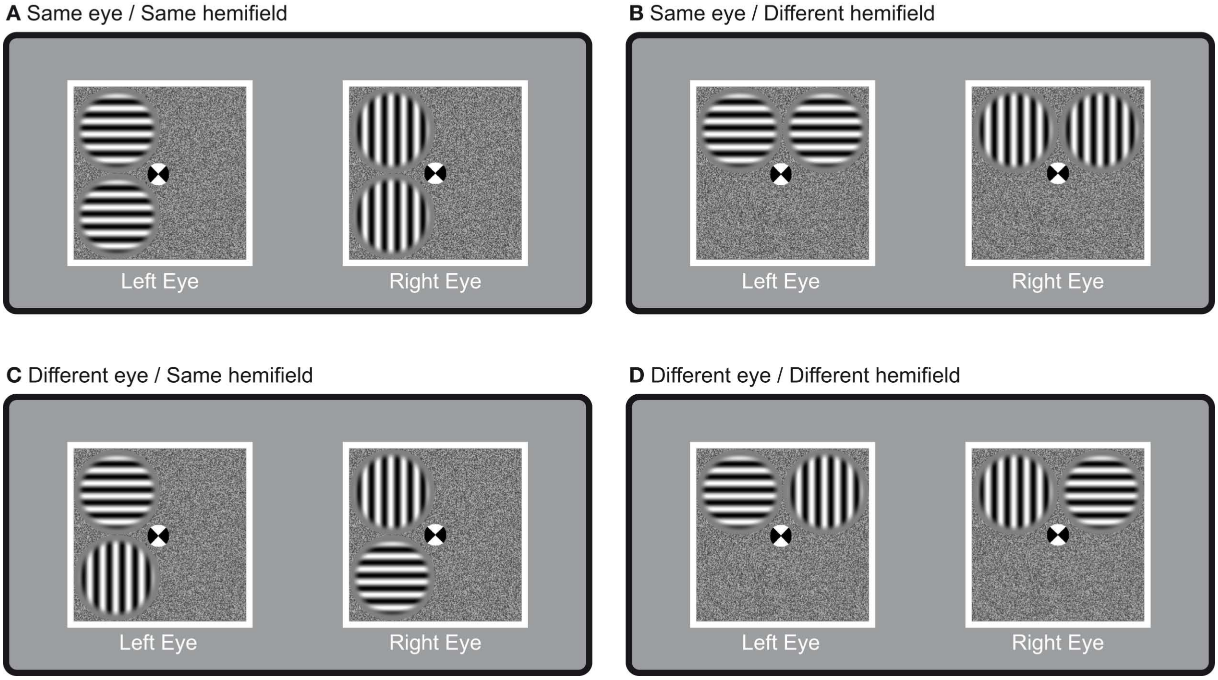


FIGURE 1 | Presentation conditions. The four different stimulus arrangements used. The rival targets were presented such that identical targets were presented **(A)** in the same hemifield for the same eye; **(B)** in different hemifields for the same eye; **(C)** in the same hemifield but for different eyes; or **(D)** in different hemifields and for different eyes. All presentation conditions were counterbalanced for eye and hemifield. Note that all rival targets had the same distance to each other as well as to the fixation point.

key). In case of a mixed percept, observers were still required to make a forced-choice. Note that the use of small gratings kept the occurrence of mixed percepts at a minimum (Blake et al., 1992). Each trial lasted 30 s. After each trial, the rivaling targets were removed from the screen. Observers were instructed to fixate on the fixation point throughout the experiment.

RESULTS

For our analyses we used two measures for grouping during rivalry: (1) Fractions of simultaneous dominance (i.e., the fraction of time images had the same or different orientations) and (2) epoch durations (i.e., the time an observer had one of these percepts). To get a first impression of the biases for grouping during rivalry we first discuss the fractions for simultaneous dominance of targets with identical cardinal orientations, followed by the underlying dominance epochs that resulted in these fractions for dominance. Subsequently, we will address the data for grouping oblique orientations. Where applicable, the *p*-values were corrected for multiple comparisons.

Our first analyses concerned the fractions of simultaneous dominance for cardinal orientations presented in the *same* or *different* hemifields and to the *same* or *different* eyes. The fractions were calculated using the time observers actually responded. This means that the duration of each trial that observers did not respond was subtracted from the 30-s trial-duration before calculating the fractions. The fractions of simultaneous dominance were interpreted as an indication of bias toward or away from grouping identical orientations. A fraction of 0.5 means that identical orientations were as often perceived as dissimilar orientations and perception was thus *unbiased* with respect to grouping.

We compared the fraction of simultaneous dominance of identical orientations across our four presentation conditions; identical orientations presented to (1) the same eye and within the same hemifield, to (2) the same eye but within different hemifields, to (3) different eyes but within the same hemifield, or to (4) different eyes and in different hemifields (**Figure 2**). A two (eye) by two (hemifield) repeated measures ANOVA revealed a main effect of eye [$F(1,7) = 45.45$, $p < 0.001$, $\eta_p^2 = 0.867$], but not of hemifield [$F(1,7) = 0.66$, $p = 0.689$, $\eta_p^2 = 0.086$]. However, an interaction between the two was apparent as well [$F(1,7) = 11.19$, $p = 0.024$, $\eta_p^2 = 0.612$]. To test the nature of the interaction we compared the effect of hemifield in the *same*-eye conditions to the *different*-eye conditions. Hemifield-effects were defined as the difference between the fraction of simultaneous dominance of identical orientations when presented in the *same* versus *different* hemifield(s) (i.e., the difference between the white and the dark gray bars in the *Same Orientation* panels of **Figure 2**). The result showed that the hemifield-effect differed depending on the (same- and different-) eye condition [paired sample *t*-test: $t(7) = 3.34$, $p = 0.0245$, $d = 1.18$]. The interaction between eye and hemifield reflects the reversal of this hemifield-effect: when identical orientations were presented to the same eye, presenting those orientations in the same hemifield *increased* grouping compared to the presentation in different hemifields. However, when identical orientations were split between the eyes, presentation in the same hemifield *decreased* the fraction of simultaneous dominance.

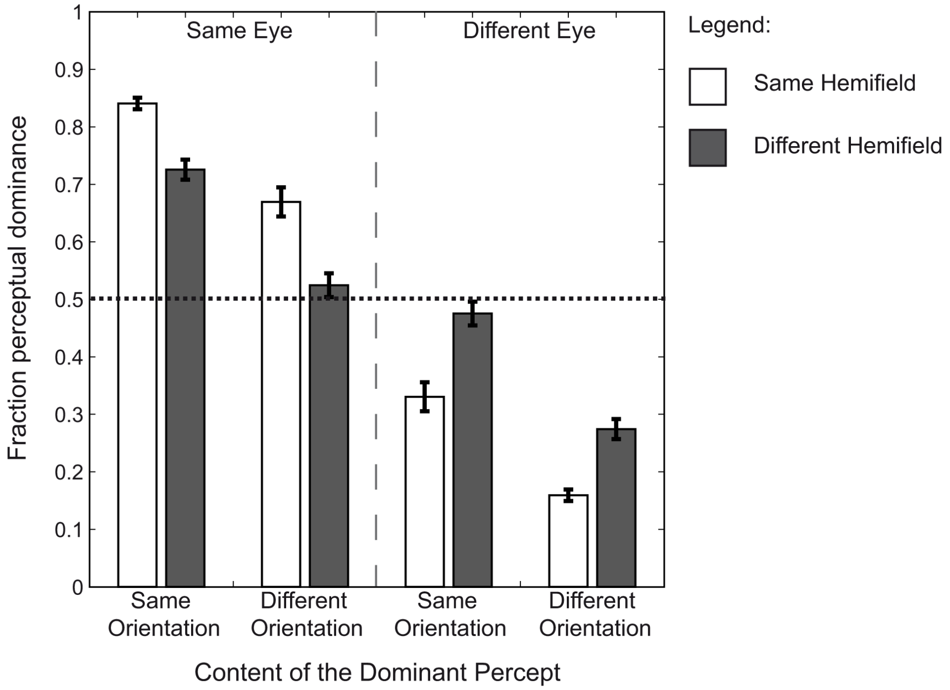


FIGURE 2 | Group means of the dominance fractions. The average fraction of simultaneous dominance across observers for all possible grouped percepts. Error bars represent SEM. Fractions are plotted for each condition. Each bar represents the fraction of dominance for two targets. The dotted line represents unbiased dominance. The results show that when identical rival targets are presented to the same eye, there is a bias toward orientation-based grouping. This is not the case when identical targets are split between the eyes. The bias toward grouping is further increased when identical targets are presented within the same hemifield as well as to the same eye. However, when identical targets are presented to different eyes, the bias is decreased (a bias away from grouping) for presentation in the same compared to different hemifields. These results suggest a strong preference for visual information presented to one eye to be simultaneously dominant.

Each fraction of simultaneous dominance of identical orientations was subsequently tested for a bias toward orientation-based grouping using paired samples t-tests. The results show that when identical orientations were presented to the same eye, there was a bias toward grouping for both the *same* and *different* hemifield conditions [$t(7) = 16.83$, $p < 0.001$, $d = 5.95$; $t(7) = 6.47$, $p = 0.001$, $d = 2.29$ respectively]. However, when the identical orientations were presented to different eyes, there was no bias toward grouping based on orientation [same hemifield, biased *away* from orientation-based grouping: $t(7) = -3.35$, $p = 0.048$, $d = -1.18$; different hemifields, unbiased: $t(7) = -0.60$, $p = 0.965$, $d = -0.21$]. These results show that there is only a bias toward grouping identical orientations when they are presented to the same eye.

The analysis of the fractions of simultaneous dominance suggests that grouping during rivalry primarily occurs between targets presented to the same eye. However, identical fractions can result from very different distributions of dominance epochs. To get a more detailed picture of the effect of grouping on perceptual dominance, we compared the dominance durations for each combination of grouped targets (identical or different orientations).

To calculate the dominance durations we used the median duration (per condition per observer) to correct for the known skewed distribution of dominance epochs (Levelt, 1967). In addition, large individual differences in dominance durations are known to be common as well (e.g., Aafjes et al., 1966). To correct for the latter, all durations were normalized to each observers' average median dominance duration across all trials, percepts (simultaneous dominance of the same of different oriented gratings) and conditions.

Throughout the experiment, simultaneous dominance of two targets can reflect grouping based on multiple cues: eye-of-origin, hemifield, and orientation (**Figure 3**). The comparison of the average duration of each of these perceptual outcomes can be used to estimate the strength of each grouping cue. Epoch durations for each perceptual outcome were compared using a two (eye) by two (orientation) by two (hemifield) repeated measures ANOVA. We found a main effect for eye [$F(1,7) = 61.54$, $p < 0.001$, $\eta_p^2 = 0.898$] as well as for orientation [$F(1,7) = 46.14$, $p < 0.001$, $\eta_p^2 = 0.868$], but not for hemifield [$F(1,7) = 1.46$, $p = 0.461$, $\eta_p^2 = 0.172$]. As was true for the analysis of the fraction simultaneous dominance of identical targets, we found an interaction between eye and hemifield [$F(1,7) = 11.35$, $p = 0.024$, $\eta_p^2 = 0.619$]. This interaction reflects the difference in the hemifield-effect when the same orientations were presented to the same eye versus when they were presented to different eyes [paired sample t-test: $t(7) = 3.37$, $p = 0.024$, $d = 1.19$]. No interaction between orientation and hemifield [$F(1,7) = 0.07$, $p = 0.960$, $\eta_p^2 = 0.010$], orientation and eye-of-origin [$F(1,7) = 2.30$, $p = 0.316$,

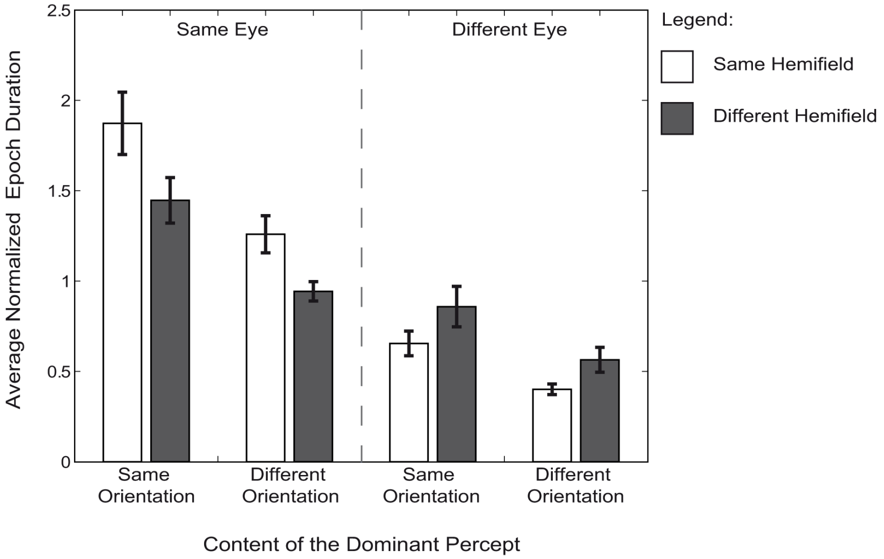


FIGURE 3 | Average epoch duration. Average normalized median durations of each particular perceptual outcome are represented for each condition. All durations are normalized to each observer's median epoch duration across all trials, percepts, and conditions. Error bars are SEM. Each bar represents the dominance duration that two targets were dominant at the same time. The durations of grouping two targets are separated by the targets' eye-of-origin, the hemifield in which they were presented and their orientation.

$\eta_p^2 = 0.248$] or three-way interaction was found [$F(1,7) = 0.76$, $p = 0.567$, $\eta_p^2 = 0.097$].

Recent evidence suggests eye-based and image-based influences on binocular rivalry vary over time (Bartels and Logothetis, 2010). Their results suggest epoch duration may become shorter as rivalry continues. Moreover, the first second of rivalry competition has been argued to be fundamentally different from the remaining rivalry period (Carter and Cavanagh, 2007). Using relatively short epoch durations, the first few seconds of each rivalry period may be overrepresented in our data. However, we found no effect of time on the different contributions to grouping in our paradigm statistically nor did we find any apparent trend to the influence of time on these contributions. The only hint to in temporal effects was a slight increase in dominance epoch durations near the end of the rivalry periods compared to the beginning of the trials.

The analysis of the fractions of simultaneous dominance suggested grouping is primarily eye-based; there was no bias toward grouping identical orientations presented to different eyes. However, the analysis of the epoch durations *did* show an effect of orientation on grouping: identical orientations are grouped for longer durations than dissimilar orientations. Importantly, this effect was *not* dependent on the eye-of-origin of the grouped targets (e.g., no interaction). This suggests a grouping effect of orientation irrespective of whether the images are presented to the same eye or not. The differential effects of grouping based on eye-of-origin and orientation cannot be fully disentangled by comparisons of the fractions of dominance. However, the analyses of epoch durations appear to be a much more sensitive measure to investigate the different grouping cues. This difference between the fraction and the epoch results is likely to stem from a difference in the underlying distributions of dominance durations; distributions for within-eye grouping were much broader than for between-eye grouping. These characteristics of the underlying distributions are lost in the comparison of the fractions of grouping during dominance. The median durations, however, are less affected by these differences in the underlying distributions.

The next step in our analysis is to quantify the respective contributions of the eye-of-origin and orientation cues for grouping (**Figure 4A**). The hemifield condition was ignored since the repeated measures ANOVA showed no main effect for hemifield on grouping targets during rivalry. Therefore, simultaneous dominance of two targets can be based on a single cue for grouping (a shared eye-of-origin *or* a shared orientation), on two grouping cues (a shared eye-of-origin *and* a shared orientation), or no grouping cues at all (simultaneous dominance of targets with different orientations and presented to different eyes). We tested whether the number of grouping cues affected the average median duration of a particular percept. Using paired sample t-tests, we found that the duration of simultaneous dominance based on a single grouping cue is longer than when there are no grouping cues at all [orientation cue: $t(7) = 4.21$, $p = 0.020$, $d = 1.49$; eye-of-origin cue: $t(7) = 10.49$, $p < 0.001$, $d = 3.71$]. Also, eye-of-origin provides a stronger grouping cue than orientation [$t(7) = 4.39$, $p = 0.016$, $d = 1.55$]. Finally, when both cues are present, the duration of simultaneous dominance is longer than for any single cue alone [compared to orientation: $t(7) = 4.98$, $p = 0.008$, $d = 1.76$; compared to eye-of-origin: $t(7) = 3.89$, $p = 0.030$, $d = 1.37$]. These results show the effectiveness of both grouping cues on the duration of particular percept as well as the relative strength of each cue.

Our final analysis is concerned with the observation that synergistic interactions among neighboring rivalry zones reinforce perception of coherent patterns during rivalry (Kovács et al., 1997; Blake, 2001; Lee and Blake, 2004). Our results for grouping

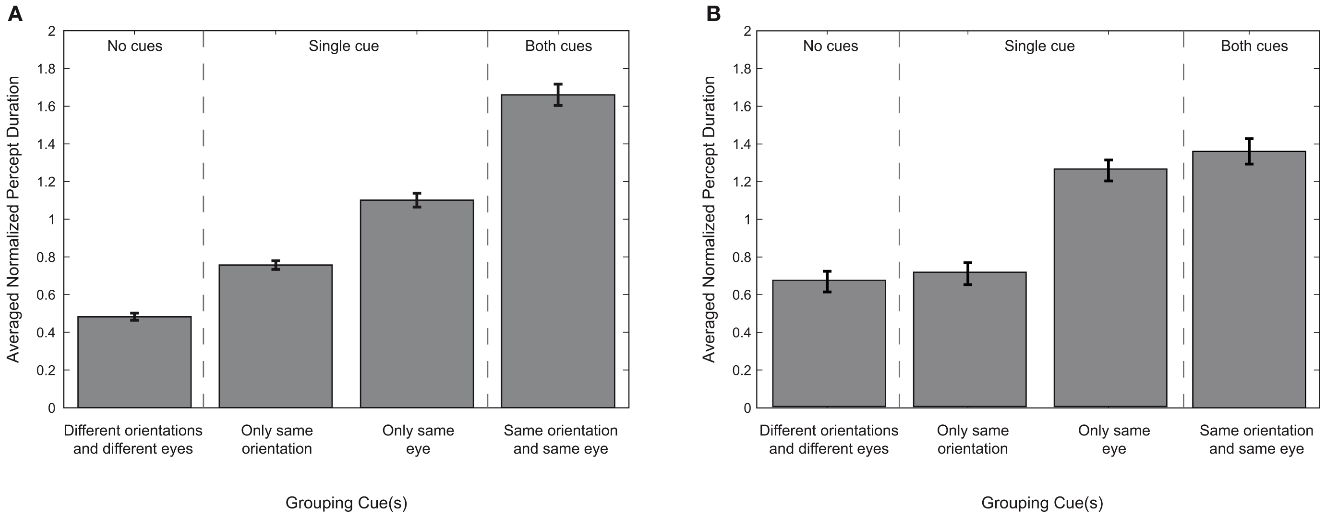


FIGURE 4 | Percept durations per grouping cue. The average median duration of each particular perceptual outcome, represented for each grouping cue. All durations are normalized to each observer's average median epoch duration of all trials, percepts, and conditions. Error bars represent SEM. The data are arranged based on the number of grouping cues associated with each perceptual outcome. The results are plotted as a hierarchy to illustrate the relative potency of certain grouping cues over others. **(A)** Displays the results for our main experiment using cardinal orientations. **(B)** Displays the results for grouping when oblique orientations are used.

cardinal orientations confirm this by showing that different cues can combine to have a synergistic effect on the duration of grouping during rivalry. To test the nature of this synergistic effect, we first took the duration of simultaneous dominance of a horizontal and a vertical oriented target presented to different eyes (the left most bar in **Figure 4A**) as the baseline duration for grouping. Next, we subtracted this baseline from the durations of simultaneous dominance based on either one or more grouping cues. These difference-scores show the additional contribution to the duration of grouping associated with each cue (**Figure 5A**). A paired sample t-test showed that the sum of the added durations of simultaneous dominance based on image-content and eye-of-origin is not significantly different from the duration of simultaneous dominance when both these cues are present [$t(7) = 1.52$, $p = 0.173$, $d = 0.54$]. This finding concurs with the lack of an interaction between the eye-of-origin and the orientation of the rival targets (see above). In sum, this suggests that the cue effects are independent, and act additively on dominance durations.

The effectiveness of the orientation cue for grouping described above is applicable to cardinal orientations. The same analysis on the data for the experiment using oblique orientations also shows an eye-of-origin effect on grouping rivaling targets [$t(6) = 3.09$, $p = 0.04$, $d = 1.17$; **Figures 4B** and **5B**]. Note that the effect is similar in magnitude compared to the experiment using cardinal orientations. However, for oblique orientations, we found no effect of the orientation cue to grouping [$t(6) = 0.71$, $p = 0.757$, $d = 0.27$]. In addition, analyses of the fractions of dominance when the rivaling grating-pairs were oblique (as is represented for cardinal orientations in **Figure 2**) only showed a significant effect of eye-of-origin [$F(1,6) = 13.69$, $p < 0.01$, $\eta_p^2 = 0.695$] and the interaction between eye-of-origin and hemifield [$F(1,6) = 10.58$, $p = 0.017$, $\eta_p^2 = 0.638$], but no effect of orientation [$F(1,6) = 1.46$, $p = 0.272$, $\eta_p^2 = 0.196$]. These results show that cardinal orientations are more readily grouped than oblique orientations during rivalry dominance. Furthermore, the lack of grouping identical oblique orientations suggests that having identical image-content is not sufficient for grouping during rivalry dominance.

GENERAL DISCUSSION

We investigated perceptual grouping of two spatially separated rival targets under a variety of spatial arrangements. Identical rival targets were presented to the same or to different eyes, and within the same or in different hemifields. For cardinal orientations, we found a bias toward grouping when identical orientations were presented to the same eye, but no such bias was evident when identical orientations were presented to different eyes. Moreover, for oblique orientations, grouping during dominance was only affected by eye-of-origin. These results show that eye-of-origin is an important factor for grouping similar orientations during binocular rivalry. The distribution of the targets across the visual field also affected grouping with respect to eye-of-origin. Grouping occurred more often for images presented to the same eye when the images were in the same hemifield. The opposite was true for images that were split between the eyes. That is, images in the same hemifield were grouped *less* often. The modulation of grouping effects by the distribution of the targets across the visual field appears independent of orientation.

The overall occurrence of simultaneous dominance of two targets during rivalry was not biased toward grouping identical orientations across the eyes. However, for cardinal orientations, the *duration* of grouping was affected by orientation irrespective of whether the images were presented to the same eye or not. Our results suggest that eye-of-origin and orientation provided independent cues for grouping during rivalry, with eye-of-origin being the superior cue. It has before been argued that synergistic

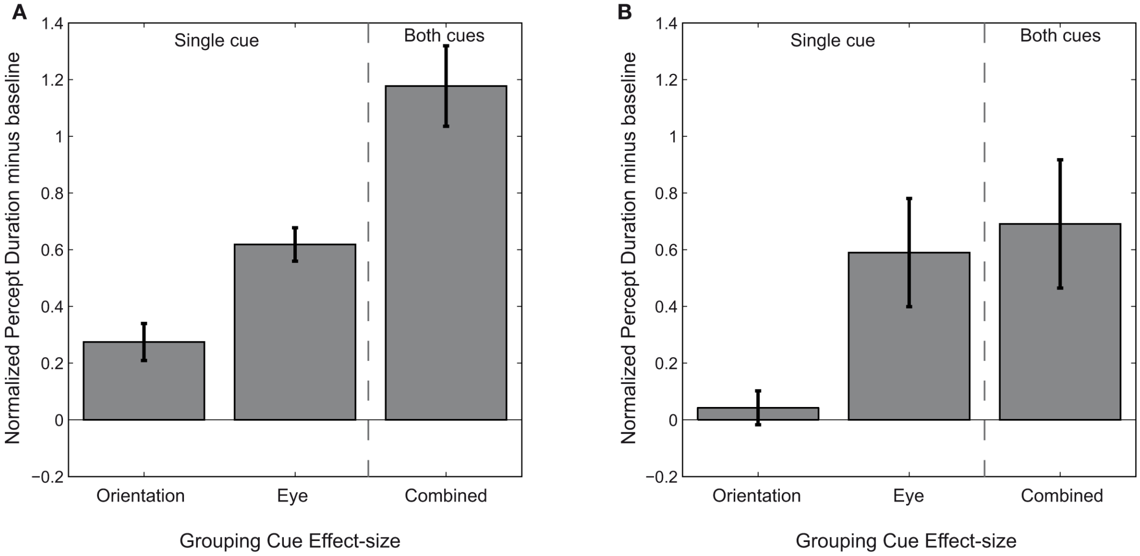
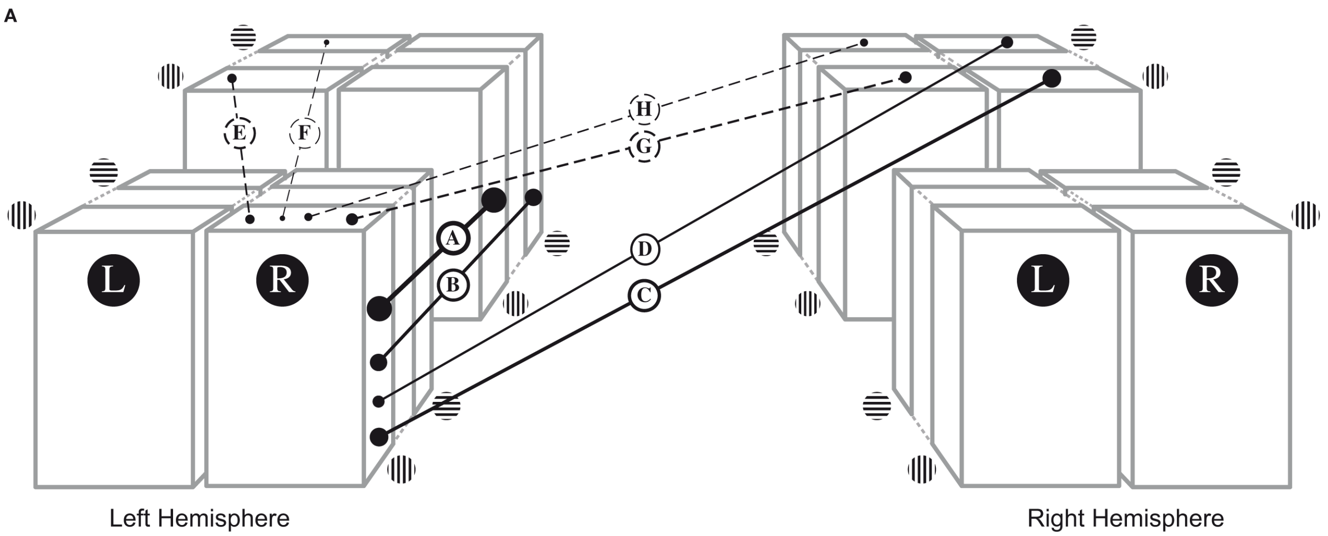


FIGURE 5 | Effect sizes of the different grouping cues. The data from **Figure 4**, displayed as difference scores by subtracting the baseline dominance duration: the duration of dominance when no grouping cues are present. The difference-scores represent the added percept duration and are represented as a function of cue effect. Note that the sum of both single cues does not differ from the dominance duration when both cues are simultaneously present. We suggest the cue effects are independent and have additive effects on dominance durations. **(A)** Show the data for cardinal orientations. **(B)** Shows the data for oblique orientations.

interactions among neighboring rivalry zones reinforce the perception of coherent patterns during rivalry (Kovács et al., 1997; Blake, 2001; Lee and Blake, 2004). We present quantitative evidence for a synergy between grouping based on image-content, and eye-of-origin. More specifically, our results show that this synergetic effect is additive in nature. However, we only found an effect of image-content for rivaling grating-pairs with cardinal orientations; no such effect was found for oblique orientations. The difference between these results likely stems from the lack of co-linearity when rivalry is between oblique grating-pairs. Both psychophysical and physiological studies have shown that facilitation of a flanking line on a target is largest when the lines are collinear (Kapadia et al., 1995). However, non-collinear parallel orientations have also been shown to group during rivalry dominance (Alais and Blake, 1999). Since the identically oriented oblique gratings are not collinear but nevertheless parallel, one would expect the grouping effects for the oblique gratings to possibly be smaller, but still present. In the present study, however, no such orientation-based grouping was found for oblique orientations. Therefore, our results suggest that the grouping effects for the oblique gratings, if present at all, are very small. We currently do not have an explanation why we found no orientation-based grouping for oblique grating-pairs. One possibility is that parallelism is not a strong cue for grouping when the rival targets are not aligned on an axis orthogonal to their orientation.

The data from this study can be used to calculate the relative contributions for all cues affecting grouping during rivalry: eye-of-origin, orientation, and hemifield. These relative contributions of each are taken directly from the normalized epoch durations as reported in **Figure 3**: the average normalized median durations of simultaneous dominance of two rival targets. The contributions are implemented as weights in **Figure 6**: a schematic representation of the cortical hypercolumns in early visual cortex. The cartoon is made for descriptive purposes only and we refrain from making strong statements about the anatomical connections underlying the (grouping) weights. A first thing to notice is that grouping is strongest for items presented to the same eye (**Figure 6**, connections A–D). Whether the items are identical or not, and whether they are processed in the same hemisphere or not, does not affect the generality of the effect. Also, eye-based grouping of two targets is stronger when they are presented in the same hemifield (**Figure 6**, connection A versus C and connection B versus D). This fits well with the decrease in joint predominance with increasing lateral separation as reported by Alais and Blake (1999), and with the decrease in connection strength as a function of increasing cortical distance (Das and Gilbert, 1995; Bosking et al., 1997). However, grouping of targets between the eyes is stronger when they are presented in different hemifields (as compared to presentation in the same hemifield; **Figure 6**, connections G and H versus connections E and F). At first sight, this result is counterintuitive, since connections between hemispheres are longer than connections within a hemisphere. We speculate that this result indicates that connections between different eyes are more inhibitory (leading to less grouping) within a hemisphere, compared to between hemispheres. In conclusion, we can draw a hierarchy of different visual structures involved in grouping: grouping of both similar and different orientations is (1) strongest across hypercolumns receiving input from a single eye and hemifield, (2) weaker across hypercolumns from a single eye between hemifields, (3) weaker across hypercolumns from different eyes and hemifields, and (4) weakest across hypercolumns from a single eye between hemifields.



B

Connection	A	B	C	D	E	F	G	H
Weight	1.87	1.26	1.45	0.94	0.65	0.40	0.86	0.56

FIGURE 6 | Schematic representation of the connections and their weights involved in grouping during rivalry. (A) Schematic representation of connections subserving simultaneous dominance. The L stands for the Left eye and the R for the Right eye. The left part of the figure represents the hypercolumns in the left hemisphere and the right part the right hemisphere. Each hemisphere has two hypercolumn representations corresponding to different locations in the visual field. Solid lines indicate connections between ocular dominance columns representing the same eye (and different retinal locations). Dashed lines represent connections between ocular dominance columns representing different eyes (and different retinal locations). The thickness of each line is adjusted to the weight of the connection. **(B)** Relative weights of each connection in A. The weight for each line is a direct representation of the data presented in **Figure 3**.

Although the above model is first and foremost descriptive for our results, we can use these weights for grouping to try and make quantitative predictions. For example, in their experiment 1, Alais and Blake (1999) measured joint predominance for pairs of collinear, parallel, and orthogonal gratings that rivaled with noise patches. The grating-pairs were presented to the same eye but in different hemifields. As such, the results of their parallel and collinear conditions are comparable to our results for perceiving identical orientations presented to the same eye and in different hemifields (i.e., connection C in **Figure 6**). The results for their orthogonal condition are comparable to our results for perceiving different orientations presented to the same eye and in different hemifields (i.e., connection D in **Figure 6**). Our results would then suggest the strength of the links between the collinear and the parallel grating-pairs to correspond to the weight of 1.45 and the orthogonal pair to correspond to the weight of 0.94. Based on these weights we would expect the grouping effect for the collinear and parallel gratings to be 1.54 times larger than that for the orthogonal pair. From Alais and Blake's Figure 1B, we see that the fraction of grouping for the orthogonal pair is about 0.31. The fractions for grouping the parallel and collinear grating-pairs are about 0.53 and 0.42 respectively. The average fraction of these two conditions (0.475) is thus 1.53 times larger than for the orthogonal condition, almost exactly the same ratio as that follows from our results. Interestingly, the images suppressed during simultaneous dominance of the different grating-pairs differed substantially between their study and ours. While we used a second grating pair, Alais and Blake used noise patches to rival with their gratings. Since their results are quantitatively similar to ours, the content of the suppressed images does not appear to affect the relative strength of grouping during dominance. This suggests another interesting feature of grouping during rivalry: the strength of grouping is based on the currently dominant images, not the suppressed ones. Note that the difference between grouping for parallel and for collinear gratings shown by Alais and Blake (1999) suggests that the collinear grating-pairs may have had the greatest influence on our grouping results. Since we did not have observers dissociated between the orientations in the dominant percept we cannot test this directly. However, with collinear being a stronger grouping cue than parallel only, this is very likely the case.

Our results also make predictions about the spread of traveling waves typically seen during rivalry alternations (Wilson et al., 2001). From our results we would expect a difference between waves traveling within one hemifield as compared to the across hemifields. Since our data suggests the linking of neighboring rivalry zones to be stronger within the same hemifield (assuming eye-based dominance of an image) we expect traveling waves to spread faster within hemifields (e.g., vertical spreading) compared to across hemifields (e.g., horizontal spreading). To our knowledge, this has not yet been tested, although the data may already be available (e.g., Lee et al., 2005). This is not unexpected since models of binocular rivalry do not typically involve any consideration as to which hemifield or -fields the image(s) is presented in, for instance, Blake (1989), Wilson (2003), Ashwin and Lavric (2010). Our results show that incorporation of the hemifield-effect may be critical in predicting dominance durations during binocular rivalry.

To summarize, we investigated grouping of spatially separated rival targets presented to the same or to different eyes and presented in the same or in different hemifields. We found that:

- Eye-of-origin is the strongest cue for grouping during binocular rivalry.
- Identical cardinal orientations are grouped in dominance for longer periods than dissimilar orientations.
- Identical image-content alone is not sufficient for grouping during dominance.
- Eye-based and orientation-based grouping are independent effects and additive in nature.
- Grouping within and between hemifields will increase or decrease depending on the presence of the eye-of-origin grouping cue.

The different contributions to perceptual grouping can be easily quantified and used to make predictions on dominance durations in other studies. Although beyond the scope of the present paper, incorporating these weights, including the dependency on hemifield, into future models of binocular rivalry, may prove useful in our understanding of the functional and anatomical basis of the phenomenon.

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Cortical microcircuit dynamics mediating binocular rivalry: the role of adaptation in inhibition

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Perceptual bistability arises when two conflicting interpretations of an ambiguous stimulus or images in binocular rivalry (BR) compete for perceptual dominance. From a computational point of view, competition models based on cross-inhibition and adaptation have shown that noise is a crucial force for rivalry, and operates in balance with adaptation. In particular, noise-driven transitions and adaptation-driven oscillations define two dynamical regimes and the system explains the observed alternations in perception when it operates near their boundary. In order to gain insights into the microcircuit dynamics mediating spontaneous perceptual alternations, we used a reduced recurrent attractor-based biophysically realistic spiking network, well known for working memory, attention, and decision making, where a spike-frequency adaptation mechanism is implemented to account for perceptual bistability. We thus derived a consistently reduced four-variable population rate model using mean-field techniques, and we tested it on BR data collected from human subjects. Our model accounts for experimental data parameters such as mean time dominance, coefficient of variation, and gamma distribution fit. In addition, we show that our model operates near the bifurcation that separates the noise-driven transitions regime from the adaptation-driven oscillations regime, and agrees with Levelt's second revised and fourth propositions. These results demonstrate for the first time that a consistent reduction of a biophysically realistic spiking network of leaky integrate-and-fire neurons with spike-frequency adaptation could account for BR. Moreover, we demonstrate that BR can be explained only through the dynamics of competing neuronal pools, without taking into account the adaptation of inhibitory interneurons. However, the adaptation of interneurons affects the optimal parametric space of the system by decreasing the overall adaptation necessary for the bifurcation to occur, and introduces oscillations in the spontaneous state.

Keywords: perceptual bistability, binocular rivalry, computational modeling, spike-frequency adaptation, spiking networks, mean-field

INTRODUCTION

Binocular rivalry (BR) is a paradigm often used to study perceptual bistability. Since the invention of the stereoscope by Sir Wheatstone (1838) and his first systematic description of the phenomenon, there has been a plethora of both experimental and theoretical studies. The beauty in BR is the capacity of the phenomenon to offer insights into conscious perception, rather than on the earlier notion that rivalry is strictly a "binocular phenomenon" which optimizes unified stereoscopic vision and is utterly unrelated to other multistable perceptual phenomena. When a subject is dichoptically presented with two conflicting images, only one image is perceived at a time while the other is suppressed from awareness (Levelt, 1968; Blake, 1989, 2001; Logothetis, 1998; see Blake and Logothetis, 2002 for review). Perception, therefore, alternates between the two visual patterns allowing a dissociation of sensory stimulation from conscious visual perception.

Theoretical studies are mostly based on competition models consisting of two selective neuronal populations whose activity encodes one of the two conflicting images. The main components of these oscillatory models are cross-inhibition and self-adaptation (Lehky, 1988; Lago-Fernandez and Deco, 2002; Laing and Chow, 2002; Wilson, 2003; Moreno-Bote et al., 2007; Shpiro et al., 2007). Cross-inhibition leads to the suppression of one of the two images, while a fatiguing process, such as spike-frequency adaptation and/or synaptic depression, eventually weakens inhibition, and causes the previously suppressed neuronal population to win the competition. This mechanism generates anti-phase oscillations of the mean firing rates of the two neuronal populations believed to represent perceptual alternations between the two conflicting visual patterns. Alternatively, alternations in perception have also been represented as switches between two attractors due to noise in noise-driven attractor models (Salinas, 2003; Freeman, 2005; Kim et al., 2006; Moreno-Bote et al., 2007). Recently, Shpiro et al.

(2009) implemented both noise and adaptation mechanisms in a common theoretical framework, and showed that both mechanisms operate in balance during perceptual bistability. Indeed, an optimal combination of adaptation and noise can explain the pattern of neuronal discharges observed in the macaque prefrontal cortex during rivalrous stimulation (Deco and Panagiotaropoulos, unpublished data), while it was recently proposed that noisy adaptation signals could represent one of the physiological mechanisms resulting in BR dynamics (van Ee, 2009; Alais et al., 2010).

Most of the computational models proposed to account for BR are rate-like models. Biophysically plausible spiking networks have also been put forward (Laing and Chow, 2002; Moreno-Bote et al., 2007). Nevertheless, the reduced models presented in Laing et al. (2010) for BR were derived heuristically from the spiking network of Laing and Chow (2002). In the present work, we present instead a four-variable reduced model consistently derived from a spiking neuronal network (Deco and Rolls, 2005; Moreno-Bote et al., 2007; Theodoni et al., 2011) with biophysically realistic AMPA, NMDA, and GABA receptor-mediated synaptic dynamics, as well as spike-frequency adaptation mechanisms based on Ca^{2+}-activated K^{+} after-hyperpolarization currents (Wang, 1998; Liu and Wang, 2001), using mean-field techniques (Brunel and Wang, 2001; Deco and Rolls, 2005; Wong and Wang, 2006). More specifically, we further reduce the extended mean-field model (Deco and Rolls, 2005) of Brunel and Wang (2001) by using a simplified mean-field approach introduced by Wong and Wang (2006). We thus reduced the original full spiking network of thousands of neurons to a four-variable rate-like model of two neuronal populations each one encoding one of two competing percepts in BR.

Both the spiking network and our four-variable reduced network consider noise and adaptation mechanisms. Our goal was to find out which of them is responsible for the perceptual alternations in BR. We based our study on behavioral data collected from human subjects experiencing BR between orthogonal sinusoidal gratings, which were presented continuously in time. The experimental data used to constrain our model consisted of dominance durations of both percepts, coefficients of variation, and parameters of gamma distribution fits to the distribution of dominance durations. When varying the strength of neuronal adaptation in the absence of noise, different dynamical regimes appear. At low levels of neuronal adaptation the system resides in a bistability regime where switches could happen only due to noise. As adaptation strength is increased, perceptual alternations are possible without noise because the system has entered an oscillatory regime. The transition regime separating the bistability from the oscillatory regime is a mixed-mode oscillations regime. By emulating the experimental paradigm for different adaptation strengths and levels of noise, we searched for parameters where our model would replicate the experimental data. In addition, we tested two extreme conditions where all inhibitory interneurons in the original spiking network are adapted or not. We found that, in order to account for the experimental data, and in both conditions, the system operates in the bistability regime near the boundary between noise-driven switches and adaptation-driven oscillations. In addition we show that in this case the model also satisfies Levelt's second revised and fourth propositions.

Interestingly, spike-frequency adaptation of interneurons, apart from decreasing the overall adaptation necessary for the bifurcation to occur when the same stimulus is applied, also influences the system behavior in the absence of a stimulus. When interneurons are not adapted, the two neuronal populations fire asynchronously and at low rates in the spontaneous state. On the contrary, adapted inhibitory interneurons lead the two neuronal populations to a higher firing and oscillatory activity in the absence of stimulus.

MATERIALS AND METHODS

BIOPHYSICALLY INSPIRED SPIKING MODEL

The network consists of four neuronal populations, three of them excitatory and one inhibitory (**Figure 1A**). Populations 1 and 2 consist of neurons selective to one or the other conflicting images in BR. The third population (labeled as ns) comprises neurons that are non-selective to the stimulus features. There is all-to-all connectivity. Note that within each population we assume homogeneity of connections for simplicity. The introduction of inhomogeneities (e.g., sparse random connectivity) does not affect the attractor landscape of the dynamics but only increases the noise (finite-size effects, see Mattia and Del Giudice, 2002). The model is based on the attractor paradigm of Amit (1995). It implements cooperation among neurons that belong to the same population, due to recurrent synaptic connectivity, and competition between neurons that belong to the two selective neuronal populations, due to feedback inhibition.

Neurons within a certain population share the same statistical properties, i.e., single-cell parameters, inputs, and connectivity. They are modeled as leaky integrate-and-fire (LIF) neurons. The subthreshold dynamics of the membrane potential of excitatory (E) or inhibitory (I) LIF neurons is described by the following dynamics

$$C_{\mathrm{m}}^{\mathrm{E,I}} \frac{dV(t)}{dt} = -g_{\mathrm{m}}^{\mathrm{E,I}} \left(V(t) - V_{\mathrm{L}}\right) + I_{\mathrm{total}}(t) \tag{1}$$

with resting potential $V_{\mathrm{L}} = -70$ mV, membrane capacitance, leak conductance, and membrane time constant for excitatory neurons $C_{\mathrm{m}}^{\mathrm{E}} = 0.5$ nF, $g_{\mathrm{m}}^{\mathrm{E}} = 25$ nS, $\tau_{\mathrm{m}}^{\mathrm{E}} = C_{\mathrm{m}}^{\mathrm{E}}/g_{\mathrm{m}}^{\mathrm{E}} = 20$ ms respectively, and for inhibitory neurons $C_{\mathrm{m}}^{\mathrm{I}} = 0.2$ nF, $g_{\mathrm{m}}^{\mathrm{I}} = 20$ nS, $\tau_{\mathrm{m}}^{\mathrm{I}} = C_{\mathrm{m}}^{\mathrm{I}}/g_{\mathrm{m}}^{\mathrm{I}} = 10$ ms, respectively. The total synaptic current to each neuron is the sum of excitatory postsynaptic currents mediated by AMPA (I_{ampa}) and NMDA (I_{nmda}) glutamatergic and $\mathrm{GABA_A}$ (I_{gaba}) GABAergic receptors, an external excitatory postsynaptic current mediated by AMPA receptors ($I_{\mathrm{ampa,ext}}$) and a slow Ca^{2+}-activated K^{+} after-hyperpolarization current (I_{ahp}):

$$I_{\mathrm{total}}(t) = I_{\mathrm{ampa,ext}}(t) + I_{\mathrm{ampa}}(t) + I_{\mathrm{nmda}}(t) + I_{\mathrm{gaba}}(t) + I_{\mathrm{ahp}}(t) \tag{2}$$

where

$$I_{\mathrm{ampa,ext}}(t) = -g_{\mathrm{ampa,ext}}^{\mathrm{E,I}} \left(V(t) - V_{\mathrm{E}}\right) \sum_{\mathrm{j}}^{C_{\mathrm{ext}}} S_{\mathrm{j}}^{\mathrm{ampa,ext}}(t) \tag{3}$$

$$\frac{dS_{\mathrm{j}}^{\mathrm{ampa,ext}}(t)}{dt} = -\frac{S_{\mathrm{j}}^{\mathrm{ampa,ext}}(t)}{\tau_{\mathrm{ampa}}} + \sum_{\mathrm{k}} \delta\left(t - t_{\mathrm{j}}^{\mathrm{k}}\right) \tag{4}$$

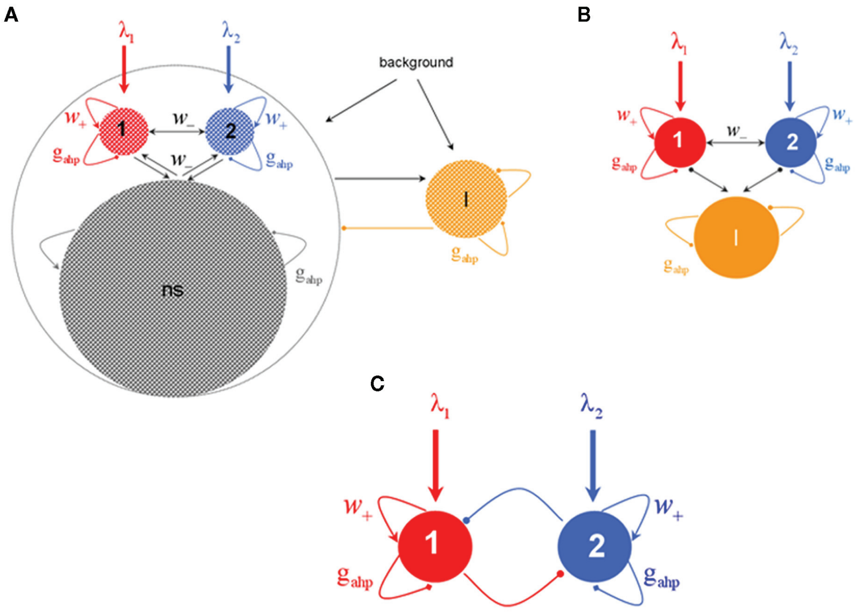

FIGURE 1 | (A) Biophysically plausible spiking network of integrate-and-fire neurons with spike-frequency adapting mechanism based on Ca^{2+}-activated K^+ hyperpolarizing currents. There are four neuronal populations: one inhibitory (orange, I), one excitatory comprised of non-selective neurons (gray, ns), and two excitatory populations (red, 1 and blue, 2) within which neurons have similar stimulus selectivity. Arrows denote excitatory connections; lines ending to circles, inhibitory connections whereas lines ending to squares, after hyperpolarizing currents with peak conductance $g_{\rm ahp}$. All neurons receive background input and selective populations receive an additional external stimulus λ_1, λ_2. **(B)** Assuming that the mean firing rate of the non-selective neuronal population is constant, the network is reduced into three neuronal populations: two excitatory (1, 2) and one inhibitory (I). **(C)** Four-variable reduced rate model of two populations with recurrent excitation, cross–inhibition, and neuronal adaptation.

$$I_{\rm ampa}(t) = -g^{\rm E,I}_{\rm ampa}\left(V(t)-V_{\rm E}\right)\sum_{\rm j}^{C_{\rm E}} w_{\rm j} S_{\rm j}^{\rm ampa}(t) \qquad (5)$$

$$\frac{dS_{\rm j}^{\rm ampa}(t)}{dt} = -\frac{S_{\rm j}^{\rm ampa}(t)}{\tau_{\rm ampa}} + \sum_{\rm k}\delta\left(t-t_{\rm j}^{\rm k}\right) \qquad (6)$$

$$I_{\rm nmda}(t) = -\frac{g^{\rm E,I}_{\rm nmda}\left(V(t)-V_{\rm E}\right)}{1+\gamma e^{-\beta V(t)}}\sum_{\rm j}^{C_{\rm E}} w_{\rm j} S_{\rm j}^{\rm nmda}(t) \qquad (7)$$

$$\frac{dS_{\rm j}^{\rm nmda}(t)}{dt} = -\frac{S_{\rm j}^{\rm nmda}(t)}{\tau_{\rm nmda,decay}} + ax_{\rm j}(t)\left(1-S_{\rm j}^{\rm nmda}(t)\right) \qquad (8)$$

$$\frac{dx_{\rm j}(t)}{dt} = -\frac{x_{\rm j}(t)}{\tau_{\rm nmda,rise}} + \sum_{\rm k}\delta\left(t-t_{\rm j}^{\rm k}\right) \qquad (9)$$

$$I_{\rm gaba}(t) = -g^{\rm E,I}_{\rm gaba}\left(V(t)-V_{\rm I}\right)\sum_{\rm j}^{C_{\rm I}} S_{\rm j}^{\rm gaba}(t) \qquad (10)$$

$$\frac{dS_{\rm j}^{\rm gaba}(t)}{dt} = -\frac{S_{\rm j}^{\rm gaba}(t)}{\tau_{\rm gaba}} + \sum_{\rm k}\delta\left(t-t_{\rm j}^{\rm k}\right) \qquad (11)$$

$$I_{\rm ahp}(t) = -g_{\rm ahp}{\rm Ca}(t)\left(V(t)-V_{\rm K}\right) \qquad (12)$$

$$\frac{d{\rm Ca}(t)}{dt} = -\frac{{\rm Ca}(t)}{\tau_{\rm Ca}} + \rho\sum_{\rm i}\delta\left(t-t_{\rm i}\right) \qquad (13)$$

$a = 0.5\,({\rm ms})^{-1}$, $\delta(t)$ is the Dirac delta-function, and $S_{\rm j}$ are the synaptic gating variables (fractions of open channels), where sums over j are over presynaptic neurons, sums over k are over spikes emitted by the presynaptic neuron j at time $t_{\rm j}^{\rm k}$, and the sum over i is over spikes of the same neuron up to time t. $w_{\rm j}$ Are dimensionless connection weights between and within the neuronal populations which define the structure and function of the network. Within the selective neuronal populations excitatory synapses are potentiated by a factor $w_{\rm j} \equiv w_+ > 1$ according to the "Hebbian" rule according to which cells that fire together are strongly connected. In the text we refer to this factor as recurrent connectivity. Excitatory synapses between the two selective neuronal populations, and excitatory synapses between the non-selective to selective populations are modified by $w_{\rm j} \equiv w_- = 1 - f(w_+ - 1)/(1-f) < 1$, where $f = 0.15$, so that the spontaneous activity of all excitatory cells is at the same level (Amit and Brunel, 1997). For the rest of the connections, $w_{\rm j} = 1$. Reversal potentials for excitatory postsynaptic currents are $V_{\rm E} = 0$ mV, and for inhibitory ones $V_{\rm I} = -70$ mV. The peak conductances for excitatory synapses are $g^{\rm E}_{\rm ampa,ext} = 2.08$ nS, $g^{\rm E}_{\rm ampa} = 104/N$ nS, $g^{\rm E}_{\rm nmda} = 327/N$ nS, $g^{\rm E}_{\rm gaba} = 1250/N$ nS, and for inhibitory $g^{\rm I}_{\rm ampa,ext} = 1.62$ nS, $g^{\rm I}_{\rm ampa} = 81/N$ nS, $g^{\rm I}_{\rm nmda} = 258/N$ nS, $g^{\rm I}_{\rm gaba} = 973/N$ nS, where N is the total number of neurons in the network. The NMDA currents are voltage-dependent, and modulated by intracellular magnesium concentration $[{\rm Mg}^{2+}] = 1$ mM, with parameters $\gamma = [{\rm Mg}^{2+}]/3.57$ and $\beta = 0.062\,({\rm mV})^{-1}$. The rise time of the NMDA mediated synaptic current is $\tau_{\rm nmda,rise} = 2$ ms, while the rise time of AMPA and GABA mediated synaptic currents are neglected for being extremely fast (<1 ms). The decay time constants are $\tau_{\mathrm{ampa}} = 2$ ms, $\tau_{\mathrm{nmda,decay}} = 100$ ms, and $\tau_{\mathrm{gaba}} = 10$ ms. The reversal potential of the potassium channels is $V_{\mathrm{K}} = -80$ mV.

When the membrane potential of an excitatory or inhibitory neuron reaches a certain threshold $V_{\mathrm{thr}} = -50$ mV a spike is emitted and transmitted to other neurons. The membrane potential is reset to $V_{\mathrm{reset}} = -55$ mV after a refractory period, $\tau_{\mathrm{ref}}^{\mathrm{E}} = 2$ ms for excitatory neurons, and $\tau_{\mathrm{ref}}^{\mathrm{I}} = 1$ ms for inhibitory neurons. During that period the neuron is unable to produce further spikes. In addition, the gating variable Ca, emulating the cytoplasmic Ca^{2+} concentration to which we will be referring in the text, increases by a small amount $\rho = 0.005$, and decays exponentially with a time constant $\tau_{\mathrm{Ca}} = 600$ ms (Liu and Wang, 2001). The $g_{\mathrm{ahp}}\mathrm{Ca}$ is the effective K^+ conductance and the g_{ahp} defines the level of neuronal adaptation or adaptation strength.

The total number of neurons in the network is N neurons. There are $C_{\mathrm{E}} = C_1 + C_2 + C_{\mathrm{ns}} = 0.8N$ excitatory neurons, where $C_1 = C_2 = fC_{\mathrm{E}}$ neurons in each of the two selective neuronal populations, and $C_{\mathrm{ns}} = (1 - 2f)\ C_{\mathrm{E}}$ non-selective neurons where $f = 0.15$. The number of inhibitory interneurons in the network is $C_{\mathrm{I}} = 0.2N$. In order to simulate the background input, each neuron in the network receives input through $C_{\mathrm{ext}} = 800$ excitatory connections, each one receiving an independent Poisson spike train with rate 3 Hz. To simulate the external visual stimulation, neurons within the two selective neural populations receive an additional Poisson spike train with invariant in time rates λ_1, λ_2 which define the stimuli strength.

To integrate the system of coupled differential equations that describe the dynamics of all cells and synapses we used a second order Runge–Kutta routine with a time step of 0.02 ms. To calculate the mean firing rate of a neuronal population, we divided the number of spikes emitted in a 50-ms sliding window, with a time step of 5 ms, by its number of neurons and by the window size.

REDUCED RATE MODEL

We derived a four-variable reduced rate model from the above described spiking network, following the simplified mean-field approach of Wong and Wang (2006). This approach is based on the mean-field approximation derived in (Brunel and Wang, 2001) which analyses networks of neurons that have conductance-based synaptic inputs when the network of integrate-and-fire neurons is in a stationary state. In the mean-field approximation, it is considered the diffusion approximation according to which the sums of the synaptic gating variables (Eqs 3, 5, 7, and 10) are replaced by a DC component and a fluctuation term. Moreover, due to the different synaptic time constants, the only noise term that remains is that of the external synaptic gating variable which is considered as Gaussian. Using this approach, the original network of thousands of spiking neurons can be reduced into a set of coupled self-consistent non-linear equations. This describes the average firing rate of each neuronal population as a function of the average input current, which in turn is a function of its average firing rate. This mean-field approximation has been extended for spiking networks including Ca^{2+}-activated K^+ hyperpolarizing currents (Deco and Rolls, 2005), such as the one described in the previous section. Here, we extend the two-variable reduced model of Wong and Wang (2006) by considering this spike-frequency adaptation mechanism in neurons.

The transfer function of a LIF neuron receiving a noisy input, I_{total}, is given by the first-passage time formula (Renart et al., 2003):

$$r = \phi\left(I_{\mathrm{total}}\right) = \left[\tau_{\mathrm{ref}} + \tau_{\mathrm{m}}\sqrt{\pi} \int_{\frac{V_{\mathrm{reset}} - V_{ss}}{s}}^{\frac{V_{\mathrm{thr}} - V_{ss}}{s}} e^{u^2}\left(1 + \mathrm{erf}(u)\right) du\right]^{-1} \tag{14}$$

where s is the amplitude of the fluctuations of the synaptic input, i.e., of the noise, $V_{ss} = (V_{\mathrm{L}} + I_{\mathrm{total}}/g_{\mathrm{m}}^{\mathrm{E,I}})$, and $\mathrm{erf}(u)$ is the error function. The remaining parameters have been defined in the description of the spiking network in the previous section. In the simplified mean-field approach, it is assumed that the driving force of the synaptic currents are constant and that the variance of the membrane potential does not vary significantly and it can be considered fixed as constant. Furthermore, instead of using Eq. 14, the input–output function of Abbott and Chance (2005) is considered:

$$\phi\left(I_{\mathrm{total}}\right) = \frac{c_i I_{\mathrm{total}} - I_i}{1 - e^{-g_i\left(c_i I_{\mathrm{total}} - I_i\right)}}, \quad i = \mathrm{E,I} \tag{15}$$

where c_i ($c_{\mathrm{E}} = 310$ (Hz/nA), $c_{\mathrm{I}} = 615$ (Hz/nA)) is the gain factor, g_i ($g_{\mathrm{E}} = 0.16$ s, $g_{\mathrm{I}} = 0.087$ s) is a noise factor determining the shape of the "curvature" of ϕ, and I_i/c_i ($I_{\mathrm{E}} = 125$ Hz, $I_{\mathrm{I}} = 177$ Hz) is the threshold current when ϕ acts as a linear/threshold function for high g_i. The values of these parameters are calculated after fitting Eq. 15 to the first-passage time formula (Eq. 14) of a LIF excitatory (E) and of an inhibitory (I) neuron, which receives AMPA receptor-mediated external Gaussian noise (Wong and Wang, 2006).

The initial spiking network can be reduced in this way into a system with $11 + 4$ variables, where the 11 are the mean firing rates of the four neuronal populations with their average synaptic gating variables. The remaining four are the average cytoplasmic Ca^{2+} concentration gating variables of the neuronal populations. While, by solving the mean-field equations, one can only determine the fixed points of the system, i.e., the stationary firing rates of the four neuronal populations describing the firing rates by the Wilson–Cowan type equations with time constant $\tau_r = 2$ ms, one can calculate their temporal dynamics. Then, the system of the $11 + 4$ variables is given by the following equations:

$$\tau_r \frac{dr_i}{dt} = -r_i + \varphi\left(I_{\mathrm{total},i}\right) \tag{16}$$

$$\tau_r \frac{dr_{\mathrm{I}}}{dt} = -r_{\mathrm{I}} + \varphi\left(I_{\mathrm{total,I}}\right) \tag{17}$$

$$\frac{dS_i^{\mathrm{ampa}}}{dt} = -\frac{S_i^{\mathrm{ampa}}}{\tau_{\mathrm{ampa}}} + \tilde{r}_i \tag{18}$$

$$\frac{dS_i^{\mathrm{nmda}}}{dt} = -\frac{S_i^{\mathrm{nmda}}}{\tau_{\mathrm{nmda}}} + \left(1 - S_i^{\mathrm{nmda}}\right) F\left(\psi_i\right) \tag{19}$$

$$\frac{dS_{\mathrm{I}}^{\mathrm{gaba}}}{dt} = -\frac{S_{\mathrm{I}}^{\mathrm{gaba}}}{\tau_{\mathrm{gaba}}} + \tilde{r}_{\mathrm{I}} \tag{20}$$

$$\frac{d\mathrm{Ca}_i}{dt} = -\frac{\mathrm{Ca}_i}{\tau_{\mathrm{Ca}}} + \rho\, \tilde{r}_i, \tag{21}$$

$$\frac{d\mathrm{Ca}_\mathrm{I}}{dt} = -\frac{\mathrm{Ca}_\mathrm{I}}{\tau_{\mathrm{Ca}}} + \rho\, \tilde{r}_\mathrm{I} \tag{22}$$

where $i = 1, 2$, ns accounts for the two selective and the non-selective to stimulus features excitatory neuronal populations, and I accounts for the inhibitory neuronal population. In Eqs 16 and 17, r_i and r_I (expressed in Hertz) are the presynaptic mean firing rate of the excitatory and inhibitory populations respectively. In Eqs 18, 20–22, $\tilde{r}_i = r_i/1000$, and $\tilde{r}_\mathrm{I} = r_\mathrm{I}/1000$ in order to be consistent with the units since the time constants are expressed in milliseconds. S_i^{ampa}, S_i^{nmda}, and $S_\mathrm{I}^{\mathrm{gaba}}$ stand for the average synaptic gating variables of the AMPA, NMDA, and GABA receptors respectively, and τ_{ampa}, τ_{nmda}, τ_{gaba} for their corresponding decay time constants. Ca_i and Ca_I stand for the cytoplasmic Ca^{2+} concentration gating variable of the three excitatory ($i = 1, 2$, ns), and the one inhibitory (I) population respectively. $\psi_i = \gamma\tau_{\mathrm{nmda}}\tilde{r}_i/(1 + \gamma\tau_{\mathrm{nmda}}\tilde{r}_i)$ is the steady state of S_i^{nmda}, $\gamma = 0.641$, and $F(\psi_i) = \psi_i/(\tau_{\mathrm{nmda}}(1 - \psi_i)) = \gamma\tilde{r}_i$ (Brunel and Wang, 2001; Wong and Wang, 2006).

Furthermore, the model can be reduced to a four-variable system if we (1) assume constant activity of the non-selective neurons, (2) consider only the slow dynamics of NMDA gating variable and of the Ca^{2+}-activated K^{+} channels, (3) linearize the input–output relation of the interneurons, and (4) consider the Ca^{2+} concentration gating variable of inhibitory interneurons as a function of adaptation strength. We will discuss this in more details in the following sections.

Constant activity of non-selective excitatory neurons

When there is no adaptation in the network ($g_{\mathrm{ahp}} = 0$ nS), the firing rate of the non-selective neurons does not change much under different conditions. This allows us to assume that they fire at a constant rate of 2 Hz, as in Wong and Wang (2006). We further assume the same when there is neuronal adaptation in the network ($g_{\mathrm{ahp}} \neq 0$ nS) in order for our four-variable reduced model to coincide with the two-variable reduced of Wong and Wang (2006) at $g_{\mathrm{ahp}} = 0$ nS. Implementing spike-frequency adaptation to all excitatory and inhibitory neurons, the mean firing rate of the non-selective population increases as a function of the level of neuronal adaptation, as shown in **Figure 2**. The mean firing rate was calculated by averaging the last 5 s of each 10 s-trial and by averaging over 100 trials. In **Figure 2A**, we show this dependence at different recurrent connectivities for an additional external stimulus to neurons belonging to the two selective populations of 40 Hz (a stimulus strength used in the simulations in the Results). We see that, for a given stimulus, recurrent connectivity does not change much the mean firing rate of the non-selective population as a function of the level of adaptation strength. This result stands for different stimuli (not shown here). In **Figure 2B**, we show the mean firing rate of the non-selective population as a function of the level of adaptation at different external inputs for a recurrent connectivity of $w_+ = 1.8$ (the recurrent connectivity used in the simulations in the Results). It is apparent that there is an increase, both as a function of level of neuronal adaptation for a given stimulus, and as a function of stimulus for a given neuronal adaptation. Nevertheless, for simplicity we decided to neglect this increase and considered that the mean firing rate of the non-selective population is constant at 2 Hz for all conditions (i.e., also when there is neuronal adaptation in the network). As a consequence of this assumption, we further neglected the extra inhibition on the selective populations evoked through the interneurons. Nevertheless, as we show in **Figures 7C,D** and **10C,D**, that the adopted assumptions do not change the results much. By assuming that the mean firing rate of the non-selective population is constant, the system is reduced to three neuronal populations as it is shown in **Figure 1B**.

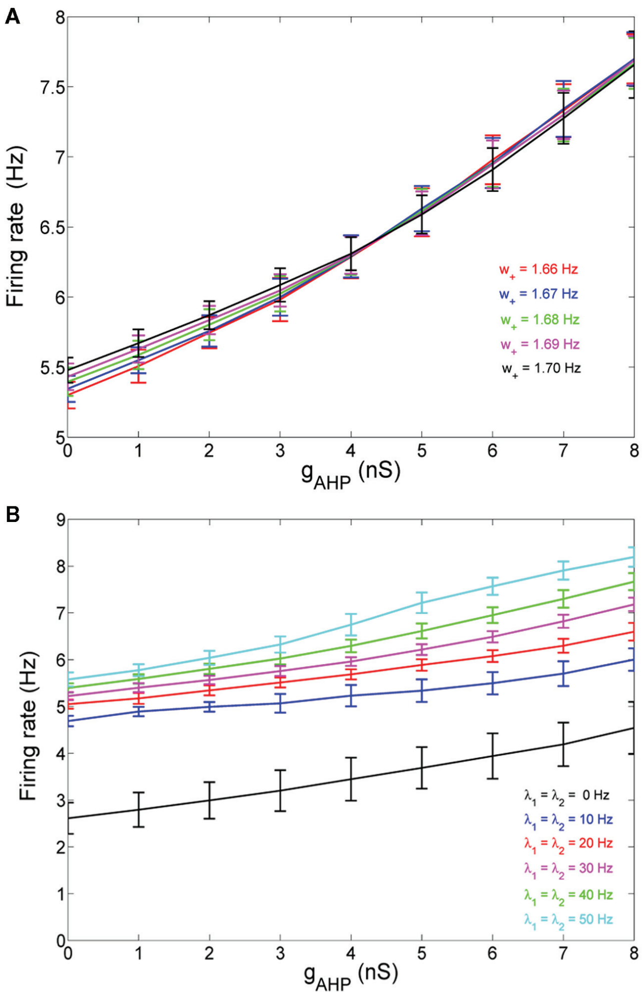

FIGURE 2 | (A) Average firing rate of the non-selective neuronal population as a function of the level of adaptation at different recurrent connectivities for external input $\lambda_1 = \lambda_2 = 40$ Hz. **(B)** Average firing rate of the non-selective neuronal population as a function of the level of neuronal adaptation at different external stimuli for recurrent connectivity $w_+ = 1.68$.

Slow dynamics of NMDA gating variable and cytoplasmic Ca^{2+} concentration

The membrane time constant of LIF neurons can be neglected since they respond instantaneously to a stimulus (Brunel et al., 2001; Fourcaud and Brunel, 2002). In addition, the fast dynamics of the synaptic gating variables of AMPA and GABA$_\mathrm{A}$ receptors, compared to the slow synaptic gating variable of NMDA receptors, may also be neglected as they reach their steady states much faster. Their average values can thus be written as proportional to the mean firing rate of presynaptic cells (Brunel and Wang, 2001; Wong and Wang, 2006). In this work, we also consider the slow dynamics of the cytoplasmic Ca^{2+} concentration that cannot be neglected. Therefore, Eqs 19, 21, and 22 remain as they were, while Eqs 16–18 and 20 become:

$$r_i = \phi(I_{\mathrm{total},i}) \tag{23}$$

$$r_\mathrm{I} = \phi(I_{\mathrm{total,I}}) \tag{24}$$

$$S_i^{\mathrm{ampa}}(t) = \tau_{\mathrm{ampa}} \tilde{r}_i(t) \tag{25}$$

$$S_\mathrm{I}^{\mathrm{gaba}}(t) = \tau_{\mathrm{gaba}} \tilde{r}_\mathrm{I}(t) \tag{26}$$

where $i = 1, 2$. The total currents in the selective populations (1, 2) and in the inhibitory (I), resulting from the simplified mean-field approach, are given by the following equations:

$$\begin{aligned}
I_{\mathrm{total},1} &= I_{\mathrm{syn},1} + I_{\mathrm{ahp},1} = I_{\mathrm{ampa,ext},1} + I_{\mathrm{stim},1} + I_{\mathrm{ampa},1} + I_{\mathrm{nmda},1} \\
&\quad + I_{\mathrm{gaba},1} + I_{\mathrm{ahp},1} \\
&= -g^{\mathrm{E}}_{\mathrm{ampa,ext}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} C_{\mathrm{ext}} \tilde{r}_{\mathrm{ext}} - g^{\mathrm{E}}_{\mathrm{ampa,ext}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} \tilde{\lambda}_1 \\
&\quad - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, w_+ \tilde{r}_1 - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \\
&\quad \times \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, w_- \tilde{r}_2 - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} \left(1 - 2f\right) C_\mathrm{E} w_- \tilde{r}_{\mathrm{ns}} \\
&\quad - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle f\, C_\mathrm{E}\, w_+ S_1 - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle f\, C_\mathrm{E}\, w_- S_2 \\
&\quad - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle \left(1 - 2f\right) C_\mathrm{E}\, w_- \psi_{\mathrm{ns}} \\
&\quad - g^{\mathrm{E}}_{\mathrm{gaba}} \left(\langle V_\mathrm{E} \rangle - V_\mathrm{I}\right) \tau_{\mathrm{gaba}} C_\mathrm{I} \tilde{r}_\mathrm{I} - \tilde{g}_{\mathrm{ahp}} \left(\langle V_\mathrm{E} \rangle - V_\mathrm{K}\right) \mathrm{Ca}_1
\end{aligned} \tag{27}$$

$$\begin{aligned}
I_{\mathrm{total},2} &= I_{\mathrm{syn},2} + I_{\mathrm{ahp},2} = I_{\mathrm{ampa,ext},2} + I_{\mathrm{stim},2} + I_{\mathrm{ampa},2} + I_{\mathrm{nmda},2} \\
&\quad + I_{\mathrm{gaba},2} + I_{\mathrm{ahp},2} \\
&= -g^{\mathrm{E}}_{\mathrm{ampa,ext}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} C_{\mathrm{ext}} \tilde{r}_{\mathrm{ext}} - g^{\mathrm{E}}_{\mathrm{ampa,ext}} \langle V_\mathrm{E} \rangle \\
&\quad \times \tau_{\mathrm{ampa}} \tilde{\lambda}_2 \\
&\quad - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, w_- \tilde{r}_1 - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \\
&\quad \times \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, w_+ \tilde{r}_2 - g^{\mathrm{E}}_{\mathrm{ampa}} \langle V_\mathrm{E} \rangle \tau_{\mathrm{ampa}} \left(1 - 2f\right) C_\mathrm{E} w_- \tilde{r}_{\mathrm{ns}} \\
&\quad - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle f\, C_\mathrm{E}\, w_- S_1 - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle f\, C_\mathrm{E}\, w_+ S_2 \\
&\quad - g^{\mathit{eff},\mathrm{E}}_{\mathrm{nmda}} \langle V_\mathrm{E} \rangle \left(1 - 2f\right) C_\mathrm{E}\, w_- \tilde{\psi}_{\mathrm{ns}} \\
&\quad - g^{\mathrm{E}}_{\mathrm{gaba}} \left(\langle V_\mathrm{E} \rangle - V_\mathrm{I}\right) \tau_{\mathrm{gaba}} C_\mathrm{I} \tilde{r}_\mathrm{I} - \tilde{g}_{\mathrm{ahp}} \left(\langle V_\mathrm{E} \rangle - V_\mathrm{K}\right) \mathrm{Ca}_2
\end{aligned} \tag{28}$$

$$\begin{aligned}
I_{\mathrm{total,I}} &= I_{\mathrm{syn,I}} + I_{\mathrm{ahp,I}} = I_{\mathrm{ampa,ext,I}} + I_{\mathrm{ampa,I}} + I_{\mathrm{nmda,I}} + I_{\mathrm{gaba,I}} \\
&\quad + I_{\mathrm{ahp,I}} \\
&= -g^{\mathrm{I}}_{\mathrm{ampa,ext}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} C_{\mathrm{ext}} \tilde{r}_{\mathrm{ext}} \\
&\quad - g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, \tilde{r}_1 - g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} f\, C_\mathrm{E}\, \tilde{r}_2 \\
&\quad - g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} \left(1 - 2f\right) C_\mathrm{E} \tilde{r}_{\mathrm{ns}} \\
&\quad - g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle f\, C_\mathrm{E}\, S_1 - g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle f\, C_\mathrm{E}\, S_2 \\
&\quad - g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle \left(1 - 2f\right) C_\mathrm{E}\, \tilde{\psi}_{\mathrm{ns}} \\
&\quad - g^{\mathrm{I}}_{\mathrm{gaba}} \left(\langle V_\mathrm{I} \rangle - V_\mathrm{I}\right) \tau_{\mathrm{gaba}} C_\mathrm{I} \tilde{r}_\mathrm{I} - \tilde{g}_{\mathrm{ahp}} \left(\langle V_\mathrm{I} \rangle - V_\mathrm{K}\right) \mathrm{Ca}_\mathrm{I}
\end{aligned} \tag{29}$$

where $g^{\mathit{eff},\mathrm{E,I}}_{\mathrm{nmda}} = \frac{g^{\mathrm{E,I}}_{\mathrm{nmda}}}{1 + \gamma e^{-\beta \langle V_{\mathrm{E,I}} \rangle}}$, E stands for excitatory, I for inhibitory, and S_1, S_2 are the average synaptic gating variables of the NMDA receptors of the two selective populations. To the external excitatory input currents to the two selective populations, $I_{\mathrm{ampa,ext},1}$, $I_{\mathrm{ampa,ext},2}$, we included the contribution of the external stimuli $\tilde{\lambda}_1 = \lambda_1/1000$ (1/ms) and $\tilde{\lambda}_1 = \lambda_1/1000$ (1/ms) respectively. $\tilde{g}_{\mathrm{ahp}} = g_{\mathrm{ahp}}/1000$ (μS), and the values of the fixed averaged membrane potentials for the excitatory and inhibitory neurons are $\langle \mathrm{V_E} \rangle = -53.4$ mV, $\langle \mathrm{V_I} \rangle = -52.1$ mV respectively, the same as the ones considered in Wong and Wang (2006).

Linearization of the input–output relation of interneurons

The mean firing rate of the inhibitory neurons lies in the range of 8–15 Hz when there is no spike-frequency adaptation encoded in the neurons of the network. However, when spike-frequency adaptation in all neurons in the network, the mean firing rate of the inhibitory neurons increases slightly and up to 20 Hz. Within the range 8–20 Hz, the single-cell input–output relation is still almost linear (**Figure 3**) and is fitted by:

$$r_\mathrm{I} = \phi\left(I_{\mathrm{total,I}}\right) = \frac{1}{g_{\mathrm{I2}}} \left(c_\mathrm{I} I_{\mathrm{total,I}} - I_\mathrm{I}\right) + r_0 \tag{30}$$

where $g_{\mathrm{I2}} = 1.7876$, and $r_0 = 11.3721$ Hz. $c_\mathrm{I} = 615$(Hz/nA) and $I_\mathrm{I} = 177$ Hz are the same as in Eq. 15. By substituting $I_{\mathrm{total,I}}$ (Eq. 29) in Eq. 30 we find:

$$\begin{aligned}
r_\mathrm{I} = &-\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}} g^{\mathrm{I}}_{\mathrm{ampa,ext}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} C_{\mathrm{ext}} \tilde{r}_{\mathrm{ext}} \\
&- \frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}} \Big(g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} C_\mathrm{E} f\, \tilde{r}_1 + g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} C_\mathrm{E} f\, \tilde{r}_2 \\
&+ g^{\mathrm{I}}_{\mathrm{ampa}} \langle V_\mathrm{I} \rangle \tau_{\mathrm{ampa}} C_\mathrm{E} \left(1 - 2f\right) \tilde{r}_{\mathrm{ns}} \Big) \\
&- \frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}} \Big(g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle C_\mathrm{E} f\, S_1 + g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle C_\mathrm{E} f\, S_2 \\
&+ g^{\mathit{eff},\mathrm{I}}_{\mathrm{nmda}} \langle V_\mathrm{I} \rangle C_\mathrm{E} \left(1 - 2f\right) \psi_{\mathrm{ns}} \Big) \\
&- \frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}} \tilde{g}_{\mathrm{ahp}} \left(\langle V_\mathrm{I} \rangle - V_\mathrm{K}\right) \mathrm{Ca}_\mathrm{I} - \frac{I_\mathrm{I}}{\eta g_{\mathrm{I2}}} + \frac{r_0}{\eta}
\end{aligned} \tag{31}$$

where $\eta = 1 + \frac{c_\mathrm{I}}{g_{\mathrm{I2}}} g^{\mathrm{I}}_{\mathrm{gaba}} \left(\langle V_\mathrm{I} \rangle - V_\mathrm{I}\right) \tau_{\mathrm{gaba}} C_\mathrm{I}/1000$. Finally, by substituting r_I (Eq. 31) in the expressions of $I_{\mathrm{total},1}(t)$, $I_{\mathrm{total},2}(t)$ (Eq. 27 and 28), the system is reduced to two populations (**Figure 1C**).

Ca^{2+} concentration of interneurons as a function of the level of neuronal adaptation

If we consider spike-frequency adaptation to the inhibitory interneurons, the model consists of five variables, two average synaptic gating variables, $S_{1,2}$, of the selective populations,

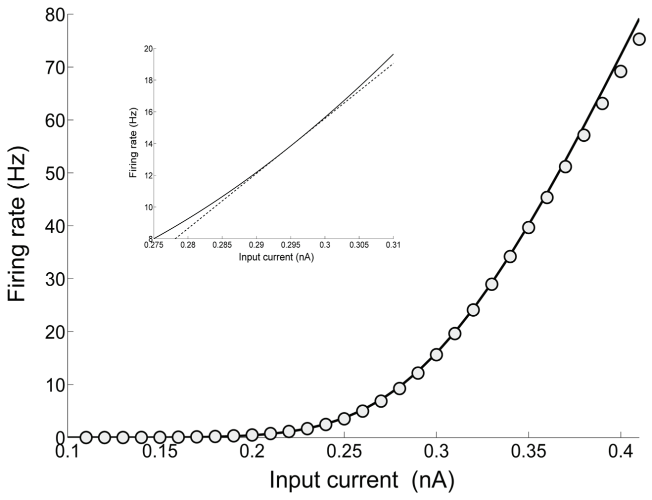

FIGURE 3 | Input–output function of an interneuron: the line is plot of the first-passage time formula of a LIF model with $\sigma = 4.2$ (Eq. 14), while the circles correspond to the fit of Eq. 15. In the inset, a close up is drawn (solid line) and the linear approximation using Eq. 30 (dashed line).

two average Ca^{2+} concentration gating variables of the selective populations, $Ca_{1,2}$, and one of the inhibitory population, Ca_I. In order to further reduce the system of equations, we assume that the Ca^{2+} concentration of the inhibitory population is constant in time at different levels of neuronal adaptation, since it changes only by a modest amount. The dependence of Ca_I on the level of neuronal adaptation is found by simulating the full biophysically plausible spiking network, as we did in Section "Constant Activity of Non-Selective Excitatory Neurons" for the mean firing rate of the non-selective population. More specifically, the Ca_I was calculated by averaging the last 5 s of each 10 s-trial, and then by averaging over 100 trials. In **Figure 4A**, we present Ca_I as a function of the level of neuronal adaptation at different recurrent connectivities for an additional external stimulus to both selective populations of 40 Hz (a stimulus strength used in the simulations in the Results). In **Figure 4B**, we present Ca_I as a function of the level of neuronal at different external inputs for a recurrent connectivity of $w_+ = 1.8$ (the recurrent connectivity used in the simulations in the Results). After fitting a quadratic function to the plot $Ca_I = f(g_{ahp})$ for recurrent connectivity $w_+ = 1.68$, and without external stimulus (black line in **Figure 4B**), we find:

$$Ca_I = 2.1 \times 10^{-5} \times g_{ahp}^2 + 8.4 \times 10^{-4} \times g_{ahp} + 0.025 \qquad (32)$$

In **Figures 4A,B**, it is apparent that the shape of this function does not change significantly under different conditions, but it is shifted to higher values at higher stimuli. Nevertheless, for simplicity, we neglected this increase and we considered Eq. 32 approximated by the value 0.025 for all g_{ahp}, i.e. $Ca_I = 0.025$ for all conditions. The consequence of this assumption is that we consider higher inhibition to the selective populations. However in **Figures 7C,D** and **10C,D** where we compare the reduced model with the spiking model, we show that both models behave similarly. We note that using Eq. 32, without approximations, we found that the final results don't change qualitatively.

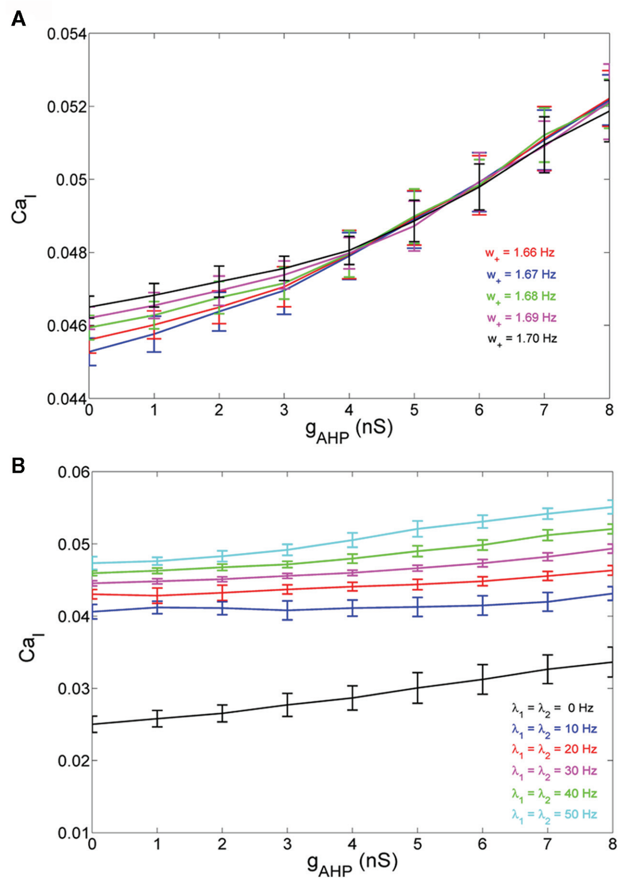

FIGURE 4 | (A) Average gating variable Ca_I emulating the Ca^{2+} concentration of the inhibitory population as a function of the level of adaptation at different recurrent connectivities for external stimulus $\lambda_1 = \lambda_2 = 40$ Hz. **(B)** The average gating variable Ca_I as a function of the level of neuronal adaptation at different external stimuli for recurrent connectivity $w_+ = 1.68$.

Reduced four-variable model

As described in the previous sections, we consistently reduced a full biophysically plausible spiking network with spike-frequency adaptation mechanism implemented to a four-variable reduced rate model (**Figure 1C**). The dynamical equations characterizing this system are:

$$r_1 = \phi\left(I_{total,1}\right) = \frac{c_E I_{total,1} - I_E}{1 - e^{-g_E\left(c_E I_{total,1} - I_E\right)}} \qquad (33)$$

$$r_2 = \phi\left(I_{total,2}\right) = \frac{c_E I_{total,2} - I_E}{1 - e^{-g_E\left(c_E I_{total,2} - I_E\right)}} \qquad (34)$$

$$\frac{dS_1}{dt} = -\frac{S_1}{\tau_{nmda}} + (1 - S_1)\,\gamma \tilde{r}_1 \qquad (35)$$

$$\frac{dS_2}{dt} = -\frac{S_2}{\tau_{nmda}} + (1 - S_2)\,\gamma \tilde{r}_2 \qquad (36)$$

$$\frac{d\,\mathrm{Ca}_1}{dt} = -\frac{\mathrm{Ca}_1}{\tau_{\mathrm{Ca}}} + \rho\tilde{r}_1 \tag{37}$$

$$\frac{d\,\mathrm{Ca}_2}{dt} = -\frac{\mathrm{Ca}_2}{\tau_{\mathrm{Ca}}} + \rho\tilde{r}_2 \tag{38}$$

The total inward currents to the populations are given by

$$\begin{aligned} I_{\mathrm{total},1} &= J_{\mathrm{N},11}S_1 - J_{\mathrm{N},12}S_2 + J_{\mathrm{A},11}r_1 - J_{\mathrm{A},12}r_2 - \lambda\mathrm{Ca}_1 + \kappa\mathrm{Ca}_\mathrm{I} \\ &\quad + I_0 + I_{\mathrm{stim},1} + I_{\mathrm{noise},1} \end{aligned} \tag{39}$$

$$\begin{aligned} I_{\mathrm{total},2} &= J_{\mathrm{N},22}S_2 - J_{\mathrm{N},21}S_1 + J_{\mathrm{A},22}r_2 - J_{\mathrm{A},21}r_1 - \lambda\mathrm{Ca}_2 + \kappa\mathrm{Ca}_\mathrm{I} \\ &\quad + I_0 + I_{\mathrm{stim},2} + I_{\mathrm{noise},2} \end{aligned} \tag{40}$$

where

$$\begin{aligned} J_{\mathrm{N},11} &= g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{I}}\langle V_\mathrm{I}\rangle f\, C_\mathrm{E} \\ &\quad - g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{E}}\langle V_\mathrm{E}\rangle f\, C_\mathrm{E}\, w_+ \end{aligned} \tag{41}$$

$$J_{\mathrm{N},22} = J_{\mathrm{N},11} \tag{42}$$

$$\begin{aligned} J_{\mathrm{N},12} &= g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{E}}\langle V_\mathrm{E}\rangle f\, C_\mathrm{E}\, w_- - g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right) \\ &\quad \times \frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{I}}\langle V_\mathrm{I}\rangle f\, C_\mathrm{E} \end{aligned} \tag{43}$$

$$J_{\mathrm{N},21} = J_{\mathrm{N},12} \tag{44}$$

$$\begin{aligned} J_{\mathrm{A},11} &= g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{ampa}}^{\mathrm{I}}\langle V_\mathrm{I}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}f\, C_\mathrm{E} \\ &\quad - g_{\mathrm{ampa}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}f\, C_\mathrm{E}\, w_+ \end{aligned} \tag{45}$$

$$J_{\mathrm{A},22} = J_{\mathrm{A},11} \tag{46}$$

$$\begin{aligned} J_{\mathrm{A},12} &= g_{\mathrm{ampa}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}f\, C_\mathrm{E}\, w_- - g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right) \\ &\quad \times \frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{ampa}}^{\mathrm{I}}\langle V_\mathrm{I}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}f\, C_\mathrm{E} \end{aligned} \tag{47}$$

$$J_{\mathrm{A},21} = J_{\mathrm{A},12} \tag{48}$$

$$\lambda = \lambda'\tilde{g}_{\mathrm{ahp}}, \quad \text{where } \lambda' = \left(\langle V_\mathrm{E}\rangle - V_\mathrm{K}\right) \tag{49}$$

$$\begin{aligned} \kappa &= \kappa'\tilde{g}_{\mathrm{ahp}} \quad \text{where } \kappa' = g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right) \\ &\quad \times \frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}\left(\langle V_\mathrm{I}\rangle - V_\mathrm{K}\right) \end{aligned} \tag{50}$$

$$\begin{aligned} I_0 &= l\cdot r_{\mathrm{ext}} + m\cdot r_{\mathrm{ns}} + n\cdot\psi_{\mathrm{ns}} \\ &\quad + g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\left(\frac{I_\mathrm{I}}{\eta g_{\mathrm{I2}}} - \frac{r_0}{\eta}\right) \end{aligned} \tag{51}$$

$$\begin{aligned} l &= g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{ampa,ext}}^{\mathrm{I}}\langle V_\mathrm{I}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}C_{\mathrm{ext}} \\ &\quad - g_{\mathrm{ampa,ext}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}C_{\mathrm{ext}} \end{aligned} \tag{52}$$

$$\begin{aligned} m &= g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{ampa}}^{\mathrm{I}}\langle V_\mathrm{I}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}\left(1-2f\right) \\ &\quad \times C_\mathrm{E} - g_{\mathrm{ampa}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}\left(1-2f\right)C_\mathrm{E}\, w_- \end{aligned} \tag{53}$$

$$\begin{aligned} n &= g_{\mathrm{gaba}}^{\mathrm{E}}\left(\langle V_\mathrm{E}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I}\frac{c_\mathrm{I}}{\eta g_{\mathrm{I2}}}g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{I}}\langle V_\mathrm{I}\rangle\left(1-2f\right)C_\mathrm{E} \\ &\quad - g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{E}}\langle V_\mathrm{E}\rangle\left(1-2f\right)C_\mathrm{E}\, w_- \end{aligned} \tag{54}$$

$$I_{\mathrm{stim},1} = J_{\mathrm{A,ext}}\cdot\lambda_1 = -g_{\mathrm{ampa,ext}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}\lambda_1 \tag{55}$$

$$I_{\mathrm{stim},2} = J_{\mathrm{A,ext}}\cdot\lambda_2 = -g_{\mathrm{ampa,ext}}^{\mathrm{E}}\langle V_\mathrm{E}\rangle\frac{\tau_{\mathrm{ampa}}}{1000}\lambda_2 \tag{56}$$

$$\eta = 1 + \frac{c_\mathrm{I}}{g_{\mathrm{I2}}}g_{\mathrm{gaba}}^{\mathrm{I}}\left(\langle V_\mathrm{I}\rangle - V_\mathrm{I}\right)\frac{\tau_{\mathrm{gaba}}}{1000}C_\mathrm{I} \tag{57}$$

$$g_{\mathrm{nmda}}^{\mathit{eff},\mathrm{E,I}} = \frac{g_{\mathrm{nmda}}^{\mathrm{E,I}}}{1 + e^{0.062\langle V_{\mathrm{E,I}}\rangle}/3.57} \tag{58}$$

$$\psi_{\mathrm{ns}} = \frac{\gamma\tau_{\mathrm{nmda}}r_{\mathrm{ns}}/1000}{1 + \gamma\tau_{\mathrm{nmda}}r_{\mathrm{ns}}/1000} \tag{59}$$

Where N is the total number of neurons in the spiking network, $C_\mathrm{E} = 0.8N$, $C_\mathrm{I} = 0.2N$ are the numbers of the excitatory (E) and inhibitory (I) neurons, $C_{\mathrm{ext}} = 800$ is the external excitatory connections, and $f = 0.15$. The rest of the parameters are: $c_\mathrm{E} = 310$ (Hz/nA), $g_\mathrm{E} = 0.16$ s, $I_\mathrm{E} = 125$ Hz, $c_\mathrm{I} = 615$ Hz/nA, $I_\mathrm{I} = 177$ Hz, $\gamma = 0.641$, $\tau_{\mathrm{nmda}} = 100$ ms, $\tau_{\mathrm{Ca}} = 600$ ms $\rho = 0.005$, $\langle V_\mathrm{E}\rangle = -53.4$ mV, $\langle V_\mathrm{I}\rangle = -52.1$ mV, $V_\mathrm{I} = -70$ mV, $V_\mathrm{K} = -80$ mV, $r_{\mathrm{ext}} = 3$ Hz, $r_{\mathrm{ns}} = 2$ Hz, $\tau_{\mathrm{ampa}} = 2$ ms, $\tau_{\mathrm{gaba}} = 10$ ms, $g_{\mathrm{I2}} = 1.7876$, $r_0 = 11.3721$ Hz, $g_{\mathrm{ampa}}^{\mathrm{ext,E}} = 0.0021$ μS, $g_{\mathrm{ampa}}^{\mathrm{E}} = 0.1/N$ (μS), $g_{\mathrm{nmda}}^{\mathrm{E}} = 0.3/N$ (μS), $g_{\mathrm{gaba}}^{\mathrm{E}} = 1.3/N$ (μS), $g_{\mathrm{ampa}}^{\mathrm{ext,I}} = 0.00162$ μS, $g_{\mathrm{ampa}}^{\mathrm{I}} = 0.086/N$ (μS), $g_{\mathrm{nmda}}^{\mathrm{I}} = 0.258/N$ (μS), $g_{\mathrm{gaba}}^{\mathrm{I}} = 1/N$ (μS), $\tilde{g}_{\mathrm{ahp}} = g_{\mathrm{ahp}}/g_{\mathrm{ahp}}1000$ (μS), and $\mathrm{Ca}_\mathrm{I} = 0.025$. In the present work, we used $w_+ = 1.68$ ($w_- = 0.88$) while g_{ahp} (nS) defines the level of neuronal adaptation, one of the parameters that we mainly varied.

Noise, $I_{\mathrm{noise},i}$ where $i = 1,2$ stands for neuronal population 1 and 2, is modeled as white noise, filtered by the fast time constant of AMPA synapses, and described by an Ornestein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930).

$$\tau_{\mathrm{ampa}}\frac{dI_{\mathrm{noise},i}(t)}{dt} = -I_{\mathrm{noise},i}(t) + \eta(\mathrm{t})\sqrt{\tau_{\mathrm{ampa}}\sigma_{\mathrm{noise}}^2} \tag{60}$$

Where η is a Gaussian white noise with zero mean and unit variance and $\sigma_{\mathrm{noise}}^2$ is the variance of the noise. In the present work, $n = \sigma_{\mathrm{noise}}$ defines the level of noise, and is the other parameter that we mainly varied.

Effective transfer function

It is not trivial to solve Eqs 33–40 since the mean firing rates are given by their inputs through the transfer function (Eqs 33 and 34), and the inputs are themselves dependent on the mean firing rates (Eqs 39 and 40). To overcome this difficulty of self-consistency calculations, we found (as in Wong and Wang, 2006), an effective transfer function $\Lambda(I_{\mathrm{total}})$. We start by defining four variables:

$$x_1 = J_{\mathrm{N},11}S_1 - J_{\mathrm{N},12}S_2 + I_0 + I_{\mathrm{stim},1} \tag{61}$$

$$x_2 = J_{\mathrm{N},22}S_2 - J_{\mathrm{N},21}S_1 + I_0 + I_{\mathrm{stim},2} \tag{62}$$

$$x_3 = \lambda\mathrm{Ca}_1 - \kappa\mathrm{Ca}_\mathrm{I} \tag{63}$$

$$x_4 = \lambda\mathrm{Ca}_2 - \kappa\mathrm{Ca}_\mathrm{I} \tag{64}$$

Then, according to Eqs 39 and 40, in the noise-free case, Eqs 33 and 34 can be written as:

$$r_1 - \frac{c_E(x_1 - x_3 + J_{A,11} r_1 - J_{A,12} r_2) - I_E}{1 - e^{-g_E(c_E(x_1 - x_3 + J_{A,11} r_1 - J_{A,12} r_2) - I_E)}} = 0 \tag{65}$$

$$r_2 - \frac{c_E(x_2 - x_4 + J_{A,22} r_2 - J_{A,21} r_1) - I_E}{1 - e^{-g_E(c_E(x_2 - x_4 + J_{A,22} r_2 - J_{A,21} r_1) - I_E)}} = 0 \tag{66}$$

Equations 65 and 66 define a system which we can numerically solve for different sets of the variables x_1, x_2, x_3, and x_4. We then fit r_1 and r_2 with an equivalent transfer function, which depends on the new variables:

$$\begin{aligned} r_1 &= \Lambda_1 (x_1, x_2, x_3, x_4) \\ &= \frac{a\left(J_{A,11}\right) x_1 - f_A\left(J_{A,12}, x_2 - x_4\right) - e\left(J_{A,11}\right) x_3 - b\left(J_{A,11}\right)}{1 - e^{-d(J_{A,11})\left(a(J_{A,11})x_1 - f_A(J_{A,12}, x_2 - x_4) - e(J_{A,11})x_3 - b(J_{A,11})\right)}} \end{aligned} \tag{67}$$

$$\begin{aligned} r_2 &= \Lambda_2 (x_1, x_2, x_3, x_4) \\ &= \frac{a\left(J_{A,22}\right) x_2 - f_A\left(J_{A,21}, x_1 - x_3\right) - e\left(J_{A,22}\right) x_4 - b\left(J_{A,22}\right)}{1 - e^{-d(J_{A,22})\left(a(J_{A,22})x_2 - f_A(J_{A,21}, x_1 - x_3) - e(J_{A,22})x_4 - b(J_{A,22})\right)}} \end{aligned} \tag{68}$$

where $J_{A,11} = J_{A,22}$, $J_{A,12} = J_{A,21}$ and

$$a = 239400 \cdot J_{A,11} + 270 \text{ (Hz/nA)} \tag{69}$$

$$b = 97000 \cdot J_{A,11} + 108 \text{ (Hz)} \tag{70}$$

$$d = -30 \cdot J_{A,11} + 0.154 \quad \text{(s)} \tag{71}$$

$$e = 301000 \cdot J_{A,11} + 270 \text{ (Hz/nA)} \tag{72}$$

$$f_A(J_{A,12}, y) = J_{A,12}\left(-276y + 106\right)\theta(y - 0.4) \text{ (Hz)} \tag{73}$$

where $\theta(x)$ is the Heaviside function. Note that the parameters *a*, *b*, *d*, and the function f_A are the same as in the two-variable reduced model of Wong and Wang, 2006, supplementary information D) where there is no spike-frequency adaptation in the neurons ($x_3 = x_4 = 0$). In that case, our four-variable reduced model coincides with the two-variable reduced model of Wong and Wang, 2006. In order to also consider spike-frequency adaptation, we included parameter *e*, which we approximated as linearly dependent on $J_{A,11}$ with parameters chosen to fit the numerical solutions. In **Figure 5A**, the average firing rate of population 1 is plotted as a function of x_1 by numerically solving Eq. 65 (line), and by fitting Eq. 67 (circles). In **Figure 5B** the average firing rate of population 1 is plotted as a function of x_1 for different couplings through AMPA synapses (from right to left: $J_{A,11} = J_{A,22} = 0, 0.0005, 0.001, 0.0015$ nA). As the couplings $J_{A,11}$, $J_{A,22}$ increase, the gain of the effective transfer function also does. The effective transfer functions Λ_1, Λ_2 do not change no matter how the network parameters (recurrent connectivities, synaptic conductances, stimulus strength) change.

Finally, our four-variable reduced rate model is given by Eqs 67, 68, 61–64, 35–38, and 60. The noise terms $I_{\text{noise},1}$, $I_{\text{noise},2}$ were included in the variables x_1, x_2 respectively.

Parameters and simulations

In the simulations in the Results, the recurrent connectivity weight used was $w_+ = 1.68$, and, hence, from Eqs 41–59, we find $\lambda' = 26.6$ mV, $\kappa' = 31.11$ mV, $I_0 = 0.3553$ nA, $J_{A,11} = J_{A,22} = 9.5402 \times 10^{-4}$ nA/Hz, $J_{A,12} = J_{A,21} = 7.1258 \times 10^{-5}$ nA/Hz, $J_{N,11} = J_{N,22} = 0.1497$ nA, $J_{N,12} = J_{N,21} = 0.0276$ nA, and $J_{A,\text{ext}} = 2.2428 \times 10^{-4}$ nA/Hz. The only parameter that we slightly changed is the external background input I_0, i.e., We used $I_0 = 0.3536$ nA in order to amplify the basin of attraction of the two unstable fixed points in the absence of stimulus and zero neuronal adaptation strength.

The mean firing rate of the two competing populations were calculated by averaging r_1 (or r_2) over a time window of 50 ms, which was sliding every 5 ms. For the numerical integration of the differential equations, we used the Euler method with a time step of 0.5 ms. The analysis of the output of the simulations is described in the Results. For the spiking simulations, we used C++ programming, for the four-variable reduced model simulations MATLAB, and for the bifurcation diagrams XPPAUT (Ermentrout, 1990).

EXPERIMENTAL DATA

During the psychophysical experiment, subjects were presented with flickering (at 18 Hz) orthogonal sinusoidal gratings to the two eyes. The gratings (spatial frequency 2.5 cycles per degree, contrast 20%) were foveally presented on independently linearized

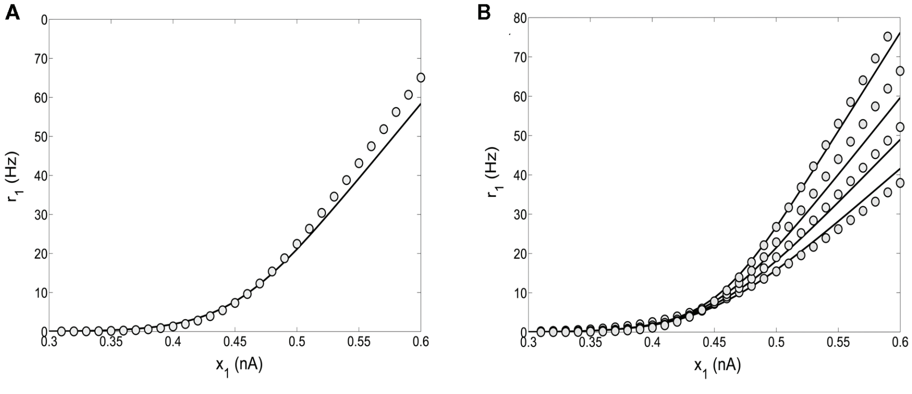

FIGURE 5 | (A) Input–output function of population 1: the line is numerical solution of Eq. 65 and the circles are fit of the effective transfer function Eq. 67. **(B)** Numerical solutions (lines) and fits (circles) as in 5A for different couplings through AMPA synapses: from right to left $J_{A,11} = J_{A,22} = 0$, 0.0005, 0.001, 0.0015 nA/Hz.

monitors facing each other (resolution 1024 × 768 at 72 Hz). The subjects viewed the gratings through a set of angled front-surfaced silver-coated mirrors in a black shielded setup (viewing distance: 118 cm). Typically, subjects underwent 5–10 observation periods. Each observation period consisted of a rivalrous stimulation that lasted 100 s, with an interval of about 20 s between each observation period. During the rivalry period, subjects responded by pressing buttons to report the perceived orientation of the grating or released the buttons when a piecemeal pattern was perceived. Sometimes, multiple datasets were collected on different days from the same subject. From the data collected in each observation period, we calculated the mean dominance time, the coefficient of variation and gamma's distribution parameters λ and r after fitting to the distribution of dominance periods:

$$f(x) = \frac{\lambda^r}{\Gamma(r)} x^{r-1} e^{-\lambda x}, \quad \Gamma(r) = \int_0^{\infty} t^{r-1} e^{-t}\, dt \tag{74}$$

where r is positive real number. Then, for each subject we averaged over all its observation periods. Mean time dominances (Td) ranged between 2.01 and 3.56 s. Coefficient of variations (CV) ranged between 0.418 and 0.704 and the gamma parameter r ranged between 2.251 and 5.446. The range of these values is what we took into account to constrain our model.

RESULTS

In a recent study, and in order to reproduce experimental data of perceptual bistability, both noise and adaptation mechanisms were implemented in a common framework. It was shown that the working point of the model, is at the edge of the bifurcation where the system transits from noise-driven switches to adaptation-driven oscillations (Shpiro et al., 2009). Here, we come to the same conclusion with our biologically realistic reduced rate model, and we study the effect of adaptation in inhibition.

We started by considering spike-frequency adaptation to all neurons, excitatory pyramidal, and inhibitory interneurons. We found that the model replicates the experimental data in a parametric region, where both noise and neuronal adaptation contribute almost in balance. Then, we tested the same for the case where there is no spike-frequency adaptation to the inhibitory interneurons of the network. Our results show that the system still operates near the bifurcation. However, when interneurons are not adapted, a stronger level of adaptation to the excitatory neurons is necessary for the bifurcation to occur. Furthermore, adaptation of interneurons has a striking effect on the spontaneous state in the absence of stimulus. We found that in the absence of stimulus, if interneurons are adapted, the system transits to an oscillatory regime, while if interneurons are not adapted, it does not. Finally, for the parameters for which the model replicates the experimental data we show that it reproduces Levelt's fourth and second revised proposition.

SPIKE-FREQUENCY ADAPTATION TO ALL NEURONS OF THE NETWORK

Bifurcation diagrams

In the original biologically realistic spiking neuronal network presented in the methods, all excitatory pyramidal neurons and inhibitory interneurons include spike-frequency adaptation. The reduction to the four-variable rate model was derived considering this condition. In **Figures 6A,B**, we show the bifurcation diagrams where the steady states of the average synaptic gating variable of one of the two neuronal populations are plotted, in the noise-free case, as a function of the level of spike-frequency adaptation, in the absence of stimulus and upon stimulus respectively. The same bifurcation diagrams stand for the other neuronal population due to symmetry in the network. Eqs 39 and 40 indicate that when interneurons include spike-frequency adaptation, there is an additional input to the selective populations due to the term:

$$\kappa \times \mathrm{Ca_I} = g^{\mathrm{E}}_{\mathrm{gaba}} \times (-V_{\mathrm{I}}) \times \left(\frac{\tau_{\mathrm{gaba}}}{1000}\right) \times C_{\mathrm{I}} \times \frac{(c_{\mathrm{I}})}{(\eta \times g_{12})} \times (-V_{\mathrm{K}}) \times \widetilde{g_{\mathrm{ahp}}} \times \mathrm{Ca_I} \tag{75}$$

In the absence of external stimulus via a supercritical Hopf-bifurcation, this additional input brings the system to a transition (at $g_{\mathrm{ahp}} = 11.2$ nS) from a stable low firing rate regime to an oscillatory one. At a higher level of adaptation ($g_{\mathrm{ahp}} = 52.5$ nS) the system returns to a new steady state of higher firing rate via another supercritical Hopf-bifurcation. At low levels of adaptation the steady state coexists with two stable and two unstable steady states which disappear in a fold bifurcation at $g_{\mathrm{ahp}} = 1.4$ nS (not shown). In the bifurcation diagrams, stable steady states are represented by thick lines, and unstable ones by thin lines. The branched curves of circles show the maximum and the minimum oscillation amplitudes of one of the two selective populations when circles are filled. Open circles correspond to unstable oscillations.

In **Figures 6C,D**, the nullclines $dS_1(t)/dt = 0$, $dS_2(t)/dt = 0$ (whose intersections are the steady states of the system) are plotted in the (S_1, S_2) phase-space of the model, for zero spike-frequency adaptation ($g_{\mathrm{ahp}} = 0$ nS). When neurons do not include spike-frequency adaptation, the phase-spaces of the model resemble the one of the two-variable reduced model (Wong and Wang, 2006). In the absence of stimulus, there are five fixed points (three stable and two unstable) and the system lies in the lower left fixed point where neurons fire at the same low rates (**Figure 6C**). When external stimulus is applied to both populations, the phase-space and the bifurcation diagram (at $g_{\mathrm{ahp}} = 0$) reconfigure (**Figures 6B,D**). The input here is $\lambda_1 = \lambda_2 = 40$ Hz. The two asymmetrical attractors are separated by an unstable steady state (saddle node), and the system is in a bistability regime. In **Figure 6B**, as the level of adaptation increases, the system first transits to a mixed-mode oscillations regime (Curtu, 2010) at $g_{\mathrm{ahp}} = 7.7$ nS and later to a stable one via two subcritical Hopf-bifurcations at $g_{\mathrm{ahp}} = 7.8$ nS. Finally, at $g_{\mathrm{ahp}} = 44.5$ nS, the system transits to a stable steady state via a supercritical Hopf-bifurcation.

Replicating experimental data

Keeping in mind the bifurcation diagrams, we simulated our reduced four-variable rate model by applying the same stimulation protocol as in the experiment. The input to both populations was $\lambda_1 = \lambda_2 = 40$ Hz. For each level of neuronal adaptation, i.e., peak conductance of the Ca^{2+}-activated K^{+} channels, g_{ahp}, we applied this stimulus for 100 s. We then calculated the mean Td of the two percepts, and the coefficient of variation. After fitting the distribution of Td to a gamma distribution, we calculated the parameter r (Eq. 74). In order to mimic the experimental protocol that each subject underwent, for each g_{ahp}, we performed 10 such

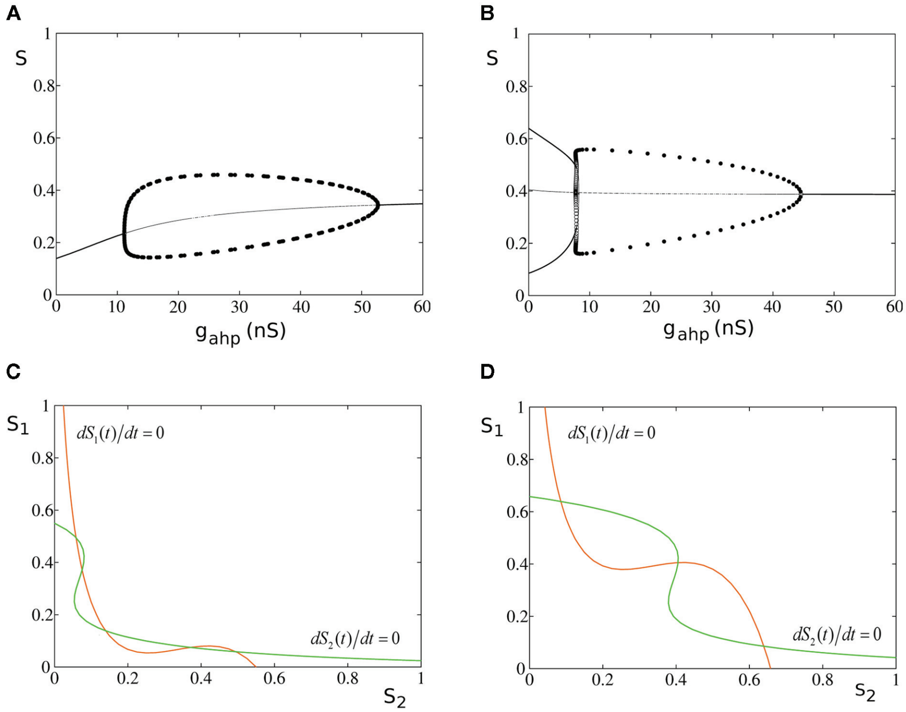

FIGURE 6 | Spike-frequency adaptation to all neurons of the network. (A) Bifurcation diagram in the absence of stimulus. Stable steady states are represented by thick lines while unstable ones by thin lines. Filled circles are the maximum and the minimum amplitudes of stable oscillations. Open circles correspond to unstable oscillations. **(B)** Bifurcation diagram in the presence of stimulus $\lambda_1 = \lambda_2 = 40$ Hz **(C)**. (S_1, S_2) phase-space in the absence of neuronal adaptation and in the absence of stimulus. The nullclines of the synaptic gating variables S_1 and S_2 are the green and orange lines respectively, and their intersections define the stable and unstable steady states. **(D)** (S_1, S_2) phase-space in the absence of neuronal adaptation but in the presence of stimulus.

trails, and computed the average values of mean Td, the coefficient of variation and the r parameter from the gamma distribution fit over these trials. Finally, we did the same with different levels of noise. One dominance period was defined as the time starting when the difference in the firing rates of the two populations was 5 Hz and ended when it became zero. In **Figure 7A**, we present the mean Td, and the coefficient of variation for five levels of noise as a function of neuronal adaptation, g_{ahp}. In **Figure 7B**, the r parameter from the gamma distribution fit is plotted as a function of level of neuronal adaptation and for the same levels of noise. The horizontal lines denote the range that the experimental data define. Vertical lines in **Figures 7A,B** are drawn at the bifurcation points where the system transits from a bistable dynamical regime to an oscillatory one, as presented in the corresponding bifurcation diagram (**Figure 6B**). We are looking for the level of noise and of adaptation at which the model results reside in the range of values defined by the experimental data. The green big circle denotes such levels ($g_{\text{ahp}} = 6.2$ nS, $n = 0.016$), and in **Figure 7C**, we plot the mean firing rates of both populations at these levels in the absence (black and green plots) and upon (blue and red plots) stimulus. For these parameters, the mean Td = 3.24 s, the coefficient of variation is CV = 0.457, and $r = 2.841$.

From our results, it is apparent that both noise and adaptation are the driving forces for the alternations in BR. The working point of our model is in the bistability regime and close to the bifurcation toward the oscillatory. Noise and adaptation contribute almost in balance to the perceptual alternations. At this point, we should note that the level of noise necessary for the model to replicate the experimental data is high enough to drive the system into the oscillatory regime (**Figure 6A**) in the absence of stimulus as one can see in **Figure 7C** (black and green plots).

Moreover, in **Figure 7D**, we plot the mean firing rates of the selective neuronal populations as we compute them by simulating the spiking network with $N = 500$ total neurons, and with the same parameters we used to plot **Figure 7C**. Thin red and blue plots correspond to the activity of the selective populations upon stimulus, and thin black and gray plots to their activity in the absence of stimulus, while thick plots are the corresponding activity after smoothing with a time window of 500 ms (sliding every 50 ms). We see that both the spiking and the reduced model exhibit similar behavior in the presence, as well as in the absence, of the stimulus. This means that the approximations we considered for the derivation of our four-variable reduced rate model (see Materials and Methods) are accurate. In addition, for these parameters, we ran 10 trials of 100 s-stimulation. From the smoothed mean firing rates, we computed the average mean Td, coefficient of variation, and r parameter from the gamma distribution fit to the distribution of the Td at each of the 10 trials, as we did with the reduced model. We found mean Td = 2.82 s, mean coefficient of variation CV = 0.582 and $r = 3.137$. These values reside in the range defined by the experimental data, similarly as we found with the reduced model.

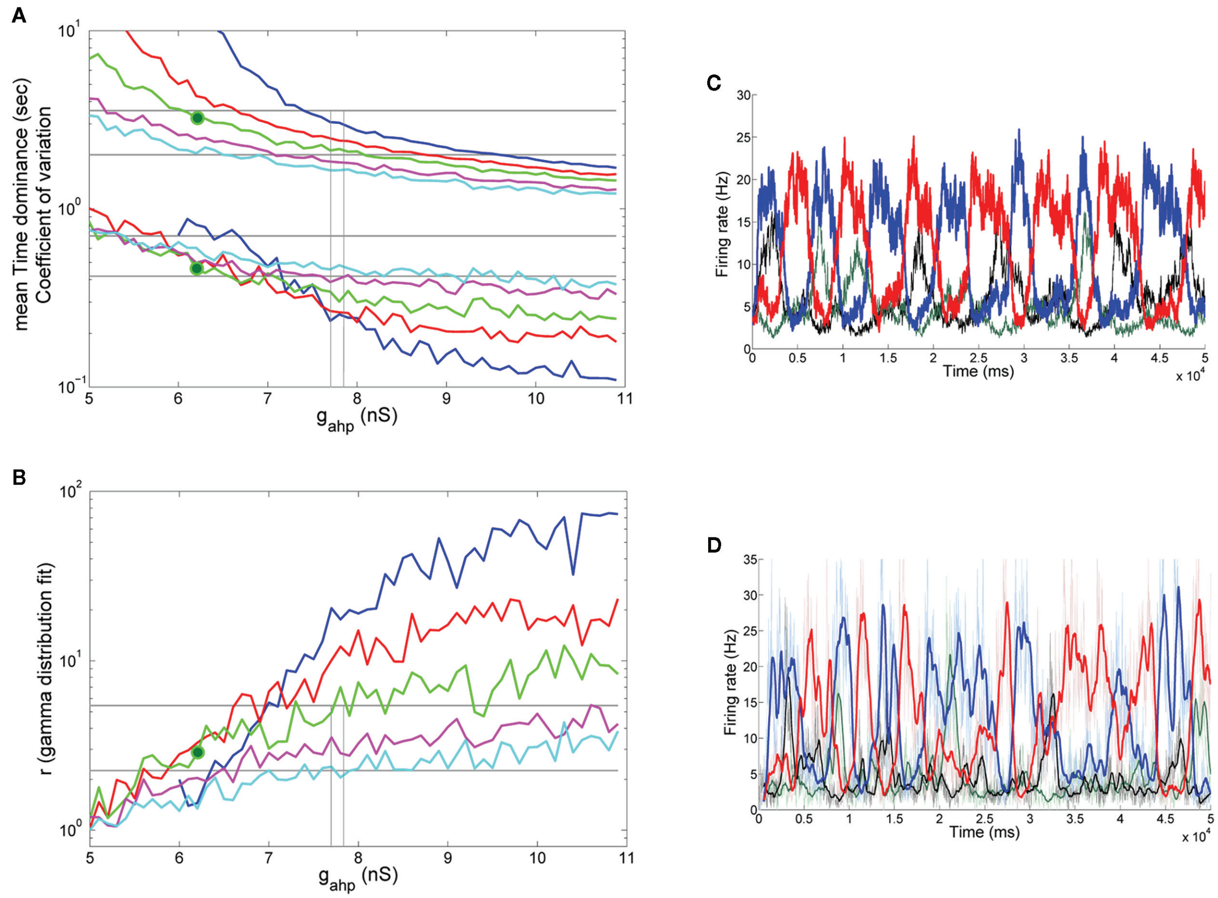

FIGURE 7 | Spike-frequency adaptation to all neurons of the network: Replicating the experimental data (A) Mean time dominance and coefficient of variation as a function of neuronal adaptation for different levels of noise (blue: $n = 0.01$, red: $n = 0.014$, green: $n = 0.016$, magenta: $n = 0.018$ and celestial: $n = 0.019$) for $\lambda_1 = \lambda_2 = 40$ Hz. (B) Parameter r of gamma distribution fit to the distribution of dominance times as a function of neuronal adaptation for the same noise levels as in **(A)**. In both **(A,B)**, horizontal lines denote the range that the experimental data define. Vertical lines are drawn at the bifurcation points where the system transits from a bistable dynamical regime to a mixed-mode oscillations and to an oscillatory regime. Green big circles at the levels $g_{\text{ahp}} = 6.2$ nS, $n = 0.016$ indicate a case where the model replicates the experimental data. We find that the model replicates the experimental data in the noise-driven regime and close to the bifurcation. **(C)** The mean firing rate of the selective populations for $g_{\text{ahp}} = 6.2$ nS and $n = 0.016$ in the absence of stimulus (black and green plots) and upon stimulus (blue and red plots). **(D)** The mean firing rate of the selective neuronal populations by simulating the spiking network (with $N = 500$ neurons) with the same parameters as the ones used simulating the reduced model **(C)**. Thin lines are plots from a trial and thick lines are the same after smoothing. We see that both models exhibit similar behavior in both the presence (blue and red plots) and absence (black and green plots) of the stimulus.

Finally we computed the bifurcation point, where the model transits to the mix-mode oscillatory regime, employing the spiking network. The total number of neurons used was $N = 20000$ in order to decrease the noise in the network as much as possible. The bifurcation point is at $g_{\text{ahp,bif,spiking}} = 6$ nS, close to the bifurcation point found with the reduced model ($g_{\text{ahp,bif,reduced}} = 7.7$ nS). The $g_{\text{ahp,bif,reduced}}$ is higher than the $g_{\text{ahp,bif,spiking}}$ due to the assumptions adopted in the Methods but mostly to the advantage of the reduced model to eliminate noise which cannot be done in the spiking network.

Furthermore, we tested the effect of increasing the external stimulus strength ($\lambda_1 = \lambda_2 = 50$ Hz) which would correspond to an increase of the stimulus contrast in the experiment. The rest of the parameters were the same as before, as well as the stimulation protocol and analysis. In **Figures 8A,B** (thick lines), we present the results for the same levels of noise, as in **Figures 7A,B**. We also plot the results for $\lambda_1 = \lambda_2 = 40$ Hz (thin lines) for comparison. Levelt's fourth proposition indicates that increasing the stimulus contrast results in an increase of the average rivalry reversal rate (Levelt, 1968), which corresponds to a decrease in the average dominance duration. This is apparent in **Figure 8A** for all levels of neuronal adaptation and of noise. In addition, by increasing the strength of the external stimulation, the bifurcation points (vertical lines) shift to lower values, while the mixed-mode oscillations regime narrows. Nevertheless, the model's results (Td = 2.49 s, CV = 0.457, and $r = 2.825$) reside again in the ranges defined by the experimental data, while working in the bistable regime (big red circle: $g_{\text{ahp}} = 5.4$ nS, $n = 0.014$) and close to the bifurcation point $g_{\text{ahp,bif,reduced}} = 5.8$ nS. Once more, for the same parameters, we simulated the spiking network (with $N = 1000$ neurons),

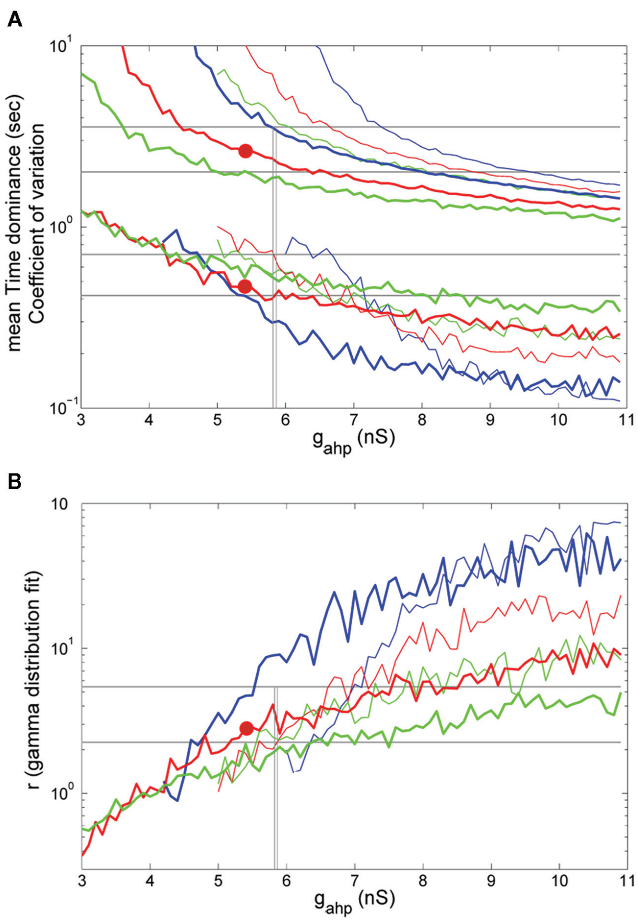

FIGURE 8 | (A) Mean time dominance and coefficient of variation as a function of neuronal adaptation for different levels of noise (blue: $n = 0.01$, red: $n = 0.014$ and green: $n = 0.016$) for $\lambda_1 = \lambda_2 = 40$ Hz (thin lines) and $\lambda_1 = \lambda_2 = 50$ Hz (thick lines). **(B)** Parameter r of gamma distribution fit to the distribution of dominance times as a function of neuronal adaptation for the same levels of noise as in **(A)**. In both **(A,B)**, horizontal lines denote the range that the experimental data define. Vertical lines are drawn at the bifurcation points where the system transits from a bistable dynamical regime to a mixed-mode oscillations and to an oscillatory regime. Red big circles at $g_{ahp} = 5.4$ nS, $n = 0.014$ indicate a case for which the model replicates the experimental data.

and found Td = 3.298 s, CV = 0.462, and $r = 3.975$. These values are close to the ones computed with the reduced model and inside the range of the experimental data. The bifurcation point as calculated by simulating the spiking network with $N = 20000$ total neurons, is at $g_{\text{ahp,bif,spiking}} = 4.3$ nS.

SPIKE-FREQUENCY ADAPTATION ONLY TO THE EXCITATORY PYRAMIDAL NEURONS OF THE NETWORK

Bifurcation diagrams

We removed neuronal adaptation from interneurons by setting $\kappa = 0$ in Eqs 63 and 64. The rest of the parameters of the model remained the same. We note that when interneurons are not adapted, the mean firing rate of the non-selective population and the mean firing rate of the inhibitory population decrease for higher adaptation strengths. Here, we again assume that the mean firing rate of the non-selective population is constant in all conditions, as we had assumed in the case of adapted interneurons (see Constant Activity of Non-Selective Excitatory Neurons of Materials and Methods). In addition, and for simplicity, we kept the same parameters of the linearization of the input–output formula (Eq. 30) as in the case of adapted interneurons. In the following we show that these assumptions do not change the results much.

In **Figure 9**, we present the bifurcation diagram of one of the two neuronal populations in the absence and in the presence of an external stimulus employing our four-variable reduced rate model. The same bifurcation diagrams also stand for the other population due to symmetry. While in the presence of a stimulus, the bifurcation diagram (**Figure 9B**) is qualitatively similar as in the case where we included spike-frequency in interneurons (**Figure 6B**), the bifurcation diagram is qualitatively different in the absence of external stimulus (**Figure 9A** compared to **Figure 6A**). Here, there is no additional input (Eq. 75) to the excitatory populations and the system remains in a stable steady state of low firing rate which decreases as level of neuronal adaptation increases (**Figure 9A**). We note that, as in the case where all neurons are adapted, at low levels of adaptation the steady state coexists with two stable and two unstable steady states which disappear in a fold bifurcation at $g_{\text{ahp}} = 0.36$ nS (not shown).

In **Figure 9B**, stable steady states are represented by thick lines, and unstable ones by thin lines. Filled circles correspond to the maximum and minimum values of stable oscillations, while open circles correspond to unstable oscillations. Upon stimulus presentation, $\lambda_1 = \lambda_2 = 50$ Hz, and at $g_{\text{ahp}} = 0$, the system transits from a stable steady state of low firing rate to a winner-take-all regime, where one of the populations fires at high rate while the other fires at low rate. The system reaches the attractor and lies in a bistability regime. Without noise, the system would remain in this attractor, being unable to transit to its anti-symmetrical (i.e., switches in perception are not possible). As adaptation increases, the basin of attraction decreases, and switches are more likely to occur upon noise introduction. Nevertheless, higher levels of adaptation drive the system into an oscillatory regime where, even in the absence of noise, alternations from one percept to the other are inevitable. More specifically, starting at high values of g_{ahp}, the system lies in a stable steady state where both populations fire at low firing rate. As g_{ahp} decreases, the system transits to a stable oscillatory regime via a supercritical Hopf-bifurcation at $g_{\text{ahp}} = 14.2$ nS. At $g_{\text{ahp}} = 9.96$ nS, the system transits into a mixed-mode oscillations regime (Curtu, 2010) via two subcritical Hopf-bifurcations. The big unstable periodic orbit coalesces with the stable periodic orbit at $g_{\text{ahp}} = 9.57$ nS, via a double limit cycle bifurcation, and the system transits to the bistability regime where two anti-symmetric attractors are separated by a saddle node fixed point. At $g_{\text{ahp}} = 11.2$ nS, the trajectories of the three unstable fixed points coalesce into an unstable fixed point via a subcritical pitch-fork bifurcation. This cumbersome dynamics of the mixed-mode oscillations regime, although very interesting, is beyond the scope of the present study. The dynamics of our model has similar characteristics as described in Shpiro et al. (2007), Curtu et al. (2008), Curtu (2010). A point to note is that, in our case, we also have recurrent excitation resulting in an asymmetry between regimes

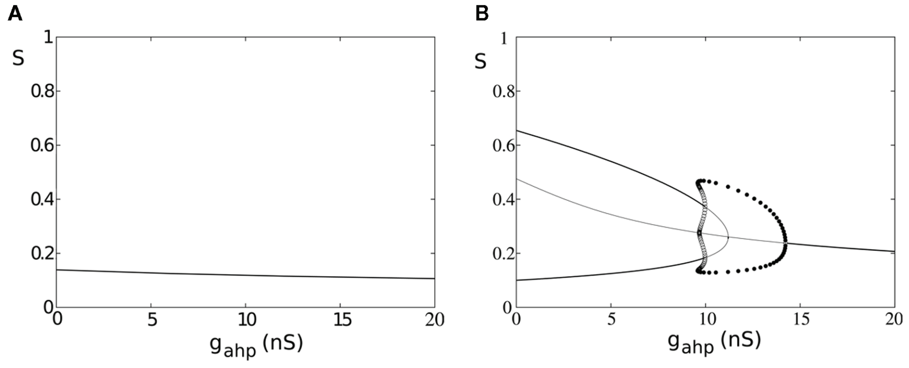

FIGURE 9 | Spike-frequency adaptation only to the excitatory pyramidal neurons of the network. (A) Bifurcation diagram in the absence of stimulus, stable steady states are represented by thick lines while unstable ones by thin lines. Filled circles are the maximum and the minimum amplitudes of stable oscillations. Open circles correspond to unstable oscillations. **(B)** Bifurcation diagram in the presence of stimulus $\lambda_1 = \lambda_2 = 50$ Hz.

of release and escape mechanisms with the release regime being small due to the recurrent connectivity in the network (Shpiro et al., 2007; Seely and Chow, 2011).

Replicating experimental data

We saw previously that when inhibitory interneurons are adapted, both noise and adaptation are responsible, almost in balance, for the perceptual alternations. Here, we follow the same stimulation protocol and analysis, as in Section "Replicating Experimental Data," for the case where inhibitory interneurons are not adapted. With the bifurcation diagram (**Figure 9B**) in mind, we applied the same fixed external stimulus to both populations, $\lambda_1 = \lambda_2 = 50$ Hz. We then computed the mean Td, the coefficient of variation and the r parameter of the gamma distributions fit to the distributions of dominance times, as a function of neuronal adaptation, at different levels of adaptation and of noise. The rest of the parameters are the same except for the exclusion of spike-frequency adaptation from interneurons by setting $\kappa = 0$ in Eqs 63 and 64. The results are presented in **Figure 10**. Different lines correspond to different noise levels. Horizontal lines denote the range that the experimental data define. Vertical lines are drawn at the bifurcation points which define the different dynamical regimes.

In **Figures 10A,B**, big blue ($g_{\text{ahp}} = 9.7$ nS, $n = 0.01$), red ($g_{\text{ahp}} = 9$ nS, $n = 0.014$), green ($g_{\text{ahp}} = 8.8$ nS, $n = 0.016$), and celestial ($g_{\text{ahp}} = 8.2$ nS, $n = 0.019$) circles are sets of parameters for which all three mean Td, coefficient of variation, and r parameter reside in the range defined by the experimental data. We find that, in all these cases, the model is in the bistability regime and near to the bifurcation point. We note that it is also possible that for a given noise-level ($n = 0.01$, blue big circle), experimental data are replicated inside the mixed-mode oscillations regime. In **Figure 10C**, we plot the mean firing rates of the two neuronal populations when level of noise is $n = 0.014$, and adaptation strength is $g_{\text{ahp}} = 9$ nS (red big circle in **Figures 10A,B**) in two conditions: in the absence of stimulus (black and green plots) and upon stimulus (blue and red plots). We see that when interneurons are not adapted neuronal populations fire at low rates and in an asynchronous state in the absence of stimulus.

Moreover, in **Figure 10D**, we plot the mean firing rates of the two selective neuronal populations, as we compute them by simulating the spiking network with $N = 500$ total neurons, and with the same parameters we used to plot **Figure 10C**. As in the case where we considered adapted inhibitory interneurons (**Figures 7C,D**), both models behave similarly in the presence and in the absence of the stimulus, indicating that the assumptions adopted for the reduction are accurate. In addition, we computed the mean Td, the coefficient of variation and the r parameter from the gamma distribution fit to the distribution of the Td simulating the spiking network (as we did in section Replicating Experimental Data). We found that the results were in the range defined by the experimental data. More specifically, we found Td = 2.64 ms, CV = 0.463, and $r = 5.147$, similar to the ones we attained with the reduced model for the same parameters (Td = 3.29 ms, CV = 0.581, and $r = 4.992$). Finally, we computed the bifurcation point by simulating the spiking network with $N = 20000$ neurons, and we found that the bifurcation point is at $g_{\text{ahp,bif,spiking}} = 8.3$ nS, close to the bifurcation point we observed with the reduced model ($g_{\text{ahp,bif,reduced}} = 9.57$ nS). As in the case where inhibitory interneurons are also adapted, the $g_{\text{ahp,bif,reduced}}$ is higher than the $g_{\text{ahp,bif,spiking}}$. This is a consequence of the assumptions adopted for the derivation of the reduced model, as well as of the noise in the spiking network which cannot be totally eliminated.

Furthermore, in **Figure 11**, we plot the mean Td and the coefficient of variation for the two extreme cases, i.e., all interneurons are all (gray lines) or none (black lines) adapted. We plot the results from the simulations where in both cases the stimulus strength is $\lambda_1 = \lambda_2 = 50$ Hz and the level of noise is $n = 0.014$. We see that by removing spike-frequency adaptation mechanism from interneurons, mean dominance duration and its coefficient of variation increase for the same level of neuronal adaptation to the excitatory neurons. The bifurcation points, where the model transits from noise-driven switches to adaptation-driven oscillations, shifts to higher values of g_{ahp}. At the same time, the level of adaptation for which the model replicates the experimental data also increases

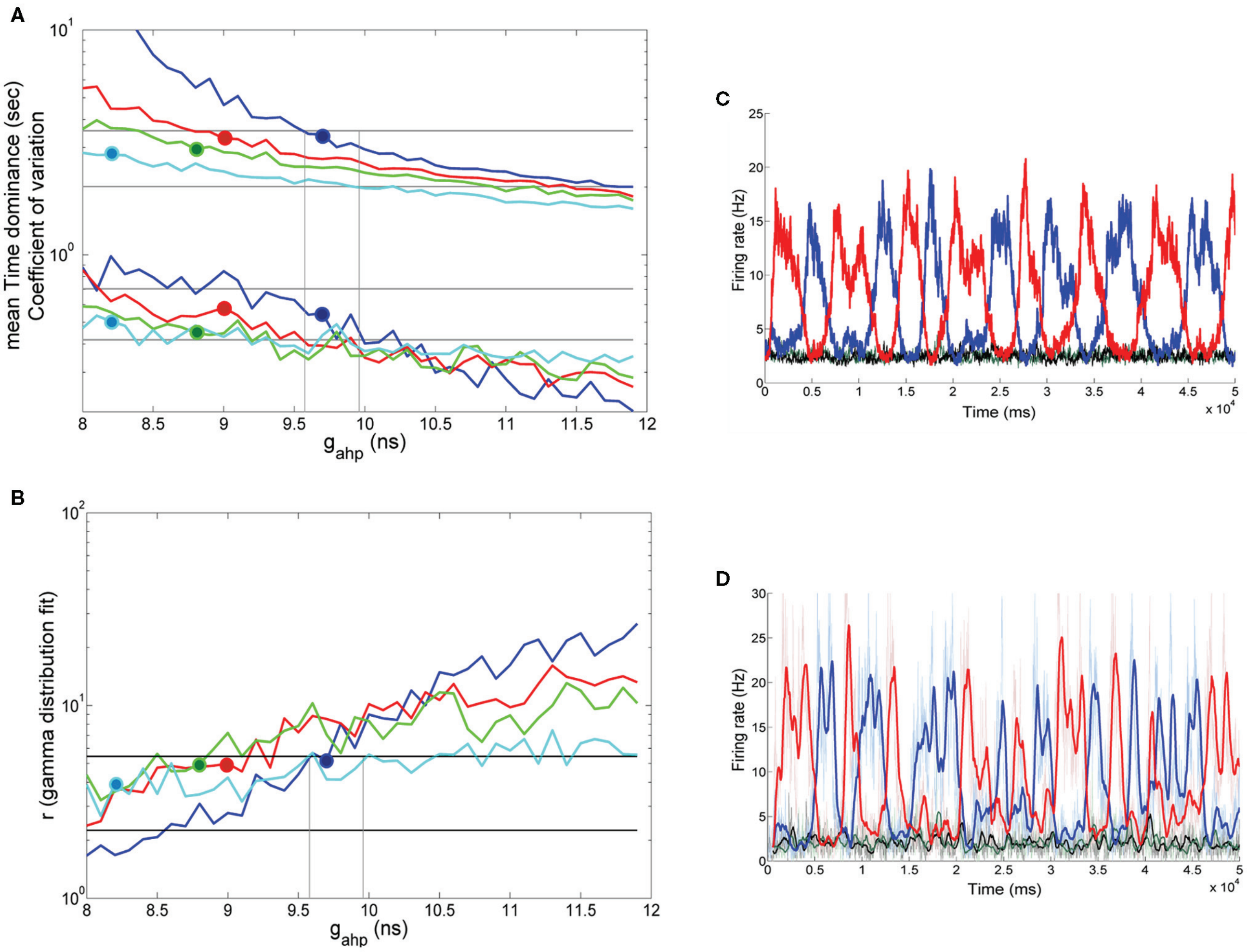

FIGURE 10 | Spike-frequency adaptation only to the excitatory pyramidal neurons of the network: Replicating the experimental data. (A) Mean time dominance and coefficient of variation as a function of neuronal adaptation for different levels of noise (blue: $n = 0.01$, red: $n = 0.014$, green: $n = 0.016$, and celestial: $n = 0.019$) for $\lambda_1 = \lambda_2 = 50$ Hz. **(B)** Parameter r of gamma distribution fit to the distribution of dominance times as a function of neuronal adaptation for the same levels of noise as in **(A)**. In both **(A,B)**, horizontal lines denote the range that the experimental data define. Vertical lines are drawn at the bifurcation points where the system transits from a bistable dynamical regime to a mixed-mode oscillations and to an oscillatory regime. Blue, red, green, and celestial big circles at $g_{\text{ahp}} = 9.7$ nS, $g_{\text{ahp}} = 9$ nS, $g_{\text{ahp}} = 8.8$ nS, and $g_{\text{ahp}} = 8.2$ nS, respectively indicate sets of parameters for which the model replicates the experimental data. We find that the model operates in the bistability regime close to the bifurcation as well as in the mixed-mode oscillation regime (blue big circle). **(C)** The mean firing rate of the populations for $g_{\text{ahp}} = 9$ nS and $n = 0.014$ in the absence of stimulus (black and green plots) and upon stimulus (blue and red plots). **(D)** The mean firing rate of the selective neuronal populations by simulating the spiking network (with $N = 500$ neurons) with the same parameters as the ones used in **(C)**. Thin lines are plots from a trial, and thick lines are the same after smoothing. We see that both models exhibit similar behavior in both the presence (blue and red plots) and in the absence (black and green) of the stimulus.

but resides in both cases within the bistability regime and close to the bifurcation.

LEVELT'S SECOND REVISED AND FOURTH PROPOSITION

Levelt's four propositions in BR (Levelt, 1968) exemplify how stimulus parameters affect the duration of perception of two conflicting images. These propositions define additional constrains to computational models candidates to explain BR. Most of the times, computational models were tested with Levelt's second and fourth proposition. Recently, Levelt's second proposition has been revised (Brascamp et al., 2006) and states that, when the contrast of one image changes the average dominance duration of the image with higher contrast is mainly affected. Levelt's fourth proposition states that when the contrast of both images increases, the average rivalry reversal rate increases, meaning that the mean Td of both images decreases.

Here, we tested Levelt's second revised proposition for four sets of noise and neuronal adaptation levels (big blue, red, green, and celestial circles in **Figures 10A,B**) for which the model's results reside in the ranges defined by the experimental data, when inhibitory interneurons are not adapted. The results are shown in **Figures 12A–C**. In the insets, we tested the same for the case where inhibitory interneurons are adapted with the same level of noise and stimulus strength (big red circle, **Figures 8A,B**) as when

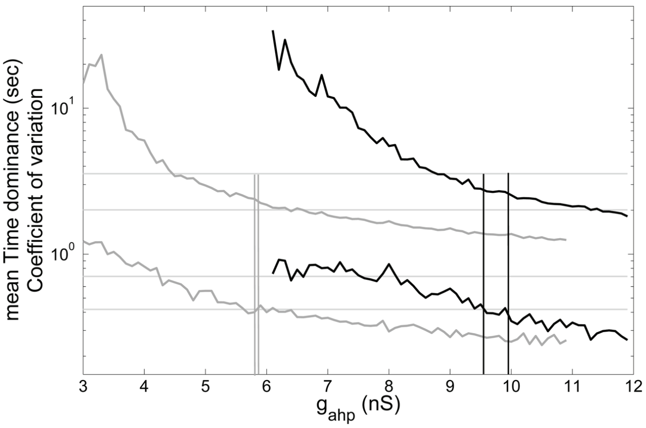

FIGURE 11 | Mean time dominance and coefficient of variation as a function of neuronal adaptation for level of noise $n = 0.014$, when inhibitory interneurons are adapted (gray lines) and when they are not adapted (black lines) for stimulus strength $\lambda_1 = \lambda_2 = 50$ Hz. Gray and black vertical lines define the bifurcation points when inhibitory interneurons are adapted and when they are not, respectively.

they are not adapted. We first applied equal stimulus for 100 s to both populations of low strength, $\lambda_1 = \lambda_2 = 45$ Hz. We then computed the mean dominance durations of each population and we averaged over 10 such trials. Then, we kept the stimulus to one of the populations fixed, $\lambda_1 = 45$ Hz, and we increased the other. The results are shown in **Figure 12A**. In **Figure 12B**, we applied equal stimulus of intermediate strength to both populations, $\lambda_1 = \lambda_2 = 47.5$ Hz, and we computed the mean Td as previously. Then, we kept the stimulus to one population fixed, $\lambda_1 = 47.5$ Hz, and we manipulated the other. Finally, we applied equal stimulus of high strength to both populations, $\lambda_1 = \lambda_2 = 50$ Hz, and computed the mean dominance periods. Then, we kept the stimulus to one of the populations fixed at this high level, $\lambda_1 = 50$ Hz, while we decreased the other (**Figure 12C**). In **Figures 12A–C**, the dashed lines are plots of the mean Td of the population receiving fixed stimulus (λ_1) while solid lines are plots of the mean Td of the population receiving variable stimulus (λ_2). Vertical lines denote the stimulus strength when it is equal to both populations. We see that Levelt's second revised proposition is satisfied by all four levels of neuronal adaptation and noise for which our model replicates the experimental data when inhibitory interneurons are not adapted as well as when they are (insets in **Figures 12A–C**). We should mention though that from Moreno-Bote et al. (2010), we know that alternation rate is higher and symmetric around equidominance, i.e., when external stimulus is equal to both neuronal populations. This would be an additional constrain for the model. In **Figure 12B**, we see that this is not always the case. Nevertheless, in the study by Moreno-Bote et al. (2010), it is shown that models best replicate this result when normalized stimuli are applied, which is not the case here.

In Section "Replicating Experimental Data," we tested Levelt's fourth proposition for two different stimulus strengths in the case where inhibitory interneurons are adapted. Here, we test Levelt's fourth proposition for the case where inhibitory interneurons are not adapted for applied stimulus strengths $\lambda_1 = \lambda_2 = 50,50,55,60$ Hz (**Figure 12D**). Each stimulation lasted 100 s, and at each trial we computed the mean dominance durations of both populations. Finally, we averaged over 10 trials. The level of noise was $n = 0.014$. In **Figure 12D**, we see that as stimulus strength increases mean dominance duration decreases. Thus our model accounts for Levelt's fourth proposition. Note that this decrease is more prominent at low levels of neuronal adaptation and at higher levels of neuronal adaptation mean Td is similar across different stimulus strengths.

DISCUSSION

In the present work, we present a theoretical approach which could provide novel insights into the microcircuit dynamics responsible for multistable perception. We consistently derived a four-variable reduced rate model from a biologically plausible spiking neuronal network, and we tested it considering experimental behavioral data of BR. We calculated the mean dominance duration of the percepts, the coefficient of variation, and the parameters of the gamma distribution fit to the distribution of dominance durations. We emulated the experiment by simulating our reduced model for different sets of noise and neuronal adaptation levels, and we looked for the optimal ones for which the model replicates the experimental data. In the noise-free condition, the range of adaptation strength defines different dynamical regimes where our model can operate. There is a bistability regime, where switches can only arise due to the implementation of noise. There is a mixed-mode oscillations regime which is the transition regime of the model from the bistability to the oscillatory regime. Finally, there is an adaptation-driven oscillatory regime where alternations can happen even without noise. By testing different levels of noise and adaptation strengths, we came to the same conclusion as Shpiro et al. (2009). In order to satisfy the experimental data, the system must operate in the noise-driven regime close to the boundary with the adaptation-driven regime. Thus, both mechanisms are responsible in balance for the perceptual alternations.

It is not the first time that a reduced spiking model is used to explain BR. Laing et al. (2010) recently presented reduced rate-like models derived from a fine scale spiking model consisting of two populations, one excitatory and one inhibitory, of Hodgkin–Huxley type neurons (Laing and Chow, 2002). Neurons are orientation selective, include both spike-frequency adaptation and synaptic depression, and each population can be thought of as lying on a ring. Nevertheless, their reduction is not derived consistently from the spiking network. Instead it is based on both intuition based on observations of the spiking network, and on data-mining tools to select appropriate variables. By processing the results of simulations, the authors determined functions that govern the dynamics of these variables. Our reduced model, on the other hand, is consistently derived from a spiking network using mean-field techniques. In addition, we studied the underlying mechanism responsible for perceptual alternations as Shpiro et al. (2009), and we extended the results by studying the effect of adapting inhibitory interneurons.

The biophysically realistic spiking network, from which we derived the reduced model, has been previously studied for perceptual bistability (Moreno-Bote et al., 2007). Their spiking

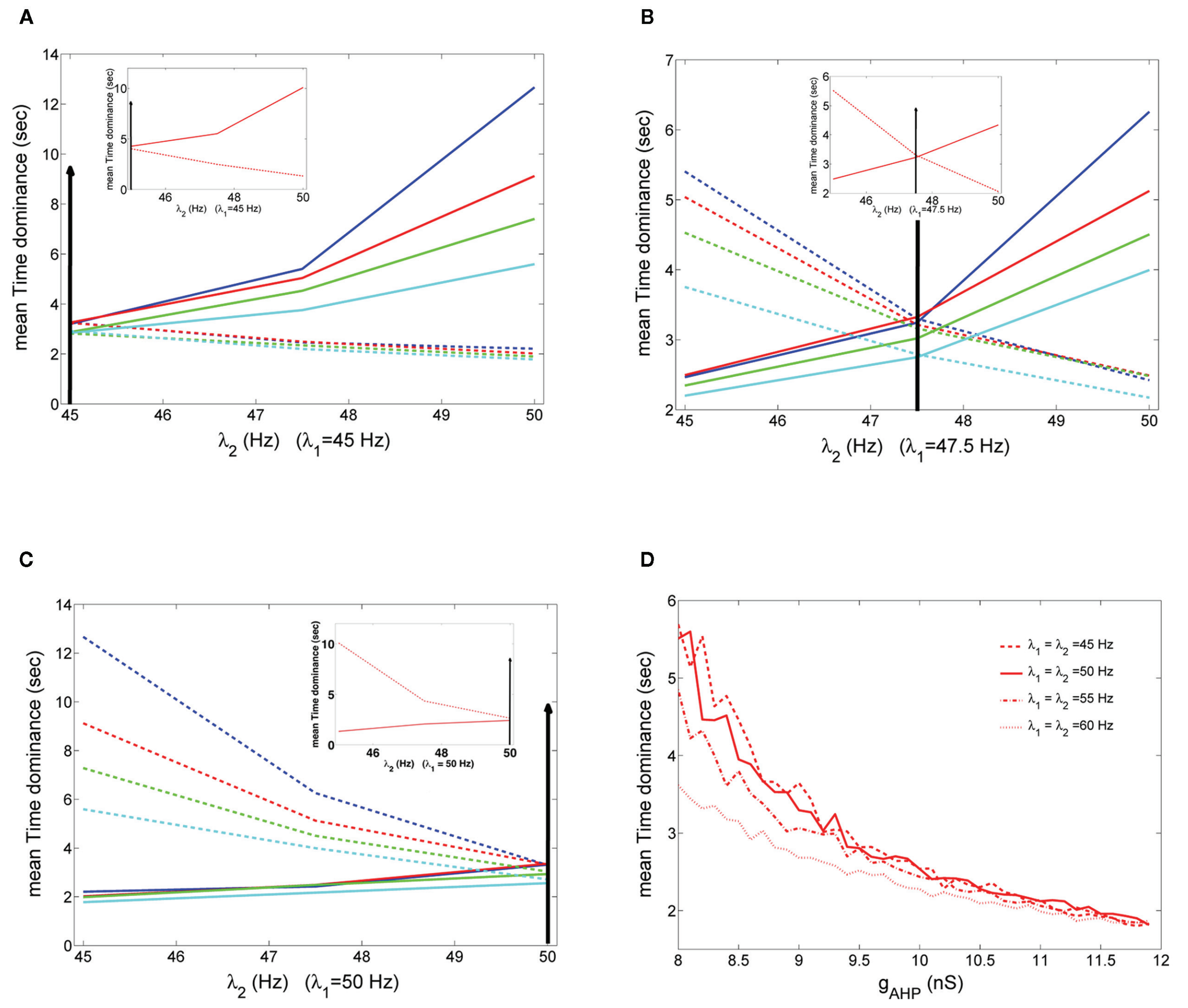

FIGURE 12 | (A–C) Mean time dominance of one of the two neuronal populations of the model receiving fixed stimulus λ_1 (dashed lines) and of the neuronal population receiving variable stimulus λ_2 (solid line), as a function of the variable external stimulus λ_2, for the four noise-adaptation points for which the model replicates the experimental data when interneurons are not adapted (big circles in **Figures 10A,B**). Arrows denote the starting point where both populations receive the same stimulus, $\lambda_1 = \lambda_2$. In the insets the same are plotted for the case where inhibitory interneurons are adapted (red big circle in **Figures 8A,B**). A: when $\lambda_1 = 45$ Hz, **(B)** when $\lambda_1 = 47.5$ Hz and **(C)** when $\lambda_1 = 50$ Hz. **(D)** Mean time dominance of both populations for different stimulus strengths when inhibitory interneurons are not adapted and $n = 0.014$.

network is very similar to ours, but the main difference is that they only include spike-frequency adaptation to excitatory pyramidal cells. Their interesting results show the effect of noise and stimulus strength in the behavior of the network. The novelty of our work is that we implemented a four-variable reduced rate-like model which we derived consistently from a similar biophysically realistic spiking network of thousands of neurons using mean-field techniques. More specifically, we performed a further reduction of the extended mean-field model (Deco and Rolls, 2005). This helps us understand the dynamics of the full original spiking network, which in turn can provide us with numerous data such as realistic synaptic dynamics, spiking time series, local field potentials, etc.

Moreover, we were able to study two extreme cases by including spike-frequency adaptation in all or in none of the network's inhibitory interneurons. Interestingly, we found that, in both cases, our model replicates the experimental data in the boundary between noise and adaptation. We thus conclude that spike-frequency adaptation of inhibitory interneurons is not relevant to the cause of perceptual alternations observed in BR. However, we demonstrate that adaptation of interneurons has an effect on the parametric space where the bifurcation is observed. When interneurons are not adapted, stronger adaptation is necessary in the remaining components of the network to induce a bifurcation. As a result, more adaptation is necessary to obtain the optimal working point of the system.

Additionally, we found that spike-frequency adaptation in interneurons generates different types of spontaneous dynamics. When the interneurons in the spiking network are not adapted, the selective neuronal populations fire asynchronously and at low rates during the spontaneous state. On the other hand, when interneurons are adapted, the model exhibits an oscillatory regime even during the spontaneous state. This type of oscillatory regime has been reported in an attractor memory network (Lundqvist et al., 2010). Here, for the set of parameters for which the model replicates the experimental data, noise is high enough to drive the system into the oscillatory regime in the absence of stimulus, when interneurons are adapted.

Furthermore, adapted inhibitory interneurons affect the reaction time at the onset of a stimulus. In Theodoni et al. (2011), it has been shown that neuronal adaptation accelerates decisions in an adaptation-related aftereffects decision making task. The spiking model studied in that work is similar to the one presented here (when all inhibitory interneurons are adapted). From our four-variable reduced model, we found that when interneurons include spike-frequency adaptation, an additional input to both selective populations is implemented which increases with adaptation strength. This results in a faster ramping activity at higher adaptation strengths, which in turn leads to faster reaction times at the onset of a stimulus. We expect that when interneurons are not adapted, we would have the opposite effect.

We would like to note that we examined two extreme conditions. Either all the inhibitory interneurons of the network are adapted or none of them. Nevertheless, for example in the prefrontal cortex, where neuronal activity follows phenomenal perception (Panagiotaropoulos et al., unpublished data), we know that there are three types of interneurons. Half of them are dendritic-targeting, and the others are divided into interneurons targeting, and perisoma targeting (Conde et al., 1994; Gabbott and Bacon, 1996). Perisoma targeting interneurons do not include spike-frequency adaptation while the rest do include (Wang et al., 2004). In our network neurons are not considered as multi-compartmental, and we cannot distinguish the inhibitory interneurons among these three types. Nevertheless, a more biophysically plausible condition would be to consider a percentage of adapted inhibitory interneurons.

Levelt's propositions show how mean dominance durations are affected as a function of stimulus strength to both or to one eye. They refer to BR but it has been shown that there is a general validity in other paradigms of visual rivalry, revealing common computational mechanisms (Klink et al., 2008). Levelt's propositions, especially the second and the fourth, have been a usual constrain for computational models of BR (Laing and Chow, 2002; Brascamp et al., 2006; Moreno-Bote et al., 2007, 2010; Wilson, 2007; Seely and Chow, 2011). In the present work, we tested Levelt's fourth proposition in both conditions, where interneurons are all or none adapted. In both conditions, we found that the reduced model satisfies this law. In addition we tested Levelt's second revised proposition (Brascamp et al., 2006), and found that the model also satisfies this law. We would like to mention that our study was not in full accordance with the recent study of Moreno-Bote et al. (2010). They showed that competition models like ours better reproduce experimental findings based on Levelt's revised second proposition when the stimuli applied to the populations are normalized, which was not the case in the present work.

In addition, we note that, in this study, we did not check for serial correlations in percept durations. Interestingly, non-zero serial correlations were reported recently in both BR and structure-from motion ambiguity paradigms (van Ee, 2009). Experimental findings in their work were replicated by implementing noise in adaptation of percept-related neurons. It would be interesting to see whether our reduced model can reproduce such serial correlations, and in what conditions. Furthermore, an open and interesting question is the freezing of perception during intermittent presentation of ambiguous stimuli (Orbach et al., 1963; Leopold et al., 2002; Maier et al., 2003). Using a reduced model consistently derived from a biologically realistic spiking network one could study the underlying dynamics, and may unravel mechanisms underlying such a phenomenon.

Lastly, BR has often been compared to cognitive processes such as attention and decision making (Leopold and Logothetis, 1999; Stoner et al., 2005). But it is only recently, that attempts have been made to study how these phenomena might be related (Braun and Mattia, 2010; Kalisvaart et al., 2011) within a theoretical framework. We have used a biophysically realistic spiking network that was initially used to model working memory (Brunel and Wang, 2001) and later decision making (Wang, 2002), attention (Deco and Rolls, 2005), and adaptation-related aftereffects in perceptual decisions (Theodoni et al., 2011). The ability of a similar spiking network to produce these different, but related, cognitive phenomena indicates that they could have similar underlying neural mechanisms.

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High-level binocular rivalry effects

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Binocular rivalry (BR) occurs when the brain cannot fuse percepts from the two eyes because they are different. We review results relating to an ongoing controversy regarding the cortical site of the BR mechanism. Some BR qualities suggest it is low-level: (1) BR, as its name implies, is usually between eyes and only low-levels have access to utrocular information. (2) All input to one eye is suppressed: blurring doesn't stimulate accommodation; pupilary constrictions are reduced; probe detection is reduced. (3) Rivalry is affected by low-level attributes, contrast, spatial frequency, brightness, motion. (4) There is limited priming due to suppressed words or pictures. On the other hand, recent studies favor a high-level mechanism: (1) Rivalry occurs between patterns, not eyes, as in patchwork rivalry or a swapping paradigm. (2) Attention affects alternations. (3) Context affects dominance. There is conflicting evidence from physiological studies (single cell and fMRI) regarding cortical level(s) of conscious perception. We discuss the possibility of multiple BR sites and theoretical considerations that rule out this solution. We present new data regarding the locus of the BR switch by manipulating stimulus semantic content or high-level characteristics. Since these variations are represented at higher cortical levels, their affecting rivalry supports high-level BR intervention. In Experiment I, we measure rivalry when one eye views words and the other non-words and find significantly longer dominance durations for non-words. In Experiment II, we find longer dominance times for line drawings of simple, structurally impossible figures than for similar, possible objects. In Experiment III, we test the influence of idiomatic context on rivalry between words. Results show that generally words within their idiomatic context have longer mean dominance durations. We conclude that BR has high-level cortical influences, and may be controlled by a high-level mechanism.

Keywords: binocular rivalry, cortical level, consciousness, perception, binocular, monocular, utrocular, semantics

INTRODUCTION AND REVIEW OF CONFLICTING EVIDENCE REGARDING SITE OF BINOCULAR RIVALRY

At any given moment our brains are busy with many tasks, including: receiving sensory information, regulating autonomous behavior, planning voluntary movements, and building memory of objects and events. Only some of these functions involve consciousness, and we are unaware of most brain activity.

Binocular rivalry (BR) has the unique property that, while physical stimuli remain constant, subjective perception changes. While two images are presented to the visual system and both are (at least partially) processed, the observer is only aware of one. Thus, BR is considered "perhaps the present most important experimental approach to finding the neural correlate of consciousness" (NCC; Crick and Koch, 1998). BR has been reviewed in more general contexts (Tong, 2003; Blake and Wilson, 2011).

LEVELS OF PERCEPTUAL REPRESENTATION

It is well known that there is a hierarchy of visual information processing (Hubel and Wiesel, 1962). Information from the eye enters, via the thalamus, low cortical levels (V1, V2, etc.) where simple features (such as lines of a specific orientation and location) are represented. Feed-forward processing leads to categorical representations, without details, at high cortical levels. Recent work by Hochstein and Ahissar (2002) suggests that there may be a reverse hierarchy of explicit visual perception. Visual information first travels in the bottom-up direction, because input from lower levels is necessary to construct a global representation, but this process may be implicit, and unavailable to consciousness. It was suggested that conscious perception begins with high-level categorical representations of the global scene. According to this reverse hierarchy theory (RHT), only later do we become aware of scene details, by reverse hierarchy return to lower level smaller receptive fields.

BINOCULAR RIVALRY

Binocular rivalry occurs when the brain cannot fuse the images seen by the two eyes because they are two completely different pictures or contain elements that differ in one or more features or attributes such as: color, orientation, size, velocity of motion, direction of motion, or depth (Blake and Logothetis, 2002). After an initial 150–200 ms, during which perception is of the two views, superimposed (Wolfe, 1996), perception alternates between two percepts. This alternation presumably reflects competition between the images for conscious perception (Crick, 1996;

Logothetis, 1998). Alternations continue about every 2–3 s, as long as both stimuli are continuously viewed. Usually the two percepts correspond to the stimuli in each eye separately. A histogram of the time intervals (t) that one of the stimuli is dominant is well fit by the gamma distribution (Fox and Hermann, 1967; Papathomas et al., 1999; but see Rubin and Hupe, 2005) with two parameters λ, r:

$$f(t) = [\lambda^r/\Gamma(r)]t^{r-1}\ \exp(-\lambda t) \quad \text{where}$$
$$\Gamma(r) = (r-1)!\ (\text{for } r \text{ positive integer})$$

To obtain fluctuation of entire pictures (exclusive rather than piecemeal rivalry), the stimuli must subtend no more than about 1 square degree for foveal targets (Blake et al., 1992; Kovács et al., 1996). One eye's view may be dominant more often or for longer periods than that of the other, as occurs for figures that are brighter, in higher contrast, moving, or of higher spatial frequency (Levelt, 1965; Blake and Logothetis, 2002). It has been suggested that strengthening one stimulus shortens its suppression durations without affecting its dominance times (Levelt, 1965; Fox and Rasche, 1969). Finally, there is a long-standing debate (dating back to Helmholtz and Hering) concerning the impact of voluntary attention or cognitive salience on dominance times (see Ooi and He, 1999; Meng and Tong, 2004; Chong et al., 2005; Paffen et al., 2006; see also Toppino, 2003; van Ee et al., 2005).

LOCUS OF BINOCULAR RIVALRY

Related to the issue of voluntary control, there is ongoing controversy regarding the low or high-level site of the BR mechanism. Supporting evidence for low-level mechanisms, include the following:

1. The fact that BR is usually a competition between monocular images suggests that the competition takes place at low cortical levels at or before the site of the transition from monocular to binocular representation; higher level cortical areas do not generally have utrocular information.
2. Basic stimulus attributes that are represented at low cortical levels affect rivalry (see above; Levelt, 1965).
3. Suppression operates to "non-selectively weaken all inputs to the suppressed eye," which is "sufficient to compromise, but not abolish, visual performance" (Blake and Logothetis, 2002). Suppression "erases" or "blocks" processing of stimuli to that eye (perhaps similar to "early selection" in attention; Broadbent, 1958; Deutsch and Deutsch, 1963; Johnston and Heinz, 1979). Together with suppressing one eye's image, detection of a probe to that eye is also reduced; blurring the picture does not stimulate the accommodation reflex; pupilary constrictions (in response to light flashes) are reduced in amplitude; and high-level adaptation effects such as the global motion after effect are reduced, though the tilt and local motion after effects remain (Lehmkuhle and Fox, 1975; Wade and Wenderoth, 1978; O'Shea and Crassini, 1981; Blake et al., 2006).
4. There is no visual priming due to suppressed words or pictures (Zimba and Blake, 1983), but priming with a certain direction of motion during suppression can bias the direction seen in a following ambiguous apparent motion sequence (Blake et al., 1998; see also Hock et al., 1996).
5. Semantic content has not been found to influence probe detection during rivalry suggesting that rivalry occurs before semantic content is extracted (Blake, 1988). However, it was recently found that a word related to a previously binocularly primed word "comes out" of suppression faster (in a flash-suppression paradigm; Costello et al., 2009). See also the new results presented later in this paper.

On the other hand, based on recent research, it seems that there are also high-level effects in BR:

1. Attention. Voluntary attention to one stimulus may increase its relative prominence, but not "save" it altogether from being suppressed and pop-out cues to one eye (initiating involuntary attention) can force a stimulus out of suppression (Ooi and He, 1999; Chong et al., 2005).
2. Patchwork rivalry. Kovács et al. (1996; see also Alais et al., 2000) used novel stimuli where two pictures were divided between the two eyes so that in order to see a coherent picture, information from the two eyes had to be integrated. Indeed the most prevalent percept was of coherent pictures, not of pictures deriving from one eye, suggesting that rivalry is mainly a high-level effect where competition is between integral percepts. Lee and Blake (1999) reject this conclusion, claiming that even low-level eye rivalry can be or patchy (as generally found for large stimuli; Blake et al., 1992). Kovács et al. (1996; see also Papathomas et al., 1999) would presumably respond that the choice of pieces which form a coherent picture would have to be high-level, proving at least a top-down influence on the rivalry mechanism. In a recent paper, Lee and Blake (2004) again challenge this interpretation, showing that swapping the dominant image to the other eye causes the percept to change; indicating that it was the eye that was dominant in that patch and not the percept. In addition, a simulation of independent regions of eye rivalry creates a dominance pattern that is similar to patchwork rivalry, demonstrating that patchwork rivalry can be explained without rejecting eye-based rivalry. Nevertheless, these authors do not deny a top-down mechanism may play a role in choosing the interocular grouping.
3. Context. When one of the rivaling stimuli is embedded in a congruent (high-level) context, its dominant periods are shorter (Carter et al., 2004) or longer (without a concomitant shortening of the suppression periods; Blake and Logothetis, 2002; Sobel and Blake, 2002).
4. Global effects. Even for large targets where piecemeal rivalry occurs, there are also periods of exclusive dominance (significantly more than chance), where the whole percept is monocular (Blake et al., 1992). Similarly, when small identical rival targets are distributed throughout the visual field they tend to fluctuate together.
5. Meaningful Content. A cognitively more salient stimulus, i.e., one with more "meaningful content," remains dominant for longer periods (Walker, 1978; e.g., an upright face: Engel, 1956 see also Zhou et al., 2010; an emotional face: Alpers and Gerdes, 2007; Bannerman et al., 2008; a recognizable figure: Yu and

Blake, 1992; a familiar figure: Lo Sciuto and Hartley, 1963; Goryo, 1969; Jiang et al., 2007). The implication of a high-level mechanism has been questioned, however, because the methods used for these studies were subjective, with a bias that could have affected the *response* rather than the percept, and because a low-level configuration detection mechanism could have affected both low-level rivalry and high-level meaning comprehension (Yu and Blake, 1992; Blake, 2000).

6. Swapping. When gratings were rapidly swapped between the eyes (at 1–3 Hz), observers report normal BR alternation rates (0.3–0.5 Hz), indicating that the pattern, not the eye, was dominant (pattern rivalry; Logothetis et al., 1996; van Boxtel et al., 2008). Following this finding, Wilson (2003) models rivalry as having both low-level and high-level mechanisms. However, Lee and Blake (1999) suggest that rapid swapping may interfere with "normal" rivalry mechanisms. More recent studies show that there actually is some rapid eye-related alternation; with the percentage of time that pattern rivalry is perceived as opposed to eye rivalry depending on the coherence of the stimuli (Bonneh et al., 2001; Silver and Logothetis, 2007).
7. Partial Rivalry. In an amazingly prescient paper, Treisman (1962) found that when each eye was shown a different colored circle (red/green) that was displaced relative to a surrounding circle, observers experienced BR between the two colored circles, in depth. The disparity information was taken into account even while the stimulus was suppressed. Superimposed orthogonal drifting gratings are perceived as a single plaid surface moving in the direction of the vector sum of the two movements. But when the two gratings are presented one to each eye, rivalry ensues. For patches small enough to ensure exclusive rivalry (0.8°), only one grating is perceived at any moment but it moves in the combined direction (Andrews and Blakemore, 1999). For larger patches, too, when one experiences piecemeal rivalry, the mosaic moves coherently, and again in the combined direction (Andrews and Blakemore, 2002). Thus, the suppressed (non-perceived) grating contributes to the perceived direction of motion (see also Alais and Parker, 2006). One may conclude that different neurons mediate rivalry of different features (motion, contour, color).
8. Rubin (2003) suggested that alternations between percepts of ambiguous figures have similar characteristics to BR alternations; (see also Carter and Pettigrew, 2003; van Ee, 2005; van Boxtel et al., 2008). Since ambiguous figure alternations are essentially between high-level interpretations, this similarity suggests that BR, too, may depend on a high-level mechanism.

PHYSIOLOGICAL INVESTIGATIONS

Physiological studies have also been used to find the site of rivalry alternation and the neural loci where activity corresponds to the conscious percept rather than to the presence of a physical stimulus. These investigators were often seeking hints at the site of the NCC but their results may tell us where to look for the alternation mechanism. These studies used a number of methodologies, including the following:

1. VEP. Using temporal tagging/labeling for two images presented to the two eyes, Brown and Norcia (1997) found correspondence between activity in the occipital cortex and perceptual changes. But this recording cannot separate between different visual areas in the brain. Studies using MEG found extended network responses modulated, but not extinguished by rivalry (Tononi et al., 1998).
2. Single-cell recordings. Leopold and Logothetis (1996; see summary Logothetis, 1998) studied alert monkeys as they viewed rivalry stimuli passively, or reported percept fluctuations. The dominance pattern was similar to that in humans. No evidence was found for any inhibition in the Lateral Geniculate Nucleus. Some of the neurons in striate cortex (20%) and early extrastriate cortex (V4, MT; 40%) showed activity modulations that corresponded to the perceptual changes, but not to the all-or-none extent experienced perceptually. In inferior temporal (IT) cortex, most of the neurons (90%) were active only when their preferred stimulus was consciously perceived – i.e., as reported by the monkey. Activity usually ceased when the preferred stimulus was suppressed, though some neurons acted in the opposite manner. Thus, area IT seems to be located at or beyond the point where the rivalry conflict is resolved.
3. Functional imaging. fMRI activity was measured in early visual cortex while subjects viewed rivaling gratings of different contrasts (Polonsky et al., 2000). Activity in V1 increased when the higher contrast was perceived and decreased when the lower contrast was perceived. These fluctuations were 55% as large as when the gratings physically alternated. The same results were found for V2, V3, V3a, and V4v. Tong et al. (1998) used pictures of a face and a house, presented respectively to each of the two eyes, and found modulations of brain activity in the Fusiform Face Area and Posterior Parietal Area that coincided with the fluctuations in the reported percept and were equal in strength to those reported when the stimuli were physically alternating, suggesting rivalry is resolved at or before these areas. It is difficult to resolve whether there is a build-up of rivalry along the hierarchy or a high-level mechanism whose results are fed back. More conclusively, Tong and Engel (2001) cleverly measured responses in the blind spot which produces a monocular region of human V1 and found fMRI modulations during rivalry which were as large as those evoked by physically alternating stimuli, suggesting that rivalry might be resolved by early interocular competition. However, supporting the above single-cell results, Brouwer et al. (2009) recently found intraparietal sulcus (IPS) sensitivity to the degree of perceptual incongruence of an ambiguous image, perhaps suggesting that this area may play a role in signaling the need to reinterpret ambiguous depth cues in the visual scene, initiating bistable perception. Similarly, Kanai et al. (2010) recently found that individual BR differences may depend on their different superior parietal lobe activations.
4. TMS. Related to the above finding, Zaretskaya et al. (2010) used TMS to individually disrupt processing in areas where fMRI activity correlated with rivalry alternations. They found that TMS over right IPS prolonged periods of stable percepts and that the more lateralized the IPS blood oxygen level-dependent signal, the more lateralized were the TMS effects. This suggests a causal, destabilizing, and individually lateralized effect of normal IPS function on perceptual continuity in rivalry,

consistent with an IPS role in selection, related to its role in attention.

5. Localized brain damage. While much has been learned in the past from studies of deficits following localized brain damage, this avenue has not been utilized extensively for the study of BR. One exception is the study by Valle-Inclán and Gallego (2006) of a patient who had most of the prefrontal cortex disconnected from the rest of the brain due to a bilateral frontal leukotomy. Results indicated that prefrontal cortex is unnecessary for perceptual alternations during BR.

SUMMARY

Thus, debate is still open regarding the locus of BR. A recently suggested and commonly held "solution" to these opposing views is that both high- and low-level mechanisms control rivalry, with local stimuli inducing alternations at lower cortical sites and complex configurations inducing high-level perceptual interpretations at high cortical areas (Rubin, 2003; Wilson, 2003, 2005; Alais and Blake, 2005; Rubin and Hupe, 2005; Tong et al., 2006). However, there may be an essential problem with this solution. What determines if the low-level mechanism initiates rivalry? If it always does, why don't we see its impact in those cases that suggest a high-level mechanism (patchwork rivalry, swapping, etc.)? And why do high-level features (such as context) affect rivalry? On the other hand, rapid access of partial information to high-level areas before processing in early stages has been completed, may explain such phenomena (see e.g., Rousselet et al., 2002). In addition, RHT (see above; Hochstein and Ahissar, 2002) predicts that high-level mechanisms guide and feedback to low cortical levels, so that (albeit pushing this argument to its extreme), high-level attention (see Chong et al., 2005) may affect even a low-level BR mechanism, or, alternatively – and more likely – a high-level rivalry mechanism may have effects at lower levels.

Since complex images and scenes are represented as such at higher cortical levels, we investigate in the following sections the impact of varying high-level characteristics of the two eyes' views, and propose that if these variations affect rivalry, it would support high-level intervention in BR, i.e., a high-level mechanism or at least a top-down effect in rivalry. We study BR with words and compare dominance durations for words and non-words. The only difference between these stimuli is high-level. Thus, any difference in rivalry pattern between words and non-words would indicate a high-level mechanism.

DOMINANCE DURATIONS WHEN WORDS COMPETE WITH NON-WORDS

INTRODUCTION AND METHODS

We study rivalry between words and non-words (i.e., strings of letters without meaning, or pronounceable nonsense words) to investigate whether high-level semantic meaning affects the time spent with each type of input.

Subjects were 11 university students (age 19–35, mean 24), naïve to the purpose of the experiment, remunerated for participation, tested for normal or corrected-to-normal vision in both eyes, with good stereovision and no strabismus.

Stimuli were superimposed semitransparent 4° × 4° diagonal texts, one in green and one in red, viewed through red/green filter glasses so that the stimuli were seen as equally salient black and each eye saw one text, as demonstrated in **Figure 1**. A black frame and black fixation cross, seen by both eyes, promoted fusion. Viewing distance was 57 cm. Texts were in Hebrew, the main language of the subjects. In our presentations, as is general in Hebrew, vowels are assumed and not explicitly written, and non-words are usually pronounceable. Words (44 in all) were common (average 0.2/thousand) short (3.2 letters), nouns (59%), verbs (11%), and simple adjectives (25%) with few cases of polysemy (9%) or homography (11%). Non-words were created using the same letters as the words. Since Hebrew words depend on a 3-letter root, changing letter order creates a totally new – and usually unrecognizable – non-word. Words were in print font and non-words in script (or vice versa), allowing responses without explicit reference to text meaningfulness. Stimuli were counterbalanced between print and script font and between red and green color. Words (and non-words) were not repeated within trials.

Subjects were asked to maintain fixation throughout the trial, and initiated trials by pressing the space-bar. There were 24 trials/session, each of 90 s during which the stimulus did not change. Subjects reported perceptual changes by briefly pressing one of three keys: PRINT (the "p" key), SCRIPT ("i"), or MIXED ("o"; subjects were instructed to indicate PRINT or SCRIPT as long as the stimulus was predominantly such).

RESULTS

The mean dominance time for non-words was longer than for words, 3.03 ± 0.08 vs. 2.58 ± 0.06 s; $p < 0.0001$ (unpaired two-tailed t-test); dominance times for print and script were not significantly different: 2.78 ± 0.06 vs. 2.83 ± 0.07 s; $p = 0.6$, as demonstrated in **Figure 2**. Furthermore, for each subject, the mean dominance time was longer for non-words than for words (or in two cases nearly identical), as shown in the scatter plot of **Figure 3** comparing average dominance times for each of the 11 subjects. Nearly all points lie above the diagonal of equality. Across-subject mean is 4.5 ± 1 vs. 3.7 ± 0.9 s; $p < 0.02$ (paired two-tailed t-test). Comparing these word-non-word competition data with dominance times for words presented to both eyes and for non-words presented to both eyes, we found an indication for competition

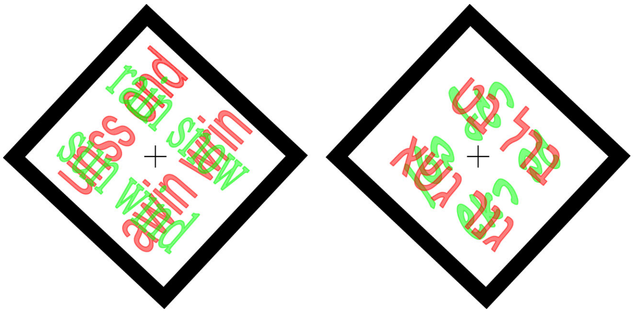


FIGURE 1 | Examples of word-non-word rivaling stimuli. Left English text (rain snow sun wind vs. unss ond awin wrin – pronounceable non-words); Right Hebrew text – as actually used in Experiment 1, since subjects were Hebrew speakers; text in print vs. script font.

leading to shortening of dominance times for words, rather than lengthening for non-words.

DOMINANCE DURATIONS WHEN POSSIBLE FIGURES COMPETE WITH IMPOSSIBLE FIGURES

INTRODUCTION AND METHODS

Having found a difference between dominance times for non-words vs. words, we asked if this difference might be more general, extending to other images beyond those of written words, in particular real, structurally possible figures compared with impossible figures. This would be consistent with previous findings that displeasing stimuli have an advantage over pleasing images (Smets, 1975).

Methods were as above, with two quite similar line drawings superimposed, one possible and one impossible, one in red and one in green, as demonstrated in **Figure 4**. Trials lasted 60 s, 20/session, 17 subjects (age 20–36; mean 25) reported their percept by pressing one of two keys (e.g., “j” for triangle pointing up; “f” for pointing down). We used two kinds of pictures: “simple” including: forks (possible and impossible), triangles (possible 3-D triangle and Penrose triangle; Draper, 1978), and squares (possible 3-D vs. Penrose-like square); and “complex” including Esher-type drawings (Thro, 1983) and similar possible objects: houses, windowpanes, wheels, and cubes. In each trial, both pictures were either simple or complex.

RESULTS

For simple figures, impossible figures were dominant for longer times. Mean dominance durations for impossible and possible figures were 2.8 ± 0.2 vs. 2.5 ± 0.2 s; $p < 0.02$ (paired two-tail t-test), as shown in **Figures 5** and **6**. On the other hand, for complex figures, dominance times were considerably longer, with no

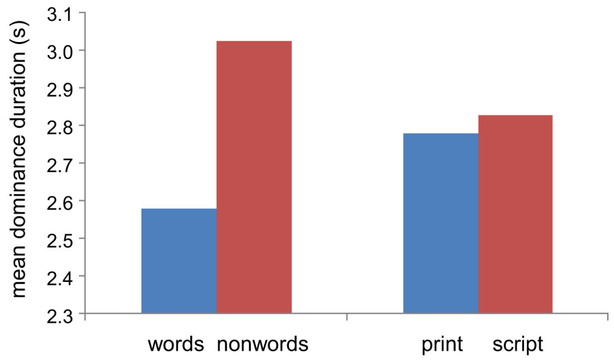


FIGURE 2 | Dominance durations. Mean dominance duration for non-words is greater than for words; no difference between print and script font. Pooled results for all subjects.

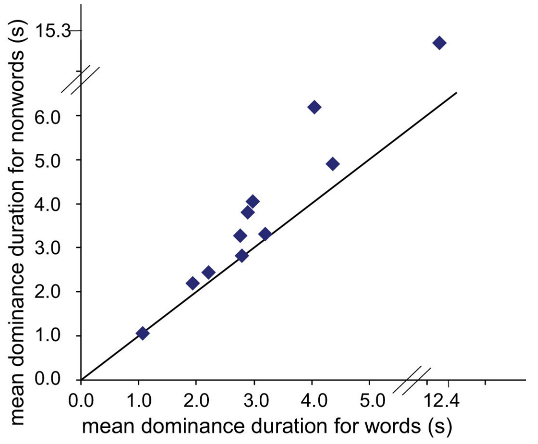


FIGURE 3 | Scatter plot showing mean dominance durations of non-words vs. words for each subject. All points are on or above the equivalence line: mean dominance durations for non-words were longer than for words. Note one observer had considerably longer dominance durations, plotted on an extended scale.

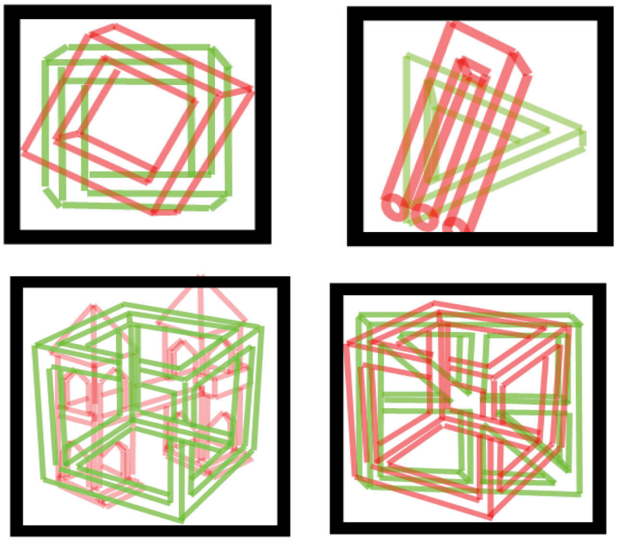


FIGURE 4 | Examples of stimuli used for possible vs. impossible figures. Simple and complex figures (top and bottom row, respectively) were used. Subjects viewed pictures through red/green filtered glasses.

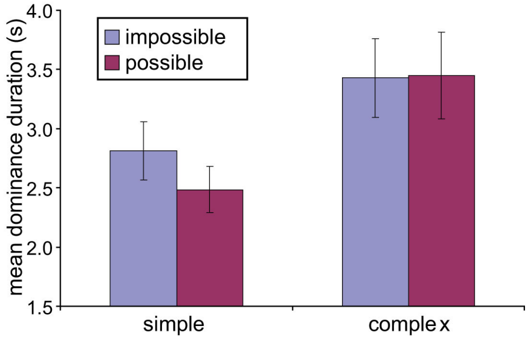


FIGURE 5 | Dominance durations – possible vs. impossible figures. Across-subject mean dominance durations for possible and impossible figures for the different classes of images. Simple impossible figures have longer dominance durations than possible figures, with no difference for complex figures.

difference between figures: 3.4 ± 0.3 vs. 3.4 ± 0.4 s; $p = 0.93$. These results are confirmed in the scatter plots of **Figure 6**, where the points for the simple impossible figures fall above the diagonal line of equivalence, but not the points for the complex figures.

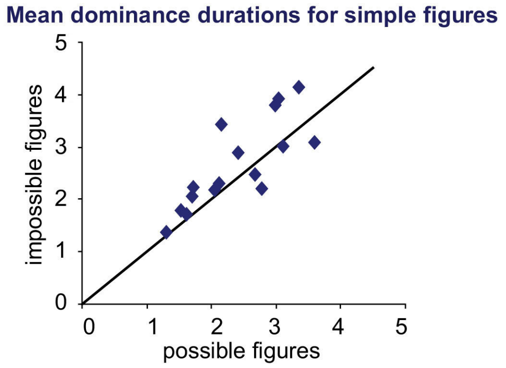
A possible explanation for this difference is that with simple figures, impossible ones are more intriguing, but for complex figures, even the possible figures were complicated enough that they were as interesting as the impossible figures, and/or their dominance times reached some ceiling of dominance time. Previous studies showed that processing structurally possible and impossible figures takes place at high-level cortical regions (Schacter et al., 1995) and that only these levels may be used for differentiating percepts of possible vs. impossible objects.

EFFECT OF IDIOMATIC CONTEXT ON DOMINANCE DURATION

INTRODUCTION AND METHODS

Having found that semantic content affects BR dominance, we tested semantic *context.* Will words imbedded in a congruent context be more salient than words incongruent with that context, increasing the dominance times? Perhaps while nonsense words attract more – longer – attention due to the variety of ways they may be read (so that subjects may be experimenting with them (consciously or unconsciously) trying to figure out a meaningful way to pronounce them, words out-of-context are easily read and their nonsense context easily rejected, so that perhaps no extra time will be spent with incongruent texts. Context effects have been tested for low-level stimuli (e.g., Sobel and Blake, 2002; Carter et al., 2004), but what about high-level context? What constitutes congruent context for words? We used well known short (Hebrew) idioms.

Mean dominance durations for simple figures



Mean dominance durations for complex figures

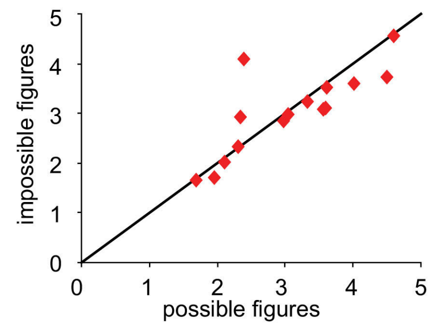


FIGURE 6 | Mean dominance duration scatter plots by subject for simple (top) and complex (bottom) figures. For simple figures, most points are above the equality line indicating longer dominance durations for impossible figures. For complex figures, points are mostly close to the equality line.

Stimuli were constructed so that with colored stimuli and glasses (as above) one eye viewed a well known short idiom and the other a modified idiom where one word was replaced with a different word (chosen to fit grammatically and to have an equal frequency in Hebrew; see http://word-freq.mscc.huji.ac.il/index.html). For example, idiom: **Mipnay seiva takum** (translation: *Rise for the elderly);* modified idiom: **Mipnay hakara takum** (translation: *Rise for the frost);* (Similar to idiom: **a stitch in time saves nine;** modified "idiom": **a stitch in time waits nine**).

Stimulus size was 3.5 × 3.5 cm viewed at 76 cm. See example in **Figure 7**. Trials lasted 60 s. Subjects tracked their percept by pressing one of three keys, "print," "script," or "mixed." They were asked to adopt a constant criterion and, press "print" or "script" even if the percept was not exclusively so.

RESULTS

Real idioms were dominant for longer periods than modified texts. Words in-context had greater predominance than words not-in-context. **Figure 8** shows mean dominance durations for individual subjects, and across-subject means for the two conditions. For almost all observers, mean dominance duration in-context was longer than when not-in-context; mean in-context 5.3 ± 0.5 s; out-of-context 4.7 ± 0.4 s; $p < 0.01$, paired t-test.

GENERAL DISCUSSION

We found a series of high-level effects in BR. The only difference between the stimuli presented to the two eyes was their cognitive semantic content. Nevertheless, there was a significant difference in the dominance periods of the two images.

In the context of the issue of the low or high cortical level of the mechanism controlling BR, these stimuli differed only in semantic content so that a low-level mechanism would treat them

FIGURE 7 | Example of stimulus for Experiment 3. Note that the idiom is in script font, the non-idiom in print.

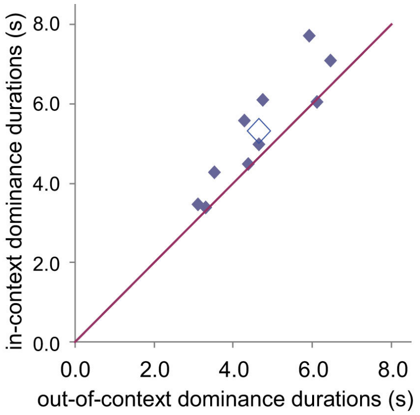


FIGURE 8 | Mean dominance durations of in-context vs. out-of-context idiom texts, for each subject (filled diamonds) and across-subject means (open diamond). In-context dominance duration is generally longer than out-of-context duration.

equally, while, at higher cortical levels, one could be preferred. In each pair, one stimulus was a group of possible words and the other impossible words composed of the same letters (Experiment 1), one was a structurally possible figure and the other impossible (Experiment 2), or one was a proper idiom and the other an idiom with a non-appropriate word interjected (Experiment 3). If the mechanism controlling BR were low-level, there should be no difference between non-words and words, between possible and impossible figures, or between words in- or out-of-context and we should find balanced rivalry (as with horizontal vs. vertical gratings). On the other hand, a high-level mechanism would be expected to distinguish between the two, and favor the more "interesting" image.

In fact, an effect in either direction would have indicated a high-level effect. We actually expected words to predominate over non-words and objects over non-objects, due to their being more familiar, containing meaning, and perhaps a "better unit" object or word in the Gestalt sense. Surprisingly, the results indicate otherwise. Non-words and impossible objects seem to be more interesting and attract longer scrutiny (see also Bonneh et al., 2001; Mudrik et al., 2011). Importantly, these results indicate that high-level interest overpowers more simple and direct familiarity.

Previous studies that attempted to differentiate between low- and high-level rivalry mechanisms (reviewed in Introduction and Review of Conflicting Evidence Regarding Site of Binocular Rivalry) used binocular effects such as patchwork images (Kovács et al., 1996) or flicker and switch stimuli (Logothetis et al., 1996) to demonstrate non-eye-related percepts and high-level image-related percepts. Others looked for manipulations that influence rivalry dominance times, such as contrast or context. Contrast would seem to indicate a low-level mechanism, context a high-level one. We now add a new approach, using high-level differences between stimuli and their impact on rivalry dominance times to demonstrate that these, too, depend on high-level effects.

The indication of a shortening of the dominance times for words when competing with non-words coincides with Levelt's famous second law that the more salient stimulus has longer dominance times because of the shortening of its suppression times. While extension of non-word dominance durations could derive from an attentional effect, shortening of non-word suppression periods more definitively suggests a high-level BR control mechanism[1]. Similar results were found by Ooi and He (1999) who manipulated attention during BR and by van Ee et al. (2007) who found a dominance dependence on simultaneous auditory stimuli. In addition, Sobel and Blake (2002) and Carter et al. (2004) found that the context surrounding simple rivalrous stimuli affects their dominance phases. The results of these authors, demonstrating an attentional or contextual involvement in rivalry, also support high-level control of dominance times. Our own new results, taken together with those of these prior studies, provide substantial support for the conclusion that rivalry is controlled or at least affected by high-level mechanisms.

Though we may not have solved the entire mystery of which part of the brain is responsible for the switching in BR, we have demonstrated a new set of stimuli for which one may be easily convinced that it is a high-level mechanism that decides which stimulus is dominant. This finding is consistent with RHT (Hochstein and Ahissar, 2002), which suggests that high cortical level effects are the first to enter conscious perception. Thus, a switching mechanism located here will have rapid effects on perception and then gradually travel down the hierarchy – in reverse order – affecting lower cortical level responses as well.

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[1] We thank an anonymous reviewer for suggesting this line of reasoning.

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Stimulus fractionation by interocular suppression

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Can human observers distinguish physical removal of a visible stimulus from phenomenal suppression of that stimulus during binocular rivalry? As so often happens, simple questions produce complex answers, and that is the case in the study reported here. Using continuous flash suppression to produce binocular rivalry, we were able to identify stimulus conditions where most – but not all – people utterly fail to distinguish physical from phenomenal stimulus removal, although we can be certain that those two equivalent perceptual states are accompanied by distinct neural events. More interestingly, we find subtle variants of the task where distinguishing the two states is trivially easy, even for people who utterly fail under the original conditions. We found that stimulus features are differentially vulnerable to suppression. Observers are able to be aware of existence/removal of some stimulus attributes (flicker) but not others (orientation), implying that interocular suppression breaks down the unitary awareness of integrated features belonging to a visual object. These findings raise questions about the unitary nature of awareness and, also, place qualifications on the utility of binocular rivalry as a tool for studying the neural concomitants of conscious visual awareness.

Keywords: awareness, interocular suppression, continuous flash suppression, temporal modulation, orientation, feature-selectivity

INTRODUCTION

Binocular rivalry fascinates us for several reasons. First, it starkly highlights the brain's strategy for dealing with ambiguous or conflicting visual information. Indeed, some believe the processes revealed during rivalry are operating at all times to resolve ambiguities inherent in the optical input during everyday vision (e.g., Hohwy et al., 2008; Sterzer et al., 2009). Second, alternations in dominance during binocular rivalry imply that conflict resolution is unstable – perception does not settle upon a single, dominant interpretation but, instead, fluctuates over time unpredictably (e.g., Levelt, 1965; Fox and Herrmann, 1967; Brascamp et al., 2005). And third, during rivalry a complex, ordinarily visible stimulus can disappear from visual awareness for seconds at a time even though that stimulus remains imaged on the retina, a remarkable act of disappearance that has been dubbed psychophysical magic (Kim and Blake, 2005). This profound, intermittent dissociation between physical stimulation and perceptual experience affords a paradigmatic case for the study of visual awareness (Crick and Koch, 2003), and the search for fluctuations in neural activity correlated with the intermittent disappearance of a stimulus has been underway for years now (Tong et al., 2006). In this paper, we focus on this third aspect of rivalry, i.e., the temporary invisibility of a stimulus.

Our question is quite simple: can we sense the physical removal of a stimulus that has already been rendered invisible owing to interocular suppression? Perceptually speaking, a suppressed stimulus temporarily ceases to exist, and the "out of sight" quality of such a stimulus naturally leads one to inquire about the extent to which such a stimulus is also "out of mind." In terms of neural events, the two circumstances are surely different. Specifically, physical removal of a stimulus has ramifications beginning at the very earliest stages of vision in the retina; removal of a stimulus from awareness during rivalry, however, does not impact retinal processing except for subtle influences on oculomotor responses (Lorber et al., 1965; Sabrin and Kertesz, 1980). Moreover, physical removal of a stimulus produces larger, more widespread changes in cortical neural activity than does phenomenal removal owing to binocular rivalry (Leopold and Logothetis, 1996; Polonsky et al., 2000; Sterzer et al., 2008). Finally, we know that a stimulus outside of awareness, because it is still present, can generate visual aftereffects arising at different stages of visual processing (Blake and He, 2005), and we know that other aspects of visual information processing associated with that stimulus survive suppression albeit often with reduced effectiveness (Lin and He, 2009). But these psychophysical results provide indirect measures of the residual effectiveness of a suppressed stimulus, serving much the same role as footprints in the sand that hint at the presence of an unseen person. For our question we are seeking more than footprints: we want to know whether people can sense the physical removal of a stimulus that has already been perceptually erased from awareness during rivalry. Answering this question could shed light on the nature of suppression and, by extension, on the often-stated assertion that binocular rivalry provides an effective means for studying the neural correlates of consciousness (e.g., van Ee, 2009; Alais et al., 2010).

Here is how we have pursued the question. Using continuous flash suppression (CFS) to create binocular rivalry (Tsuchiya and Koch, 2005), we presented a dynamic Mondrian to one eye and a circular gabor pattern to the other eye. While the gabor pattern was suppressed, we removed either the top half or the bottom-half of the pattern and required observers to judge which half was removed, top or bottom (two-alternative spatial forced-choice). We reasoned that if suppression of the gabor pattern is equivalent to physically removing it, it should be impossible to judge which half is physically removed when the pattern is suppressed (because, perceptually speaking, both halves are already gone). By way of preview, this simple question led to the realization that suppression does not operate in a wholesale fashion on a stimulus but, instead, selectively impacts certain features of the stimulus. This finding squares with earlier results obtained using different techniques, and it reveals that phenomenal suppression is quite different from physical absence.

METHODS

EXPERIMENT 1

A total of 16 participants (6 men), including 2 of authors (Asieh Zadbood and Randolph Blake), participated in the first experiment (mean age ∼28 years). Eleven of them were naïve and had no previous experience in psychophysical experiments nor any familiarity with binocular rivalry. All had normal or corrected to normal vision, and each gave written consent to procedures as approved by the IRB office at Seoul National University.

Observers viewed the stimuli on a CRT monitor (1024 × 768 resolution, 60 Hz) through a mirror stereoscope attached to a head/chin rest. The distance between eyes and display was 71 cm, and the head/chin rest stabilized head position and viewing distance. All the experiments were programmed using MATLAB, ver. 7.4 and Psychtoolbox, ver. 3 (Brainard, 1997; Pelli, 1997).

Unless otherwise specified, all experiments involved presentation of a CFS display to one eye and a Gabor patch comprising horizontal contours to the other eye (**Figure 1**). For the CFS display we used grayscale Mondrian patterns (4.34° × 4.34°) normalized to 70% contrast (root mean square). Each Mondrian frame comprised overlapping rectangles of variable dimensions and variable luminance. A new Mondrian image was presented every 100 ms (10 Hz) throughout the duration of each trial. As noted by others (e.g., Tsuchiya and Koch, 2005), this dynamic, richly contoured display is a potent generator of interocular suppression, as evidenced by its long durations of dominance when paired with a rival stimulus to the other eye.

The target stimulus viewed by the other eye was a counter-phase flickering, horizontal Gabor patch (3.1° × 3.1°grating + Gaussian envelope SD = 0.95°) the spatial frequency of which was 1.3 c/degree; the pattern flickered in counterphase (Levinson and Sekuler, 1975) at 1 Hz. The spatial position of the Gabor patch was precisely situated so that the pattern's zero crossing was located at

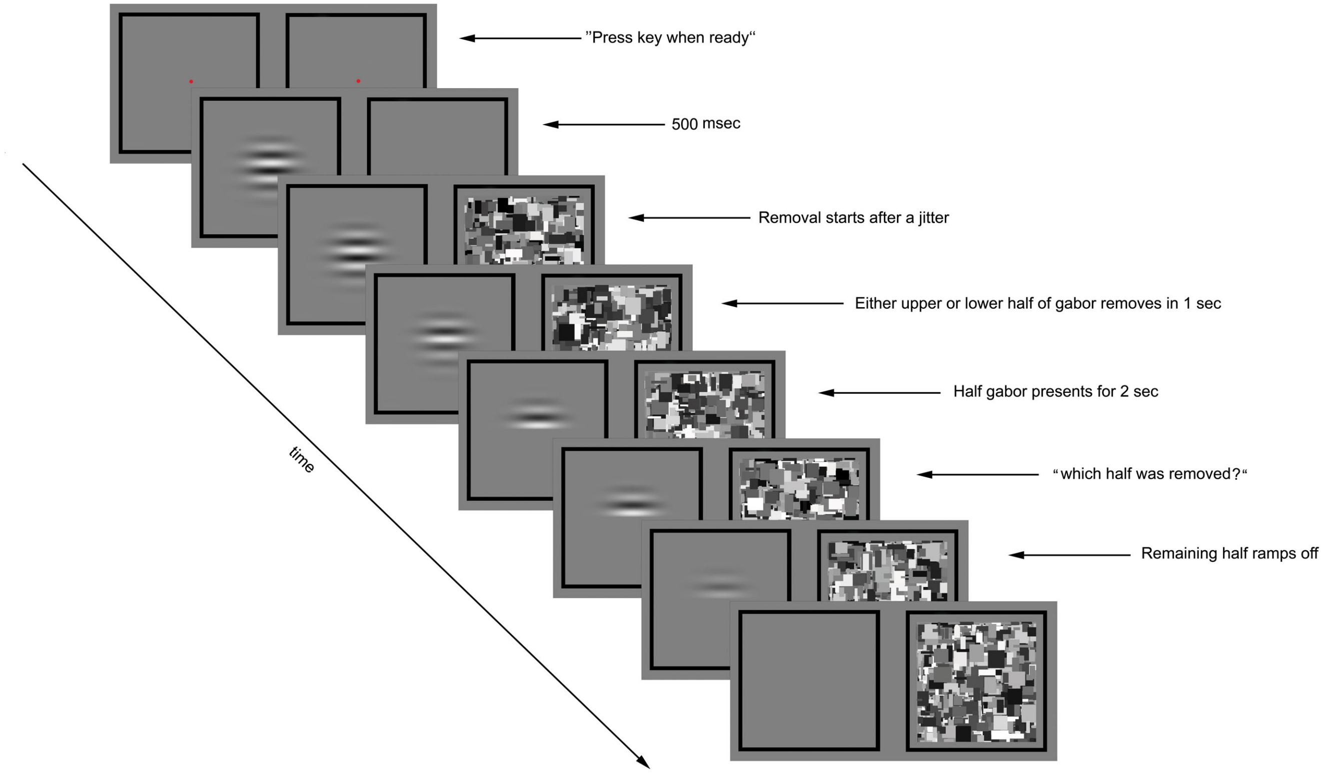

FIGURE 1 | Experimental paradigm for preview condition of Experiment 1. The trial was initiated by the observer's key press. A flickering gabor was presented to one eye and blank gray square to the other eye. After 500 ms the Mondrian images were displayed to the other eye at 10 Hz. Following a variable time period (0, 200, or 400 ms) the contrast of either the upper or lower half of the gabor was gradually ramped to zero over a 1000-ms period. The other half remained unchanged for 2 s before the prompt screen asked about the half removal side, at which time the remaining half of the gabor was removed over a 300 ms period. The CFS was displayed to the other until the observer made his/her response.

the exact middle of the display during all phases of the sinusoidal flicker cycle. Four different contrast values (0.05, 0.1, 0.2, 0.4) were used in this first experiment.

To achieve and maintain stable binocular alignment, a test session started with presentation of two black square frames (4.94° × 4.94°) with a red circle (0.25° × 0.25°) in the middle as the fixation point; the observer started each session by adjusting the mirrors of the stereoscope using the cover/uncover test, pressing a key when refixation eye movements associated with repetitive monocular viewing of the two half-images had been eliminated.

During each test session, two exposure conditions were randomly intermixed, one called preview and the other called post-view. On preview trials, the Gabor patch was presented to one eye followed 500 ms later by presentation of the CFS animation to the other eye (**Figure 1**). On post-view trials, the CFS animation was presented first followed 500 ms later by presentation of the Gabor patch, whose contrast was ramped on to its given value for that trial over 500 ms. On all trials, the upper or the lower half of the Gabor patch was gradually removed; because the contours were horizontal and the pattern was centered at its zero crossing, removal of half of the Gabor produced no change in average luminance. On preview trials (Gabor preceding the Mondrian), removal of the upper or the lower half of the Gabor patch occurred 0 (simultaneous), 200, or 400 ms after presentation of the Mondrian, with the delay determined randomly for each trial. On post-view trials (Gabor following the Mondrian), removal of half of the Gabor patch occurred either 500, 700, or 900 ms after appearance of the Gabor, with that delay value randomly determined for each trial.

The rest of timeline was same for preview and post-view conditions: the removal was completed gradually in 1000 ms and the remaining half of the Gabor was not removed until 2000 ms later. The CFS animation was shown to the other eye during the whole period of trial. Then a screen prompt instructed the observer to indicate by button press which half of the Gabor had been removed, guessing if necessary. At the same time the remaining portion of the Gabor patch was removed and the CFS animation remained on during this response period, to mask any lingering afterimage associated with removal of the Gabor patch. Observers were asked to respond as quickly as possible, and they were told that the entire Gabor patch would be gone at the time they made their response so they should judge based on what they experienced during the trial not what they experienced at the time of the screen prompt.

All timing conditions, preview and post-view trials, stimulus removal location (upper vs. lower) and stimulus eye assignments were randomized and counterbalanced across trials.

Each condition (preview vs. post-view for each of four contrast values) was repeated 108 times, and each observer completed 864 trials in this task.

EXPERIMENT 2

Part one

Fifteen observers from the first experiment participated in this experiment (including the two authors).

The CFS display and timeline were the same as in the previous experiment. The Gabor patch was the same, too, except that its contrast was 0.4 and it had one of two counter-phase flicker rates, 1 or 5 Hz. The Gabor patch was always presented first (preview mode), and either the upper or the lower half of the Gabor was removed with the same timing used in the first experiment. The observer's task was the same, and there were 108 trials per each condition and a total of 216 trials for each observer.

Part two

Eight of the participants in part one also completed the second part of Experiment 2.

The stimulus was a Gabor patch with the same properties explained above in first part but it was not flickering. The task and timing conditions were the same. Each observer completed 108 trials.

EXPERIMENT 3

Six observers participated in this experiment. Target stimuli were two gabor patches (2° × 2° gratings smoothed by a Gaussian envelope with SD = 0.57°). These two gabors were centered immediately above and below a central fixation point (**Figure 2**), and their contours were diagonally oriented such that one was 45° and the other was 135°; the orientation/location pairing was random over trials. The spatial frequency of each gabor patch was 2 c/degree, and on each trial both flickered in counterphase at one of four temporal frequencies: 0.5, 1, 2, or 5 Hz. The contrast values of the two gabor patches were identical and were established for each observer based on performance in Experiment 1 and in pilot testing for Experiment 3. The CFS display again comprised a sequence of grayscale Mondrian patterns (70% contrast), with a new image presented every 100 ms. For this experiment, the CFS was enlarged to 5.5° × 5.5°, to match the larger size of the rival stimuli presented to the other eye.

The session began with presentation of a pair of binocular fusion frames, one viewed by the left eye and the other by the right eye. Each frame consisted of a thick black square (6.2° × 6.2°) with small, central fixation mark. Once the observer had adjusted the mirrors of the stereoscope to achieve stable binocular alignment of these fusion frames, he/she pressed a key that triggered presentation of the CFS display to one eye or the other. Then, 500 ms after presentation of CFS, the pair of gabor patches was ramped on, creating the post-view condition described earlier. Then after a short interval lasting either 500, 700, or 900 ms, one of the two gabor patches was gradually removed over a 1000-ms period time. The other gabor remained present for two more seconds, at which time its contrast dropped to zero and the observer was cued to make two judgments: (1) the orientation of the initially removed grating and

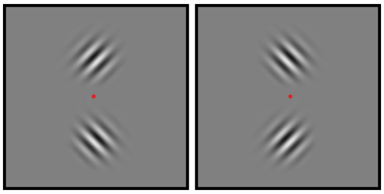

FIGURE 2 | Target stimuli for Experiment 3. Two gabor patches, one tilted 45° clockwise and the other tilted 45° counterclockwise, were located above and below the central fixation point.

(2) the location (above vs. below fixation) of the initially removed grating. During the response period, the other eye continued to view the CFS display until both responses were made. All trial-related variables – eye receiving the pair of gabor patches, orientation/location of the gabor patches and temporal frequency – were randomized with the stipulation that all combinations be presented an equal number of trials. Observers completed 216 trials for each of the four temporal frequency values.

RESULTS

RATIONALE OF THE PRESENT STUDY

Before presenting our results, we start with a description of the rationale that guided our design of these experiments. In principle, the most straightforward way to answer the question of the equivalence of phenomenal and physical absence is simply to determine whether or not observers can tell if a stimulus has been presented to one eye (on some trials it is, on other trials it is not), with the other eye always viewing the dynamic Mondrian. We rejected this simple approach, however, because it does not capture the essence of "absence" that we are interested in: the removal of a stimulus from phenomenal awareness because of interocular suppression. We wanted to know, in other words, whether physical removal is distinguishable from phenomenological removal, and that means presenting a stimulus on every trial and removing it on some trials but not others.

With that in mind, we initially tried a "yes/no" procedure whereby a gabor patch was presented to one eye at the same time as the CFS Mondrian was presented to the other eye. On half of the trials the entire gabor patch faded off after 1–2 s, leaving just the CFS display; on the other trials, the gabor patch remained present. Knowing that afterimages can mimic real patterns in rivalry (Wade, 1974), we flickered the gabor patch on all trials to preclude induction of a residual afterimage on those trials when the pattern was removed (Gilroy and Blake, 2005). Observers were cued with an instruction to guess whether or not the gabor patch was removed. Observers characterized the task as impossible, and the d' values confirmed that observers could not tell on which trials it was removed. While implying that awareness of absence is not noticeable during absence of awareness, we were unwilling to accept this as a definitive answer to our question. Instead, we elected to employ a forced-choice technique wherein either the top- or bottom-half of the gabor patch disappeared on every trial and observers made a forced-choice judgment about which half was removed, guessing if necessary. We moved to this procedure knowing that forced-choice testing typically produces better performance than does the yes/no procedure (e.g., Macmillan and Creelman, 1991; Kroll et al., 2002), a textbook example being the above-chance localization performance that can be obtained in the blind hemifield of at least some individuals with unilateral occipital lobe lesions (e.g., Weiskrantz, 1990). In addition to the more sensitive nature of 2AFC task, this new design differs from the original one in a subtle but important way: removing only half of the suppressed stimulus, not all of it, provides a potential reference frame in the region spatially contiguous with the region of interest, thereby allowing observers to sense subtle differences by directly comparing physical absence and phenomenal absence.

For this 2AFC experiment, we made several strategic decisions concerning the test stimulus that would be partially removed. First, we decided to test two methods for presenting the gabor patch, one involving its presentation shortly before appearance of the CFS Mondrian and the other involving its presentation shortly after appearance of the CFS Mondrian. We did this reasoning that the former would insure that a neural representation of the gabor patch would be formed before the onset of suppression induced by the Mondrian; we could not be sure this would happen when gabor patch followed the Mondrian. Second, we chose this particular range of gabor patch contrasts because, with these contrasts, it was trivially easy to see which half was removed when the monocularly presented pattern was dominant owing to the absence of the Mondrian; every participant performed flawlessly on this condition. What happened, however, when the gabor patch was suppressed by CFS?

EXPERIMENTS 1 AND 2

Results are shown in **Figure 3**, which plots percent-correct (chance = 50%) as a function of the contrast of the gabor patch. We have pooled results across each observer's left and right eyes, as separate analyses contingent on the eye receiving the gabor patch disclosed no systematic performance differences [$F(1,15) = 0.96$, $P = 0.34$].Several features are obvious from these psychometric functions. First, some, but not all, observers found the task impossible regardless of contrast. Those whose performance did climb above the chance level (>58% correct, based on the binomial distribution with 108 trials/condition) generally showed improved performance primarily at the higher contrasts. Among observers who were at least partially successful, there was no obvious tendency for them to perform better when the gabor patch appeared before being suppressed [$F(1,9) = 0.8$, $P = 0.39$] – evidently the neural representation of the gabor patch is attenuated equivalently whether or not its initial neural representation is established prior to succumbing to interocular suppression.

Observers who were able to perform the task offered a revealing account of the cue they relied on: they described seeing faint ripples within either the top- or bottom-half of the dynamic Mondrian pattern a few moments after onset of a trial, and the location of these ripples in either the top or the bottom portion of the Mondrian informed their forced-choice judgment. As is obvious from **Figure 3**, these ripples were inconspicuous at low contrasts. Once these ripples were discovered within the CFS, it was possible to discern that they were also faintly visible when the entire gabor patch was present, although they were much more conspicuous when half of the gabor patch was removed. The first author was one of those for whom the ripples were noticeable, and she quickly understood that the ripples coincided with the counterphase flicker of the gabor patch. To confirm that this rippling cue was indeed tied to the flicker, we retested a subset of observers using a non-flickering, stationary gabor patch with highest contrast, and performance was at or near chance for all observers (mean = 0.6, SD = 0.08) including those whose performance was previously high.

These results – and the anecdotal descriptions of the residual flicker signal associated with the suppressed gabor patch – prompted us to retest observers at two different rates of

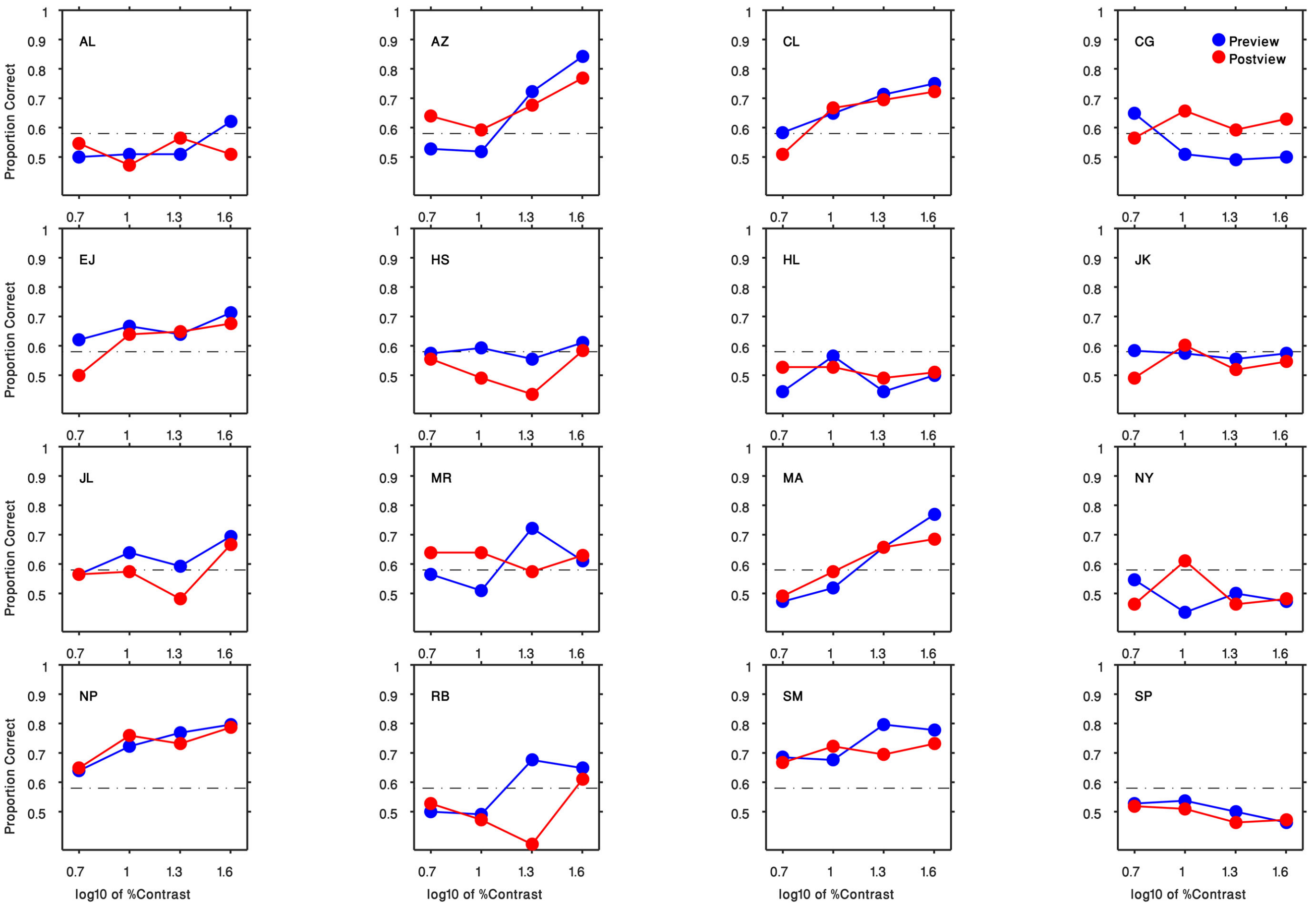

FIGURE 3 | Results of Experiment 1 for all 16 participants. Each panel indicates the result of an observer (initials indicated in the top left corner). The preview condition is shown in blue circles and the post-view condition is shown in red circles. Horizontal axis is the $\log_{10}$ of the gabor patch percent contrast (5, 10, 20, 40). Vertical axis plots the proportion of correct responses. The black dashed lines denote the level of performance significantly above-chance level (58% correct, based on the binomial distribution with 108 trials/condition).

counter-phase flicker, 1 and 5 Hz. For these measurements we tested using the preview procedure only (i.e., gabor patch introduced before the Mondrian), and we tested at the high contrast only, 40%. Results from those conditions are plotted in **Figure 4A**, where it can be seen that observers performed much better at 5 Hz, a flicker rate where the faint ripples were now sufficiently strong to make the disappearance cue more conspicuous [$t(14) = -7.43$, $P < 0.0001$]. The third author was retested, this time including intermediate flicker values, and his results confirm that this cue becomes increasingly more salient with flicker rate (**Figure 4B**). We have not yet tried to identify the upper flicker rate beyond which this cue begins to weaken, but based on our knowledge of the effect of temporal frequency on contrast sensitivity (Robson, 1966) there is bound to be a point at which one begins to lose sensitivity to this cue.

So, it appears that interocular inhibition induced by a dynamic Mondrian can effectively erase from awareness the form information associated with our test stimulus while exerting a less robust suppression effect on the temporal information carried by that stimulus.

EXPERIMENT 3

The ripples within the CFS that betray the location of the removed portion of a gabor patch themselves convey a vague sense of form, in the same way that waves in a body of water portray form in virtue of their spatial extension. In the parlance of contemporary vision science, we would characterize such waves as second-order, or non-Fourier, patterns defined by temporal modulation, not by luminance (Lin and Wilson, 1996). In this third experiment, we asked whether interocular suppression induced by CFS exerts differential effects on absence of awareness of this second-order form information compared to absence of awareness of stimulus location disclosed by temporal modulation. To pursue this question, we exploited the increasing salience of higher rates of flicker as a cue for location (recall **Figure 4**). Does identification of second-order contour orientation covary with increasingly improved location performance? To find out, we modified our previous task to turn it into a 2 × 2 forced-choice task that assesses performance on two tasks concurrently (Nachmias and Weber, 1975; Watson and Robson, 1981).

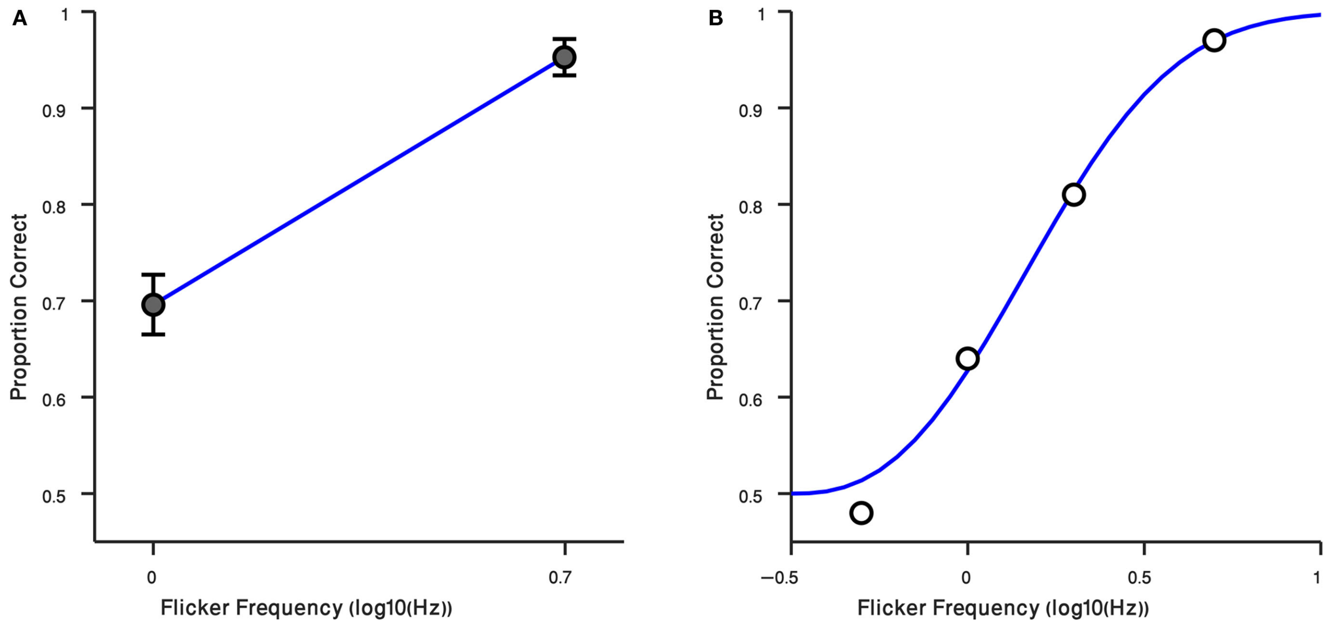

FIGURE 4 | Result of Experiment 4. (A) Performance of observers in two flicker frequency conditions (1 and 5 Hz). Error bars indicate ±1 SEM. **(B)** Result of Randolph Blake in four flicker frequency conditions (0.5, 1, 2, 5 Hz) are shown in black circles. The blue curve is a Weibull function fitted to data. Horizontal axis is the $\log_{10}$ of flicker frequency. Vertical axis plots the proportion of correct responses.

In this third experiment, we modified the display presented to one eye so that it contained two flickering gabor patches situated above and below a central fixation point (**Figure 2**), with one comprising contours oriented clockwise and the other comprising contours oriented anticlockwise; the other eye viewed the CFS display. From trial to trial the orientation/location pairings of the gabor patches were randomized, as was the eye receiving the pair of gabor patches. On each trial the observer judged the orientation and the location of the gabor patch that was removed 2 s before removal of the second gabor patch.

For each observer these dual 2AFC tasks produced two sets of data, one associated with identification of the orientation of the initially removed pattern and the other associated with identification of the location of the initially removed pattern. For each observer we analyzed those two sets of results in the following way. We first used a maximum likelihood procedure to fit a Weibull psychometric function to each data set (examples of the two extremes in performance among the six observers are shown in the upper panels of **Figure 5**). Using those best-fitting psychometric functions, we next applied a parametric bootstrapping technique (Wichmann and Hill, 2001) to estimate the 95% confidence intervals of the flicker frequency value associated with 65% correct performance on the location task and on the second-order orientation task. If performance on those two tasks were perfectly yoked, we would expect those estimated threshold values to be statistically indistinguishable.

The lower left scatterplot in **Figure 5** reveals that the threshold for judging the location of the removed stimulus was consistently higher than the threshold for judging the orientation of that same stimulus. For all observers, in other words, there were trials on which they could perceive the location of the removed pattern but could not perceive its orientation. Once again, observers described using a process of elimination to perform the location judgment: either the upper or the lower region of the CFS display ceased to exhibit that vague sense of rippling produced by the temporal modulation of the gabor patch, enabling the observer to deduce whether the initially removed gabor was the one located above or below fixation. Evidently this cue was less salient for perceiving the orientation of that initially removed pattern (or, for that matter, less salient for specifying the orientation of the remaining gabor patch which, by process of elimination, would enable observers to deduce the orientation of the initially removed pattern).

This dissociation between absence of awareness of stimulus orientation and stimulus location was further evidenced by an analysis of performance of the orientation task contingent on correct performance on the location task. Specifically, for each observer we computed the conditional probability of correct orientation judgment given a correct location judgment, $P(C_\mathrm{O}/C_\mathrm{L})$, and the conditional probability of a correct location judgment given a correct orientation judgment, $P(C_\mathrm{L}/C_\mathrm{O})$. For all six observers, $P(C_\mathrm{O}/C_\mathrm{L})$ was lower than $P(C_\mathrm{L}/C_\mathrm{O})$, again pointing to a dissociation between performance on the two tasks (lower right scatter plot in **Figure 5**).

DISCUSSION

This study was initially conceptualized as an attempt to learn whether awareness of absence is distinguishable from absence of awareness. Based on what we have learned from our three experiments, we have no doubt that it is possible to create conditions where observers cannot notice the physical removal of a stimulus that was already erased from awareness by interocular suppression. But in the course of performing these experiments, we stumbled

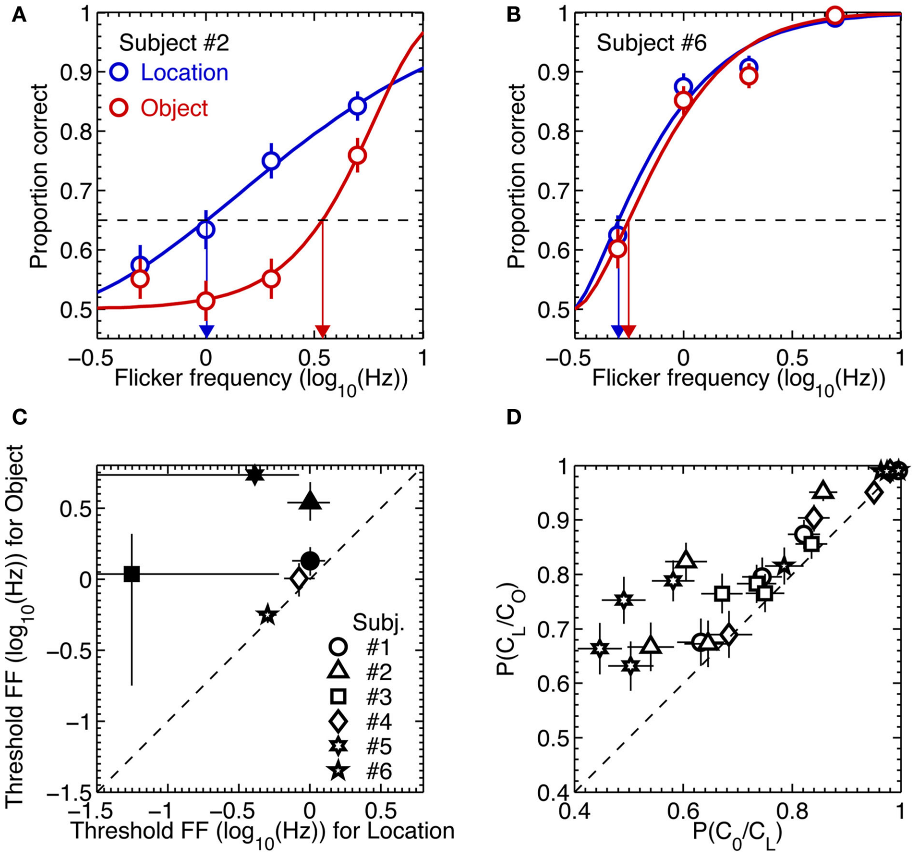

FIGURE 5 | Results of Experiment 3. (A,B) Example psychometric function fits to the data from two most extreme observers. The blue and red symbols are data from the location and object tasks, respectively. The thick lines are Weibull functions fitted to the data. The blue and red arrows indicate 65% (the broken horizontal lines) threshold flicker frequencies for the location and object tasks, respectively. The error bars are the standard errors of proportion correct, estimated from binomial distributions. **(C)** Threshold flicker frequencies from the location task are plotted against those from the object task. The different symbols represent different observers. The statistically significant differences in threshold between the two tasks are indicated by the solid symbols. The error bars are 95% confidence intervals, estimated from 2000 parametric bootstrap samples. **(D)** The conditional probability of being correct in the object task given correct location judgment are plotted against the conditional probability of being correct in the location task given correct object judgment for each of flicker frequency and for each subject. The different symbols represent different observers. The error bars are the standard errors of proportion correct, estimated from binomial distributions.

upon an additional observation that provides a more refined view of interocular suppression's effect on a stimulus, namely that temporal information can be less susceptible to interocular suppression than is form information.

In retrospect, this finding is not so surprising, for several other lines of evidence hint at a differential effect of interocular suppression on spatial vs. temporal information. We know, for example, that interocular differences in rate of luminance flicker do not produce binocular rivalry alternations in the absence of form differences (O'Shea and Blake, 1986). We also know that the perceived direction of motion of a pattern dominant during rivalry can be influenced by the motion direction of the suppressed pattern, implying that motion information from the suppressed eye remains partially effective (Andrews and Blakemore, 1999, 2002). Perhaps most relevant to our findings, are results from a study by Carlson and He (2000) in which observers dichoptically viewed two different forms flickering at different rates. Observers could readily perceive the visual "beats" produced by integration of the two flicker rates even when they were consciously aware of only one of the two forms. Flicker and form information, in other words, were dissociated in perception (see He et al., 2005, for more on this dissociation and its possible relation to the parvo- and magnocellular pathways). Flicker and form are not the only stimulus qualities that can be dissociated during suppression. Hong and Blake (2009) noted that, "the color of an object, suppressed from awareness during CFS, could nonetheless be experienced as a diffuse, somewhat faint cloud appearing transparently on the grayscale rectangles forming the Mondrian patterns. This impression of color did not seem to be a surface property of the Mondrian itself but, instead, to be a transparent overlay with no defined shape. (p. 403)." Hong and Blake documented this dissociation in a series of experiments, including one that involved monocular presentation of colored, drifting gratings. Results from that latter condition showed that increasing the speed of motion of a colored grating made its color more difficult to identify during suppression but made its direction of motion easier to identify. This latter finding, of course, dovetails with the frequency-dependent modulation of detection of absence found in our Experiment 2. (In an email exchange with one of the authors (Randolph Blake), Bahador Bahrami, University College, London, described a similar phenomenon when using CFS to suppress a drifting grating, writing that the contrast polarity of the grating was invisible but the drift was still evident "like a mirage in a desert.")

Putting these various findings together, one is led to the conclusion that neural information associated with some aspects of a stimulus are less susceptible to interocular suppression than are other aspects of that stimulus. Interocular suppression thus can operate like the chemical process of fractional distillation, separating the qualia comprising conscious visual awareness from the objects or events themselves. The idea that the contents of awareness can be fractionated by suppression is intriguing within the context of the view that awareness is a constructive process that operates to unify/integrate sensory information (e.g., Baars, 2005; Mudrik et al., 2011). While not contradicting this view, fractionation of awareness by suppression implies that perceptually bound features can become temporarily unbound without losing access to consciousness. That being said, we are reluctant to push this idea too far, for the very notion of qualia is highly controversial as evidenced by the lively debates over this notion among philosophers (see the Wikipedia entry for qualia http://en.wikipedia.org/wiki/Qualia to see what we mean).

In the vision literature, people often speak of the depth of suppression when referring to binocular rivalry (e.g., Nguyen et al., 2001) or to interocular suppression associated with strabismic amblyopia (Holopigian, 1989). Our findings suggest that it may be useful to think about awareness as having depth, in that awareness can penetrate to different levels depending on the composition of the stimulus and, perhaps, the nature of the task being performed. We are currently exploring whether the depth of awareness is dependent on task demands and whether it can be modified by practice and, if so, the extent to which such modification generalizes to other tasks or categories of stimuli.

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