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INHIBITION IN THE PROCESS OF FEATURE BINDING

Topic Editor
Snehlata Jaswal



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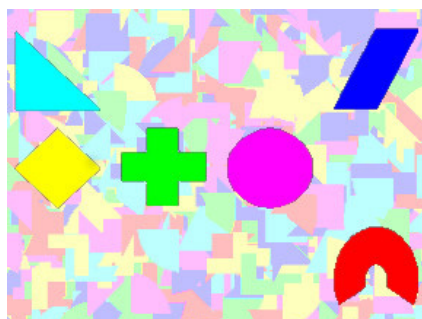
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INHIBITION IN THE PROCESS OF FEATURE BINDING

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Feature binding is the process whereby different features such as shape, colour, size, orientation, location, etc. are linked together to form a coherent representation of the object. It is a ubiquitous physiological sequence and an essential phase in information processing, for it provides the basis of mental representations, which in turn, are requisite for all cognitive functions.

It is important to realize though, that binding is not an isolated process. There are myriad stimuli

impinging on our senses at all times, vying to gain entry into our consciousness. Further, not only does sensory input emanate from a complex, dynamic environment, but it also enters a neural system that is already activated by previous inputs and is oriented towards future goals. Which aspects of the momentary sensory input are selected for further processing depends as much on the state of the system as it does on the sensory input itself. Indeed, some fundamental questions one may ask about binding are whether, why, and how, some features are selected for binding at the cost of others.

The bottom-up view of information processing is that the input received by the brain is processed in a largely automatic way to the higher centers in the brain. The physiological basis of binding is postulated to be either conjunctively coding neurons, or synchrony among participating neural networks to encode features and out of phase neural activity to encode separate objects. But, mere perceptual integration of features, whether by synchrony or by specialized neurons, does not even begin to capture the implication that binding results in coherent objects, fundamental for further information processing. An object is not only a bundle of features. At the very least, the features need to be integrated so that the object can be distinguished from other objects. This implies selection and manipulation of the basic information supplied by separate features. The top-down view of information processing contends that binding is more influenced by the reentrant processes (the downward and

lateral feedback to the lower areas, emanating from the higher centers of the brain). Reentrant processes not only help to confirm what is correct but also resolve competition. These top-down processes are linked to attention and higher cognitive functions help select relevant input.

We aim to debate what happens to the irrelevant information in the process of binding. Are irrelevant features simply lost from the system over time, or are they deliberately deleted? Is there any inhibitory process involved in binding? What is the empirical evidence for such a process at the behavioral level? Is such a process active and resource-demanding or relatively passive and automatic? What do neuropsychological studies show? What are the physiological underpinnings of such a process? How is it incorporated in computational models to increase our understanding of the binding process? The idea is to bring together diverse views on 'Inhibition in Feature Binding' with the ultimate aim of better understanding the process of binding and invoking informed and insightful future research.

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The process of feature binding

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The integration of different stimulus properties as an object is the process of feature binding. The research topic “Inhibition in the process of feature binding” aimed to debate which features bind together, why, and how; and what happens to features which are not integrated.

The authors of the review articles took up the debate in earnest. Wyatte et al. (2012) emphasize that the process of binding does not require any special neural substrates. The two mechanisms of inhibition and top-down feedback are sufficient to explain the process of object recognition. Their computational model describes how these established principles of neural processing work over time to solve the binding problem. Particularly critical of the idea of neural synchrony, often held forth as “the” mechanism underlying feature binding, they contend that it helps only to create a contrast between relevant and irrelevant features. It is top-down feedback, which reinforces relevant information.

The relevance of features is the key factor in the process of binding for Jaswal (2012). She attempts an integration of physiological and psychological literature, highlighting that only relevant features bind together in a rather slow process, which concomitantly ensures that the irrelevant features are actively inhibited. In a more expanded overview, Velik (2012) reaches similar conclusions—that irrelevant information is deleted from the system in the process of binding. However, whilst Jaswal (2012) bases her conclusions on empirical studies, Velik (2012) presents a computational model in which filter mechanisms work to suppress irrelevant information. Krummenacher and Müller (2012) review evidence from behavioral and ERP studies to confirm that separate feature dimensions are important in the pre-selective phase of feature binding. However, once the bound object emerges, feature based effects are not as dominant. This corroborates with the aforementioned views that only relevant features are carried forward.

Herzog et al. (2012) also address how we process features prior to and during the process of binding. Using the sequential meta-contrast paradigm, they explore binding as a sub-process in the Gestalt experience of grouping elements into wholes. They contend that computation of features is in itself a process and not an instantaneous event. Stimulus representations are dynamic and binding probably occurs simultaneously with the processing of independent features.

Meier and Rey-Mermet (2012) discuss episodic context binding using bivalent stimuli. The ambiguity of bivalent stimuli is itself a “feature” that enters binding and influences subsequent behavior in consonance with the bivalency effect. It is interesting

that Meier and Ray-Mermet propose that this conflict is not relevant to the task. In fact, this ambiguity and concomitant conflict is a cardinal feature of bivalent stimuli, which reactivates whenever the context is reintegrated.

Moving from features to objects, Dent et al. (2012) review behavioral and physiological evidence for the process of distracter inhibition in visual search. They postulate that it is a resource demanding active process, which is parallel in nature, such that all distracters are deleted, and the target alone remains as the item to be processed further.

The four articles contributing original research extend the study of binding to novel avenues. As merits empirical investigations, all studies not only document details of current work in these new areas, they also indicate hypotheses for future investigations.

Delogu et al. (2012) enter the arena of audition to investigate the link between location and temporal order. The recall of temporal order is weakened more than locations, whilst binding in visual as well as auditory domains. This suggests that location is encoded relatively automatically during binding, but recall of temporal order is resource demanding. Similar results across visual and auditory domains suggest that binding of location and temporal order may involve shared, modality-independent physiological mechanisms. This special link between “when” and “where” features, merits future explorations.

Giersch et al. (2012) scale up from features to explore grouping and regrouping between objects among schizophrenics and healthy controls. Patients were particularly slow to detect connected targets when the attentional focus was on unconnected pairs. This effect was found only for targets presented within the same hemifield. Thus, schizophrenics do not regroup stimuli in the same way as healthy controls. Speculations can be made regarding the role of connectivity between hemispheres in grouping. Further, grouping and regrouping are different (maybe parallel) mechanisms, the former relying on automatic processing, whilst the latter demand attentional resources.

The two original research articles based on computational models conceptualize binding as part of other processes. Schrobsdorff et al. (2012) propose that binding is an essential phase in inhibition. In their model of the negative priming effect, features are activated, bound into object entities, and related to their context. Inhibitory processes and changing thresholds implement the concept of selective attention. Thus, binding becomes a sub-process in a general model of inhibition. Davelaar (2013) evokes the concept of binding to explain the Gratton effect in the Eriksen flanker task. The Gratton effect is the reduction in

the interference due to flankers after incongruent, as compared with congruent trials. Results of experiments that separate the contributions from target, flanker, and response repetition, show that flanker repetition alone is sufficient to produce congruency effects in sequences of trials. He postulates that representations of targets, flankers, and response(s) are associated in a task set. This work is an excellent example of how the concept of binding is used to understand other ideas and paradigms.

The aim of this research topic was to consider the process of binding from various perspectives such that an integrated

view emerged to guide future research and theory. Challenging the assumption that feature binding is an automatic “event” driven by bottom up processes dependent on conjunctively coding neurons or synchrony, the collection of these articles yield the conclusion that the emergence of a bound object capable of further processing, is itself a sub-process, which is heavily contingent on re-entrant mechanisms and is probably resource demanding. Future investigations may explore feature binding as a basic process in myriad behavioral sequences of diverse populations.

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The role of competitive inhibition and top-down feedback in binding during object recognition

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How does the brain bind together visual features that are processed concurrently by different neurons into a unified percept suitable for processes such as object recognition? Here, we describe how simple, commonly accepted principles of neural processing can interact over time to solve the brain's binding problem. We focus on mechanisms of neural inhibition and top-down feedback. Specifically, we describe how inhibition creates competition among neural populations that code different features, effectively suppressing irrelevant information, and thus minimizing illusory conjunctions. Top-down feedback contributes to binding in a similar manner, but by reinforcing relevant features. Together, inhibition and top-down feedback contribute to a competitive environment that ensures only the most appropriate features are bound together. We demonstrate this overall proposal using a biologically realistic neural model of vision that processes features across a hierarchy of interconnected brain areas. Finally, we argue that temporal synchrony plays only a limited role in binding – it does not simultaneously bind multiple objects, but does aid in creating additional contrast between relevant and irrelevant features. Thus, our overall theory constitutes a solution to the binding problem that relies only on simple neural principles without any binding-specific processes.

Keywords: binding, competitive inhibition, feedback, computational model, object recognition

INTRODUCTION

The term “binding” has several meanings within psychology and neuroscience. The central assumption is that partial representations must in some way be “bound” together into a full representation (Treisman, 1996, 1999). In particular, the term is used in the context of visual processing; however, the issue is relevant in understanding brain and psychological mechanisms in general. The need for binding mechanisms is highlighted by the fact that neurons early in the visual system respond to (and therefore represent) simple visual features while meaningful objects consist of very particular conjunctions of many of these features (e.g., perpendicular lines meeting at their ends compose corners; corners that line up compose rectangles, etc.). Some mechanism appears to be needed to track which of these features belong together; that is, which ones originated from a coherent construct in the real world, and so should be combined to produce an accurate and meaningful internal representation of that construct.

We seek here to clarify the neural mechanisms involved in the process of binding. In doing so, we describe a theory of how binding can be explained using only simple, generic principles of neural processing. Our perspective on binding has much in common with that of other theorists (Reynolds and Desimone, 1999; Shadlen and Movshon, 1999; Treisman, 1999; Bundesen et al., 2005). In fact, the amount of convergence on the binding problem in recent years is striking; the novelty of our contribution is therefore largely in adding specificity to these proposals in terms of the biological mechanisms that underlie binding in the brain.

Our core proposal is that competitive neural inhibition, combined with top-down feedback and learned selectivity for some features over others, accounts for binding in the brain. More specifically, the computational role of inhibition and top-down feedback in binding is to ensure that only neurons with the most support become substantially active and ultimately drive behavior. Cortical inhibition thus performs contrast enhancement by suppressing activity of neurons with significant but lower levels of excitatory input (Kandel et al., 1995; Carandini and Heeger, 2012). Neurons tuned to the less relevant information (such as features from objects outside the focus of attention) are thus out-competed, and so downstream neurons respond only to the most relevant “winning” features.

Top-down feedback supplies an extra set of criteria for which features are most relevant in a given context, supplying useful biases to this competition (Desimone and Duncan, 1995). Top-down feedback can thus be contrasted with feedforward, stimulus-driven signals, that mainly convey information about the sensory environment. However, the neural mechanisms that underlie these two information pathways are exactly the same: standard excitatory synaptic inputs (O'Reilly, 1996; O'Reilly and Munakata, 2000). Putative top-down signals include those from frontal and parietal areas that direct spatial attention (Thompson et al., 2005; Bressler et al., 2008), and those from prefrontal areas that convey information related to the current task or goals (Miller and Cohen, 2001), but might also include those originating from areas only slightly higher up in the visual system that convey “working hypotheses” as to object identities or higher-level features

(Fahrenfort et al., 2007; Boehler et al., 2008; Roland, 2010; Koivisto et al., 2011). In each case, the type of information and therefore the exact constraints supplied to the competition are different; but the fundamental computational role in guiding the local competitions that lead to binding the most relevant features is the same.

We motivate our proposal with a recent review by Vanrullen (2009), which posits two distinct types of binding. One is an “on-demand” process for binding together simple but arbitrary feature dimensions into conjunctive representations (e.g., a red circle stimulus in a visual search experiment contain both “red” and “circular” features). Much of research on binding to date has involved visual tasks that use these arbitrary feature conjunctions which have been proposed to be solved by top-down attentional mechanisms as well as inhibitory mechanisms (Treisman, 1996, 1999; Reynolds and Desimone, 1999). A second type of binding, referred to as “hardwired” binding, involves grouping together pre-established conjunctions of features. Experiments using visual object categorization have been used to motivate the need for hardwired binding, with the major finding being that they proceed rapidly in the absence of top-down attentional mechanisms (Riesenhuber and Poggio, 1999b; Serre et al., 2007; Vanrullen, 2007).

We focus here on the case of hardwired binding. However, we propose that the same mechanisms involved in on-demand binding are also present during hardwired binding. Inhibition and top-down feedback interact to select only the most relevant elements of visual features for further processing, eliminating less contextually relevant features, thus minimizing binding errors. We argue that these mechanisms are just as important for activating the learned feature combinations used in visual object recognition as they are in visual tasks involving arbitrary feature combinations.

Thus, our approach focuses on the binding problem inherent in the problem of object recognition, but applies to the problem more generally. When presented with visual information, whether it be in the context of a single isolated object or an array of multiple objects, the brain relies on the same basic neural mechanisms to form a coherent (properly bound) representation. While abstract cognitive strategies may be important for dealing with different tasks (e.g., visual search), it is unlikely that they are implemented differently at the neural level or require special binding processes. Instead, they operate on the same basic representation formed by simple visual processing.

We explicitly demonstrate our proposal using a biologically realistic model of visual processing (O'Reilly et al., under review; see Methods for overview). We demonstrate three particular aspects of our proposal in the context of a realistic object recognition task that requires binding together learned object features into a single, coherent object (i.e., part binding; Treisman, 1996). First, we show how neurons that code complex visual features compete during processing over the full course of recognition. Inhibitory competition ensures that only the most relevant features are active, while less relevant ones are ultimately suppressed. We further show that systematically reducing the number of category-relevant visual features in the stimulus by an occlusion degradation weakens these competition effects, ultimately causing binding errors in which relevant and irrelevant features become co-active in the bound representation. Second, we show how

top-down feedback reinforces category-relevant features, including those that may have been weakened by degrading factors like occlusion, providing some robustness to binding errors. Finally, we investigate the case of multiple object recognition, which has special importance in the study of binding as it can produce illusory conjunctions of features across objects (Treisman, 1996, 1999). We find that the same mechanisms of inhibitory competition and top-down feedback contribute to solving the problem of properly binding learned features when selecting among multiple objects.

The novelty of our contribution to the ongoing discussion on binding is a synthesis between binding and object recognition theories using only the general neural mechanisms of neural inhibition and top-down feedback. Others have put forth similar solutions to the binding problem using only general neural mechanisms (e.g., Reynolds and Desimone, 1999; Bundesen et al., 2005), and we expand on this work with explicit simulations that make predictions about the temporal dynamics of these mechanisms during a hardwired binding task. Our theory can be contrasted with more complex theories of binding, especially those that involve multiplexed neural synchrony (e.g., Singer, 1993, 1999; Singer and Gray, 1995; Uhlhaas et al., 2009). While there might be additional binding-related phenomena (such as those involving working memory; see Raffone and Wolters, 2001) that require such mechanisms, the standard object recognition functions of visual cortex targeted by existing work on binding appear to only require the mechanisms that we focus on here. We conclude by discussing some of the predictions and limitations of our model with respect to other binding theories.

NEURAL INHIBITION SUPPRESSES IRRELEVANT INFORMATION

In the simplest sense, a bound representation in the brain consists of the current set of actively represented features. The brain represents information in a code distributed across a large number of neurons (Kandel et al., 1995), and thus, can represent many features simultaneously. Binding errors can thus occur when features that belong to different objects in the external world are incorrectly bound together into the brain's representation of a single object. To minimize binding errors, the brain relies on several mechanisms to ensure that only the features that belong together get bound together in the long run. One such mechanism is neural inhibition.

Within a given brain area, only a small percentage of neurons are ever active at any given time. One reason for this is that cortical neurons inhibit each other through disynaptic connections with local inhibitory neurons. These inhibitory interneurons are known to perform the function of limiting overall activity levels throughout cortical areas. Within an area, connections to and from inhibitory neurons seem to be relatively non-selective (Swadlow and Gusev, 2002), making this competitive effect general: every excitatory neuron competes with every other excitatory neuron, to roughly the same extent. This picture of inhibitory function is, of course, somewhat oversimplified, but it is sufficient to capture the role neural inhibition in solving the binding problem. This competitive inhibition is one mechanism of contrast enhancement (Carandini and Heeger, 2012), and it is useful to think of the

mechanism as enhancing contrast between firing rates of neurons representing more- and less-appropriate features.

As an example that illustrates the role of inhibition in hard-wired binding, we use the LVis model described in O'Reilly et al. (under review) to demonstrate how the brain binds together a visual representation of a fish for recognition (see Methods for model details). Visual object recognition is thought to be subserved primarily by inferotemporal (IT) cortex, which responds to moderately complex visual features (Logothetis et al., 1995; Tompa and Sary, 2010). IT cortex contains a columnar organization (Tanaka, 1996; Tompa and Sary, 2010), in which columns of neurons that subtend horizontal patches of the cortex code different visual features. While the specific dimensions of stimuli to which a given IT column respond are not yet well-understood (Kourtzi and Connor, 2010), IT neurons can be conceptualized as responding to object “parts” that represent a specific object exemplar at the population level (i.e., combination coding, Ungerleider and Bell, 2011).

As a concrete example, one column of IT neurons might be tuned to a fish's fin, ideally firing when in the presence of a viewed fish. A neighboring column might be tuned to a completely different visual feature such as a bird's wing, and thus should be silent when viewing the fish. These columns project onto inhibitory interneurons that create competition among columns (Mountcastle, 1997), effectively making some combinations of columns mutually exclusive.

In **Figure 1**, we show the firing patterns of simulated columns of IT neurons when presented with a fish stimulus. Initially, a large number of IT neurons fire, some of which belong to columns that code fish-relevant features and some of which belong to columns that do not. The columns selective to fish-relevant features (e.g., a fish fin, a fish tail), however, quickly out-compete columns selective to fish irrelevant features since the former constitute a better fit with the fish stimulus, increasing their initial evoked response. In turn, the columns selective to fish features inhibit columns selective to irrelevant features, effectively stopping irrelevant neurons from firing and becoming part of the bound representation. Thus, competitive inhibition among detected features helps ensure that a valid combination of features ultimately is bound by driving firing of IT neurons, eliminating invalid conjunctions of features that might lead to binding errors.

Inhibition might be especially important when visual objects are highly ambiguous. We demonstrate this idea in **Figure 1** by partially occluding the presentation of a fish, which removes diagnostic visual features and impairs recognition accuracy. Other conditions may also create stimulus ambiguity, such as a non-standard view of an object (such as a fish's underbelly), or an atypical exemplar (an exotic fish, perhaps). Visual occlusion, however, allows us to parametrically measure the effects of ambiguity on activity levels of IT neurons in our model. The general effect of occlusion is an attenuation of the category selective IT response due to the decreased stimulus-driven signal, a finding that has

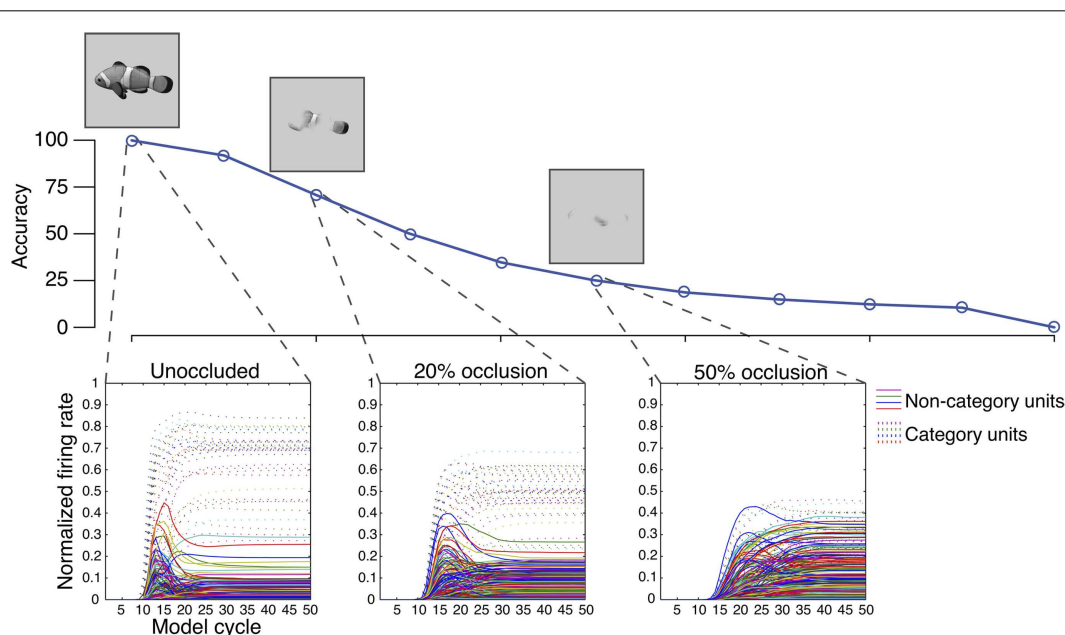


FIGURE 1 | Neural inhibition in visual binding. We use the LVis model described in O'Reilly et al. (under review) to demonstrate how IT level visual features are suppressed by inhibitory mechanisms over the course of visual processing. **Top:** Visual occlusion was varied as an independent variable to measure its effect on IT firing patterns during object categorization. Increased occlusion results in a monotonic impairment in categorization accuracy. **Bottom:** Firing rates were recorded for each IT unit in the model and grouped according to whether they were strongly tuned to the fish category

exemplars (dotted lines) or tuned to other categories (solid lines). The first wave of responses from the model's IT units area code a large number of features, only some of which are category-relevant. Inhibitory competition, however, suppresses the responses of irrelevant non-category units, leaving the features coded by relevant category units to compose the final bound representation. This competitive advantage disappears at higher levels of occlusion (e.g., 50% occlusion) due to fewer category-relevant features being specified in the stimulus.

been also demonstrated in neurophysiological studies of occlusion (Kovacs et al., 1995; Nielsen et al., 2006). Moreover, because neurons in category selective columns fire at a lower rate, they indirectly exert weaker levels of inhibition toward competing columns. The result is an overall increase in the response of neurons that are selective to category irrelevant features. Thus, both the weakened response to category-relevant features and the erroneous heightened response to irrelevant features may play a role in binding errors when stimulus conditions are highly ambiguous, leading to impaired recognition accuracy.

TOP-DOWN FEEDBACK REINFORCES RELEVANT INFORMATION

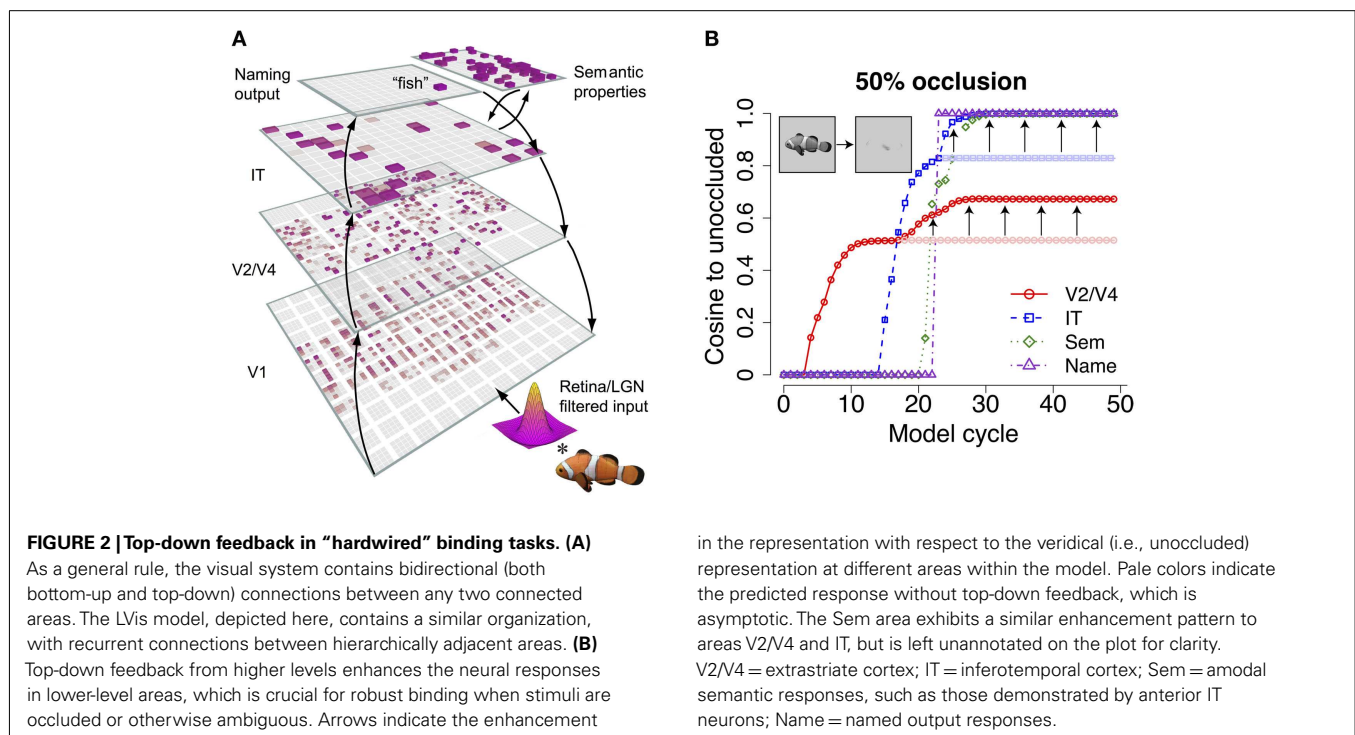
It is well-known that the brain contains numerous top-down connections that descend from higher levels of brain systems to lower levels (Felleman and van Essen, 1991; Scannell et al., 1995; Sporns and Zwi, 2004; Sporns et al., 2007). In the context of vision, one commonly suggested function of top-down connections is to convey attentional signals to sensory based areas of visual cortex. These top-down signals can take the form of spatial attention (originating in the frontal eye fields and posterior parietal cortex, Thompson et al., 2005; Bressler et al., 2008) or executive attentional control (as enacted by maintained representations in prefrontal cortex; Miller and Cohen, 2001; Herd et al., 2006).

In the case of spatial attention, top-down feedback about the attended region of space determines which features are relevant by selecting for features within a small spatial area and enhancing them relative to features from neighboring, unattended areas of space. Top-down feedback reflecting executive attentional control works the same way, except that relevancy is determined by more abstract feature dimensions such as color or category (Maunsell and Treue, 2006).

In either case, top-down feedback does not require any representation of what to exclude. Instead, it simply signals what to attend to by providing additional excitatory bias to the sensory representations, causing the representative neurons to fire more strongly. This bias reinforces the activation of relevant features, encouraging their binding at the highest levels of processing. This explanation of attention is a further explication of the biased competition framework of (Desimone and Duncan, 1995), and has been supported by considerable empirical evidence, most notably that of Reynolds and colleagues (see Reynolds and Chelazzi, 2004, for a review).

While top-down feedback has been shown to be crucial for on-demand binding tasks that require the cognitive flexibility to bind arbitrary features together at arbitrary locations (Treisman, 1996, 1999), it is not yet understood whether top-down feedback similarly plays a role in hardwired binding tasks like object recognition and categorization. Computational models have suggested that these tasks can be solved in the brain in a primarily feedforward manner with little to no influence from top-down feedback (Riesenhuber and Poggio, 1999b; Serre et al., 2007; Vanrullen, 2007, 2009). However, there are a number of reports of top-down feedback playing a fundamental role in early visual processes including object recognition (Bar et al., 2006; Fahrenfort et al., 2007; Boehler et al., 2008; Roland, 2010; Koivisto et al., 2011).

In an attempt to reconcile these data, we recently described a computational model of object recognition that contains both feedforward and feedback connections between feature processing layers (O'Reilly et al., under review). One of the key findings, which we review here, is that top-down feedback promotes robust recognition when bottom-up signals are weak and ambiguous due to occlusion (**Figure 2**). While occlusion generally attenuates



neural responses resulting in reduced recognition accuracy, the model often exhibits intact category selective responses and correct recognition, a property that we attribute to top-down feedback. Specifically, top-down reinforcement enhances the responses of neurons at lower levels that may have been weakened due to occlusion. This enhancement is repeated across multiple recurrently connected areas, essentially recovering the occluded visual features and resulting in a complete representation. Conceptually, visible features like the fish's dorsal fin might evoke a partial response in IT cortex, which could provide reinforcement to the encoding of other relevant features that might not be visible at lower levels like V2 or V4. Similarly, entertaining the possibility that one might be viewing a fish (i.e., partial activation at the "Naming Output" level of our model) can reinforce fish-relevant features encoded by IT columns. Functional neuroimaging experiments have indicated that the brain exhibits a similar object completion process in which visual information is recovered despite its omission from a visual stimulus (Kourtzi and Kanwisher, 2001; Lerner et al., 2004; Johnson and Olshausen, 2005; Juan et al., 2010).

BINDING MULTIPLE OBJECTS

Thus far we have focused on the problem of binding visual features into a singular, coherent object, and have proposed that both neural inhibition and top-down feedback play important roles in this process. Do these same mechanisms aid in proper binding when multiple objects are present in a display? Proper binding when multiple objects are present is a challenging problem because high-level visual areas such as IT cortex have receptive fields that span large portions of the visual field (generally 10° to 20°; Kobatake and Tanaka, 1994; Rust and Dicarlo, 2010). Thus, IT neurons respond, by default, to visual features regardless of where they are within the visual display, even when they occur in the context of a second object's features. Although the large receptive fields of IT neurons are thought to be necessary for promoting tolerance to changes in object position, scale, and rotation (Logothetis et al., 1995; Tanaka, 1996; Riesenhuber and Poggio, 2002; Rolls and Stringer, 2006), they exacerbate the possibility of illusory conjunctions being formed between the features of separate objects.

We propose that neural inhibition combined with top-down feedback can solve the problem of binding when multiple objects are present in a similar manner to the way they aid in binding visual features into singular, coherent objects. We demonstrate the plausibility of this idea in **Figure 3**. As is the case with single objects presented in isolation, a large number of IT neurons fire initially when multiple objects are present. Grouping these neurons according to the object to which they are selective illustrates the interactions between inhibition and top-down feedback. Generally, neurons that code visual features shared by both objects are the first to respond, since they constitute the best overall fit with the stimulus itself. In the case of the gun and bicycle pictured in **Figure 3A**, these first responders might be neurons that code the horizontal edges that compose the barrel of the gun and the top tube of the bicycle. Neurons that code unique features for each of the object categories are the next to respond. However, inhibition between these columns of neurons ensures that the features of only one of these objects are selected in the end, "winning" the competition (in this case, the bicycle neurons) and contributing

to the final bound representation. When a single object is selected for the bound representation, top-down feedback can reinforce neurons that code meaningful features from that object that may not have initially responded (possibly due to initial inhibitory influences from neurons corresponding to the "losing" object).

Binding errors can occur when neurons representing irrelevant features are not entirely out-competed (**Figure 3B**). This allows invalid feature conjunctions to manifest, which subsequently get reinforced from top-down feedback, resulting in the formation of illusory conjunctions. To determine more specifically how inhibition and top-down feedback contribute to minimizing illusory conjunctions, we tested the effect of removing top-down feedback and both top-down feedback and inhibition from the model¹ (see Methods for details). The results of these tests are indicated in **Figure 4**.

For the LVIS model (which contains both inhibition and top-down feedback), illusory conjunctions occurred on only 4.7% of trials. Removing top-down feedback, but leaving inhibition intact, had virtually no effect on the number of illusory conjunctions. However, removing both top-down feedback and inhibition caused illusory conjunctions to occur with much higher frequency, on 19.3% of trials.

We also computed the ratio of relevant IT responses to irrelevant responses (where relevance was determined by whether the responses corresponded to the model's output) which can be thought of as a kind of "signal-to-noise ratio" (**Figure 4B**). A decrease in this number reflects lower proportions of relevant information and higher proportions of irrelevant information at the IT level, which could lead to more illusory conjunctions being made. Accordingly, the purely feedforward model, which made the most recognition errors, also exhibited the lowest ratio of relevant to irrelevant information.

Removing feedback from the LVIS model also lowered the ratio of relevant to irrelevant information, but recognition performance remained unchanged. This suggests that there is a critical signal-to-noise ratio (in terms of relevant and irrelevant responses) above which recognition remains robust, without many illusory conjunctions. Inhibition was intact in this model, consistent with our proposal that inhibitory competition is the critical mechanism that selects relevant information over irrelevant information, thus providing a relatively stable baseline signal-to-noise ratio. Top-down feedback can further highlight relevant information, increasing the signal-to-noise ratio, but it is unnecessary for well-learned tasks with little ambiguity. Top-down feedback is likely more important in tasks where objects are degraded (e.g., from visual occlusion), which we discussed in the previous section, or in cases where there is more feature overlap across items (e.g., conjunctive visual search).

GENERAL DISCUSSION

We have presented an account of binding in the brain that depends only on well-established mechanisms of neural processing that

¹ Note that it is impossible to test the remaining condition in which top-down feedback is left intact but inhibition is removed from the model, as some mechanism is necessary to control the overall response levels, which would saturate quickly with repeated processing.

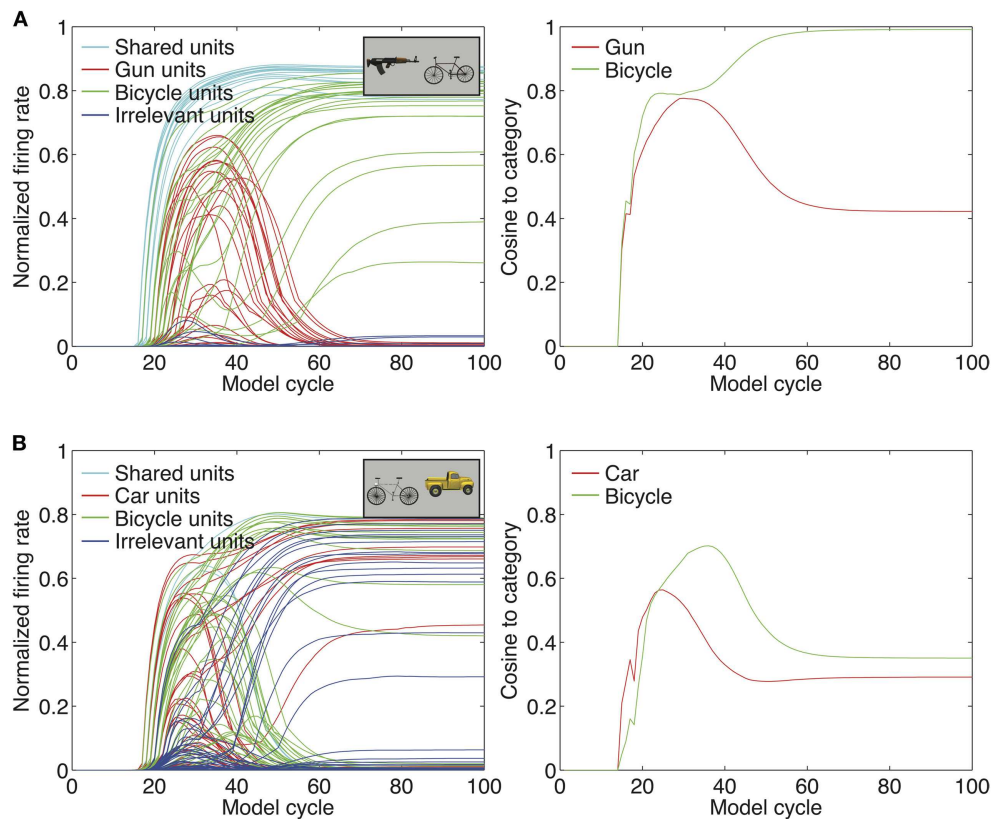


FIGURE 3 | Binding multiple objects. (A) The same mechanisms of neural inhibition and top-down feedback extend to binding when multiple objects are present in a display. The competition created from having multiple IT units active that represent multiple objects causes one set of units to “win” and one set to “lose” (in this case, the bicycle units win). Inhibition suppresses the responses from units corresponding to the losing object as well as

responses from completely irrelevant units. Top-down feedback serves to reinforce units from the winning object that may not have been initially active. **(B)** Binding errors occur when completely irrelevant units become erroneously active, leading to the inability to suppress invalid responses. This creates illusory conjunctions of features across the objects in the display, leading to a representation that does not resemble either category.

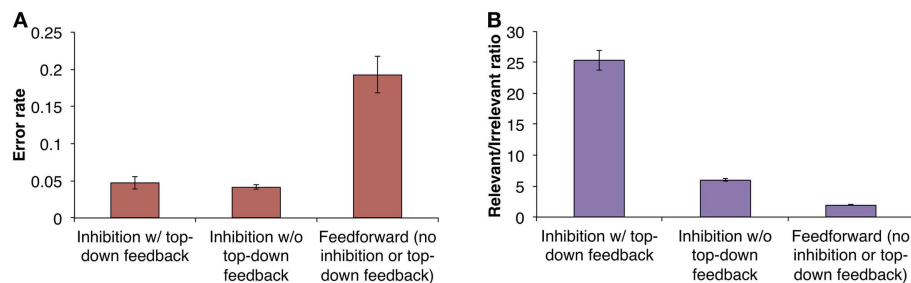


FIGURE 4 | Results for multiple object binding. (A) We tested the effect of removing top-down feedback and both top-down feedback and inhibitory competition from the model. The purely feedforward model missing both of these critical mechanisms made the most recognition errors. **(B)** Grouping responses according to whether they were corresponded to the model's

output (relevant responses) or not (irrelevant responses) suggests that the reason for the purely feedforward model's poor performance was that it had a higher overall signal-to-noise ratio (mean relevant response divided by mean irrelevant response). This type of representation could lead to illusory feature conjunctions and thus, recognition errors.

interact over time. Two such mechanisms that we focus on here are neural inhibition and top-down feedback. Together, these mechanisms create an environment of local competition within a brain area that selects only the most relevant features for the bound representation that influences perception and behavior.

We have taken a general neural processing approach to explaining how these mechanisms relate to binding. We illustrate the mechanisms explicitly in an object recognition task that requires binding together learned object features into a single, coherent object, as well as a variant of this task that requires selecting from

and identifying multiple objects. Despite our focus on “hardwired” binding, we believe that the same mechanisms perform “on-demand” binding (e.g., conjunctive visual search). In on-demand binding, top-down influences bias processing toward items in a particular region of space, and consequently, competitive inhibition eliminates those features in nearby areas of space, allowing a properly bound representation of the novel item.

One natural consequence of our proposal is the suggestion that perception and behavior are largely driven by an interactive process that integrates bottom-up information with dynamic constraints including top-down, conceptual knowledge. It is somewhat surprising then, that a large class of extant theories of visual processing treat early perceptual processing as a feedforward set of stages that simply transform information from one level of the visual system to the next (Riesenhuber and Poggio, 1999b; Serre et al., 2007; Vanrullen, 2007). Models that instantiate this feedforward theory often include a “max” operation that selects the largest response at each processing level, which can be viewed as a form of inhibitory competition that suppresses less relevant responses (Riesenhuber and Poggio, 1999a). These models, however, lack top-down feedback to reinforce relevant information, which can emerge at any time over the course of processing.

Competitive dynamics reflecting inhibitory and top-down influences within visual areas are clear if one examines population level responses. For example, initial IT population responses convey information about many individual object parts, but information about the object as a whole begins to emerge over the full time course of their response (Brincat and Connor, 2006; see also Sugase-Miyamoto et al., 2011). Other single-cell analyses have indicated that the selectivity of IT neurons changes over time, beginning with a quick burst of broadly tuned activity that gradually becomes more selective (Tamura and Tanaka, 2001). Similar temporal dynamics have been demonstrated at other levels of the visual system, such as areas V2 and V4 (Hegde and van Essen, 2004, 2006). The fact that the information content of neural responses changes over time strongly suggests that some aspects of the representation are being selected over others. Our account of binding suggests that relevancy is a significant determining factor of what parts of the representation are ultimately selected for the bound representation at the highest levels.

Our proposal is highly congruent with many previous descriptions of binding (Reynolds and Desimone, 1999; Shadlen and Movshon, 1999; Treisman, 1999; Bundesen et al., 2005). Our contribution is novel in implementing a biologically grounded neural network model that embodies these theories, and in further specifying the mechanisms involved, and how they interact. One notable relation is to the role of top-down feedback in the form of spatial attention in Treisman’s Feature Integration Theory (Treisman, 1996, 1999). Top-down feedback in our model does not directly perform binding, however, but simply prevents mis-binding by highlighting some features over others and relying on competitive inhibition to suppress the others.

Our proposal also has much in common with (Reynolds and Desimone, 1999) biased competition model, which cites the importance of competitive inhibition between populations of neurons and top-down biasing of relevant features. However, the biased competition model has traditionally focused on frontal

and parietal cortices as likely sources of the biasing signal. While attentional signals from these areas are clearly capable of biasing perceptual processing (Miller and Cohen, 2001; Thompson et al., 2005; Herd et al., 2006; Bressler et al., 2008), our approach provides a more general characterization of biasing. Specifically, any area that sends feedback to an earlier area has the potential to bias its computations. In our simulations, this allows for representations that are beginning to emerge at high-level areas to bias lower-level areas, which itself can be viewed as a form of emergent feature-based attention.

Theories centering on the role of synchrony have also been proposed as a solution to the binding problem (Singer, 1993, 1999; Singer and Gray, 1995; Uhlhaas et al., 2009). There is ample evidence that neural firing does synchronize to some degree, and that synchrony plays a role in attentive object recognition (Gray et al., 1989; Buzsaki and Draguhn, 2004). We agree that synchrony does play a role in the competitive selection process that is the core of our proposal, acting as another form of contrast enhancement by providing mutual excitation among concurrently active neurons via recurrent feedback and lateral connections (Roland, 2010). Synchrony thus effectively gives the winners of competition an extra advantage in controlling responses at higher levels.

This role of synchrony in sharpening neural competition should be differentiated from early proposals that synchrony can simultaneously bind multiple objects. No data of which we are aware indicates that the brain performs “multiplexed synchrony,” in which neurons representing each object remain in phase with others representing the same object, but reliably out of phase with neurons representing other objects. Theories of multiplexed synchrony for binding have been strongly criticized on the grounds of being both biologically implausible and unnecessary (Shadlen and Movshon, 1999; O’Reilly et al., 2003). While it seems intuitive that we are aware of many objects simultaneously, recent research on change blindness indicates that we do not maintain detailed representations outside the current focus of attention (Beck et al., 2001; Lamme, 2003; Simons and Rensink, 2005).

Because of the level of noise from incidental processing in the brain (compared to models, which are idealized and thus use little to no noise) multiplexed synchrony seems likely to be unstable beyond extremely short time periods. This drawback severely limits the use of this mechanism for binding in working memory, the other case in which intuition and some evidence suggests we maintain several representations simultaneously (Raffone and Wolters, 2001). One alternative to true multiplexed synchrony is that binding in working memory is performed by maintaining separate neural substrates for separate items within prefrontal cortex, as in the model of working memory developed by our group, reviewed in O’Reilly et al. (2010).

Rather than supposing that the brain can represent and interpret several arbitrary conjunctions of features simultaneously, it seems more parsimonious to assume, as in our proposal, that all features represented simultaneously are bound together. Instead of using a particular firing phase to “tag” each neuron as belonging to one object or another, the brain simply represents only one object (or concept, etc.) at a time when binding is difficult, thus serializing a computation that would pose unique difficulties for parallel processing.

While previous work on binding has presented many possible mechanisms and argued that they are needed to solve the brain's binding problem, the necessity of mechanisms beyond the most basic neural mechanisms has not been clearly demonstrated. We have presented a solution to the binding problem of that relies on only generic neural mechanisms to bind together features into objects. While our proposal clearly demonstrates that the mechanisms of inhibition and top-down feedback contribute in part to solving the brain's overall binding problem, it is possible that there exist binding-related situations that warrant additional mechanisms and processes (e.g., working memory). Only after attempting to explain these phenomena with basic neural mechanisms (as in the proposals mentioned above) should more complicated theories be considered.

METHODS

The LVis (Leabra Vision) model and its training/testing methods are briefly described here. See O'Reilly et al. (under review), for a detailed description. The model consists of a hierarchy of feature processing layers that roughly correspond to areas within the ventral stream of the brain – primary visual cortex (V1), extrastriate cortex (V2/V4), inferotemporal cortex (IT) – as well as higher-level layers that represent amodal semantic properties and named output responses (**Figure 2A**). The model processes grayscale bitmap images with filters that capture the response properties of the retina and lateral geniculate nucleus (LGN) of the thalamus, the results of which are used as inputs to the V1 layer. The model's V1 layer consists of a retinotopic grid of 3600 units that represent V1-like features at multiple spatial scales. The V2/V4 layer contains 2880 units that receive from neighborhoods of 320 V1 units. Neighboring V2/V4 units receive from overlapping portions of the V1 layer. The IT layer contains 200 units that receive from the entire 2880 V2/V4 units, and thus do not contain a retinotopic organization.

Overall, the model can be viewed as an expansion on a large class of hierarchical feedforward models of visual processing in the brain (Riesenhuber and Poggio, 1999b; Delorme and Thorpe, 2001; Masquelier and Thorpe, 2007; Serre et al., 2007). The primary innovation of the model is that hierarchically adjacent layers (e.g., V1 and V2/V4; V2/V4 and IT) are recurrently connected, providing an account of top-down feedback connections within the brain's ventral stream. Feedforward connections generally contribute 80–90% of the total input to a receiving layer and feedback connections contribute the remaining 10–20% of the total input. Overall layer activations are controlled using a *k*-winners-take-all (*k*WTA) inhibitory competition rule (O'Reilly, 1996; O'Reilly and Munakata, 2000) that ensures only the *k* most active units remain active over time. The specific *k* value varies for each layer in the model, but is generally in the range of 10–20% of the number of units in the layer.

SINGLE OBJECT SIMULATIONS

The model was trained to categorize images from the CU3D-100 dataset (<http://cu3d.colorado.edu>) using an extension of the Leabra learning algorithm (O'Reilly, 1996; O'Reilly and Munakata, 2000). The entire dataset consisted of 18,840 total images. Training proceeded for 1000 epochs of 500 trials, each of which consisted of

a random image selected from the dataset which was transformed with small variations in position, scale, and planar rotation. Images of two exemplars from each category (4000 images total) were reserved for a generalization test. After training, the final mean generalization accuracy was 91.9%.

Category selective representations were obtained for each of the 100 categories by averaging the response patterns of the model's IT units to all training and testing images from each category. In general, a distribution of 10–20% of the 200 units were selective to a given category, reflecting the level of *k*WTA inhibition within the IT layer. The category-relevant units for a given category were then isolated using a simple threshold over the category selective representations. For the fish category used in the simulations here, a value of 0.3 was used such that a higher response level indicated a category-relevant unit while a lower response level indicated a category irrelevant unit. Small variations in this parameter produced very similar results.

To create the plots in **Figure 1**, the firing rate from each of the model's IT units was recorded and averaged across every training and testing fish image (180 total images), then grouped according to whether the unit was category-relevant or irrelevant. This procedure was repeated with a visual occlusion manipulation that used a Gaussian-based filter to delete pixels from the input image. The filter was defined as 1.0 within a circle of radius 5% of the image size and then fell off outside the circle as a Gaussian function. The σ parameter of the Gaussian was set to 5% of the image size. The filter was applied to the image a variable number of times, with more applications corresponding to higher levels of occlusion.

To create the plot in **Figure 2B**, the model was presented with an unoccluded image of the fish and the response pattern was recorded from the model's V2/V4, IT, Semantic, and Naming Output layers for 50 processing cycles. The model was subsequently presented with a 50% occluded image of the fish, and the resulting response patterns were used to compute the similarity to the unoccluded response patterns for each layer as a function of time. The cosine angle between the unoccluded and occluded response vectors was used as the similarity metric in this calculation.

MULTIPLE OBJECT SIMULATIONS

The multiple object simulations involved training the model to recognize smaller versions of the CU3D-100 stimuli and testing its ability to generalize to presentations of multiple small stimuli. Training methods for these simulations were generally similar to the single object simulations described above, but a subset of the dataset was used. Five (5) exemplars from 5 categories (500 total images) were selected from the full dataset (*bicycle*, *car*, *donut*, *doorhandle*, and *gun*). Each image was downsampled to 50% of its size (originally 320 × 320 pixels, downsampled to 160 × 160 pixels) and randomly placed on either the left or right half of a new 320 × 320 image with variation in the *y* axis position. This was repeated 25 times for each of the 500 original images, resulting in 12500 new images. The model was trained on images from this dataset of 4 exemplars from each category to ensure proper generalization without over fitting. Training proceeded for 50 epochs of 500 trials. This was repeated for five instances of the model using different combinations of the 4 training exemplars

from each category and randomized initial weights. After training, the final accuracy over the training stimuli was 100% for each model.

To create the multiple object stimuli that were used for testing, images from each possible pairing of categories were randomly combined with one 160×160 image on the left half of a new 320×320 image and one 160×160 image on the right half. This was repeated 25 times for each category pairing, resulting in 250 new images containing two objects. In testing over these images, the model was ran for 100 cycles, as it often did not fully converge in the standard 50 cycles used in single object presentations. A testing trial was counted as correct if the model's output matched either of the two categories in the image.

We tested the effect of removing top-down feedback and inhibitory competition from the model on recognition accuracy for the multiple object stimuli. To remove influence from top-down feedback only, unit inputs from top-down feedback connections (e.g., Naming Output to IT, IT to V2/V4) were simply multiplied by zero during the testing phase. Removing influence from both top-down feedback and inhibitory competition required training a variant of the model that contained only feedforward connections (allowing for negative weights between units) with a backpropagation algorithm. This feedforward model required training for 100 epochs of 500 trials on the training stimuli before reaching 100% accuracy. Aside from these differences, the model was architecturally equivalent to the LVIS model in terms of layer organization and numbers of units and used otherwise identical training and testing methods.

The same method that was used in the single object simulations was used to isolate category selective representations for each of the 5 categories, except that IT units were further grouped into those shared across category pairings (e.g., gun and bicycle units) as well as those that were unique to each category. These groupings were used to create the plots in **Figure 3**. Similarity to category selective representations was also measured to determine how much the overall pattern of responses across the IT layer approximated the category selective response to the single objects. The cosine angle between the category selective representation and the IT response vector was used as the similarity metric in this calculation.

To investigate how category-relevant responses were related to a model's output (**Figure 4**), the firing rates of units that corresponded to the model's output were isolated into one grouping (*relevant* responses) while the firing rates of all other units were isolated into another grouping (*irrelevant* responses). Our decision to refer to these responses as "relevant" and "irrelevant" was made to keep with the theme of relevant and irrelevant responses when a single object was presented in isolation, but one should note that irrelevant responses encompassed what could be considered to be relevant responses. For example, if a presented stimulus contained a gun and a bicycle and a model responded *gun*, the responses from units that corresponded to the *gun* category were considered to be the relevant responses while the units that corresponded to all other categories (including *bicycle*) were considered to be irrelevant. Other reasonable labels for these two groupings might be selected/unselected or attended/unattended responses.

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The importance of being relevant

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This review aims at an understanding of the binding process by synthesizing the extant perspectives regarding binding. It begins with a consideration of the biological explanations of binding, viz., conjunctive coding, synchrony, and reentrant mechanisms. Thereafter binding is reviewed as a psychological process guided by top-down signals. The stages and types of binding proposed by various researchers are discussed in this section. The next section introduces Working Memory (WM) as the executive directing the top-down signals. After that it is described how WM works by selecting relevant sensory input, followed by a detailed consideration of the debate regarding objects vs. features with the conclusion that relevance is the key factor determining what is processed. The next section considers other factors affecting the selection of relevant input. Then, we shift focus to describe what happens to irrelevant input – whether it is discarded at the outset or is gradually inhibited, and whether inhibition is a perceptual or post-perceptual process. The concluding section describes the process of binding as currently understood on the basis of the literature included in the review. To summarize, it appears that initially the “object” is conceptualized as an instantaneous bundle of all features. However, only relevant features of stimuli are gradually integrated to form a stable representation of the object. Concomitantly, irrelevant features are removed from the object representations. Empirical evidence suggests that the inhibition of irrelevant features occurs over time and is presumably a process within WM.

Keywords: feature binding, top-down and bottom-up processing, inhibition

Binding is the process whereby separate entities are linked together to form a unified, coherent representation of the world around us. Feature binding refers to linking various characteristics of the stimulus to form a coherent representation of the stimulus. Cognitive scientists postulate binding to be one of the basic processes in information processing ranging from object identification to consciousness (Crick and Koch, 1990, but, see Singer and Gray, 1995; Crick and Koch, 2003; Zimmer et al., 2006).

People from myriad backgrounds study binding. Philosophy debates whether the solution will be neurobiological, functional, computational, or a completely different kind. Empirical science focuses on how a person solves the binding problem at the neural or behavioral level. Rapid strides have been made in our understanding of the binding problem from the biological as well as the psychological perspectives, since the concept came into focus in the early 1990s. Nevertheless, researchers from diverse backgrounds often work within their microcosms, scarcely appreciating the similar nature of work in other researchers' worlds. Moreover the diversity of current views regarding the process causes concern that the field may become excessively fragmented. Thus, this review is primarily attempting a synthesis of the existing views regarding binding. It particularly tries to bring together insights from the biological and psychological perspectives regarding binding. The theme that emerges is that relevance of features is crucial in the binding process. Only relevant features are integrated to form strong clear objects, whilst the irrelevant features are excluded. The review begins with a consideration of the biological underpinnings of the binding process.

BRAIN MECHANISMS UNDERLYING FEATURE BINDING: CONJUNCTIVE CODING VERSUS SYNCHRONY

The reality that is perceived is contingent upon information of diverse kinds located in many different areas of the brain. The binding problem exists because information about the features of every object in the external world is processed to disparate areas of the brain. Researchers have attempted to study different mechanisms whereby the brain brings together information that is initially represented in distinct areas of the brain. The modularity of the brain for processing different kinds of information is long established. Usually, however, we transcend these disparities, and accurately and effortlessly bind the myriad of information to create a holistic representation. So what is the underlying brain process, which binds together information that is represented in distinct areas of the brain? Almost all researchers assume that the answer lies in the identification of specialized neurons or networks that participate in the same cognitive process at the same time.

When Nobel prize winners Hubel and Wiesel provided evidence for conjunctively coding cells in the striate cortex of cats (Hubel and Wiesel, 1959, 1962), and monkeys (Hubel and Wiesel, 1968), it seemed clear that specialized neurons existed to code the different objects that are encountered in the environment. Researchers soon proposed that specialized cells attuned to specific conjunctions of features are responsible for binding, and that these cells come together in a workspace that enables the flexibility of binding and unbinding, and further processing. Fodor and Pylyshyn (1988) distinguished between vertical “modular faculties” and a distinct “central horizontal system” capable of sharing information

across modules. Baars (1988) distinguished between a vast array of unconscious, specialized, parallel processors, and a single, limited capacity, serial workspace that allows exchange of information. Dehaene and Changeux (2004) proposed the “neuronal workspace hypothesis,” which distinguishes two computational spaces in the brain, each characterized by a distinct pattern of connectivity. They proposed a network of “specialized processors,” attuned to particular type of information, but sharing the characteristics of specialization, automaticity, and fast feed-forward processing, as well as “cortical workspace neurons” that break the modularity of the cortex because they are able to send and receive projections to many distant areas through long range excitatory neurons. However, the idea of binding due to specialized neurons had a problem with sheer numbers. The quandary was how to grapple with the numerous stimuli, account for transience of binding, and at the same time limit the huge number of conjunctively coding neurons required for all the binding operations. Computational models attempted to show how the magnitude of numbers could be significantly reduced. Mel and Fiser (2000) use an algorithm that gradually “acquires” a representation by choosing features that are statistically most likely to distinguish objects from their noisy environments. In the process, the system invokes any available strategy to limit processing to one or a small number of objects at a time, including biological mechanisms such as the fovea, or psychological ones such as attention. Proposing different types of bindings, O’Reilly and his associates suggest that higher order bindings can result from coarse coded representations. In fact, Cer and O’Reilly (2006) held that the posterior cortex deals with low order conjunctions with distributed coarse coded representations, the hippocampus deals with higher order conjunctions such as episodes or locations, whilst the prefrontal cortex actively maintains transient bindings in service of current goals. As is evident, these models reduce the problem of huge numbers only by proposing additions to the architecture or subdivisions within their models, either of which increase the complexity of the explanation.

Synchrony thus gained in popularity as an apparently more parsimonious alternative physiological explanation for binding. It was Von der Malsburg (1981) who first contended that a complex environment requires parallel processing of information related to different objects or events, and posited neural synchrony as the mechanism whereby such information is bound together. Singer and Gray (1995) suggested that binding is explained by transient and precise synchronization of neuronal discharges, discovered in their laboratory by Gray et al. (1992) in the cat striate cortex. Indeed, synchronization was later reported in species ranging from locusts (MacLeod et al., 1998), to cats and monkeys (Gray, 1999), and of course, in humans (Singer, 1999). The idea of synchrony assumes that binding occurs throughout the brain, synchronous firing of cortical neurons leading to binding of features. The proposal faces two problems. The first is with respect to how two (or more) bound objects are differentiated. Although oscillation between out of phase firing has been proposed as a possible mechanism to encode separate objects, it is difficult to imagine how such a precise timing mechanism is implemented, considering that there are always multiple objects in the external world, and in addition to that, the brain itself is a highly noisy environment. The second

problem is related to the implication that the same neurons encode all binding operations, entailing that binding is transient. Precisely, the problem is how to account for permanence of representations after the stimulus is no longer there. Thus, synchrony seems to be an adequate explanation of binding, only for a single object, and that too only when it is present as a percept.

Nevertheless, physiological evidence exists for specialized processors as well as synchrony, and is hard to refute. Thus, many researchers tried to resolve the dispute between synchrony and specialized neurons by proposing different kinds of bindings, but in the process merely ended up reiterating the debate. Crick and Koch (1990) differentiated three kinds of bindings. First, bindings “hardwired” by genes or the experience of distant ancestors that determine the response to natural stimuli. Second, bindings learnt due to experience such as those required for recognizing familiar faces, or the letters of the alphabet; and third, transient bindings of novel stimuli which require focal attention. These are presumably based on neural synchrony, and if the stimulus is repeated often enough, develop into the second kind of bindings. Baddeley (2007) mentioned two types of bindings, passive binding, contingent on automatic processes; and active binding, which requires attention. The examples used by him suggest that while the former refers to binding elements of the natural world for which humans are “prepared” in an evolutionary sense, the latter type refers to binding of arbitrary, learnt elements. He further adds that long term episodic memory provides a third source of binding. Clearly these ideas are similar to the tripartite distinction by Crick and Koch (1990). VanRullen (2009) also distinguishes between hardwired binding of natural/frequently encountered objects, and on-demand binding of meaningless/arbitrary feature conjunctions, asserting that while the latter always requires attention, the former requires attention only if there is competition between multiple objects, thus emphasizing the inhibitory function of attention. Hommel and Colzato (2009) similarly hold that binding can take place through neural synchronization of all features present at a time, or because a stored detector exists for real/familiar objects. They too, admit the possibility of both processes acting together.

BEYOND PERCEPTUAL INTEGRATION: RECURRENT PROCESSES

Despite this measure of acceptance, there is also a sense that mere perceptual integration of features, whether by synchrony or by specialized neurons, simply does not encapsulate all characteristics of bindings as coherent objects essential for all information processing. An object cannot be defined only as a cluster of features. Different features not only need to be integrated into a whole, but this “whole” needs to be consistent, distinct, and meaningful. Consistency would come from object persistence, distinctness is a concomitant of clarity and contrast from other objects; and meaningfulness implies that the object is of some consequence in the information processing sequence. To achieve these characteristics, the basic information supplied by separate features has to be transformed. This transformation is achieved by top-down processes that presumably select only the relevant features for processing.

At the physiological level, the selection of relevant features is done by the reentrant processes in the brain. These are the downward and lateral connections that feedback information to lower levels in the brain. As in any good communication system, the

brain too relies on feedback mechanisms. In the visual system, for example, the lower level neurons in Area V1 send signals for forward processing, but it is also true that all higher visual centers have reentrant (downward) connections with Area V1. An important characteristic of reentrant connections is that they not only feedback to the original neurons, but also “receive” signals back from them. Communication between brain areas is therefore a continuous, iterative process.

The dichotomy between synchrony and specialized neurons is thus currently transcended by proposals that ascribe paramount importance to the evidence of reentrant processes in the brain. These top-down processes are linked to higher cognitive functions. Edelman (1978) first proposed that reentrant signaling may be important in integrating disparate cortical areas and higher brain functions. Damasio (1989) specifically argued that recall and recognition involve reactivation of the same areas that were involved in initial registration of conjunctions. This is done by means of “convergence zones” that enable retroactivation of multiple regions in the brain.

The crux of the reentrant theory is that brain processes are inherently iterative because of the hierarchical nature of the system and the fact that as information is processed in the higher areas the receptive fields become larger and lose their feature specificity. Thus one or more cycles are required to establish a stable representation. Reentrant processes confirm the correct features, resolve competition, and thus allow accurate bindings to take place (Di Lollo et al., 2000; Lamme and Roelfsema, 2000; Bullier, 2001; Hochstein and Ahissar, 2002; Hamker, 2003).

As far as the visual system is concerned, such signals emanate from the parietal cortex. Saalmann et al. (2007) studied how parietal output influences early sensory areas in macaques performing a visual matching task. They found that output from parietal areas increased activity in the early areas, and concluded that this represented top-down feedback from the parietal cortex to early sensory areas that helped to focus attention on relevant locations. Silvanto et al. (2009) used triple pulses of TMS over PPC to find that they led to excitation in the visual areas when applied unilaterally, demonstrating the top-down modulation of the visual areas by PPC.

Reentrant connections in the brain may also be combined with dynamic changes in synchronous activity to explain how the bound object is distinguished from the background, or indeed from other objects (Seth et al., 2004; Van der Togt et al., 2006). Thus reentrant processes are now accepted to be crucial for binding. Indeed, so compelling is this evidence that it has led to a rethink regarding the very concept of binding among many researchers. From the initial idea that all features are inevitably, instantaneously, and automatically bound together, there is a change to the view that reentrant connections confirm and integrate only some of the features in an iterative, resource-demanding process. There is a clear and discernible shift from the assessment of binding as a product to conceptualizing it as a process.

BINDING AS A PROCESS GUIDED BY TOP-DOWN SIGNALS

Treisman (1996) proposed three sequential mechanisms to solve the binding problem: selection of particular locations by a spatial attention window, inhibition of locations from feature maps

containing unwanted features, and top-down activation of the location containing the currently attended object for further processing. She also speculated that reentry to area V1 or V2 mediated all these three different mechanisms, proposing that reentrant connections from parietal areas mediate spatial attention, from extra-striate areas mediate feature based selection, and from the inferior temporal cortex mediate object based selection. Treisman (2006) holds that the initial response of the brain is to activate feature detectors in the early striate and extra-striate areas that automatically connect to compatible temporal lobe object nodes, and perhaps inhibit the conflicting ones. The parietal cortex then controls a serial reentry scan of the V1 and V2 areas to retrieve the features present in each, and then these are combined to form integrated object representations or bindings.

Humphreys (2001) and his co-workers also propose a two stage account of binding (Humphreys et al., 2000, 2009; Cinel and Humphreys, 2006; Braet and Humphreys, 2009). The initial evidence for this two stage process came from a patient GK with bilateral parietal lesions (Humphreys et al., 2000). The patient could bind form elements into shapes, but could not integrate shapes with color. This prompted the idea that the initial stage of binding results in shapes, and thereafter, surface features are associated with the shapes. Cinel and Humphreys (2006) proposed that in the initial noisy stage, visual elements are weakly bound, and these bindings can dissipate unless they are consolidated into more stable and stronger representations by being reinforced by top-down attentional feedback modulated by the posterior parietal cortex. Humphreys et al. (2009) showed that form conjunctions were easier to detect than difficult feature targets by controls and parietal patients alike, whereas parietal patients were significantly impaired in detecting other cross domain conjunctions. Braet and Humphreys (2009) respectively used feature detection errors and conjunction errors as inversely related measures of feature detection and binding, and found that a patient with bilateral parietal lesions generated illusory conjunctions with unusually long display durations. Also, when transcranial magnetic stimulation was applied to the parietal cortex in normal participants, it led to an increase in conjunction errors, but only 150–200 ms after stimulus onset. Thus, they held that binding occurs due to reentrant communication emanating from the posterior parietal cortex.

Roelfsema (2006) postulates two mechanisms in the visual system responsible for binding – base grouping and incremental grouping. Base groupings are coded by single neurons tuned to multiple features, and reflect the selectivity of feed-forward connections. But, all possible feature combinations cannot be coded by dedicated neurons. Therefore, a second, flexible form of grouping called incremental grouping needs to be posited. Incremental grouping augments the responses of the set of neurons coding separate features that are bound in perception. It takes more time than base grouping because it relies on horizontal and feedback connections, besides the feed-forward ones. The modulation of neuronal response strength, i.e., the firing rate of neurons, during the incremental grouping stage parallels the behavioral fact that attention is directed to features that are indicated by the enhanced neuronal response, and those features are then bound together. Base grouping takes place initially in the system, followed by incremental grouping in the cortex. This basic theory has been enhanced

to propose a computational model that predicts figure-ground separation as well as binding (Jehee et al., 2007).

Zimmer et al. (2006) distinguish between transient binding and more durable binding, implying that different mechanisms probably bind features at different points in time, and/or there is a process of consolidation that transforms transient binding into durable binding. Shifting the focus to a very late stage in the binding process and thus proposing an integrated model of binding in WM and long term memory, Murre et al. (2006) also distinguish between transient and permanent binding, suggesting that while the former reflect the capacity of WM to select task relevant information for processing, the latter is the capacity of the neural system to store coherent patterns in LTM. Their emphasis, nevertheless, is that there is a constant interaction between these two. "What is transiently bound in WM governs what is temporarily and eventually permanently bound in long term memory. In turn, what is permanently bound affects transient binding in WM. The interplay of these binding processes determines how the brain develops into a structured system that is cumulatively correlated with its environment, thus implementing a process that is able to lift itself to higher levels of cognitive functioning" (Murre et al., 2006, p. 244).

Emphasizing the top-down factors even more, Hommel and Colzato (2009) propose that memory for a binding is controlled by two kinds of priming processes. Offline priming happens before the stimulus is presented, due to foreknowledge about the relevant features, task instructions, manipulation of mental set, etc. Online priming is induced by stimuli that have entries in long term memory, such as familiar objects. These are detected in a non-selective fast feed-forward sweep, followed by recurrent processes refining the input according to the operating principles of the attentional set for that task.

Summary so far

In line with these ideas, one may conclude that binding is a continuous process that begins with the sensory input which goes to myriad areas of the brain and ends when the bound object emerges in memory such that it is strong enough to be manipulated further for higher cognitive processes. Features are initially perceived together either through synchrony or by neurons coded to detect conjunctions. This integration is a largely automatic, non-conscious process, which thereafter is refined by iterative processes and ultimately allows differentiation and dissemination of information in conscious states.

WORKING MEMORY AS THE EXECUTIVE DIRECTING TOP-DOWN REENTRANT PROCESSES

The process of binding inevitably begins with the physical continua impinging on the sense organs. But it is equally true that the information regarding stimuli does not enter an empty box. The brain has its own ideas! The top-down control of behavior by mental representations of goals, instructions, and ideas is perhaps as undeniable as the source of behavior in bottom-up processing of stimulation. A logical assumption is that since the reentrant signals emanate from the cortical regions higher up in the processing hierarchy, they reflect top-down modulation of the process of binding. The question still remains as to what is at the "top"?

What directs the reentrant processes? Working Memory (henceforth WM) seems to be the executive guiding all processes of the brain in the service of current goals. The prototype model of WM (Baddeley and Hitch, 1974; Baddeley and Logie, 1999) emphasized that different kinds of information are processed by distinct mental systems that act together to deal effectively with tasks confronting a healthy human adult. Baddeley and Hitch (1974) distinguished two subsystems, the phonological loop and visuo-spatial sketchpad, and a control system called the central executive. To deal with the fact that the information processed in these subsystems is often combined, and indeed, is at some stage also linked to information in the long term permanent store, Baddeley (2000) proposed a fourth component, the "episodic buffer." The episodic buffer was initially theorized to be controlled by the executive, but was primarily a storage system linked to conscious awareness, that binds together information from different sources in episodes. Thus, the episodic buffer was proposed as the answer to the binding problem (Baddeley, 2003).

Logie (2003) conceptualized WM as a mental workspace that deals with integrated objects identifiable on the basis of prior knowledge. He maintains that sensory input reaches WM only after it has activated the knowledge base. Thus what reaches the workspace is the result of an amalgamation of the sensory input and the knowledge base. Since another source of input into the workspace is retrieval generated by processes in WM such as imagery, he holds that WM does not act as a gateway for processing information into LTM (substantiated by Van der Meulen et al., 2009). The workspace model implies that feature binding takes place concomitantly with or before the object representation evokes prior knowledge, which in turn, precedes the manipulation of the object in the mental workspace. Nevertheless, other kinds of binding, such as between objects and their semantic associates, or between percepts and images, or between images, or among sequentially presented objects, presumably takes place in the workspace that is WM. The basic units in WM are thus perceived objects. Nevertheless, the model can also be interpreted to accommodate the idea that features themselves might evoke prior representations in LTM and then the processes of WM refine the representation so that it emerges as an object.

Although there are many interpretations of WM as a concept and consequently many different models exist in current literature (reviewed by Miyake and Shah, 1999; Osaka et al., 2007), consensus exists on two important characteristics. First there is a general assumption that physiological level explanations are tenable for the WM phenomena observed at the behavioral level. Second, attention has a crucial and largely inhibitory role to play in all models of WM. Both these characteristics imply that WM is the top executive, the "controller," managing the stimuli. It is in this sense that one may conceptualize WM as the source of top-down influences directing recurrent processes.

HOW DOES WORKING MEMORY WORK – BY SELECTING RELEVANT INPUT?

The advocates of top-down processes regularly invoke and use the concept of WM as the top executive in their theories. The biased competition theory by Desimone and Duncan (1995) proposed that WM content in terms of instructional set, task goals,

etc., facilitates the selection of matching sensory input. The biased competition model rests on the assumption that attending to an object causes a bias signal to be sent by higher areas to the lower sensory areas which increases their tonic activity without necessarily increasing the neural responses evoked by the external stimulus itself. Behaviorally, this assumes that incoming sensory stimulation is matched with a template which specifies the relevance or otherwise of the received stimulation. Although Duncan (2006) concedes that in principle, competitive bias can begin anywhere in the system and then spread to the higher and/or lower levels, he also reiterates the role of task relevance and an associated pattern of fronto-parietal activity that he calls the multiple demand pattern because it is produced by many different kinds of cognitive demands. No wonder that his theory is usually taken to be a prime exemplar of the emphasis on top-down processing.

Based on studies using single unit recordings in macaques (Chelazzi et al., 1993), it was held that a state of competition always exists among the variety of sensory inputs at any moment. Stronger sensory inputs usually win out, but the representations in WM bias the competition such that inputs matching them are the ones that are strengthened and selected for further processing. The contention that competition is essential for attention to emerge is supported by neuroimaging evidence that the posterior parietal cortex, which is activated when visuo-spatial attention is focused, promotes feature binding when there is a potential for confusion with the simultaneous presence of other objects. Kastner et al. (1998) used fMRI evidence to substantiate that when stimuli are simultaneously presented, their cortical representations interact in a competitive and suppressive way in the ventral (object recognition) pathway. However, this was not evident when stimuli were presented sequentially. In a second experiment, spatial attention focused on the objects was found to counteract the suppressive effect, and more so in the simultaneous as compared to the sequential presentation condition. Using fMRI, Shafritz et al. (2002) established that the posterior parietal cortex was active when multiple objects were simultaneously presented, but not when they were sequentially presented in the same location (at fixation).

WHAT IS SELECTED AS RELEVANT INPUT? OBJECTS OR FEATURES?

Currently, there is conflicting evidence regarding the level to which distracters are represented in the brain. Some researchers propose that all objects and features are automatically and implicitly represented in the brain up to a level that excludes semantic processing (reviewed by Thoma et al., 2004). Nevertheless some studies indicate that even unattended objects are habitually processed to the semantic level (Pins et al., 2004; Altmann et al., 2005). Attempting a resolution, Martinovic et al. (2009) used EEG to find evidence that induced gamma band activity was enhanced due to the presence of distracter objects under low load conditions, thus providing evidence for cortical representation of distracters. However, as perceptual load increased, attentional selection played a more important role, and gamma band activity was limited to the attended object with a general suppression of all activity linked to surrounding information. This corroborates Duncan's views regarding suppression of distracters by attention in consonance with top-down directions.

Emphasizing the integrated nature of processing of objects, Duncan (1996, 1998, 2006) held that since the object features are encoded in an integrated fashion across different cortical regions, if attention is directed to one feature, all features of the object, whether relevant or irrelevant, become dominant in their respective regions of the brain. Support for this idea came from fMRI data by O'Craven et al. (1999) who found that neural activity increased in response to the attended as well as non-attended task-irrelevant attribute of the stimulus. Nevertheless, their studies also provided evidence for differential level of activity, with the absolute amount of activity being stronger for relevant features than for irrelevant ones in the attended object. More definitive data were provided by Schoenfeld et al. (2003) who recorded event related potentials as well as event related magnetic fields together with fMRI to find that the irrelevant feature was activated rapidly enough to participate in the perceptual integration and binding of the attended object. Using event related potentials, Winkler et al. (2005) found evidence that pre-attentive binding of relevant as well as irrelevant features occurs "normally" in visual as well as auditory modality, and that attention is required for correct binding only under special circumstances when high load displays are processed under high time pressure.

Thus, in considering the difference between relevant and irrelevant, the distinction between features and objects is crucial in Duncan's theory. Duncan (1980) asserted that only targets are selectively processed through the limited capacity system, non-target objects are identified and rejected by initial parallel and unconscious processes. Nevertheless, this selectivity is not assumed to operate on features. Duncan (1984) showed that perceptual identification of properties inherent in two different objects is much more difficult than when the features are combined in a single object. However, if two features are combined within a single object, the visual system finds it as easy to encode a combination of two features such as orientation and texture, as to encode them separately. Duncan (1998) provided evidence that it is also hard to identify two separate targets presented within the same modality, though there is no problem in detecting targets that differ between modalities. Thus, the features of an object are integrated such that they are processed together in an all or none fashion. Directing attention to a selected object enhances the representation of all its features together (Egley et al., 1994; Duncan et al., 1997). The objects compete with each other and the winner is processed further at the cost of widespread suppression of the distracters or the 'to be ignored' objects. Competition is biased and ultimately resolved in favor of task relevant objects, and typically this state is achieved over 100–200 ms and is sustained by attention.

Luck and his associates also contend that the basic units on which VWM operates are objects rather than features. Luck and Vogel (1997) held that VWM was object based because remembering one feature such as color allowed the recall of another without any additional cost. Vogel et al. (2001) confirmed that VWM can hold three to four chunks of information, be they features or bound objects. This evidence suggests that VWM stores integrated objects rather than features, and objects are thus the basic units of VWM. Woodman and Luck (2007) tested the prediction of the biased competition model that a match between the template held in WM and the sensory input always leads to a facilitation

of performance. They used a dual-task paradigm and asked participants to perform a visual search task while maintaining object representations in VWM at the same time, but found no such facilitation of performance. Nevertheless, the reaction time was faster for matching distracters. When the participants knew beforehand that the target would never match the item retained in memory, they could direct attention away from the items that matched the WM representation. Thus they found an inhibitory effect and concluded that participants can use the content of WM strategically to inhibit as well as facilitate attentional processing. Moores and Maxwell (2008) also found that prior stimuli in WM captured attention even in the absence of bottom-up priming, and influenced the response of the participant, despite the influence being detrimental to the task. Indeed one important purpose of VWM is postulated to be the control of eye movements (denoting attention), specifically the initial direction and subsequent correction of gaze toward particular objects in visual search (Hollingworth et al., 2008; Hollingworth and Luck, 2009).

In contrast to these theories emphasizing the top-down nature of processing of integrated objects, are accounts of behavior that stress the role of different features of the stimuli to be processed. These accounts vary in their espousal of top-down mechanisms. For example, the feature integration theory (Treisman and Gelade, 1980; Treisman, 2006) and contingent capture theory (Folk et al., 1992, 1993; Folk and Remington, 2006) ascribe paramount importance to top-down factors implemented through attention. At the other extreme are the accounts of stimulus driven capture (Theeuwes, 1992, 2004), and dimension weighting (Muller and Krummenacher, 2006), which primarily emphasize the importance of bottom-up factors in capturing attention. Nevertheless, they are similar in stressing one or more features as being relatively more important in the process of binding.

The feature integration theory (Treisman and Gelade, 1980; Treisman, 1988, 1998) suggests that attention to particular locations is the most important factor in feature binding, implying that all features present at a particular location are inevitably bound together if attention is focused on them. Treisman and Zhang (2006) reiterated the importance of locations in binding in VWM as well. This view makes binding a relatively automatic process triggered off by attention to particular locations. Basically, it postulates a master map of locations, and as attention is focused on any area of this map, the object in that location is encoded. Also, while detection of features is contingent on independent maps for each feature, other types of searches, particularly conjunction search, is driven by the master map of locations that integrates information from other maps to produce the signals that make each stimulus salient (Treisman and Sato, 1990; Wheeler and Treisman, 2002).

Kahneman et al. (1992) proposed the object file theory, according to which objects are primarily identified by their positional marker or spatial index. Thereafter, other properties of the object, color, shape, etc., are associated with the spatial index. Spatiotemporal continuity is essential for maintaining object file representations, whereas non-spatial properties such as color and shape are unimportant. Direct evidence in support of this idea comes from the object reviewing paradigm (Kahneman et al., 1992; Mitroff and Alvarez, 2007), the multiple object tracking paradigm (Pylyshyn, 2004), visual search in dynamic displays (Horowitz and Wolfe,

1998; Alvarez et al., 2007); and developmental evidence showing that young infants rely on spatiotemporal rather than surface features or identity information to make sense of their visual world (Feigenson and Carey, 2005).

Applying the feature integration theory and the idea of object files specifically to the binding process, Treisman (2006) maintained that pre-attentively, features, and locations are registered in different maps, and focused attention binds them together. She mentioned three components of the binding process, and suggests that we shift attention in space to select one object after another, suppress features of other objects, and finally bind selected features together into “object files.” Note that she contends that initially, features are processed in parallel and stored as separate traces, which are only inhibited, but not completely eradicated, in the binding process. Revisiting the feature integration theory, Chan and Hayward (2009) have provided fresh evidence for dissociation between feature detection and localization, involving respectively parallel and focal search.

To completely grasp the implications of Treisman’s ideas, it is instructive to contrast them with Duncan’s model. One difference is their view of binding. For Duncan, binding happens at a very early stage in the visual process and the basic units in his theory are bound representations or objects. For Treisman, binding is a process of continuous refinement, during which features become linked to a master map of locations. Features remain bound only as long as attention is focused on them. Any irrelevant features continue to exist in an attenuated form. Another related but important point of distinction lies in their disparate view of the role of attention in binding. While Treisman views attention to be a selective process essential for binding, Duncan assumes that features are already bound into objects (probably through conjunctive coding by neural detectors) and then biased competition between objects occurs accompanied by a state of attention. Attention is thus an emergent property of the system, and the mechanism that aids top-down biased selection of some objects over others. It follows that Treisman holds attention to be an earlier process than Duncan. Finally the most important influence in the process of attention for Treisman is location, so attention is basically spatial in nature, whereas for Duncan, it is an emergent property of the system that is weighted in many ways, but essentially by task relevance more than anything else. Despite these differences, both agree that attention is necessary for binding separate features into a coherent object.

Treisman’s insistence that attention was primarily spatial also conflicted with experiments showing attention capture by abrupt onsets, the tendency of anything unusual in the field to attract involuntary attention, even if participants are set to ignore them (Remington et al., 1992). Nevertheless, the contingent capture theory (Folk et al., 1992, 1993; Folk and Remington, 2006) holds that attentional capture, as for example, by abrupt onsets, is contingent on top-down attentional control settings. This was because the original experiments showed that abrupt onset cues captured attention when the task was to identify onset target, but color cues captured attention when the task was to respond to color targets. Folk et al. (2008) have established that non-spatial attention is also subject to capture that is contingent on top-down settings. In their experiments, a change in the color of the distracter such that it matched the target, decreased target detection. Folk et al.

(2009), showed that even non-spatial distracters which did not capture attention, nonetheless, influenced responses to a target.

The guided search model (Wolfe et al., 1989; Wolfe, 1994) had a rather different concern regarding the feature integration theory. Wolfe et al. (1989) pointed out that except for locations, the feature integration theory did not differentiate between other features of the stimuli. Further, it presumed that parallel processing of features in the initial pre-attentive stage did not have any impact on the later attentive serial search. The guided search model proposed that the features which were processed in the parallel stage guided attention in the subsequent serial stage, primarily by dividing the stimuli into distracters and probable targets. Further, they provided evidence that search for conjunctions defined by three features was more efficient than conjunctions of two features, simply because more number of features guided search for triple conjunctions. Wolfe (1994) acknowledged the special role of location by modifying the model to suggest that the output of processing in the initial massively parallel stage guided spatial attention and thus the second serial stage processed input from a limited portion of the visual field. Note that this reverses the sequence of the relative influence of location and other features postulated by the feature integration theory which holds that other features are attached to a master map of locations and hence spatial attention precedes and guides attention to features (Treisman and Sato, 1990).

The idea that each feature is coded within its own feature map was extended by Vidal et al. (2005) to include the notion of “structural gist.” Their Experiments 1, 2, and 3 using a change detection task with a study-test interval of 1000 ms showed that it was more difficult to detect changes of only color, only shape, or only orientation, in a target item, if the distracters also changed on the same dimension as compared to a condition where there was no change in distracters. Experiment 4 showed that change detection was impaired when an item that remained on screen during the study-test interval changed in the same dimension as the target, demonstrating that encoding relational information was possible even when it was not presented simultaneously. In Experiments 5 and 6, they compared conditions when distracters could change on the same dimension as the target, or on a different dimension. Changes in a different dimension, however, did not have an effect on performance, whereas changes in the same dimension did affect performance. It was more difficult to detect feature changes when the distracters also changed features on the same dimension, as compared to when the distracters changed on some other feature dimension. Thus they proposed that each item in each feature map is encoded in terms of individual as well as configural information. The effects of relational information are particularly strong within each feature map. Their experiments considered only changes in colors, shapes, and orientation, keeping location constant. However, Jiang et al. (2000) had earlier reported that detection of changes in color was impervious to change in locations of non-targets.

The dimension weighting account (Muller and Krummenacher, 2006), which may also be considered an extension of the guided search model, holds that attentional weights are allocated to basic visual dimensions (such as color, orientation, etc.), on the basis of stimuli defined by features (red, tilted, etc). Enhanced feature contrast within a dimension, e.g., red vs. green rather than

yellow vs. green, and amplified saliency signals about a dimension to the overall saliency map, can facilitate detection of targets defined by that dimension, or alternatively target detection may be delayed if the target dimension changes across trials, shifting the weight to a new target defining dimension. They propose that the dimension weight can never be set to zero and indeed, may reflect the speed of processing associated with various dimensions. Weighting effects are proposed to be pre-attentive, influencing dimension based saliency signals before the overall saliency computation which is the basis of attentional selection of objects. Nevertheless, weight shift can be modulated through expectancies set up by cues, instructions, past experience, etc. In this sense the role of top-down processes is acknowledged. Muller et al. (2009) used the singleton salient distracter paradigm and showed how distracter influence varied with relevant practice, such that participants could learn to suppress distracters depending on the incentive to use suppression which in turn was presumed to vary with the probability of occurrence of the distracter. Nevertheless the costs of dimensional cueing in these studies could be, in part at least, due to task switching in general. Pan et al. (2009) studied the effect of dimensional cueing when the relevant dimensions were known to the participants. In fact, participants were explicitly instructed to prepare the relevant dimension on congruent trials and discard the irrelevant dimension on incongruent trials. Participants received a dimensional cue to be held in memory, and were subsequently tested on it either before or after a test of attention. Response latency was more on incongruent trials and less on congruent trials as compared to neutral trials. The benefits of congruency were enhanced when the cued dimension had to be held in memory throughout the trial, i.e., when the memory test was given after the attention test. This study demonstrates that the contents of WM can have an effect, and in fact, have more positive than negative effects on performance.

Theeuwes and his colleagues have consistently adhered to a strict bottom-up account of behavior (Theeuwes, 1992, 2004; Theeuwes et al., 2006). Their paradigm essentially investigates the effect of a singleton distracter defined by a different dimension than the one defining the singleton target. Theeuwes (1992) used a distracter defined by color (the only red among all green), and a target defined by shape (the only diamond among circles). The initial check confirmed that RTs were quicker to color than to shape, showing it to be more salient. Then participants performed under two conditions, one in which the distracter was present, and the other in which it was not. Results showed significant distracter interference in that RTs were significantly slower when the distracter was present. The embarrassing question for adherents of top-down influences was why participants were unable to ignore the distracter; despite the fact that they knew what dimensions were defining the target and the distracters. Schreij et al. (2008) reported that abruptly occurring distracters produce costs in performance even in the presence of a top-down set for color. They argue that these results show that abrupt onset of new objects captures attention independent of a top-down set and thus, provides conclusive evidence against the idea that attention capture is contingent only on top-down attention control settings.

It is, of course, possible to take an eclectic view of the tripartite competition among researchers who have proposed

objects, locations, or features to be the units of visual processing. Humphreys (1998) proposing a dual coding account of representation of objects in space, contends that we have a rather poor representation of space *per se*. However, objects are spatially represented in two ways, within object representations, where elements or features are encoded as part of objects, possibly in the ventral stream with some dorsal involvement; and between object representations, where objects are coded in relation to each other, presumably involving the dorsal stream. Both these kinds of representations exist in parallel. Visual processing capacity is limited by the competition to encode elements within an object, the number of objects that can be encoded at the same time, and the relevance of within object or between object representations to the task. In this view, unlike the feature integration theory, there is no attempt to assign a special role to locations. Indeed, the bottom line is that the objects in space are important. Space in itself is not significant. The feature that is important here is form, for form elements are bound in the absence of focal attention and are later associated with surface features such as color. In giving this account, Humphreys also diverges from Duncan, and proposes that competition may exist within the elements of an object as well, and further, this competition can be biased by task relevance. Thus the differential effect of features can itself be influenced by top-down factors.

Linnell and Humphreys (2004) have shown how object based selection can overrule the central bias, the fact that attention is primarily directed at fixation and performance decreases as eccentricity of the targets increases. Linnell and Humphreys (2007) used the odd man out paradigm of visual search and found that when the participants knew in advance about the feature defining a target, detection was enhanced due to grouping on that target feature, and the participants then limited search to that group only. This grouping by features overruled the central attentional bias by allowing the grouping of peripheral targets with centrally presented distracters. They concluded that visual search can be space, object, or feature based, and in fact, performance is often determined by an interaction of all three. The real winner is top-down modulation which directs which of these three are relevant to the task at hand.

OTHER FACTORS AFFECTING THE SELECTION OF "RELEVANT" INPUT

Current research has largely moved away from the debate among objects, locations, and features, to focus on *how* top-down WM factors influence the encoding and retention of stimuli. An influential idea delineating how WM deals with distracters is the load theory of selective attention and cognitive control (Lavie et al., 2004; Lavie and De Fockert, 2005, 2006). It suggests that WM provides goal-directed control of visual selective attention by decreasing interference by goal-irrelevant distracters. Lavie and De Fockert (2005) tested this idea with the singleton paradigm. They showed that attention capture by an irrelevant color singleton during shape search critically depends on availability of WM to the search task. When WM was loaded by a concurrent yet unrelated verbal short-term memory task, capture increased. Increasing WM load also results in greater distracter interference in Stroop-like tasks (De Fockert et al., 2001; Lavie et al., 2004). In fact, increasing WM load leads to greater distracter interference whereas increasing

perceptual load reduces distracter interference (Lavie et al., 2004). Park et al. (2007) demonstrated that the type of WM load is crucial to this effect using the flankers task with houses and faces as stimuli. Distracter interference increased when the memory load items overlapped with the targets, but decreased when they were similar to the distracters. These findings suggest two selective attention mechanisms: a perceptual selection mechanism serving to reduce distracter perception in situations of high perceptual load that exhaust perceptual capacity in processing relevant stimuli and a cognitive control mechanism that reduces interference from perceived distracters as long as cognitive control functions are available to maintain current priorities (low cognitive load).

Forster and Lavie (2008) reasoned that in real life situations, there is as much need to avoid external irrelevant distracters as there is to suppress relevant distracters. Laboratory studies usually focus on relevant distracters alone. Thus they compared the effects of perceptual load on task-irrelevant and task relevant (response competing) distracters. They found that an entirely irrelevant distracter can interfere with task performance to the same extent as a response competing distracter. High perceptual load in the task eliminated the effect of both types of distracters with similar effectiveness. Forster and Lavie (2007) showed that although individual differences in reported distractibility were correlated with distractibility in a response competition task performed in the laboratory, high levels of perceptual load in the task reduced distracter interference for all participants. Forster and Lavie (2009) demonstrated how a high perceptual load, demanding task relevant processing, concomitantly decreased the frequency of task unrelated thoughts, and thus reduced "mind wandering." When one needs to focus on a task, it is easier to inhibit both external and internal sources of interference.

Olivers et al. (2006) found that singleton distracters interfered more with visual search when an additional memory task had to be performed at the same time. The interference effect was even stronger when the distracters were virtually the same or related to the object held in memory. Houtkamp and Roelfsema (2006) studied whether items in WM influence the deployment of attention. Using line drawings of simple objects, they asked participants to remember two objects. After a blank interval of 1000 ms, while the participant was instructed to search for one of the two items as a target, the other memory item was sometimes presented as one of the distracters in an array of items. They found that the distracter had an effect only if the target was absent. Whenever, the target was present, the memory item had no effect as a distracter. Eyes were unlikely to be fixated on the distracter, and if they did, fixation duration was very short. Thus attention was primarily oriented toward the target, and memory items had an effect only if the target was absent. The special processing of the target has been found with objects in real world scenes as well. Details of targets and distracters related to targets are better retained than the distracters that are unrelated to the targets, maybe because they are looked at more frequently as shown by eye movement recordings (Williams et al., 2005). Brisson et al. (2009) investigated whether contingent capture required capacity-limited central resources by incorporating a contingent capture task as the second task in a dual-task paradigm using N2pc as a marker of spatial attention. N2pc is an ERP component that appears in the right hemisphere if

the participant pays attention to the left visual field, and vice versa, appears in the left hemisphere if attention is focused on the right visual field. The N2pc was significantly reduced in high concurrent central load conditions, indicating that even though it is involuntary, the deployment of visual-spatial attention occurring during contingent capture depends on capacity-limited central resources.

Soto and Humphreys (2008) found that when the WM item that was used as a cue for one of the distracters, did not match the subsequent search display, search performance was worse as compared to a neutral baseline. This effect of WM content on search was reduced when cognitive load was increased, and when articulatory suppression was used. Soto et al. (2008) reviewed evidence emanating from their lab regarding the influence of WM on search for relevant information from the environment. They contend that WM automatically guides selection, even if it is detrimental to performance. Further, on the basis of fMRI evidence (Soto et al., 2007) they assert that this modulation is a top-down process quite distinct from bottom-up processes such as priming. When a stimulus held in WM appeared in the search array, there was enhanced activity in the superior frontal gyrus, mid-temporal, and occipital areas. In contrast, implicit repetition priming (which involves mere repetition of a stimulus) elicited a suppressive response. Also WM probably affects the early process of attention that controls the entry of information into awareness. Soto and Humphreys (2009) assessed whether guidance by WM is limited to single task relevant dimensions, or does it differentially affect bindings of those dimensions. Participants were asked to remember the shape of a colored object in memory. Then they were to search for a target line amongst distracter lines, each embedded within a different object. On some trials, one of the distracter objects in the search display matched the memory item on the shape, the color, or both dimensions. Relative to a neutral baseline, where there was no match between the memory and the search displays, search performance was reduced when a distracter object matched both the color and the shape of the memory cue, demonstrating that WM had a greater impact on bindings as compared to single dimensions. Relevance of stimulus input to task goals thus seems to be the overriding factor in the process of binding.

WHAT HAPPENS TO IRRELEVANT INPUT? DISCARDED AT THE OUTSET OR GRADUALLY INHIBITED?

Searching for direct evidence, we (Jaswal and Logie, 2011; Logie et al., 2011) studied the effect of task relevance of features in the process of feature binding at study-test intervals from 0 to 2500 ms. All experiments used a version of the change detection task. The task presents two stimulus arrays to the participant who has to decide whether there is a change between the two arrays. The task requires not only the formation of mental representations, but also the maintenance or storage of these representations across time so that they can be compared in successive frames. As such, it is a perceptual as well as a memory task. Simply by manipulating the study-test interval one changes it from a test of perception to a test of memory.

The difference in the change detection task, if it occurs, may be in terms of the addition of a new stimulus, deletion of an old one, or a swap in the already presented stimuli. Binding is required only

for the last kind of change, a swap between two stimuli. In fact, the swap detection task was introduced by Wheeler and Treisman (2002) specifically to study bindings. It is not possible to perform this task by remembering which features were presented, for all the same features appear in the study as well as the test display. It is essential to remember how the features were “combined” to find which ones swapped. Alvarez and Thompson (2009) have used the term “feature switch detection” to describe this task. Their work has also shown that although this task underestimates the binding capacity of VWM, it is an efficient paradigm for studying the factors affecting the fragile nature of bindings.

Since the aim was to study the effect of an irrelevant feature in an experiment, reducing the binding problem to its essentials, stimuli were defined concomitantly by three properties. The three features chosen to define the stimuli were location, shape, and color. The operational problem was how to design a task that would “break off” one of these elements to study the link or “binding” between the other two. One solution could have been to hold this element constant. For example, presenting various shapes in various locations, and swapping any two, whilst keeping the color of all the stimuli unchanged. Indeed this has been the procedure followed by many researchers in the field (e.g., Vogel et al., 2001; Wheeler and Treisman, 2002). However, it is questionable how far this manipulation prevents the inclusion of the irrelevant feature in the bound representation on each trial. If a feature is present constantly, it can still function as an informative cue. In fact, other features may be accessed through this feature. On the other hand, it may also block the effect of other features.

In the literature on conditioning, following Rescorla (1967), it is well established that the way to make a stimulus truly irrelevant and non-informative, is to randomize it. This idea was applied to the design of experiments by randomizing one feature between the study and test displays to render it non-informative, while testing memory for the combinations of the remaining two features of each object in the array. Using the swap detection task, location was randomized between the study and the test display with memory tested for the color-shape combinations in the study display. Analogously, shape was randomized to study the link between location and color, and color was randomized to study the link between shape and location.

In each case, binding between two of the features was studied whilst the third was rendered irrelevant through randomization. The focus was to study how far performance would be disrupted when a feature was rendered irrelevant through randomization in comparison to a condition in which it was unchanged. If there were no differences between unchanged and randomized conditions, it would indicate that participants can remove the unwanted irrelevant features right from the outset in accordance with task instructions. Reduced performance in the randomized feature condition would suggest that all features automatically participate in the initial representation even if they are irrelevant to the task. If a convergence occurs over time, it would suggest that relevant features can be consolidated and irrelevant features can be inhibited only gradually through the control processes of VWM. Thus, performance in the randomized feature condition was compared to when the feature was unchanged, to study *whether and when* the feature could be deleted from the visual system.

It was expected that performance in detecting change in bindings would be reduced when a feature is randomized from study to test as compared to when it is unchanged, if the feature had an initial representation, despite that the instructions were to ignore the feature and it was rendered completely non-informative and irrelevant to performance. It was also expected that as the visual system consolidated the binding of relevant features, this irrelevant feature would be inhibited, leading to a convergence of performance at longer study-test intervals.

This expectation was confirmed across experiments where locations were the irrelevant feature and color-shape bindings were to be detected. There was a convergence of performance at study-test intervals of 1500 ms or beyond. A similar pattern of interaction was also found when shapes were randomized to study color-location binding, and when colors were randomized to study shape-location bindings (see Logie et al., 2011, for details). This not only suggests that the effect is very robust, but also attests to the overriding importance of top-down factors in binding irrespective of the features involved. All features are treated the same way in VWM. They are selectively consolidated if they are relevant, and removed from the mental representation if they are irrelevant.

In the randomized condition, the task used in these experiments is a further variant of the swap detection task in the sense that in the test display, not only does the target change, but the distracters also change. The task becomes even more difficult, for participants have to decide whether there is a change in the binding of two features, when the third feature also changes. They have to ignore the changes in the one feature, and focus on finding the swap in the other two. This presumably involves a more demanding and central cognitive process in which the subject has to consider each of the stimuli in the test array, and compare whether the binding is the same as for the ones he holds in his memory.

Nonetheless, there is no denying the differential processing of features. In line with physiological studies (Zeki et al., 1991; Moutoussis and Zeki, 1997; Lamberts, 2002; Aymoz and Viviani, 2004) and psychophysical evidence (Magnussen et al., 1996; Magnussen and Greenlee, 1997; Magnussen, 2000), differential processing of features was found. There is greater disruption of performance when locations are randomized than when shapes or colors are randomized, with the disruption due to randomization of colors being the least. In addition, the removal of locations from the initial representation takes a much longer time than the removal of shapes or colors.

The differences among the three features, locations, shapes, and colors, follow the differential perceptual processing of these features. Location swaps are easiest to detect and location is the most difficult feature to ignore. Color swaps are the most difficult to detect, and color is the easiest feature to ignore. The results for shape fall between these two. This is in consonance with researchers showing that locations are processed in the dorsal stream, which is relatively automatic and works on an earlier time scale than the ventral stream (Velichkovsky, 1982, 2007; Vecera and Palmer, 2006). Between shape and color, differentiation of forms happens before the surface features are filled in (Cinell and Humphreys, 2006; Humphreys et al., 2000, 2009). To be speculative, the differential processing of features might happen with other features such as orientation, size, textures, etc., as well.

The differences in the amount of disruption experienced by the participants, imitate the importance of the “to be ignored” feature in our daily lives. The disruptive effect is least when color is the feature to be ignored, with a greater amount of disruption when shape is to be ignored, and the maximum disruption when location is to be ignored. The correct perception of the location of objects in space has survival value in our daily navigation of the world, and reflecting that importance, randomizing location disrupts performance to the greatest extent in these experiments.

These results go against the overwhelming importance accorded to locations by many researchers (e.g., Wolfe, 1994; Treisman, 2006). Perception may be location based, but memory may be not only location based, it might well be object based, or feature based. Just as it is possible to ignore other features, it is possible to ignore locations too. It is only more difficult, not impossible. As compared to other features, location is special. But, in itself, it loses its importance in the binding process if it is not relevant. Thus relevance of features overrides the differential processing of features.

Summary so far

The account of the binding process that emerges is that features may not be bound together instantaneously and all at the same time. Instead, their processing in the visual system continues at different rates. This differential processing affects *when* they are bound in object representations. Object representations involving shape-location bindings are formed most easily or are the strongest, followed by color-location bindings, followed by shape-color bindings. Certainly, there is no clear, coherent, strong object right from the outset. It is also clear that there is a selective process that binds only some features together. The task relevance of features determines *whether or not* they are bound into the object representation, i.e., they are bound in the object weighted by their task relevance. Features are consolidated if relevant, and discarded if irrelevant, but only as a gradual process.

IS INHIBITION A PERCEPTUAL OR POST – PERCEPTUAL PROCESS?

Any discussion regarding binding of relevant features cannot be complete without discussing “relevant for what?” Adaptive organisms that we are, the ultimate goal of the process of binding is necessarily some sort of action. Kahneman et al. (1992) suggested that we create object files that contain all the perceptual information about an object. Nevertheless, as discussed, binding is not restricted to perception. Via WM, it is linked to actions. As such, the ideas of “instances” (Logan, 1988) or “event files” (Hommel, 1998, 2004, 2005) containing perceptual as well as action related information assume importance. Indeed, Davelaar (2011) postulates that all real world tasks can be denoted as “goal representations” which are bindings of their sub representations. The sub representations are for perceptual inputs, conceptual rules, and/or motor responses bound together by a memory trace. One infers that the sub representations are themselves bindings as well, for example, comprising the task relevant features of sub-states, or the properties of task-specific control representations.

Hommel (2004) postulated the importance of task relevance as a factor at the time of initial binding. However, experimental evidence shows that the inhibition of irrelevant features is gradual and requires some time to occur (Logie et al., 2011). In another

study (Jaswal and Logie, 2011), the display duration was increased from 200 to 900 and 1500 ms. This improved performance overall, but had no differential effect at the two study-test intervals of 0 and 2000 ms. This indicated that the inhibition of irrelevant features did not happen during the presentation of the study display, and is not operational during encoding, but that it is a post-perceptual process within WM (see Experiment 1, Jaswal and Logie, 2011, for details). Inhibition was used in many different ways in this experiment. The stimuli in the study display always being above capacity, focusing is required to select a region, objects, or features. This uses the prioritization function of attention. This selection process necessitates that the rest of the locations, objects, and features are deselected. These would not influence or reappear in performance. Thereafter, from the selected representations, of features, objects, or locations, there is a process of removal of the irrelevant, unwanted feature. This process begins only after encoding is complete. This crucial process is presumably a part of the central executive component of WM, and comes into play to extract meaning from an otherwise confusing array of stimulus dimensions. Gradually, this inhibitory process is complete, and the object comprising relevant features emerges to be maintained in WM, ready for further processing. Supportive evidence comes from fMRI studies by Sala and Courtney (2007) who found reduced activity over time in reaction to “conjunction” stimuli in cortical regions dedicated to “what” and “where” stimuli. Interestingly, this reduction does not happen for only “what” or only “where” stimuli. It happens only following bound stimuli which use both these streams of processing. Analogously, a number of studies with the preview search procedure (which is very similar to the task described here) have suggested that “active inhibition” is a higher order process that follows the initial registration of the stimuli (reviewed by Soto et al., 2008). Thus, inhibition of irrelevant features occurs over time and is presumably a process within WM.

This inhibitory process is rather different from the orientation function of attention that allows selection of locations and/or objects from the stimulus display that is presented. Indeed it is possible to focus and use this latter type of attention even before the stimuli are displayed or in the complete absence of distracters (Henderson, 1996). In contrast, the inhibitory process occurs after stimulus presentation and seems to be directed at everything that is irrelevant in the stimulus display – be it features or objects. In this sense, it is similar to distracter suppression, which appears only after the distracters are identified (Luck and Hillyard, 1994a,b; Luck et al., 1997; Luck, 1998).

In the area of WM, an inhibitory process was first proposed by Hasher and Zacks (1988) to account for differences among older and younger adults in WM. They proposed that successful processing implied allowing relevant information in and keeping irrelevant information out. However, they did not apply this idea to features within bindings, and restricted their view to objects in WM. Subsequent studies have shown that the memory problems of older adults are not so much regarding individual features but about bindings of those features (Chalfonte and Johnson, 1996; but, see Brockmole et al., 2008). The gradual process of deleting or inhibiting a feature that is task-irrelevant and possibly disruptive has been identified as an important aspect of WM executive functions (Miyake et al., 2000; Friedman and Miyake, 2004).

Summary so far

All features and objects, indeed the whole display, enter the sensory register of the participants, and gradually, from this representation, the relevant features and objects are selected and retained, and the irrelevant ones are discarded. Whether the features participate in a preliminarily integrated percept to be refined thereafter or whether the features are held in separate feature maps is a moot point. The vast literature on information processing theory has shown that parallel representation of stimulation followed by serial decision making is a much more efficient procedure, than selecting each object one by one and making decisions about it (e.g., Sternberg, 1966, 1967). It being easier to encode all stimuli and then make the decisions, participants might loosely represent the irrelevant as well as relevant features initially, deleting the irrelevant ones only after the display is gone, and no more relevant features can be committed to memory. Certainly, there is no clear, coherent, strong object right from the outset. The deletion of features from within a representation, such that it becomes a coherent strong object capable of further manipulation, takes time and resources, and is a preliminary phase in the online processing of objects in WM. Thus, the emergence of the bound object is a result of an active inhibitory process in WM.

CONCLUSION: THE PROCESS OF BINDING

The process of binding as understood on the basis of research reviewed above is illustrated in **Figure 1**. The five stages represent cross-sections of the process to aid understanding, otherwise the process is assumed to be continuous. The area covered by the ovals gradually reduces to depict the decrease in the amount of information available to the participant, and also increasingly focused attention. It is, nevertheless, accepted that attention plays different kinds of roles in this process. The gradual completion of the boundaries is used to show the increasing clarity of the representations.

The whole process is dictated and delimited by instructions from WM which define the goal for the participant. Even before the trials begin, the participant is set to ignore the irrelevant feature. Stage 1 represents stimuli in the real world. Stage 2 is the initial representation of the stimulus dimensions, which includes almost all the various features defining the stimuli. However, there is some loss of information even at this early stage, as a proportion of the stimuli impinging on the sense organs are selected to be processed further. This stage contributes to the binding process by holding information as an almost veridical representation of reality which can be organized and further consolidated. It corresponds to retinotopic iconic memory, and is vulnerable to an immediate mask. It is also difficult to build up this representation with sequential presentation when one item vanishes as the subsequent one is presented.

Stage 3 is a spatiotopic representation with a greater loss of information than Stage 2, but which has much more information available than the later stages. Presumably it corresponds to the fragile VSTM proposed by Sligte et al. (2008). The process of active inhibition is dominant between the Stages 3 and 4, and removes the irrelevant feature, in this case locations. The inhibitory process is otherwise a necessary component of top-down processes

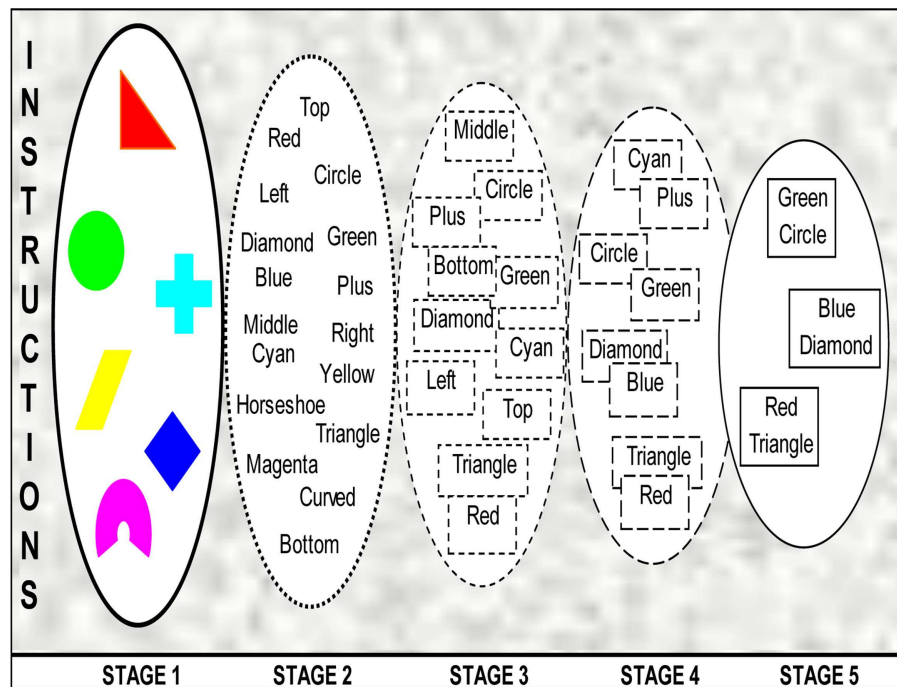


FIGURE 1 | The process of binding.

which select relevant information and inhibit irrelevant information and operates throughout the binding process. This top-down processing is achieved by reentrant processes. Notice how reentrant processes recover the relevant feature “blue” to be amalgamated with “diamond” as represented in the next stage. Stage 4 represents only the relevant features, with increasing overlap between them to show the strength of binding at this stage. Stage 5 shows features bound as objects in VWM ready for further processing.

Though the illustration uses location as the feature to be ignored, it is assumed that analogous processes operate if color or shapes (or other stimulus dimensions) are to be ignored. The total duration of this process will vary with the stimulus dimensions involved. As per experimental evidence (Logie et al., 2011), the duration of the process is shorter when shapes or colors are to be ignored.

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From simple receptors to complex multimodal percepts: a first global picture on the mechanisms involved in perceptual binding

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The binding problem in perception is concerned with answering the question how information from millions of sensory receptors, processed by millions of neurons working in parallel, can be merged into a unified percept. Binding in perception reaches from the lowest levels of feature binding up to the levels of multimodal binding of information coming from the different sensor modalities and also from other functional systems. The last 40 years of research have shown that the binding problem cannot be solved easily. Today, it is considered as one of the key questions to brain understanding. To date, various solutions have been suggested to the binding problem including: (1) combination coding, (2) binding by synchrony, (3) population coding, (4) binding by attention, (5) binding by knowledge, expectation, and memory, (6) hardwired vs. on-demand binding, (7) bundling and binding of features, (8) the feature-integration theory of attention, and (9) synchronization through top-down processes. Each of those hypotheses addresses important aspects of binding. However, each of them also suffers from certain weak points and can never give a complete explanation. This article gives a brief overview of the so far suggested solutions of perceptual binding and then shows that those are actually not mutually exclusive but can complement each other. A computationally verified model is presented which shows that, most likely, the different described mechanisms of binding act (1) at different hierarchical levels and (2) in different stages of “perceptual knowledge acquisition.” The model furthermore considers and explains a number of inhibitory “filter mechanisms” that suppress the activation of inappropriate or currently irrelevant information.

Keywords: perception, binding problem, combination coding, temporal coding, population coding, focus of attention, knowledge, inhibition

INTRODUCTION

The binding problem in perception is concerned with answering the question how information from millions of sensory receptors, processed by millions of neurons working in parallel, can be merged into a unified percept. Finding an answer to this question is on the one hand crucial for understanding the functioning of the brain and therefore tackles researchers from various disciplines of brain sciences. On the other hand, gaining insight into this topic is also highly valuable for a subfield of engineering called “Brain-Like Machine Perception” (Velik, 2008). Brain-Like Machine Perception is concerned with developing brain-inspired concepts and technologies for a new generation of information processing and automation systems. The motivation for the research presented here comes exactly from this latter discipline and originated from the following challenge: sensor technology is getting smaller and smaller while at the same time becoming cheaper and cheaper. The consequence is that in future, systems like robots or building automation systems will be equipped with a larger number (up to millions) of individual sensors. This will enable completely new application domains. However, today’s technical approaches cannot cope with the processing and interpretation of such a flood

of incoming data. Novel concepts are needed (Velik et al., 2011). One way to find a potential solution to this challenge is to take inspiration from the brain – a system that is capable of processing information from millions of sensory receptors and merging them into unified percepts.

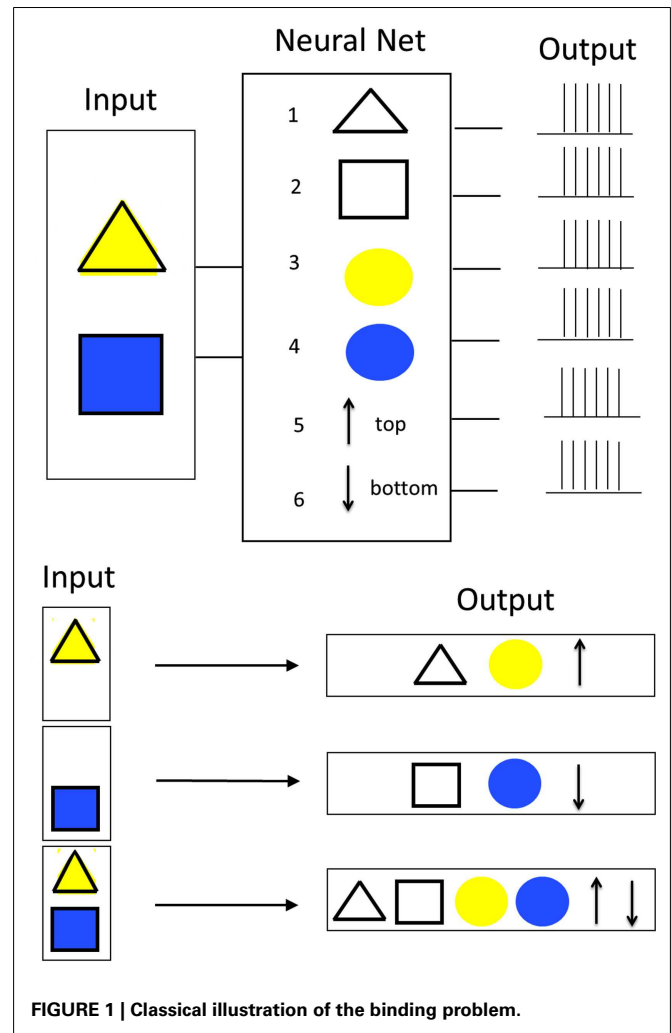
Driven by this idea, we formed an interdisciplinary research team of engineers and brain scientists and worked on the development of a technically implementable model of the human perceptual system of the brain – a task which included also an extensive study of the binding problem in perception. During the course of this research, we did not only develop innovative concepts and methods for future engineering systems, but also gained new insights and formulated new hypotheses concerning brain functioning. While engineering aspects of this work and a first draft of the overall model from the viewpoint of cognitive sciences have already been presented elsewhere (see for instance Velik, 2010a,b,c; Velik and Boley, 2010), the article of this special issue shall now particularly focus on a description of newly gained insights and hypotheses concerning the binding and inhibition mechanisms involved in perception. For this purpose, we first give a summary of so far suggested potential solutions to the binding

problem and their strengths and weak points in Chapter 2 followed by a presentation of our proposed perceptual binding model in Chapter 3. The model is based on a conclusive combination of so far suggested potential solutions to the binding problem and further supplementary considerations and hypotheses including several inhibition mechanisms coming from feedback connections and top-down guided mechanisms. The principal functionality of the resulting model is validated via computational simulations. The next step to take, which is not covered by this article, is to search for physiological support of the suggested hypotheses by experiments and observations in animals or humans. With this article, we would like to encourage other research groups to join this verification process.

STRENGTHS AND WEAK POINTS OF CURRENT BINDING HYPOTHESES

WHAT IS THE BINDING PROBLEM? – A FIRST SIMPLIFIED EXPLANATION

The binding problem in perception takes its origin in the field of Gestalt psychology, which was concerned with trying to understand by what principles visual features tend to be grouped to particular perceived objects. According the identified Gestalt principles, such a grouping is done based on properties like proximity, continuity, simplicity, closure, similarity, figure-ground distinction, and common fate (movement into same direction). The binding problem as considered today goes a step further and tries to investigate what processing mechanisms lie behind such “grouping effects” within and across modalities. The principal problem that current brain science has with understanding how information is “bound” in perception is probably best explained by a concrete example (see **Figure 1**). The most extensive discussion of binding has so far concerned binding in visual perception. The presented example constitutes an extended version of F. Rosenblatt’s classical illustration of the binding problem from his book “Principles of Neurodynamics: Perceptrons and the Theory of Brain Mechanisms” (von der Malsburg, 1995, 1999). The example concerns binding of visual information. At the input of a hypothetical neural network consisting of six neurons, different visual images are presented that can either be yellow or blue triangles or rectangles in an upper or lower position. In order to process the incoming information, in analogy to observations made in the visual cortex, different neurons of the network respond to different features of those objects. In the example, two neurons respond to the shape of objects (neuron 1 to triangles, neuron 2 to squares) and two further neurons respond to the color of objects (neuron 3 to yellow, neuron 4 to blue). Last but not least, the two remaining neurons represent the position of the objects (neuron 5 means upper position, neuron 6 means lower position). If now for example either a yellow triangle in the top position or a blue square in the bottom position is presented, always the three corresponding “feature neurons” are activated. However, a problem occurs in the case that not only one but two objects are presented to the network simultaneously. In this case, all six feature neurons are activated concurrently and without further measures, it cannot be concluded which feature belongs to what object. Finding out how the brain solves this issue to come to unified correct percepts is the so-called binding problem. The binding problem is not limited to perception. Similar



mechanisms are also necessary for other brain functions including sensor-motor function, memory, and consciousness (Roskies, 1999). For this reason, the binding problem is considered as one of the key questions to brain understanding (Triesch and von der Malsburg, 1996).

Within the last decades, researchers have intensively worked on finding a solution to the binding problem. We already presented an extensive overview and discussion of so far suggested solutions to the binding problem in (Velik, 2010d). In the following sections, we give a summary of this information as far as it is relevant for understanding the model and hypotheses that will be described in Chapter 3. While Section “Proposed Binding Mechanisms” describes individual so far suggested mechanisms, Section “Proposed Combinations of Binding Mechanisms” is concerned with illustrating what combinations of those individual mechanisms have so far been proposed.

PROPOSED BINDING MECHANISMS

Combination coding

In the 1960s, the Noble prize winners Hubel and Wiesel (1962) reported that the visual cortex shows a hierarchical organization. Each hierarchical level receives and processes information from

earlier levels. This way, incoming information is merged and condensed from layer to layer leading to more and more complex perceptual representations in higher levels that cover information from larger receptive field sizes.

Based on this notion, the hypothesis of combination coding (also called convergent hierarchical coding or grandmother-cell hypothesis) was introduced. Combination coding cells (also called connector cells, cardinal cells, or grandmother cells) always receive convergent input from neurons or populations of neurons of earlier levels and therefore only react to particular combinations of features. This way, incoming information from earlier processing stages is integrated and condensed more and more at higher levels. A simple example for how combination coding can work is given in **Figure 2** (left). Similar like in the example in **Figure 1**, the task that shall be performed by the hypothetical neural network is to detect the simultaneous presence of a yellow triangle in the upper position and a blue square in the lower position. According to the combination coding hypothesis, in order to achieve this task, there has to exist a particular neuron for each possible combination of the features (shape, color, and position). The image representations currently present then result in an activation of the appropriate neurons.

According to combination coding, neural representations are becoming increasingly complex from level to level. At each particular level, a single neuron or a small group of neurons receives convergent input from neurons or populations of neurons from lower hierarchical levels. As noted by Sir Charles Sherrington in his book “Man on His Nature” (1941), following this integration scheme, this could in the extreme case lead to one ultimate pontifical cell as the climax of the whole system. Sherrington however rejected this idea as improbable. In accordance with this, Barlow (1972) suggested that the concept of the pontifical cell should be replaced by a number of “combination cells” from which only a few fire concurrently in order to represent the current perception of the body and the environment.

Evidence for the combination coding hypothesis has been reported particularly for the visual cortex which shows a gradual decrease of retinotopic specificity from layer to layer together with an increase in receptive field size and an increase in complexity of stimulus features to which neurons respond (Hubel and Wiesel, 1962). Models that map these observations of a hierarchical feed forward architecture for simple form recognition have been presented by Riesenhuber and Poggio (1999, 2002).

Although at first sight, the combination coding hypothesis seems to be very intuitive, it suffers from certain weak points. The first criticism concerns the question of how cell connectivity patterns of such high specificity should be formed. To acquire them by learning would need many examples of all possible objects, shapes, colors, sizes, rotations at all possible locations of the perceptual field. On the other hand, prewiring cell connections would require the storage of all this information in the genes, which is also unlikely (Triesch and von der Malsburg, 1996). A second criticism concerns the fact that combination coding could need as many connector cells as there are distinguishable objects. If a connector cell was to represent a whole class of objects, it would not be able to represent fine object details. On the other hand, if there

existed a cell for all objects showing general similarities but differences in details (e.g., one and the same face with different facial expressions), this would quickly lead to a *combinatorial explosion*. Furthermore, this would mean that many cells would have to be silent for long times (up to decades) before their patterns appear again (von der Malsburg, 1981).

Population coding

A proposed alternative to overcome the combinatorial explosion of convergent hierarchical coding is population coding (also called distributed coding; Gray, 1999; Goldstein, 2002). The principle of population coding is explained by the example given in **Figure 3**.

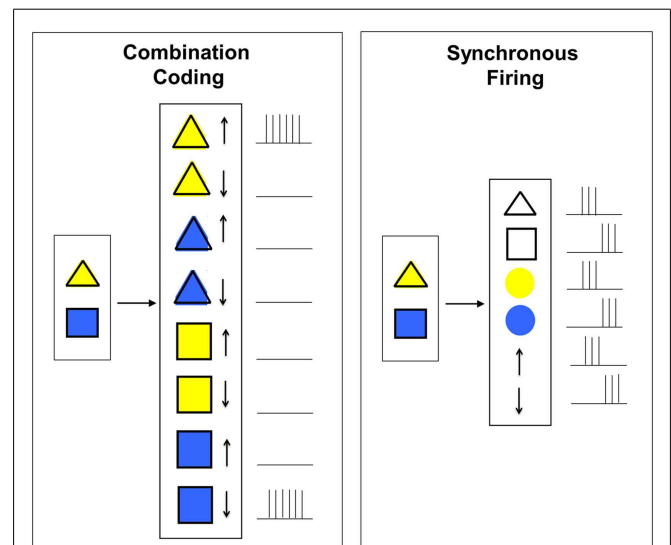


FIGURE 2 | Combination coding vs. binding by synchronous firing.

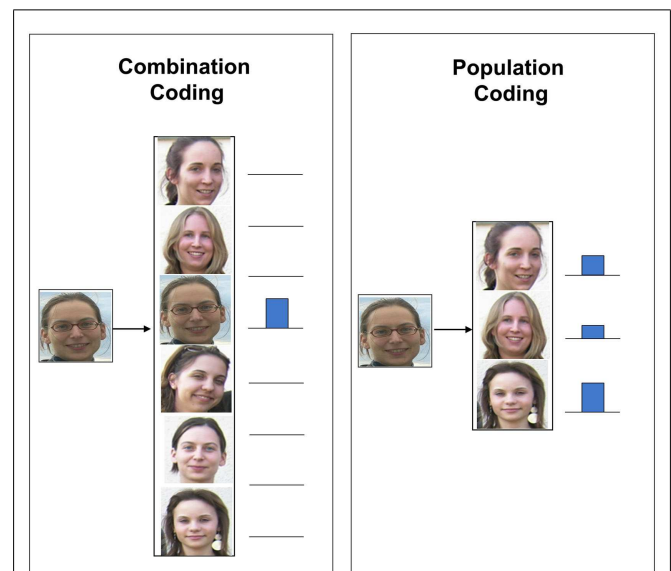


FIGURE 3 | Combination coding vs. population coding.

In this example, a particular face shall be recognized. While in combination coding, there would exist a particular neuron (or group of neurons) for each known face, population coding would follow another principle. According to population coding, such complex features are not represented by individual nerve cells but by a whole population of distributed neurons of the same or different cortical levels. A particular sensory input pattern then activates a particular firing pattern in this population. To make this concept plausible, one could imagine that the population of neurons consists of individual neurons representing archetypical faces. If now a particular face shall be recognized, the “archetype faces” are activated more or less strongly depending on the grade of similarity with the presented image thus leading to a specific activation pattern inside the neural population. In comparison to combination coding, by this coding scheme, the representational capacity of the network would be greatly increased as the number of possible distinct stimulus patterns is by far higher than the number of neurons necessary to represent them. Thus the issue of combinatorial explosion would no longer pose a problem.

The theory is supported by physiological evidence from sensory and non-sensory cortical areas and has shown to mesh well with various aspects of the physiological and anatomical organization of the visual cortex. For instance, Haxby et al. (2001) showed using functional magnetic resonance imaging that in the ventral temporal cortex, the representation of faces and objects is widely distributed and overlapping. Similarly, O’Toole et al. (2005) reported for the same brain area that object categories with shared image-based attributes have shared neural structures. Quiñan Quiroga et al. (2007a,b) conducted experiments in the medial temporal lobe to investigate population vs. combination coding and pleaded for this brain area in favor of a spares but not “grandmother-cell” coding.

Although population coding seems to play an important role in binding, the theory again seems to be incomplete. A problem with this hypothesis arises when more than one object of the same group appears in the same scene. The unanswered question – referred to as *superposition problem* – is how a particular pattern can be identified from the many other patterns represented by the same network concurrently without interference.

Synchronous firing

To avoid the combinatorial explosion that would follow from combination coding and furthermore overcome the superposition problem of population coding, the hypothesis of binding by synchronous firing (also called binding by synchrony, temporal binding, or temporal correlation hypothesis) was suggested by Legendy (1970), Milner (1974), and von der Malsburg (1981) who formulated it independently from each other (von der Malsburg, 1999). The basic principle of binding by synchronous firing is illustrated in **Figure 2** (right) and suggests that binding can be solved by temporal correlations in firing patterns. The task to perform in **Figure 2** is again the same as described in the examples in the Sections “What is the Binding Problem? – A First Simplified Explanation” and “Combination Coding.” With the hypothesis of temporal coding, a temporal dimension is invoked to cell responses. This means that neurons representing features (in our case shape, color, and position) belonging to the same object

are correlated in time while neurons representing features of different objects are anti-correlated in time, i.e., their firing patterns are independent. This way, multiple feature combinations can coexist in the same network (Treisman, 1996; Ghose and Maunsell, 1999; Fries, 2005).

The temporal binding hypothesis seems plausible as the output patterns of neurons depend on the precise timing of their synaptic inputs. Ghose and Maunsell (1999) have reported that humans are sensitive to timing differences down to 150 μ s. In the last 15 years, experimental evidence from the visual system has been provided that supports the temporal coding hypothesis (Ghose and Maunsell, 1999; Jacobs et al., 2007). Gray et al. (1989) found in-phase neural oscillations for neurons with overlapping receptive fields and non-in-phase oscillations for cells with no such overlap. Amongst others, Gray (1999), von der Malsburg (1999), and Gabriel (2004) suggested a time range of 1–10 ms for synchronous firing. Usrey et al. (2000) support this statement by physiological evidence and report that the time window for reinforcement of heterosynaptic interaction is shorter than 7 ms in the cat geniculocortical pathway. Singer (2001) describes oscillatory modulations of neural firing patterns in the gamma-frequency range (30–90 Hz). Fries et al. (2001) discovered that gamma-frequency synchronization causes spikes to coincide in a range of 10 ms.

Despite these results, the role of synchronous neuron firing in feature binding is still controversial. Grossberg and Grunewald (1996) suggest that synchronization rather has the function of “perceptual framing” of non-constant retinal images. According to them, in case of motion in the retinal image, a mechanism is needed to ensure that parts in the image belonging together are still processed together. Otherwise, illusory conjunctions can occur. Via perceptual framing, parts of an image are re-bound by resynchronizing network inputs with a temporal offset less than a critical delay.

Sharkey (1998) expresses her doubts about temporal binding and points out that there is no evidence that neurons can respond to synchronous input with the precision that would be necessary. Furthermore it is criticized that the observations of synchrony were made in anesthetized animals. The correlation might therefore have been a consequence of anesthesia. Stryker (1989) pointed out that further work is needed demonstrating that those oscillatory phenomena are also definitely present in awake animals. Schultz et al. (2001) analyze the limits in terms of amount of information that can be extracted from an observer from such a synchronous code in order to determine if this amount is sufficient to allow for computational processes like feature binding. However, no final conclusion is drawn by them. Another point of discussion is that observed synchronous firing could also just be an artifact of binding instead of the crucial binding mechanism (Ghose and Maunsell, 1999). The hypothesis of temporal binding is only about how binding is signaled, not about how it is computed. Thus synchrony could be rather the result than the cause for binding. Ghose and Maunsell (1999) point out that this therefore begs the question how synchrony is achieved. Stryker (1989) indicates that the observation of rhythmic oscillations and their correlation with particular stimuli does not allow the conclusion that the brain makes use of this information.

Golledge et al. (1996) indicate that physiologically, the establishment of synchrony is too slow to account for normal object recognition in familiar situations. In order to provide a binding mechanism, synchronous firing would have to occur very close to stimulus onset. However, observations have shown that synchronization is not phase-locked to the onset of the stimulus and starts at a variable time after presentation of the stimulus. Later studies of Fries et al. (2001) and Stefanics et al. (2005) however partly invalidated this criticism by reporting about findings of partly phase-locked stimuli onsets in the gamma-frequency range.

Sharkey (1998) reports that maybe binding by synchronous firing is not computed in the primary cortex but instead imposed via top-down feedback connections from higher levels (see also Top-Down Synchronization).

Ghose and Maunsell (1999) indicate that binding by synchrony was suggested in order to overcome the hypothetical combinatorial explosion emerging with convergent hierarchical coding. They however provide calculations concerning the number of neurons needed in the visual cortex in order to represent all possibly occurring distinguishable visual perceptions and conclude that the combinatorial explosion is not really a problem and that thus temporal correlation is no compelling need for binding. Based on their findings, Ghose and Maunsell (1999) suggest that, although there is no absolute need for temporal binding in everyday life situations, it could be important during recognition learning (see On-Demand vs. Hardwired Coding).

Attention

A problem with the hypothesis of binding by synchrony is that spatial information of combined features is lost. Treisman and Gelade (1980) suggested that focused attention plays a crucial role in solving the binding problem. They suggest that visual information is first coded in several separate dimensions including color, brightness, orientation, and direction of movement. Via focused attention, those features are then related to each other to form objects. For this purpose, not all information is processed and integrated simultaneously but is limited top-down to one object per space and time. Once this information is processed, the features of the next object are merged. Thus, information processing is “serialized” via focal attention. The favorite metaphor for visual attention is therefore a spotlight. Only information that is currently in this “mental beam of light” is processed. This way, spatial information of features is obtained indirectly by restricting the current binding area to a certain region (Hommel and Milliken, 2007). This “beam of attention” can either be directed to small areas to obtain information with high resolution or to larger areas which results in a perception with less detail. Chun and Wolfe (2001) suggest that via attention currently relevant information is selected and interfering or irrelevant information is ignored according to the goals and state of the perceiver.

Ghose and Maunsell (1999) indicate that attention may also play a role in differentiating objects which at first glance seem the same. They describe further discrimination as a sequential process that requires sequential processing. This way, perceptions of higher detail level can be achieved.

Treisman and Gelade (1980) report that attention is needed for the correct perception of conjunctions. However, the mechanism

of focused attention, by which information processing is “serialized,” cannot be reconciled with the speed with which object recognition can take place. Riesenhuber and Poggio (1999) and Gray (1999) therefore suggest that object recognition does not base on focus of attention alone but that there have to act mechanisms prior to attention, which additionally serve to attract it (see Bundling and Binding).

Knowledge, memory, and expectation

While more classic approaches consider the perceptual system and the brain as a whole rather as a passive, stimulus-driven system, more recent theories point out the active nature of perception, which seems to be controlled by top-down processes. Apart from focus of attention, further top-down processes acting on perception and taking a role in binding are semantic knowledge, context knowledge, memory, expectation, and mechanisms related to these concepts. This notion is today supported by various researchers. Engel et al. (2001) indicate that sensory-motor processes, cognition, and behavior are to a large extent not reflex-like, based on incoming (sensory) stimuli, but also heavily influenced by expectations derived from generalized knowledge and experience coded in cortical networks. Similarly, Ernst and Buelthoff (2004) report that for interpreting (ambiguous) sensor signals, prior knowledge is often necessary. Wolfe and Cave (1999) point out that different patterns could be produced by the same stimuli due to different expectations of a subject. Engel et al. (2001) point out that top-down processes assure perceptual and cognitive processing to be fast and reliable. Using these mechanisms, predictions about forthcoming stimuli can be made, which are then continuously matched against signals from the environment and body. Treisman and Gelade (1980), who suggested focused attention to be a binding mechanism, furthermore indicated that contextual information and past experiences take a role in the binding process. Accordingly, it is for instance unlikely that we will perceive a blue sun and a yellow sky even if attention is directed elsewhere. Additionally, they point out that features, once correctly bound by focused attention, continue to be perceived and stored this way. The same observation was made by Hommel (1998) who indicates that not all phenomena can be explained by temporal integration through attention alone, like for example the experience of object constancy despite changes in some features over time. Without additional mechanisms, as soon as attention is shifted, this information would be lost again. There is thus some kind of memory and knowledge needed acting top-down to preserve the information (Wolfe and Cave, 1999; Engel et al., 2001). In the process of applying top-down mechanisms on incoming stimuli, the prefrontal and parietal cortex seem to play a particularly important role (Frith and Dolan, 1997; Miller and Cohen, 2001).

Models incorporating top-down processes usually suggest that predictions about features of the surrounding are expressed by firing patterns traveling from higher to lower hierarchical processing levels via feedback connections where then a comparison of predicted perceptions with sensory input takes place (Engel et al., 2001). Ullman (1995) indicates that the interaction between top-down and bottom-up processes can occur at any intermediate level. The only condition is that they have to arrive simultaneously. Engel et al. (2001) suggest that a mismatch of bottom-up

and top-down signals causes an extinction of signals in early levels while a match leads to an amplification.

Despite its many advantages, the usage of knowledge, memory, and expectation can also be cause of misperceptions. In familiar situations, top-down prediction of objects and events can lead to fast and efficient information processing. However, in unfamiliar situations with misleading context, predictive expectations can lead to wrong interpretations of stimuli. While top-down processes usually interact with incoming sensory stimuli to “create” perception, in some cases, they can even act in complete absence of incoming stimuli. This situation occurs in perceptual hallucinations of subjects with schizophrenia but also in normal subjects during mental imagery (Frith and Dolan, 1997).

PROPOSED COMBINATIONS OF BINDING MECHANISMS

As reported in (Treisman, 1996) different binding mechanisms suggested so far are not mutually exclusive. Accordingly, as described in the following sub-sections, different authors have already suggested a combination of particular binding mechanisms for explaining feature binding.

On-demand vs. hardwired coding

In Section “Synchronous Firing,” it was outlined that temporal coding is particularly flexible and economic in terms of cognitive structure. However, it has been criticized as this mechanism would not be able to perform binding with the speed necessary in familiar environments as even features that are very likely to occur together would need to be bound anew every time. Therefore, Colzato et al. (2006), Hommel and Colzato (2009), and VanRullen (2009) suggested that there exist two distinct binding mechanisms in perception. For frequently encountered and important objects, hardwired binding (combination coding) is applied. For more arbitrary or meaningless feature combinations, an on-demand temporal coding mechanism is used. VanRullen (2009) suggested that on-demand binding is always mediated by attention. In contrast, hardwired binding can work without attention for single objects but needs attention if multiple objects are present in the receptive field.

Golledge et al. (1996) propose that, rather than for the perception of familiar objects, temporal binding might take a particular role in recognition learning, which can have a longer time course. von der Malsburg (1995) indicates that binding by synchrony has a limited bandwidth of neural signals. However, stereotypical tasks show very short reaction times that cannot be explained by temporal binding. Thus he suggests that the more time-expensive synchronous binding is only used for novel situations. Once a cellular binding structure has turned out to have a long term value, it is stabilized into faster but less flexible specialized circuits. This hypothesis would be in line with Hebb’s cell assembly theory (Hebb, 1949) according to which cells that fire together (i.e., show synchronous firing patterns) start wiring together until they result in faster and therefore more efficient hardwired structures. Singer (2001) supports this hypothesis by indicating that neural connection achieved via temporal binding can be stabilized through learning. In this process, synchrony could be invoked either via focus of attention or maybe in-phase firing patterns of topographically correlated cells.

Bundling and binding

In Section “Attention,” attention was suggested as a binding mechanism. However, as described there, attention alone cannot explain the speed with which perception takes place. Accordingly, Treisman and Gelade (1980) proposed for visual perception that conjunctions are also formed in the absence of focused attention, however rather on a random basis. Thus, if attention is overloaded or directed elsewhere, illusory conjunction can occur. In accordance with this view, patients with parietal lobes damage in the regions involved in allocation of attention have shown to lead to illusory conjunctions (Reynolds and Desimone, 1999). Reynolds and Desimone (1999) report that the number of incorrectly bound feature conjunctions increase exponentially with the number of objects in the receptive field. Thus higher receptive levels representing larger receptive fields are more sensitive to erroneous feature conjunctions. Attention is the mechanism to resolve these incorrect feature bindings by restricting the spatial area in which information is processed at a certain moment.

In relation to this, Wolfe and Cave (1999) suggest that binding involves an early pre-attentive and a later attentive stage of processing. In the early levels of processing, i.e., the primary visual cortex, features are represented by spatially organized (topographic) maps of the visual field. This means that neighboring neurons in the retina project their information on neighboring neurons in the primary cortex. Thus, at those lowest levels, this implicit location information serves as means for interrelating features belonging to a particular object and therefore prevents features from “free floating.” Nevertheless, although all necessary information is present at those early levels, those features are rather “loosely bundled together than tightly bound.” Without attention, it is probably not possible to recode those interrelations of features into memory. In higher processing levels, the specific location information of features is no longer available as there, information is no longer arranged topographically. Therefore, selective attention is necessary for binding it at those higher stages.

Feature-integration theory of attention

According to the feature-integration theory of attention suggested by Treisman and Gelade (1980), which shows some similarities to the bundling and binding theory, features like color, brightness, direction of movement, orientation, etc. are detected automatically and in parallel in early levels of visual processing. In contrast, objects are registered separately in later stages. Awareness for objects is obtained in two different ways: (1) through focused attention and (2) via top-down processes basing on contextual knowledge and memory of past events/percepts. Usually, those processes work synergistically. However, in extreme cases, they might work almost independently.

Top-down synchronization

In Section “Synchronous Firing,” it was outlined that synchronous neural firing might play a role in binding. However, the question what the function of neural synchrony in early processing levels is and how it can be achieved is controversial. Several authors suggest that synchronous neural firing might be imposed via top-down feedback connections from higher cortical areas representing functional relationships during stages of attention or

expectancy (Sharkey, 1998; Engel et al., 2001; Fries et al., 2001; Fries, 2005). In the process of synchronous firing, also different neurotransmitter systems (e.g., cholinergic or dopaminergic) and astrocytes could theoretically play a role, which are however not further discussed in the current article.

Fries (2005) proposes that via the top-down mechanisms, a modulatory input is provided to selected neural cell groups of earlier cortical levels. In the case of attention, neural groups are defined by their topographic position in the receptive sensor map. Thus, by synchronous firing induced by attention mechanisms, currently relevant areas are selected and transformed from a spatial (topographic) code to a temporal code. Apart from locations, attention can also be directed toward different modalities or particular object features (e.g., color or movement; Engel et al., 2001). In support of this hypothesis, recent studies of Fries (2005) have shown that spikes coming from neurons representing attended features are more precisely gamma-band synchronized than the spikes of neurons representing unattended stimuli. Fries (2005) further reports that thalamic nuclei and other “broadcasting centers” with widespread reciprocal connections within the cortex could take over the function of distributing the synchronization rhythms. Selectivity could be achieved via specific rhythms sent to particular areas. Engel et al. (2001) report about studies according to which, apart from attention, also states of “anticipation” and “expectancy” can be represented via temporally synchronized activity patterns that occur before the appearance of stimuli.

Engel et al. (2001) suggest that the synchronization effect caused by attention is detectable in the primary cortical areas. Nevertheless, the extent to which synchronization can be observed

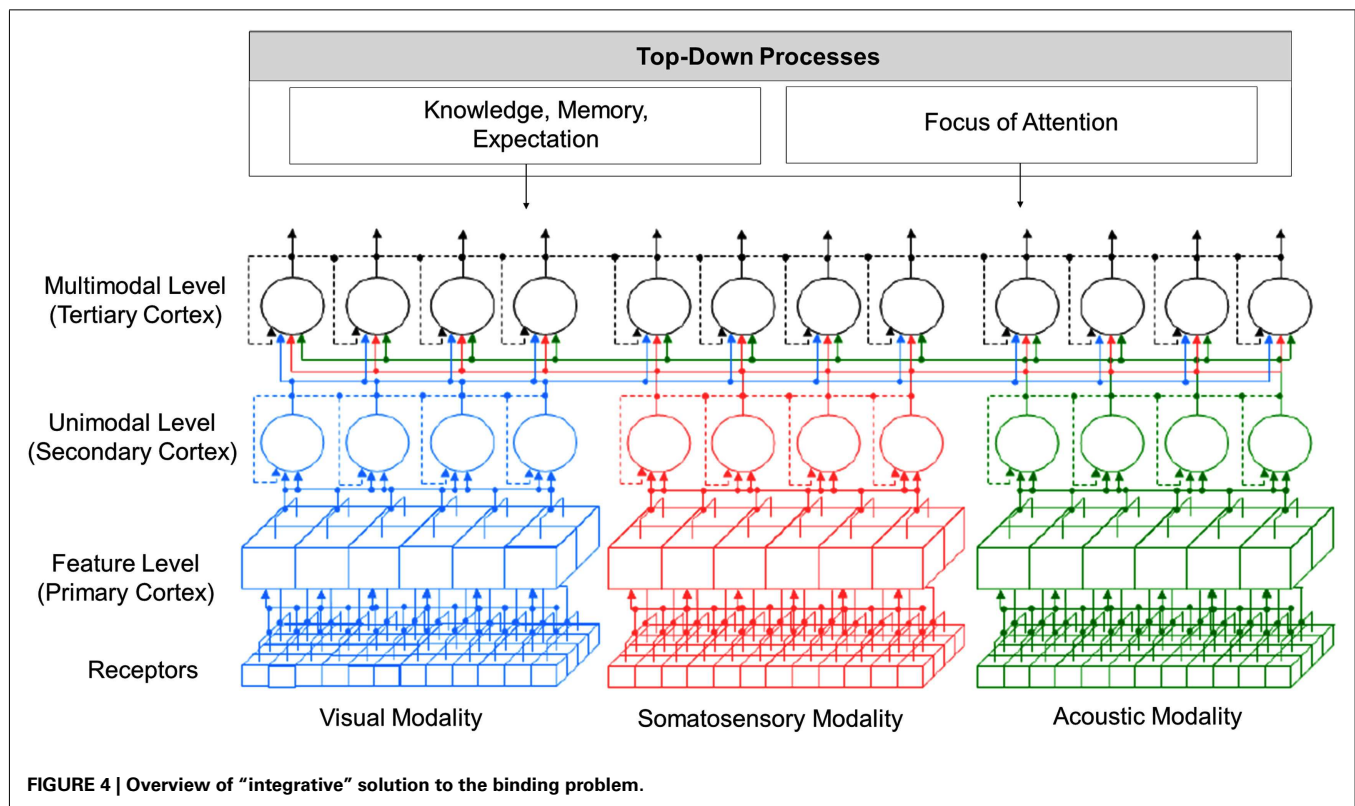
increases in higher cortical levels. However, this effect might not be caused by attentional mechanisms (alone) but also by knowledge, memory, and expectation.

INTEGRATIVE SOLUTION

In Chapter 2, different so far suggested hypotheses concerning the binding problem have been presented. Each of the proposed mechanisms seems to address some important aspects of binding. Nevertheless, none of them could so far give a complete answer. As the different solutions are however not contradictory, a conclusive combination of them might lead to a more satisfactory explanation of how binding in perception works. In this Chapter, such an “integrative” solution is proposed and the underlying perceptual model is described.

MODEL OVERVIEW

In Figure 4, an overview of the proposed model is presented. The model covers perceptual information processing from the level of sensory receptors up to the level of multimodal perception and includes the visual, auditory, and somatosensory modality. Following research findings reported by Luria (1973), perceptual information processing in the model is divided into three levels, from which each level can consist of several sub-layers (Velik, 2008). In the first two levels, corresponding to the function of the primary and secondary perceptual cortex, information for each sensory modality is mainly processed separately and in parallel (see Representation of Location Information for exceptions). In the first level, neurons – here represented by cubes – respond to relatively simple features. For the visual modality, examples for



processed features are lines, edges, colors, or movements in to a certain direction always at a certain location of the receptive field. Examples for the acoustic modality could be sounds of a certain frequency. The primary cortices are topographic, meaning that for each modality, neighboring receptors project on neighboring neurons in the cortex. Information is therefore highly location dependent. On the second level, activated neurons (or groups of neurons) – here represented by circles – respond to whole unified percepts of each modality. Examples for the visual modality would be faces, objects, persons, etc. and for the acoustic modality voices, melodies, etc. Representations are independent of the concrete location, orientation, size, etc. of the perceptual images. On the third level, corresponding to functions of the tertiary cortex, information from different sensory modalities is merged. An example for processing in this level would be the correlation of a visual image of a person with a voice to recognize that those two percepts belong together and that a particular person is currently talking.

The model shows a feedforward “simple-to-complex” hierarchy as reported by Hubel and Wiesel (1962) but additionally comprises feedback connections (see Feedforward and Feedback Connections). Furthermore, perceptual processing does not only depend on information coming from receptors but is also heavily influenced by top-down processes like knowledge, memory, and expectation (see Focus of Attention) and focus of attention (see Representation of Location Information).

FEEDFORWARD AND FEEDBACK CONNECTIONS

A clarification of the function of the different layers and their interconnections is probably best explained by concrete (simplified) examples. **Figure 5** shows an example schematically illustrating visual feed forward information processing from the receptor level up to the unimodal level.

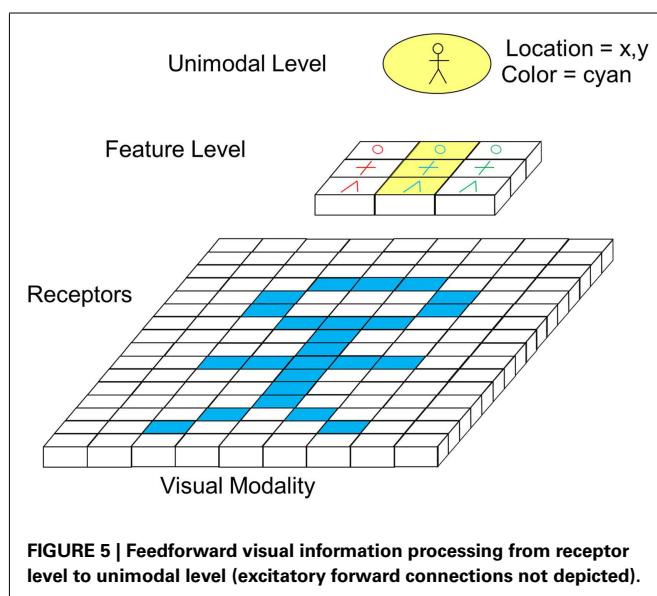
In the example, a “person symbol” in cyan color shall be recognized. For this purpose, receptors are connected to cells of the feature level and cells of the feature level are connected to the

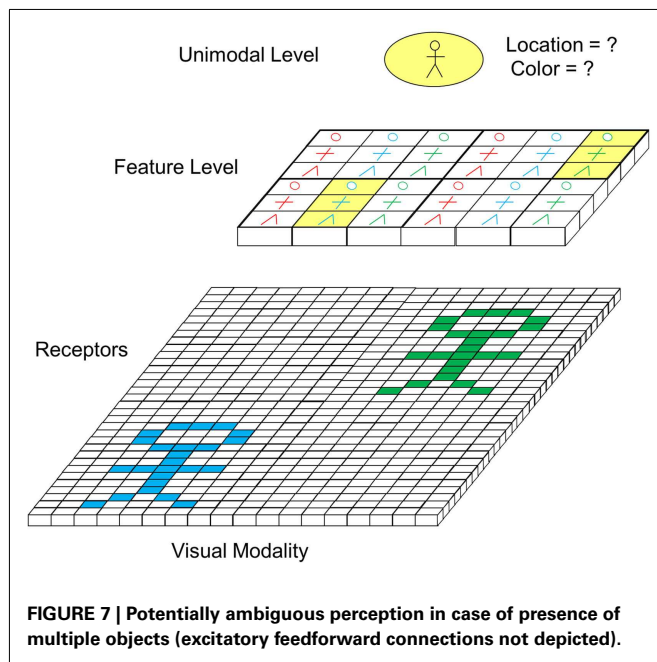
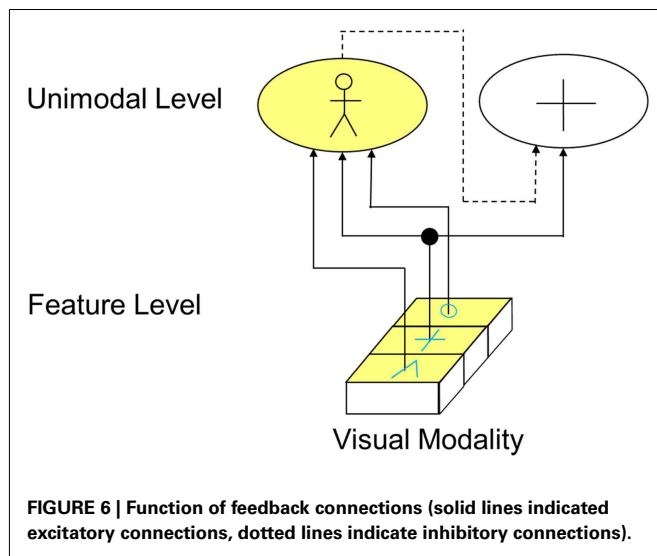
unimodal level via exhibitory connections. For reasons of clarity, the connections are not depicted in the figure. Activated cells are highlighted with yellow color. The feature level shows a topographic structure, meaning that neighboring receptors project on neighboring feature cells. As indicated by its name, cells of the feature level respond to different features of a visual image. In the given example, cells respond to shapes like circles, crosses, or edges of a specific color. In **Figure 5**, just one segment of the whole visual field is shown. Other segments of the visual field project on other cells of the feature layer. Cells on the unimodal level now receive input from feature cells of different sectors. In the concrete example, the depicted cell recognizes a person if a circle, a cross, and an edge feature are recognized in the right spatial arrangement at a certain location. Unlike assumed in F. Rosenblatt’s classical illustration of the binding problem (see **Figure 1**), this model therefore suggests that location information on the feature level is not just an additional feature like color, shape, and orientation but the crucial mechanism for binding, which is at this level coded in the spatial arrangement of cells. From the unimodal level upwards, spatial integration of information is no longer achieved via topographical representations but coded by other means (see later sections). Options for this could be specific firing patterns, the activation of cross-modal neurons, or focus of attention. At the unimodal level, cells generally respond to visual images (e.g., a person) independent of the color, size, orientation, etc. of the image except if those features are very characteristic for the object. Therefore, like for location information, these characteristics have to be coded by additional means.

Besides feedforward connections, the visual cortex also shows a number of feedback connections. The function of those connections is however not yet well understood. In the example of **Figure 6**, it is shown what important role inhibitory feedback connections can have in perception. Let’s assume that, similar like in the example of **Figure 5**, three neighboring cells representing a circle, a plus, and an edge are active at the feature level. On the unimodal level, there does however now not only exist a cell representing a person but another cell representing a cross. Via the depicted exhibitory forward connections alone, now both the “person cells” and the “cross cells” would be activated. However, the activation of the “cross cell” would be inappropriate. To avoid this concurrent undesired activation, there exists an inhibitory feedback connection (depicted as dotted line). By this means, the activation of the “cross cell” is deactivated as soon as the “person cell” representing the actual perceptual image is activated.

FOCUS OF ATTENTION

A further mechanism taking an important role in perceptual binding is focus of attention. Focus of attention comes in to play if several objects are present in the environment concurrently. This is well illustrated by the example of **Figure 7**. There, two person symbols, one in cyan and one in green are present in the visual field at the same time at different locations. On the feature level, which is topographic, this would lead to an activation of feature cells in two different areas (marked in yellow). On the unimodal level, this could lead to an activation of the “person cell.” However, at this level, a binding problem occurs as two persons are present and no conclusive information about the location and color (i.e.,





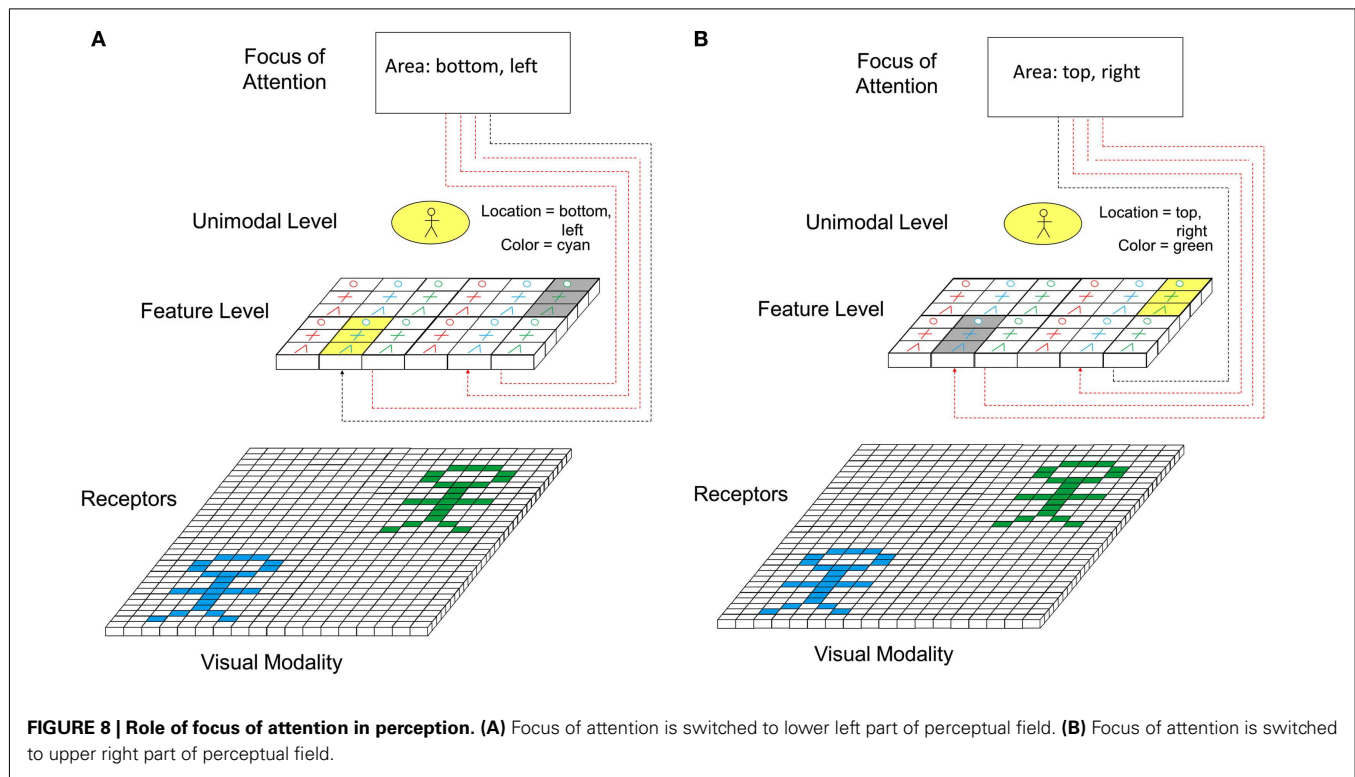
the details) of the person symbol can be obtained. To resolve this problem, focus of attention can be applied.

Figure 8 shows the principle how focus of attention interacts with perception. In the model, focus of attention interacts on the feature level. Via inhibitory connections from the focus of attention, the activation of all feature cells outside a certain spatial range is reduced in comparison to the range to which the focus of attention is currently directed. This way, only information currently “inside” the focus of attention is further processed in higher levels (see **Figure 8A**). Once processed, the focus of attention is shifted to the next area (see **Figure 8B**) and the features activated there are now processed. Apart from directing focus of attention toward particular spatial areas of the perceptual field, it is also conceivable that focus of attention can be directed toward particular

features (e.g., particular colors, particular shapes, etc.). Seen from a physiological perspective, focus of attention could be represented by a top-down-induced pattern of synchronous firing of neurons representing features being currently in the focus of attention.

REPRESENTATION OF LOCATION INFORMATION

As already outlined in the previous sections, information about the location where particular features, objects, and the like are perceived has an important role in binding. This becomes particularly important for correctly binding features to higher-level concepts in case multiple objects/events occur at the same time. As explained in Section “Feedforward and Feedback Connections,” up to the feature level, location information about features is represented topographically. Thus binding in those first layers particularly occurs between features represented by spatially proximal neurons. However, the unimodal and multimodal level of perception no longer show these topographic representations. Thus other mechanisms need to act in later levels of perception to code location information. A particularly interesting question in this context is how unimodal representations of different sensory modalities are bound to correct multimodal perceptions if different objects and events occur at the same time. One example could be that two persons are currently perceived in a room at different locations from which one is currently talking and the other is not. How can perceptual information be correctly bound in order to perceive which of the two persons is currently talking? Apparently, the information where in the room a voice was heard and where in the room the two persons were seen has to be matched adequately and the acoustic and visual information having been perceived in an overlapping spatial range has to be merged while the other visual information should not be considered. One possible way to achieve this merging is the mechanism of focus of attention introduced in Section “Focus of Attention.” In this case, the spatial range within which information is considered and therefore can be merged would be limited in each moment of time. The question is however if focus of attention is the only mechanism available as it is quite exact but relatively time consuming. As suggested in Section “Synchronous Firing,” synchronous firing of neurons could have the function to translate the topographic representation of location information of the feature level into a temporal representation in the unimodal level and above. One mechanism to induce synchronous firing could be focus of attention, which however has the disadvantage to be relatively slow. Therefore, other alternatives are conceivable. On the one hand, theoretically, concurrently activated neurons of the feature level in a proximal spatial range could produce such a firing pattern. However, when going beyond information processing for just one particular modality, the question is how synchronization in firing between different sensory modalities can be achieved for representing the same spatial ranges. This would be necessary for multimodal merging of information. One possible mechanism suggested here for achieving this inter-modal synchronization could be cross-modal (i.e., multimodal) cells in levels lower than the multimodal level having the function to spatially interrelate representation of different modalities. Until recently, the general view in neuroscience was that multimodal integration is mainly limited to higher cortical levels after extensive unisensory processing has taken place (i.e.,



in the multimodal level of our model). However, recent studies report that cells responding to activations of more than one sensor modality can already be found in lower levels of perception (Ghazanfar and Schroeder, 2006; Cappe et al., 2009). The question that has so far not been completely clarified is what the function of those cross-modal neurons is. As outlined above, we propose that their function (or at least one of their functions) is to establish a “spatial correlation” between different modalities. This suggestion is in accordance with findings from Pascual-Leone and Hamilton (2001) who report about recordings of patterns from cross-modal neurons in the visual cortex responding to both visual and acoustic stimulation. Results showed that none of these neurons demonstrated a frequency tuning curve comparable to what can be obtained in the primary auditory cortex. Instead, the acoustic responsiveness of the “audio-visual” cells depended on the location of the sound source in space. Accordingly, they conclude that those neurons are engaged in the representation of the spatial localization of stimuli independent of the sensory modality. Therefore, these cells could play an essential role in “location-sensitive” binding of stimuli of different modalities.

KNOWLEDGE AND MEMORY

In certain situations, perceptual information originating from sensor values can be ambiguous. Furthermore, perception needs mechanisms to preserve the outcome of feature binding to avoid continuous reprocessing of information and to be able to consider former relevant percepts no longer activating sensory receptors. Top-down processes like knowledge, memory, and expectation can help to resolve “conflicts” and store processed information. An example for how the interaction of those top-down processes

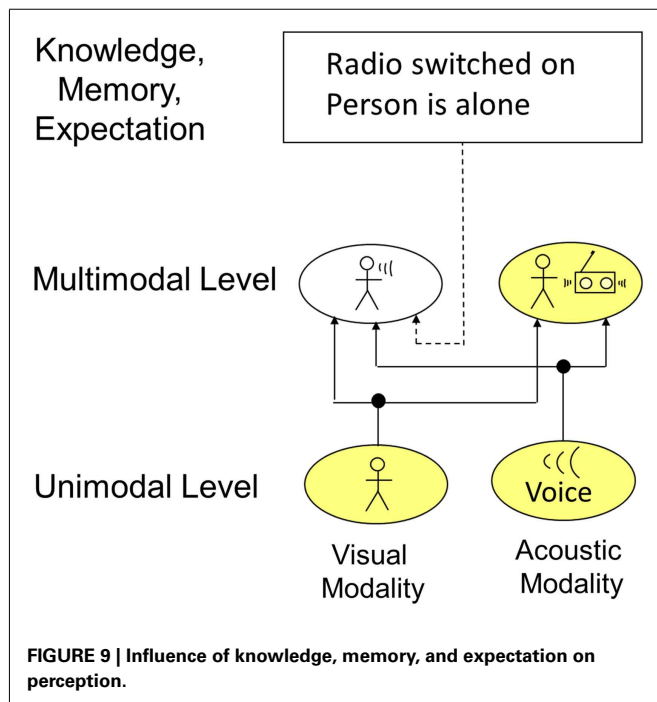
with perception takes place is given in **Figure 9**. The example shows information processing on the unimodal and multimodal level. In the visual modality, the presence of a person is detected. In the acoustic modality, a voice is recognized. On the multimodal level, this information could now lead to two different conclusions: (1) the person is talking, (2) the person is listening to the radio positioned right next to him. Taking just the current time instant is not enough to reach an unambiguous recognition. Therefore, memory and knowledge interact at this level. By these mechanisms, it can be memorized that the person switched on the radio several minutes ago. Additionally considering that the person is alone in the room and usually does not talk to himself, it can be concluded that the person is listening to the radio. Accordingly, the activation of the cell representing the “person talking” is deactivated by those top-down mechanisms via inhibitory connections. Principally, the interaction of perception and knowledge, memory, and expectation can take place at every level. However, simulation results showed that interaction at higher levels corresponding to the unimodal and multimodal level are more efficient and therefore more likely. Furthermore, inhibitory as well as excitatory top-down connections would principally be possible. However, computer simulations and system theory showed that a too large number of excitatory top-down connections can negatively influence system stability (Velik, 2008).

OVERVIEW OF INVOLVED BINDING MECHANISMS

Based on the processing mechanisms described in the last sections, this section shall now give a suggestion what binding mechanisms are applied at different levels of perception (see **Figure 10**). One central point that has to be considered is that information about

the location of perceptual images of one layer is crucial for a correct binding in the next higher layer.

The model suggests that at the feature level, which is topographic in structure, combination coding is the means of choice for binding as at this level, the activation of cells is highly specific to particular features concerning shape, color, movement, etc. at a certain position. Information about the location of features is coded in the topographic maps. The represented features are features that occur very frequently in the environment. Therefore, combination coding is the most efficient option to handle it.

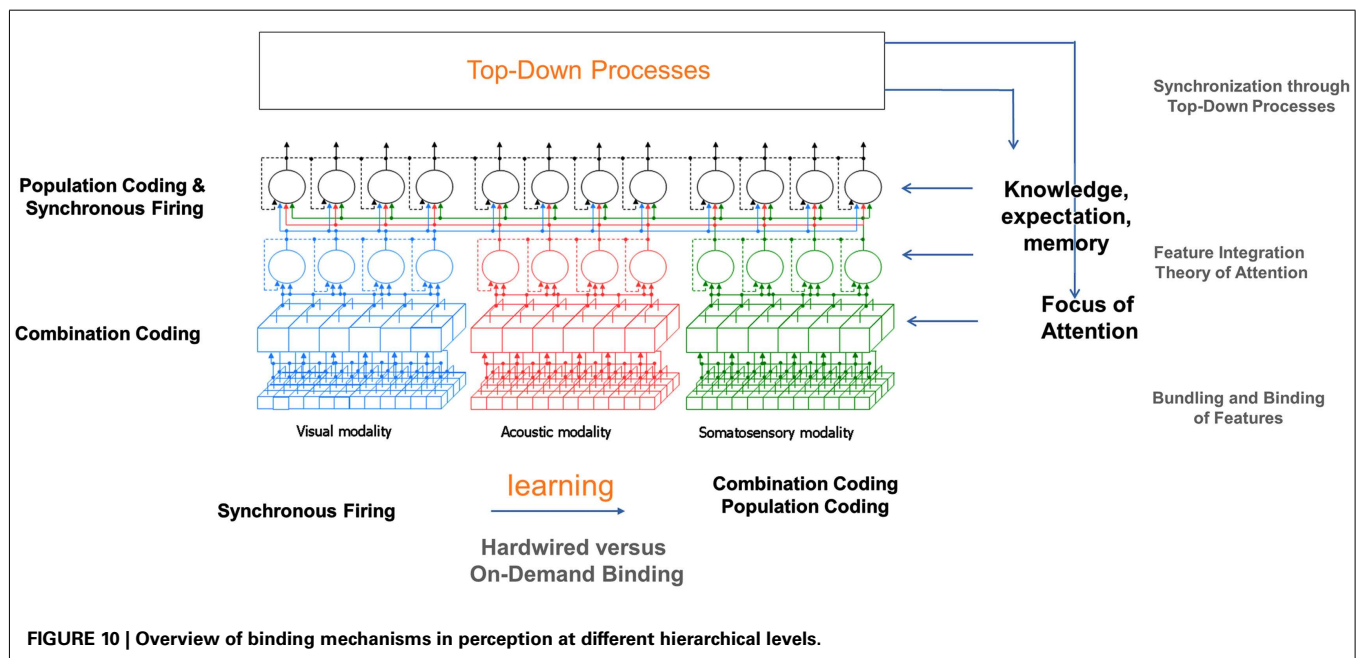


The parallel coding assures that all information in the perceptual field is quickly accessible. Only in later stages, filter and selection mechanisms are applied to reduce the amount of information that has to be processed at each time instant.

On the unimodal and multimodal level, a combination of population coding and binding by synchrony seems to be the dominating binding mechanisms. At his levels (groups of), cells are activated by particular perceptual images independent of the concrete location, size, orientation, etc. of those images. Location information is no longer represented topographically but via other mechanisms. A possible candidate for preserving this information is some kind of temporal pattern. Further mechanisms involved could be cross-modal cells responding to features of two or more modalities concurrently and focus of attention (see Representation of Location Information). The transition from the feature level to the unimodal level is of course no abrupt junction but rather a continuous change over the layers from smaller to larger perceptual fields and accordingly from more location specific and simple to less location specific and more complex features.

Additionally to the "bottom-up" processes just described, the mechanisms of focus of attention and knowledge, memory, and expectation support perceptual binding in a top-down manner. A description of how this interaction takes place has already been given in Sections "Focus of Attention" and "Knowledge and Memory."

Concerning binding in the lower levels of perception, particularly the feature level, it is conceivable that at early development stages, on-demand binding is prevalent basing on binding by synchrony and focus of attention. Only later on, commonly occurring feature combinations become hardwired. To achieve this, Hebb's law of correlations in activations could come into action: Connections of cells being frequently activated concurrently are strengthened more and more until they represent particular feature combinations in a stable way.



The remaining so far suggested “combined” binding hypotheses (see Feedforward and Feedback Connections) are simply a combination of a subset of the above mentioned mechanisms.

The bundling and bounding theory correlates to the described topographic binding mechanisms at the feature level plus the “focus of attention”-restricted processing in higher levels to allow unambiguous binding. However, unlike the model suggested here, the bundling and bounding hypothesis makes no concrete statement on how and at what level focus of attention interacts with perception. In comparison to the bundling and bounding theory, the feature-integration theory of attention additionally considers the mechanism of knowledge, memory, and expectation. However, again, in contrast to the above described model, no concrete statement is made about the possible ways of interaction. Finally, the theory of top-down synchronization covers aspects of the concepts of binding via focus of attention and binding via knowledge, memory, and expectation. However, once more, prior to this model, no statements about the concrete ways of interaction were made.

CONCLUSION

In this article, an overview was given about so far suggested solutions to the binding problem in perception. It was shown that the different existing solutions are not contradictory but that it is actually very likely that all of them play a crucial role in binding, however each of them only at specific hierarchical levels of perception and during specific periods of “perceptual knowledge

acquisition.” Accordingly, a new model for perceptual binding was suggested.

To our knowledge, prior studies about binding have mainly focused on the visual cortex and either on a description of one individual binding mechanism only or (to a much less extend) a combination of two (or at maximum three) concepts. However, an integration of the full range of binding mechanisms in to one conclusive model, which reaches additionally from the receptor level up to the multimodal level of perception, has not been provided yet. This article presented a model answering the question what binding mechanisms act at what level in what way and how the interaction of the different mechanisms can take place. We think that having available such a first “global” model will make it much easier to elaborate further details on specific binding mechanisms in different areas and hierarchical levels (e.g., by applying dynamic system theory) and also to integrate newly upcoming insights (e.g., if neurotransmitter systems or astrocytes play a role in binding). Computer simulations (Velik, 2008; Velik and Boley, 2010) showed that this “integrative” concept of binding can provide a conclusive and feasible solution for merging sensory information. The next step is now to validate the model by searching for physiological evidence of the hypotheses presented. This work can however not be performed by one single research group alone. With this article, we would therefore like to encourage the research community to validate our model and hypotheses and to either confirm their validity or to provide constructive critique and/or suggestions for adaptations.

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Dynamic weighting of feature dimensions in visual search: behavioral and psychophysiological evidence

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Dimension-based accounts of visual search and selection have significantly contributed to the understanding of the cognitive mechanisms of attention. Extensions of the original approach assuming the existence of dimension-based feature contrast saliency signals that govern the allocation of focal attention have recently been employed to explain the spatial and temporal dynamics of the relative strengths of saliency representations. Here we review behavioral and neurophysiological findings providing evidence for the dynamic trial-by-trial weighting of feature dimensions in a variety of visual search tasks. The examination of the effects of feature and dimension-based inter-trial transitions in feature detection tasks shows that search performance is affected by the change of target-defining dimensions, but not features. The use of the redundant-signals paradigm shows that feature contrast saliency signals are integrated at a pre-selective processing stage. The comparison of feature detection and compound search tasks suggests that the relative significance of dimension-dependent and dimension-independent saliency representations is task-contingent. Empirical findings that explain reduced dimension-based effects in compound search tasks are discussed. Psychophysiological evidence is presented that confirms the assumption that the locus of the effects of feature dimension changes is perceptual pre-selective rather than post-selective response-based. Behavioral and psychophysiological results are considered within in the framework of the dimension weighting account of selective visual attention.

Keywords: visual attention, visual search, feature-based attention, dimension-based attention, inter-trial effects, redundancy gains, dimension weighting, ERPs

INTRODUCTION

The selection of sensory data that are relevant for the control of behavior and thinking is a key cognitive ability and models of selection constitute a core component of cognitive theories. The notion that the neural activations representing a limited set of visual features in the brain are modulated by a process prioritizing a circumscribed part of the visual field has turned out to be a powerful account of selective attention. In her seminal Feature Integration Theory (FIT), Treisman (1988; Treisman and Gelade, 1980) proposed that visual objects are selected by a mechanism involving two consecutive processing stages. On an initial stage, representations of visual attributes or features are created. Features of a set of independent visual dimensions color, orientation, motion, size, etc. (referred to, by Wolfe and Horowitz, 2004, as attention-guiding attributes) are coded independently of each other in a topographic fashion. The generation of coherent representations of objects requires the allocation of the focus of attention to a specific spatial location in order to integrate visual features coded at the same location of the separate dimensional representations. Focal attention binds feature representations into object files that are compared to object descriptions stored in long-term memory for object recognition and identification. Feature binding and comparison occurs in a serial fashion, that is, object files are processed in turn.

Going beyond FIT, in the Guided Search (GS) model of selection, Wolfe (1994; see also Wolfe et al., 1989) proposes that entry-level feature coding feeds into the generation of a saliency representation of the visual scene. The saliency representation is conceived of as a stimulus-based (bottom-up¹) map of activations (peaks and troughs), which reflect the conspicuity, or differentness, of each feature at a given spatial location relative to their surroundings. The focus of attention is guided by the strength of the saliency activation, with the highest peak being attended first, the next peak second, etc. Visual information within the focus of attention is gated through to mechanisms of object recognition and response selection. Visual information within the focus of attention is made available to a processing stage of limited capacity that essentially processes one object at a time.

According to Treisman and Gelade (1980, p. 98), “features are registered early, automatically, and in parallel across the visual field.” Similarly, Wolfe (1994, p. 202) states that GS “distinguishes between a pre-attentive, massively parallel stage” of feature

¹Note that in GS (Wolfe, 1994) representations of particular features can be enhanced top-down by foreknowledge of feature relevance and, as a consequence, saliency activations are modulated according to the strength of the feature representation.

processing which is followed by “a limited-capacity stage that performs other, more complex operations.” In both models, assuming a dichotomy between parallel and serial processing phases, a capacity-unlimited stage of parallel feature processing prepares the scene for capacity-limited serial processing.

In the present paper we review recent behavioral and electrophysiological evidence demonstrating that dimension-based mechanisms mediating the generation of saliency signals, by drawing on limited processing resources, selectively modulate the relative strength of dimension-based saliency representations; consequently, ensuing selection processes are also modulated. The Section “Priming in Pop-Out Search” briefly introduces findings showing that search for a conspicuous target is expedited when the feature or dimension that defines the target is repeated across consecutive experimental trials. In the Section “Dimension Weighting” the Dimension Weighting account (DWA, Müller et al., 1995, 2003), a model accounting for the dynamic modulation of search performance is presented and empirical evidence in its support is discussed. The Section “Locus of Dimension-Based Modulations: ERP Evidence” considers the debate on whether dimension-based weighting occurs at perception-based processing stages prior to selection by focal attention or at response-based stages following selection. The argument here draws on the patterns of event-related electro-cortical potentials that, in previous electrophysiological studies, have been shown to reflect stimulus-based and response-based processing. Overall, behavioral and electrophysiological findings provide converging evidence in support of the assumption of a pre-selective locus of dimension-based dynamics as proposed by the DWA.

PRIMING IN POP-OUT SEARCH

Search for a stimulus that differs from distractors by one salient feature is efficient and independent of the number of distractor items present in a search array. For example, a red vertical bar presented among green vertical bars is detected seemingly effortlessly. Analysis of the search reaction time (RT) function relating the time it takes to discern the presence vs. the absence of an odd-one-out item in the array to the number of distractor items (set size) shows that RTs do not increase with increasing set size: Independently of how many green bars there are in the display, the red bar is detected efficiently – phenomenally, it “pops out” of the display. Interestingly, it has been shown that increasing the number of distractors can expedite search. Bravo and Nakayama (1992) had participants decide on the shape of a diamond target; in detail, they had to indicate whether the diamond’s left or right edge was cut off. The target was the only red diamond among green distractor diamonds or the only green among red diamonds. When the assignment of target and distractor colors changed randomly across experimental trials, the increase of the number of distractors resulted in expedited RTs. The finding is consistent with the concept of a bottom-up saliency representation. Adding distractors increases the strength of the feature-based saliency activation. Note that the shape judgment, a discrimination task, requires the selection of the target by focal attention; other tasks in the study of Bravo and Nakayama (1992) involving the mere detection of the presence of a feature that do not require focal attention were not expedited when set

size was increased (see also, Turatto et al., 2010). The decision that no target is present is made almost as rapidly as a target-present decision, that is, there is hardly a difference between target-present and target-absent RTs. The phenomenon of pop-out constitutes the core evidence for the assumption that feature extraction and processing are automatic in nature (e.g., Treisman, 1988).

The automaticity assumption was called into question by Maljkovic and Nakayama (1994, 1996). They showed that the RT in a task requiring the detection and processing of a target item that differed from distractors by its color was affected by whether the color of the target item (and associated with it, that of the distractor items) was repeated or changed across consecutive trials. In more detail, search items were red or green diamonds with the target item being the uniquely colored item. Repeating the target- (and distractor-) defining color resulted in a RT benefit on the current trial compared to the preceding trial(s), whereas changing the target color (i.e., swapping it with that of the distractors) across trials incurred an RT cost. Maljkovic and Nakayama’s (1994, 1996) findings demonstrate that, at variance with the automaticity assumption, processing of information within a visual dimension (color) is subject to modulation by variations of the stimulus. Given the additional finding that RTs were apparently not modulated by pre-knowledge of the upcoming target feature, Maljkovic and Nakayama (1994, 1996) interpreted their findings in terms of the concept of implicit memory of the target-defining feature yielding “visual priming”; as a result, repetition of the target-defining feature yields faster processing on the current, compared to the preceding, trials (but see also, Leonard and Egeth, 2008).

DIMENSION-BASED MODULATIONS IN FEATURE SEARCH

Müller et al. (1995) investigated the effects of presenting observers with pop-out targets defined, within a given block of trials, either within a single dimension (i.e., orientation) or varying across dimensions (i.e., orientation, color, size). Distractors in all conditions were small vertical gray bars. Targets were right-tilted, left-tilted, or horizontal bars in the within-dimension condition, and right-tilted, black, or large bars in the cross-dimension condition. Analyzing search RTs to the right-tilted (orientation) target presented in both conditions revealed the RTs in the cross-dimension condition to be significantly slower than in the within-dimension condition (see also Treisman, 1988). That is, variability of the target-defining dimension within a block of trials incurs a substantial RT cost relative to the target features varying within a constant dimension.

Based on these findings of cross-dimension RT costs, Found and Müller (1996) used inter-trial analyses in a feature pop-out task to further examine whether it is the target dimension or feature on the preceding trial $n - 1$ that critically influences search performance on the current trial n . In their Experiment 1, distractor items were green vertical bars; targets were either red or blue vertical (color targets) or green left-tilted or right-tilted bars (orientation targets). Observers’ task was to indicate, as quickly and accurately as possible, whether or not an odd-one-out item was present in the search array (see Figure 2, left-hand panel, for an example of a search display). Two types of change were compared to repetitions of the target feature: feature-based (within dimension) and dimension-based (across dimension). Results showed

that changing the target-defining dimension across trials (e.g., color on trial $n - 1 \rightarrow$ orientation on trial n) incurred a RT cost relative to a repetition, across consecutive trials, of the target-defining dimension (e.g., orientation on trial $n - 1 \rightarrow$ orientation on trial n). By contrast, changing the target-defining feature across trials (e.g., left-tilted on trial $n - 1 \rightarrow$ right-tilted on trial n) did not incur any cost compared to repeating the feature (e.g., right-tilted on trial $n - 1 \rightarrow$ right-tilted on trial n), neither for the color nor the orientation dimension.

Significant RT costs on dimension change relative to repetition trials were also observed in a task in which the response required knowledge of the target feature (e.g., red, left-tilted: response 1 vs. blue, right-tilted: response 2). Separate analyses of orientation and color trials showed that there were no additional costs associated with changes of orientation features while there was some evidence that feature changes incurred a cost in the color dimension. There were additional costs associated with the requirement to access the level of feature representations (see also Müller et al., 2004).

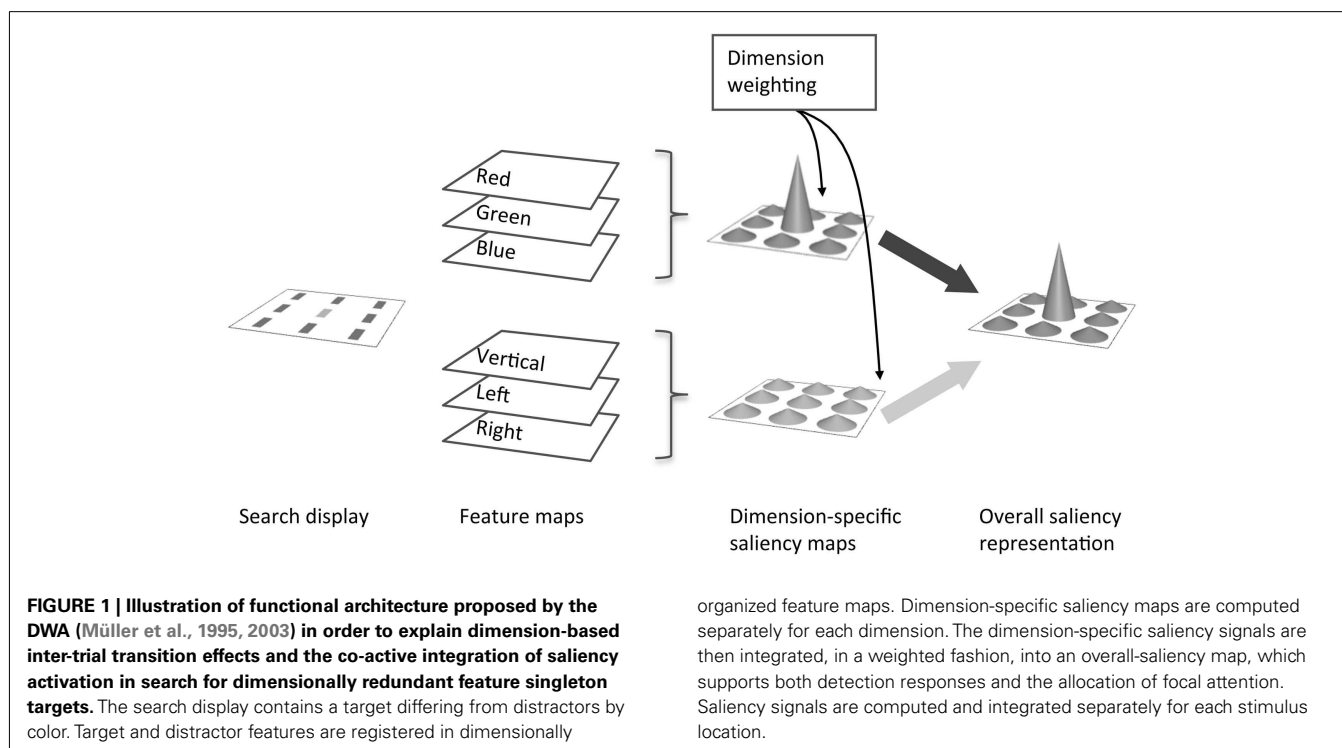
The absence of feature-based inter-trial transition effects in color and orientation trials of Experiment 1 and the orientation trials of Experiment 2 in the Found and Müller (1996) study is at variance with the findings of significant feature change vs. repetition effects in a number of studies. As stated above, Maljkovic and Nakayama (1994) observed benefits of feature repetition as opposed to feature changes within the color dimension, which they interpret in terms of bottom-up priming. More recently, Leonard and Egeth (2008) also found stimulus-driven RT benefits of feature repetitions within the color dimension. Furthermore, they also showed that foreknowledge of the target feature expedites search RTs, providing evidence for independent mechanisms of bottom-up and top-down enhancement of individual features in

search tasks. The contrasting results give rise to the question of how the divide can be resolved theoretically. The color dimension is at the core of the divergent findings. Accordingly, Found and Müller (1996) suggest that the color dimension might be conceived of as comprising a series of sub-dimensions coding colors such as red, green, and blue. They base their proposal on theories of color perception assuming the perceived colors are the result of a comparison process, which in turn could be likened to the computation of saliency signals. Importantly, provided the proposal is accepted, the mechanisms of the DWA would apply within the color sub-dimensions. Further research is required to provide empirical support for the hypothesis.

The results of dimension-based effects in feature detection tasks require a modification of models of visual search to reflect the dynamics at the level of dimension-based processing. The model proposed by Müller et al. (1995, 2003; Found and Müller, 1996) is discussed in the following section (see **Figure 1** for an illustration of the functional architecture of the DWA).

DIMENSION WEIGHTING

Müller et al. (1995; Found and Müller, 1996) interpreted their findings in terms of a DWA of search. Similar to GS (Wolfe, 1994), the DWA assumes that saliency activity integrated across separate dimensions (i.e., a supra-dimensional saliency map) signals the presence of a target in the search array and guides the allocation of focal attention. In contrast to GS, the DWA assumes that the dimension in which the target is defined is tracked by a mechanism that weights dimension-based feature contrast signals by allocating a limited-capacity resource (attentional weight). As the total amount of weight is limited, an increase of weight assigned to one dimensional module (e.g., orientation) entails a reduction of



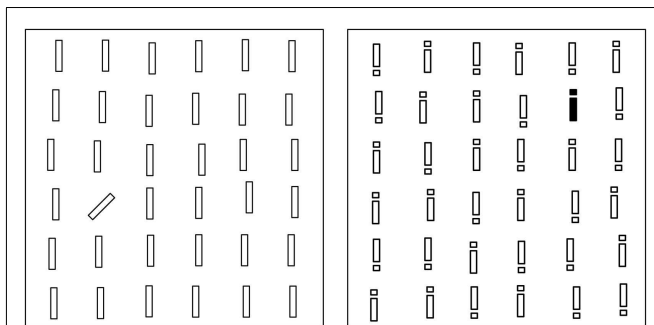


FIGURE 2 | Examples of search displays used in the empirical studies discussed in the present review.

Left-hand panel: Singleton feature search. The target item differs from the distractors by its color or orientation (shown) in non-redundant target trials or by color and orientation in redundant target trials; distractors all have the same color and orientation. **Right-hand panel:** Compound search task. The to-be-detected target differs from distractors by its color (shown) or orientation; the response is defined by the position of the gap cut into the target item at the top or bottom part. Distractors all have the same color and orientation. Cuts are located in the upper and lower parts, respectively, in half the items. Spatial locations of all the search items are randomly shifted relative to center of the cell of a virtual grid underlying the spatial arrangement of the search display. Note that the number and spatial arrangement of the display items varied according to the research issue under investigation. Note that the present example displays are not drawn to scale.

the weight assigned to other modules (e.g., color, etc.). The distribution of attentional weights established on a given trial episode (i.e., a number of sequential trials) persists across trials, at the least the weight established on a particular trial persists into the next trial episode. Shifting attentional weight between dimensions is achieved in a time-consuming process. Therefore, if the target on the current trial n is defined in the same dimension as that on the preceding trial $n - 1$, no weight shift is required and RTs are faster compared to a trial sequence that, following a change of the target-defining dimension, requires attentional weight to be shifted. The finding that a change of the target-defining feature across trials does not affect RTs relative to a repetition of the feature suggests that attentional weighting modulates the output of dimension-based saliency computations. Stated differently, weighting occurs prior to the integration of the dimension-based saliency activations by the overall-saliency representation. In sum, the results so far suggest that the strengths of dimension-based saliency activations are modulated by dynamic shifts of processing resources (attentional weights) to potential target-defining dimensions.

In the remainder, the research conducted to empirically examine the characteristics and predictions of the DWA is discussed. One key issue refers to the question whether the allocation of processing resources may be controlled or modulated by top-down foreknowledge of the dimension on which the target is defined in the upcoming experimental trial. Note that, in contrast to features, dimensions are abstract entities: Whereas features are used to describe objects such as for example “a red apple,” statements such as “a colored apple” do not convey any useful information. Both FIT (Treisman and Gelade, 1980; Treisman, 1988) and GS (Wolfe, 1994) propose that top-down modulation is at the level

of the representation of concrete features; the question whether dimension-based processing mechanisms are susceptible to top-down modulation is in part motivated by the nature of these feature-based processes.

TOP-DOWN MODULATION OF ATTENTIONAL WEIGHT

Dimensional weighting (e.g., as demonstrated by Found and Müller, 1996) seems to be largely driven by stimulus characteristics, and weight shifting does not require any conscious effort on the part of the observer (e.g., Müller et al., 2004). But does (semantic) pre-knowledge of the dimension of the upcoming target influence search performance? Müller et al. (2003) investigated the issue by presenting participants, before the onset of the display in a pop-out search task, with a symbolic cue. The cue indicated, with high validity, the dimension in which the target on the imminent trial was defined. In more detail, in their Experiment 1, targets were defined in either the color or the orientation dimension. A symbolic cue, the word “color” or “orientation,” was presented at the start of each trial to pre-cue the likely target dimension, with a cue validity of 80%. As an example, following the pre-cue “color,” that target was color-defined in 80% of the trials (valid trial) and orientation-defined in 20% of the trials (invalid trial). RTs to search displays preceded by valid and invalid dimension cues were compared to a baseline condition in which the cue word “neutral” was presented. Results showed that RTs were significantly faster on valid relative to neutral trials, and significantly slower on invalid relative to neutral trials. To more closely examine whether the effect indeed reflects weighting at the level of dimensions, rather than features, in another experiment, cue words (“red,” “blue,” “left,” “right”) indicating the exact target feature were presented prior to search display onset. For example, the cue “red” meant that the target was defined by the feature red in 79% of (valid) trials and the features blue, left-tilt, or right-tilt on each 7% of the (invalid) trials. The DWA assumes that cues, independently of whether they indicate a specific feature (e.g., red) or a dimension (e.g., color), primarily bias the weighting to favor any signals defined in the encompassing dimension (i.e., in the example, color) and only secondarily to a specific feature value within this dimension (e.g., red, blue). In line with this prediction, an invalid feature (e.g., blue) within the cued dimension (i.e., color), following the cue “red” produced shorter RTs compared to targets defined in the invalid (orientation) dimension.

These results show that dimensional weighting is susceptible to (top-down) modulation on the basis of pre-knowledge of the upcoming target, at least to some extent. Converging evidence for this position was provided by a comparison (in Experiment 1) of the inter-trial (dimension repetition/change) effects on valid and invalid trials relative to those on neutral trials. As expected, dimension-based effects were observed in the neutral condition: RTs were significantly slower on dimension change than on repetition trials (feature change did not affect RTs). The size of this effect was significantly reduced, compared to the neutral condition, on both valid and invalid trials. Thus, a cue that, for example, validly predicted the (changed) target dimension on a dimension change trial significantly reduced the RT cost that is typically incurred by the change (feature changes were not affected). A similar reduction was evident on invalid compared to neutral

trials; this time, however, the reduction was due to a relative slowing of RTs on dimension repetition trials. In other words, the RT slowing occurred when the cue was misleading, incorrectly predicting that the target would be defined in a changed dimension, when it was actually defined in the same dimension as on the preceding trial. While this pattern provides strong evidence that top-down (knowledge-based) weighting processes can modulate dimensional weight settings established (bottom-up) in response to the stimulation, the top-down influence is limited: dimension change/repetition effects remained evident even when the pre-cue was 100% valid.

The findings of Müller et al. (2003; see also Zehetleitner et al., 2011) cuing study show that dimension-based processing modules can be modulated by semantic foreknowledge of the target item in a dynamic (trial-by-trial) fashion. A related question is whether a top-down attentional set affects dimension-based processing for an extended time range such as the duration of an experimental block or an entire experiment. The question is of theoretical interest because continuous weighting of a relevant dimension relative to irrelevant dimensions might constitute a strategy to avoid capture by stimuli defined on an irrelevant dimension (cf. Bacon and Egeth, 1994). The issue was investigated in a series of three studies that are discussed in the following section.

Longer-term effects of dimensional attentional set on search performance were demonstrated in a series of studies concerned with the phenomenon of “attention capture.” Theeuwes (1992) had shown that the presence of a salient singleton color distractor affects RTs if observers search for a (somewhat less salient) singleton form target; distractors that are less salient (e.g., form) than the target (e.g., color) do not affect RTs. Theeuwes (1992) argued that the more salient stimulus automatically captures attention and that, when the distractor is more salient than the target, RTs to the target are increased by capture preventing the direct allocation of focal attention to the target. In Theeuwes’ (1992) experimental setup, observers were instructed to respond to the form singleton (in which case the color singleton is the distractor) or to the color singleton (in which case the form singleton is the distractor) and to ignore the respective other singleton. Vis-à-vis the DWA, the question arises why observers appear unable to down-modulate the weight of the “salient” irrelevant dimension so as to eliminate, or at the least reduce, the adverse effect of a singleton defined in this dimension on performance. Müller et al. (2009) addressed this question in a study in which they systematically varied the proportion of distractors presented in a given block of trials. Observers’ task was to identify a form target while ignoring a (more salient) color distractor. Within a given block, color distractors were present in 0, 20, 50, 80, or 100% of the trials; further, in the very first trial block, distractor proportion was either 0 or 100%, providing observers with either no practice or with extensive practice to deal with distractors. The results showed that distractor interference is differentially modulated by both the initial condition (0 vs. 100% distractor trials) and the likelihood of a distractor occurring. Generally, distractor interference was high for observers who had never encountered a distractor before (0% initial condition) and when distractor probability was low; by contrast, interference was substantially reduced, if not completely eliminated, when distractor probability

was high, in particular for observers who had experienced ample initial exposure to distractors. Müller et al. (2009) argued that the amount of distractor interference observed in the different conditions is explained by a strategy of (top-down) suppressing the distractor dimension. How efficiently this strategy can be or is applied depends on experience with distractors generally (prior practice) and the incentive to consistently operate this (effortful) strategy (which is high when distractor probability is high). Consistent with the latter, when the incentive is low, the first distractor after a no-distractor trial causes maximum interference, because the occurrence of the first distractor leads to the recruitment of top-down control. Interference is greatly reduced on the next trial if it also contains a distractor. Taken together, these findings suggest there does exist a mechanism capable of (actively) down-modulating the effects of salient stimuli defined in an irrelevant dimension (see also Geyer et al., 2008).

Sayim et al. (2010) recently showed that the ratio of distractor trials also affects the proportion of saccades directed to an additional onset distractor presented at a location not occupied by a distractor. The observers of Sayim et al. were instructed to execute a saccade to the one of six disks (presented on the circumference of an imaginary circle) that changed its color while ignoring the onset of a salient distractor disk. Distractors were presented on 0, 20, 50, 80, or 100% of trials. Results show that the proportion of saccades going to distractors significantly decreased as distractor proportion increased (from about 2/3 of all saccades in the 20% to about 1/5 of saccades in the 80% distractor condition). This finding could be taken to suggest that modulation may occur at early processing stages before the generation of cortical representations. The block-wise variation of the likelihood of distractor ratios used by Sayim et al. (2010) limits the generality of the finding somewhat because potential effects of different inter-trial contingencies might affect performance. Recently, Moher et al. (2011) demonstrated that the adjustment of the oculomotor system in response to foreknowledge occurs very rapidly on a trial-by-trial basis. In detail, Moher et al. had participants execute a saccade to a shape target while, in a proportion of trials, a color distractor appeared. At the start of each trial, a cue reliably indicated the likelihood (low: 10%, high: 90%) of a distractor. The results show that on high-likelihood trials, costs associated with the presentation of a distractor were significantly reduced compared to low-likelihood trials. In sum, Moher et al.’s findings can be taken to suggest that the top-down modulation is able to respond to current conditions in a highly flexible manner.

LOCUS OF DIMENSION-BASED EFFECTS: BEHAVIORAL EVIDENCE

The following section is dedicated to the question whether dimension repetitions and changes across trials affect selection at the level of response selection mechanisms. The issue came up because some researchers (e.g., Maljkovic and Nakayama, 1994, 1996 in their shape judgment studies or Theeuwes, 1991, 1992 in his capture studies) used compound search tasks and some argued that the dimension-based effects arise at the level of response selection (e.g., Mortier et al., 2005; Theeuwes et al., 2006). Whereas in simple feature (pop-out) search tasks observers simply discern target presence vs. absence, in compound tasks the detection-critical and response-critical features of the target are dissociated; that is,

detection and response features may vary independently across trials (see **Figure 2**, right-hand panel, for an example of a compound search display). As in feature search tasks, the target differs from the distractors by a salient feature, for example, its color or orientation, allowing for efficient target detection. An additional, response-relevant feature, for example, the tilt of a line presented within a square or a gap near the top or bottom end of a bar, defines the required response (e.g., left-/right-hand key press for left-/right-tilt or upper/lower gap). Note that, as a rule, a target is present on each trial in compound tasks. Although changes of the target-defining dimension were also shown to affect response decision making in compound search tasks, the dimension-based inter-trial effects are greatly reduced in compound search relative to feature search tasks (Krummenacher et al., 2002b; Theeuwes et al., 2006). Theeuwes et al. (2006) had taken the reduction to suggest that the locus of inter-trial effects is post-selective, at the level of response selection processes – rather than pre-attentive, at the level of saliency signal computation, as proposed by the DWA (Müller et al., 1995, 2003). However, there exist more parsimonious alternative explanations consistent with the DWA; these are discussed below.

In the study of Krummenacher et al. (2002b), observers were presented with an array of colored squares; the target differed from distractors either by its color (e.g., being the only red among green items) or orientation (e.g., being the only square rotated by 45° relative to the orientation of the distractors). The response was defined by the orientation of a line presented within the target item (lines were also presented within the non-target items): a left-/right-pointing line required a left-/right-hand key press. While dimension-based inter-trial effects were reduced in this task, there was also an asymmetry between color and orientation trials: dimensional effects were observed for color-defined targets, but not for orientation-defined targets. The authors argued that this pattern was owing to the requirement to switch attention from the target- to the response-defining dimension: as the response dimension was invariably orientation, observers would always need to weight the response-defining (orientation) dimension on any given trial n , irrespective of the dimension of the target-defining feature. Therefore, in the subsequent trial ($n + 1$), weight would be on the orientation dimension and the dimension-based processing stage would be biased toward processing orientation-defined targets. Accordingly, dimension change effects from color-defined to orientation-defined targets tended to be small while they were large when the target was color-defined requiring the shift of attentional weight from the orientation to the color dimension.

Another important aspect contributing to the reduced magnitude of cost/benefits of dimension-based changes/repetitions in compound relative to feature detection tasks was revealed by an analysis of the change of the target-defining feature contingent on the change of the response-defining feature (see, e.g., Müller and Krummenacher, 2006). Trial sequences involving changes were compared to repetition sequences. The results revealed an interaction between the two factors: there were costs associated with a change relative to a repetition of the target dimension from trial $n - 1$ to trial n , but only when the response feature remained the same; when the response feature changed, dimension change

costs were abolished. This pattern explains the general reduction of dimension-based inter-trial effects in compound relative to feature search tasks. Although the two types of change, of the target- and response-defining features, are statistically unrelated, the processing system behaves as if they were correlated. The target-defining attribute (color, orientation) is available to the system before the post-selective stage of (focal-attentional) processing at which the response-defining attribute (orientation) is extracted. If the target attribute on the current trial n is the same as on the preceding trial $n - 1$, the system behaves as if it assumed that the response-defining attribute would also remain the same – thence, an unchanged response is facilitated, and a cost is incurred when the response attribute changes. If the target attribute changes, any response priors are discarded and processing starts from scratch, that is, processing on the current trial n is unaffected by processing on the preceding trial $n - 1$. In their explanation of the contingencies between target-defining and response-defining features, Müller and Krummenacher (2006), referring to a similar line of reasoning by Kingstone (1992) (see also Hillstrom, 2000), argue that the linkage between selection-relevant and response-relevant features might arise because it is easier to abandon both of these parameters than to abandon one of them while maintaining the other one.

A further aspect that contributes to the reduction of dimension-based inter-trial effects in compound as opposed to feature search relates to the nature of the processing required to solve the tasks. Krummenacher et al. (2009) compared RTs and inter-trial effects in feature and compound search tasks. In the feature search condition, observers indicated whether a color (red, blue) or orientation (left-tilted, right-tilted) target bar was present in an array of green vertical distractor bars; in the compound condition, the target also differed from distractors by its color or orientation, but the response was defined by whether a gap was positioned near the top or the bottom of the target bar (see **Figure 2**). The results showed that inter-trial effects in the feature detection condition were dimensional in nature and largely uninfluenced by cross-dimensional variations of the spatial location of the target in the search array. Conversely, in the compound search condition, the effect of dimension changes was markedly reduced while there was a significant effect of the distance between the locations of the target on the previous and on the current trial: RTs to the target on trial n increased linearly with increasing distance from the target on trial $n - 1$. Krummenacher et al. (2009) interpreted this finding as suggesting that dimension change/repetition effects are modulated by the amount of attentional focusing required by the task, with space-based attention altering the integration of dimension-specific feature contrast signals at the level of the overall-saliency map: When the task does not, or only minimally, require focal-attentional processing of the target (as in simple detection tasks), dimension-based inter-trial effects can operate across the whole search array; by contrast, when focal-attentional analysis of the target is required (as in compound search tasks), dimension-based effects become confined to a narrow region around the target location (the focus of attention).

Krummenacher et al. (2010) went on to show that dimension-specific and feature-specific effects of the target definition on the preceding trial on search RTs to the target on the current trial

constitute a marker of the level (depth) at which the target was processed. Processing at the level of dimensional saliency signals entails dimension-based, but not feature-based, inter-trial effects, whereas processing at the feature level gives rise to feature-based inter-trial effects (in addition to dimension-based effects). Krummenacher et al. (2010) presented observers with search displays containing either a color (red or blue vertical bar) or orientation (green left-tilted or right-tilted bar) target embedded in an array of homogeneous distractors (green vertical bars) or a single target or distractor item that was presented in isolation. When search arrays were presented, repetition or change of the exact feature defining the target on the preceding trial $n - 1$ would not affect the RT on the current trial n because participants responded on the basis of the overall-saliency activation signaling the presence of a target. By contrast, when the item was presented in isolation a feature change incurred a RT cost because observers processed items at the feature level in order to assign the item to the target or non-target category.

In summary, the studies discussed above show that the magnitude of the dimension-based costs associated with cross-trial alterations of the target is modulated by task demands. Compound search tasks as compared to feature detection tasks give rise to effects that are related to response processing such as the requirement to shift weight to the response-relevant feature or the abandonment of settings from the previous trial if the target dimension changes. Further, compound searches require focalization of attention as reflected in space-based inter-trial effects. Feature-based effects are observed when processing of individual features is required to perform the tasks. While some of these effects can be explained by feature-based attention (see, e.g., Egeth et al., 1984; Bichot et al., 2005; Maunsell and Treue, 2006), the DWA is able to theoretically integrate the full picture of findings obtained in the above studies.

FEATURE INTEGRATION

Analyses of inter-trial effects revealed benefits and costs associated with repetitions and changes of dimensions across trials in feature search tasks that can be explained by the DWA (Müller et al., 1995, 2003). However, as the vast majority of objects in the real world are defined by multiple rather than single feature differences, inter-trial effects give rise to the question whether the integration of features also draws on the processing resources involved in feature detection².

Krummenacher et al. (2001, 2002a) addressed the issue by examining the mechanisms underlying the integration of dimension-based saliency signals into the overall-saliency representation guiding focal attention, adapting the so-called redundant-signals paradigm (see, e.g., Mordkoff and Yantis, 1991) to feature search. In their adapted paradigm, search performance for feature targets differing from distractors in one dimension (e.g., color or orientation: a red vertical bar or a green right-tilted

bar presented in an array of green vertical bars) is compared to performance in search for targets differing from distractors in two dimensions (e.g., color and orientation: a red right-tilted bar among green vertical bars). In principle, integration of dimension-based saliency signals into the overall-saliency representation may be serial, parallel, or parallel co-active in nature. Analyses of mean RTs and RT distributions can be employed to differentiate between the three possible integration mechanisms. On a serial account, dimension-based signals are integrated in a sequential fashion, resulting in increased RTs for targets differing from distractors in two dimensions compared to just one dimension³. On parallel accounts, mean RTs are determined by the faster of the two single-definition RTs. If the response is based on a parallel-race between signals, overall mean RTs to targets defined in two dimensions are expected to be somewhat faster than the overall mean RTs to targets defined in a single dimension, because the response is always elicited by the faster of the two signals. Stated differently, slow RTs in the on average faster dimension are compensated for by fast RTs in the on average slower dimension. Parallel races produce a RT benefit or RT redundancy gain that is referred to as “statistical facilitation” (Raab, 1962). However, the amount of mean RT redundancy gain compatible with the assumption of a parallel race of signals is bound by properties of the (probability) distributions of RTs to single-dimension targets. Miller (1982) proposed a distribution-based procedure to test whether RT gains are compatible with the assumption of a parallel race, the “race model inequality” (RMI): $P(\text{RT} < t|C\&O) \leq P(\text{RT} < t|C) + P(\text{RT} < t|O)$. The RMI states that the probability P of having responded to a target defined in two dimensions (e.g., color C and orientation O) at a given point in time t after display onset [$P(\text{RT} < t|C\&O)$] must be smaller or equal to the probability of having responded to a color target at time t after onset [$P(\text{RT} < t|C)$] plus the probability of having responded to an orientation target at time t after onset [$P(\text{RT} < t|O)$]. Violations of the RMI then provide evidence for parallel co-active processing of signals; that is, signals are integrated into a common representation before activating subsequent processes such as response selection and execution.

Krummenacher et al. (2002a) had their participants respond to feature targets defined in the color, the orientation, or both the color and orientation dimensions. Distractors were always green vertical bars; the target could be a red or blue vertical bar (one-dimension color target), a 45° left or right-tilted bar (one-dimension orientation target) or a bar that was red and left-tilted, red and right-tilted, blue and left-tilted, or blue and right-tilted (two-dimension color and orientation target). The results showed that RTs to targets defined in two dimensions were significantly faster than RTs to targets defined in one dimension [RTs to two-dimension targets were also significantly faster than RTs to targets of the faster of the two single-dimensions (color)]. Importantly, the distribution-based analyses showed violations of Miller’s (1982) RMI that provides evidence for parallel

²Note that the term feature integration in the following discussion refers to the integration of dimension-based feature contrast saliency activations into an overall-saliency representation rather than the integration of distinct feature representations into a coherent object representation (as in, e.g., Treisman and Gelade, 1980; Treisman, 1998).

³For an example see Krummenacher et al. (2010), who reported serial processing of multiple features in a task that required observers to categorize objects along multiple dimensions.

co-active integration of dimension-based saliency signals into the overall-saliency representation.

Krummenacher et al. (2002a) further investigated whether multiple feature signals are integrated if they are presented at spatially different locations. Observers were presented with single (e.g., a red vertical bar or a green left-tilted bar) and dual (e.g., a blue vertical and a green right-tilted target) feature targets among green vertical distractors. Search RTs of four dual target distance conditions were compared to RTs of single target conditions. Different-dimension (color and orientation) and same-dimension (color and color; orientation and orientation) dual signals were presented either at (horizontally, vertically, or diagonally) neighboring display locations (distance d1), locations separated by one distractor item in between two targets (d2), or separated by two distractor items (d3). Additionally, different-dimension dual signals were presented at the same (d0) location (i.e., a single red and left-tilted target, as in the paradigm described in the previous paragraph). Results showed that (i) RTs to single targets defined in two dimensions (d0) and RTs to dual targets (d1 to d3) were significantly faster than RTs to single targets defined in one-dimension only; (ii) RTs to dual same-dimension targets were slower than RTs to dual different-dimension targets, and both were slower than RTs to single two-dimension targets. Testing for violations of Miller's (1982) RMI showed parallel co-active processing of dimension-based signals in the single and dual different-dimension conditions, however, in the latter condition violations were observed only when the spatial distance between the two (different-dimension) target signals was small (d0 and d1). By contrast, same-dimension dual targets, though producing significantly faster mean RTs than single targets, are processed in parallel-race mode. Consequently, the finding suggests that co-active signal integration requires the presence of saliency activation in more than one dimension.

Detailed analyses of RMI violations demonstrate that co-active integration of dimension-based saliency is modulated by the topographic location of dimensional saliency signals. Presentation of dual targets at neighboring locations (d1) produces mean RT gains together with violations of Miller's (1982) RMI, a result that provides evidence for parallel co-active signal processing; presentation of dual targets with one or two distractor items in between (d2, d3) only yields mean RT gains without RMI violations, suggesting a parallel race of signals. The pattern of co-active vs. parallel processing is explained by the assumption that saliency activations of dual targets presented at the same (d0) or neighboring (d1) locations are integrated (summed) into a single overall-saliency representation while saliency activations of dual targets at larger distances generate separate representations at the level of the overall-saliency representation. Further, dual targets defined on the same dimension, while producing RT gains, do not violate Miller's (1982) RMI; that is, dual signals defined on the same dimension are processed in parallel-race mode.

In sum, processing of single and dual targets defined on the same or different dimensions each generate specific RT patterns that in turn can be explained by the spatial distribution of saliency activation. Results showed that in trials with multiple target signals, mean search RTs to both different- and same-dimension redundant targets were significantly faster than

mean RTs to single targets (compared to the faster of the two single dimensions). Analyses of RT distributions using Miller's (1982) RMI revealed that different-dimension dual target trials are processed in co-active activation mode, same-dimension dual targets, though significantly faster than single targets, are processed in a parallel race.

Krummenacher et al. (2002a) had argued that redundancy gains arise at the pre-selective processing level at which dimension-based bottom-up saliency activations are integrated into an overall-saliency representation before focal attention is allocated. However, some researchers claimed that co-active integration is post-selective, that is, that redundancy gains arise the response selection or execution stage. Krummenacher et al. (2002a) addressed the issue by examining whether RTs to redundantly defined targets are expedited if observers have pre-knowledge of the location where the target is highly likely to appear relative to when there is no advance knowledge; in other words, they investigated whether feature integration depends on the previous allocation of focal attention or whether integration occurs pre-attentively, before the allocation of focal attention. The authors used a symbolic pre-cue – an arrow presented prior to the onset of each search display – to indicate, with a validity of 80%, the display quadrant in which the target item would appear. The arrow instructed observers to shift the focus of attention to the indicated quadrant. The results showed that the pattern of RT gains was unaffected by whether the cue validly or invalidly indicated the quadrant containing the target. However, overall RTs in valid-cue trials were significantly faster than RTs in invalid-cue trials. Krummenacher et al. (2002a) interpreted the finding to suggest that the mechanism underlying dimension-based signal integration is not affected by whether it takes place under focal attention or not.

Overall, the results strongly suggest that dimension-based saliency signals are integrated before focal attention is allocated to a particular location of the search display. In addition, the findings show that (saliency) information from the slower of the two dimensions (in single dimension trials) is able to further increase the processing speed of the faster of the two dimensions, when two signals are presented. This finding provides converging support for the assumption that dimension-based signals are integrated into a common activation, in a co-active fashion, before the attentional focus is allocated to a display location (i.e., independent of focal attention; but see Cohen and Feintuch, 2002; Feintuch and Cohen, 2002).

Even though the behavioral results discussed above provided strong evidence in support of the assumption that redundancy gains arise at a pre-selective processing stage, the use of event-related potentials (ERPs) of the electroencephalogram (EEG) is an approach that is ideally suited to decide between the perceptual pre-selective and post-selective response-based accounts. ERPs measure changes in the electro-cortical potential associated with specific stimulus or response events.

LOCUS OF DIMENSION-BASED MODULATIONS: ERP EVIDENCE

The DWA (Müller et al., 1995, 2003) assumes that the allocation of limited attentional resources (i.e., dimensional weighting) occurs at an early pre-selective (or perceptual) stage of processing.

The assumption of pre-selective weighting has been challenged by researchers postulating that the dimensional inter-trial change and repetition effects arise at the stage of response preparation and/or execution. Cohen and colleagues (e.g., Cohen and Feintuch, 2002) proposed a Dimension Action (DA) model that, akin to GS (Wolfe, 1994) or the DWA, assumes dimension-based processing modules. In contrast to GS and DW, the DA model claims that each dimensional module has its own response selection devices. Dimension-based response selection is operated by a winner-takes-all process that excludes all but one of the mutually inhibitory dimensional activations with the winner activating the response execution stage. In an empirical investigation of the DA model, Cohen and Shoup (1997) used a variant of the flanker paradigm (e.g., Eriksen and Eriksen, 1974) in which the target and distractor stimuli activate multiple dimension-based response units (associated with different effectors) in parallel. In detail, Cohen and Shoup (1997) presented observers with a central target stimulus that was flanked by two distractor stimuli. In an exemplary experiment, the target required a left-hand response when it was a right-tilted red bar or a left-tilted green bar and it required a right-hand response when it was a right-tilted green or a left-tilted red bar. Flanking stimuli could be compatible or incompatible with the central stimulus. Cohen and Shoup (1997) argue that competition between responses elicited by the irrelevant incompatible flanking and the relevant central stimulus is resolved by allocating focal spatial attention to the task-relevant central stimulus. According to the DA model, RT redundancy gains observed in conditions in which relevant and irrelevant stimuli activate the same response, compared to the conditions in which relevant and irrelevant stimuli activate different responses, occur at a post-selective stage. In order to contribute to the resolution of the debate and to produce evidence in favor of the DWA or the DA model, the pattern of ERP signatures associated with perceptual-selective as opposed to response-related processes were examined in a series of studies the main findings of which are presented in the following.

Gramann et al. (2007) examined the (non-lateralized) N2 component of the ERP following dimension changes vs. dimension repetitions in search for color and orientation feature targets to identify brain-electric correlates of the weight shifts associated with dimension changes. The anterior N2 had been associated with the detection of pop-out targets in visual search (Luck and Hillyard, 1994) and Gramann et al. hypothesized that dimension changes may be reflected by N2 modulations. The results showed that the N2 amplitude at anterior electrode sites was enhanced in dimension change compared to dimension repetition trials in tasks that required the mere detection of a target or the identification of the target-defining dimension. Gramann et al. (2007) argue that the N2 modulation mirrors the detection of a dimension change and the initiation of the attentional weight shift. Their interpretation relies on the results of imaging studies by Pollmann and colleagues (Pollmann et al., 2000, 2006; Weidner et al., 2002; Pollmann, 2004) that revealed a fronto-posterior network of cortical areas involved in dimension-based weight shifting. Although modulations were also observed in other ERP components (P3, slow wave), the authors concluded that results are consistent with the assumption

that dimension change costs are caused by perception-related processes.

Töllner et al. (2008) analyzed the modulation of ERPs that are directly linked to perceptual and response-related processes, namely the (lateralized) N2pc and the lateralized readiness potential (LRP) in a compound search task that allows independent changes or repetitions of the search-relevant (color, form) and response-relevant features (line orientation). The N2pc is an enhanced negative-going deflection over posterior visual brain areas of the hemisphere contralateral to the location of an attended stimulus with a maximum in the N2 time range. The N2pc has been interpreted as reflecting the allocation of focal attention on the basis of perceptual stimulus attributes (Luck and Hillyard, 1994; Eimer, 1996) and it can be taken to mark the end of pre-attentive sensory coding; therefore, N2pc latencies indicate the speed of pre-attentive processing. The LRP can be tied to the time of the stimulus onset or the response. The stimulus-locked LRP reflects processing prior to the activation of a specific response while response-locked LRP mirrors the time taken by the production of the response. If dimension-based processes are pre-selective in nature, the N2pc component is modulated, if they are post-selective the LRP component is modulated by dimension change vs. dimension repetition across consecutive trials.

Observers in Töllner et al.'s (2008) study searched for color (e.g., red among green) or form (e.g., square among circle) targets; the response was determined by the orientation (horizontal, vertical) of lines running through the objects. The results showed that, irrespective of the (motor) response, dimension changes were reflected in shortened latencies and enhanced amplitudes of the (stimulus-locked) N2pc component. Analyses of the response-locked LRP revealed that, irrespective of dimension changes, motor response changes were accompanied by enhanced amplitudes of the LRP. The response-locked LRP is generally interpreted as mirroring preparation or activation of a motor response (e.g., Smulders and Miller, 2011) and, on account of the way it is computed, is agreed to cancel out any perceptual and/or cognitive processes. In sum, the ERP results demonstrate that dimension changes are reflected in an early N2pc modulation while response changes are mirrored in a later LRP modulation. This finding provides further evidence for a pre-selective mechanism of dimension-based effects. However, as the LRP results show, a later, response-based contribution to the effect cannot be ruled out.

Recently, Töllner et al. (2011), also in an ERP study, used the redundant-signals paradigm to obtain further evidence to establish the locus, perceptual vs. response-related, of dimension-based effects. The approach was mainly based on Krummenacher et al.'s (2001, 2002a) findings, discussed above, suggesting that redundant dimensional signals are integrated before the activation of response processes. Feintuch and Cohen (2002), challenging the pre-selective interpretation by Krummenacher and colleagues, claimed that redundancy gains arise at the stage of response rather than perceptual processing. Using a feature identification task in which participants were required to respond if one of three possible color or/and one of three possible orientations was present, Feintuch and Cohen (2002) observed redundancy gains only if

focal attention was directed to two visual objects both of which were defined by a target feature (Recall, however, that Krummenacher et al., 2002a – at variance with the finding of Feintuch and Cohen, 2002, and also Miller et al., 2009 – had shown that integration of dimensional signals in search for redundantly defined targets is independent of the allocation of focal attention.) Therefore, Töllner et al. (2011) examined ERP components to provide further evidence for the assumption that dimension-based signals are integrated before the response processing stage. The authors again focused on the N2pc and LRP components asserting that N2pc modulations reflect pure processing at the perceptual level and LRP modulations pure processing at the motor level. Analysis of the ERPs demonstrates that both amplitude and latency of the N2pc to redundantly defined targets differ significantly from the N2pc wave of color and orientation targets. No difference between waveforms whatsoever was observed in the response-locked LRP. Therefore, the ERP study by Töllner et al. (2011) provides clear evidence for an early locus of dimension-based redundancy gains.

The visual perceptual locus of redundancy gains was confirmed in an ERP study by Grubert et al. (2011) using a similar experimental paradigm as Töllner et al. (2011). Importantly, in addition to replicating Töllner et al.'s findings, Grubert et al. further showed that the occurrence of behavioral and ERP redundancy gains is modulated by top-down task set. Grubert et al. (2011), in a variant of the redundant-signals paradigm, instructed participants to respond only if the odd item in the display was defined on one of the two possible target-defining dimensions (color or orientation) while an odd item defined on the respective other dimension could be ignored and did not require a response. Target items differed from distractors on the relevant dimension or ("redundantly") on both the relevant and the irrelevant dimensions; that is, while the relevant (i.e., target) dimension required a response, the irrelevant (i.e., non-target) dimension did not require a response. The ERP results show reliable N2pc components to odd items defined on the target and the non-target dimension; importantly, however, the amplitudes of the N2pc to (odd-one-out) items defined on the non-target dimension were significantly reduced compared to items defined on the target dimension and to items defined on the target and the non-target dimensions. Grubert et al. (2011) argue that the finding can be taken to suggest that the stimulus-based saliency signal that is generated at the perceptual processing level is top-down modulated by the task set.

As the psychophysiological studies discussed above employed the lateralized N2pc component of the EEG it could be argued that the dimension-based effects revealed in the search experiments are contaminated by aspects of space-based processing. Zhang and Luck (2009) produced evidence that can be taken to disprove this objection. They showed that feature-based attention can influence feed-forward sensory activity, as reflected by the P1 wave of the EEG. Similarly, Gramann et al. (2010) demonstrated dimension-based modulations of the P1 component. In Zhang and Luck's (2009) experiment, a continuous stream of intermixed red and green dots was presented in one (e.g., the left) visual half-field. Observers attended to either the red

or the green dots in that half-field to detect occasional luminance decrements in the attended color. To test the assumption that feature-based attention can influence feed-forward sensory processing and that the modulation is independent of spatial attention, red-only or green-only probe arrays were presented in the other (e.g., the right) half-field. If the task-irrelevant probe arrays of the unattended half-field elicit a larger P1 wave when they appeared in the attended, as opposed to the unattended, color, the P1 modulation would constitute convincing evidence for a (space-independent) attentional influence on feed-forward sensory processing. Results show that after about 100 ms post-stimulus amplitudes of the P1 component over the cortex contralateral to the probe were significantly larger for probes presented in the attended (rather than the unattended) color. That is, visual signals can be modulated at processing stages that are activated briefly after stimulus onset by a non-spatial mechanism.

CONCLUDING REMARKS

In summary, the behavioral and electrophysiological results discussed in the present review suggest that the processing of dimension- or feature-based information is dynamically modulated by a mainly stimulus-driven process of dimension weighting. The mechanism underlying dimension weighting is located at a pre-selective, perceptual processing stage, and dimension weighting can be modulated by symbolic knowledge such as cues and task set.

In terms of the brain systems that might be involved in the dimension-based modulations, a number of potential candidate structures were proposed in the literature. In an account that integrates extensive psychophysical and neurobiological evidence, Fecteau and Munoz (2006) proposed a distinction between saliency and priority representations. Saliency refers to bottom-up processing of search items by spatially selective neurons that do not encode particular visual characteristics. Priority combines saliency with the relevance of a particular stimulus with respect to the observer's goals. Fecteau and Munoz (2006) argue the saliency and priority are represented by the structures of the oculomotor system with the superior colliculi and the frontal eye field constituting the core components. Bisley and Goldberg (2010) suggest that the parietal cortex, in particular the lateral intraparietal area (LIP), combining bottom-up sensory and top-down intentional information, represents saliency (see also, Gottlieb et al., 1998). Similarly to Fecteau and Munoz (2006), Serences and Yantis (2006) reject the concept of a single saliency representation made by psychological models in favor of the assumption of multiple representations associated with the structures of the oculomotor system.

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The fate of visible features of invisible elements

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To investigate the integration of features, we have developed a paradigm in which an element is rendered invisible by visual masking. Still, the features of the element are visible as part of other display elements presented at different locations and times (sequential metacontrast). In this sense, we can “transport” features non-retinotopically across space and time. The features of the invisible element integrate with features of other elements if and only if the elements belong to the same spatio-temporal group. The mechanisms of this kind of feature integration seem to be quite different from classical mechanisms proposed for feature binding. We propose that feature processing, binding, and integration occur concurrently during processes that group elements into wholes.

Keywords: feature binding, feature processing, feature integration, sequential metacontrast paradigm, feature inheritance

RESEARCH QUESTIONS

Does binding operate on pre-processed features or are feature processing and binding concurrent operations? What is the relationship between features and their carriers? What happens to features whose carriers become invisible? How do the inhibitory processes that operate on carriers affect feature processing and binding? Why and when features are segregated or integrated? Does attention play a role in these processes?

INTRODUCTION

To make sense of the world surrounding us, the brain has to extract and interpret information from the vast amount of photons impinging on our photoreceptors. The interpretation of information requires the establishment of spatio-temporal relations between different elements. How these processes of information extraction and interpretation lead to perception, learning, development, and knowledge have been fundamental problems in philosophy, psychology, neuroscience, and artificial intelligence. For example, empiricism and behaviorism are based on the principle of association. Elements that co-occur repetitively or persistently in spatial and/or temporal proximity become associated, i.e., relations are established among them so as to bind them into more complex entities. The Hebbian postulate offers a possible mechanism whereby such associations can be implemented in neural systems (Hebb, 1949). In contrast to these hierarchical approaches that build more complex entities from combinations of simpler entities, Gestalt psychologists suggested that stimuli become organized into wholes, or Gestalts, that cannot be reduced to associative combinations of their parts. Both associationist and Gestaltist views are still prevalent today as one considers the binding problem at its various levels, from perception to knowledge.

In visual perception, most approaches to the binding problem are guided by the parallel and hierarchical organization of the early

visual system. Information is carried by parallel pathways from the retina to higher levels of cortex, for example, by retino-cortical magnocellular and parvocellular pathways, and cortico-cortical dorsal and ventral pathways. Neurons in different visual areas generate distinctive responses to different stimulus attributes. For example, neurons in area MT are sensitive to motion whereas neurons in the blob regions of V1 are particularly sensitive to color. There appears to be a hierarchy within pathways; for example, complex shape selectivity appears to result from a hierarchy in the ventral pathway, starting with orientation selectivity, leading to curvature selectivity, and finally to complex shape selectivity (Connor et al., 2007). This hierarchy has been suggested to be accompanied by a shift in reference frames, from retinotopic reference frames in early areas to object-centered reference frames in higher areas (Connor et al., 2007). If different attributes of a stimulus are processed in different parts of the brain according to different reference frames, how are they associated with each other to underlie the unified percepts that we experience?

The hierarchy in the visual system is often interpreted to support the associationist view. It is assumed that the early visual system computes a set of stimulus attributes (e.g., oriented boundary segments, color, texture) and the binding consists of selectively associating different attributes with each other by, for example, hierarchical convergence (e.g., Riesenhuber and Poggio, 1999b), neural synchrony (Singer, 1999), or by an attentional scanning mechanism (Treisman and Gelade, 1980; Treisman, 1998).

In analyzing the binding problem in its broader context, one has to recognize that there are several stimulus attributes that need to be bound together, thereby leading to a variety of binding problems. Treisman (1996) pointed out the existence of at least seven types of binding, including “property binding” (e.g., how color and shape of the same object are bound together), “part binding” (how different parts of an object, such as boundary segments,

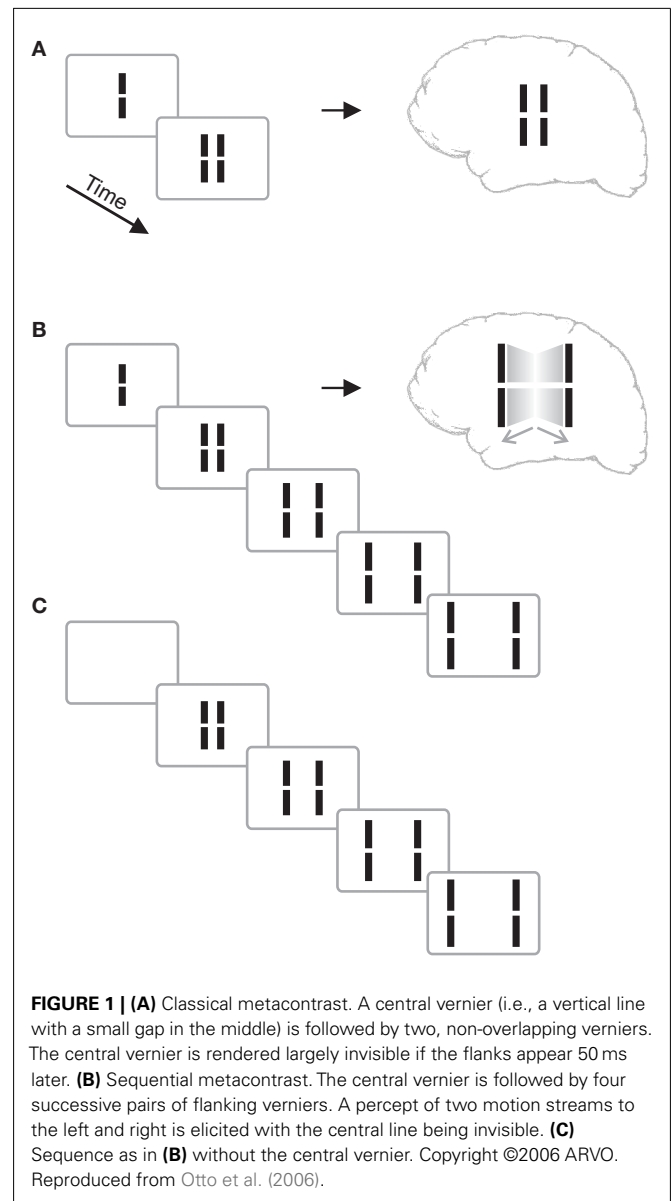
are segregated from the background and bound together), “location binding” (how shape and location information, believed to be represented in ventral and dorsal pathways, respectively, are bound together) and “temporal binding” (how binding operates across time when an object moves). It is highly likely that these different types of binding operations are not independent from each other but work in an interactive way. Furthermore, while most theoretical approaches assume as a starting point simple “features,” such as oriented line segments and color patches, it is highly likely that the computation of even these basic features is not independent from their binding operations. To appreciate this last point, one needs to first recognize that the computation of features is not instantaneous, but takes time. Second, under normal viewing conditions, our eyes undergo complex movements. Many objects in the environment are also in motion and thereby cause dynamic occlusions. As a result, the representation of the stimulus in retinotopic areas is highly dynamic, transient, and intermingled. Under these conditions, one cannot assume that features are already computed and ready for binding operations; instead, one needs to address the problem of how to simultaneously compute and bind features through interactive processes. Consider for example a moving object. Due to occlusions, the features of the moving object will overlap with those of the background or with those of other occluding objects. The receptive fields of neurons in retinotopic areas will receive a succession of brief and transient excitations from a variety of features, some belonging to the same object, some belonging to different objects. To compute features, the visual system should be able to decide whether to segregate information (when it belongs to different objects) or integrate information (when it belongs to the same object). The object file theory (Kahneman et al., 1992) assumes that an object file is opened and indexed by location and features are inserted to this file over time to allow processing. However, this poses a “chicken-and-egg” problem: In order to decide distinct objects, one needs to have access to their features; but unambiguous processing of features, in turn, needs the opening of distinct object files. This vicious circle suggests, again, that the processing of features need to co-occur with their binding.

In this paper, we summarize our recent findings from studies where we examined the spatio-temporal dynamics of feature processing and integration. In order to assess the temporal interval during which the stimulus is processed, we used brief presentations of features (a vernier offset presented for 20 ms).

THE SEQUENTIAL METAcontrast PARADIGM

We presented a vernier stimulus that comprises a vertical line with a small gap in the middle. The vernier was presented for 20 ms, followed by blank screen (inter-stimulus interval, ISI) for 30 ms, and then a pair of lines neighboring the vernier. The central vernier stimulus is rendered invisible because the flanking lines exert a metacontrast effect (Figure 1A; Stigler, 1910; Alpern, 1953; Bachmann, 1994; Breitmeyer and Ögmen, 2006).

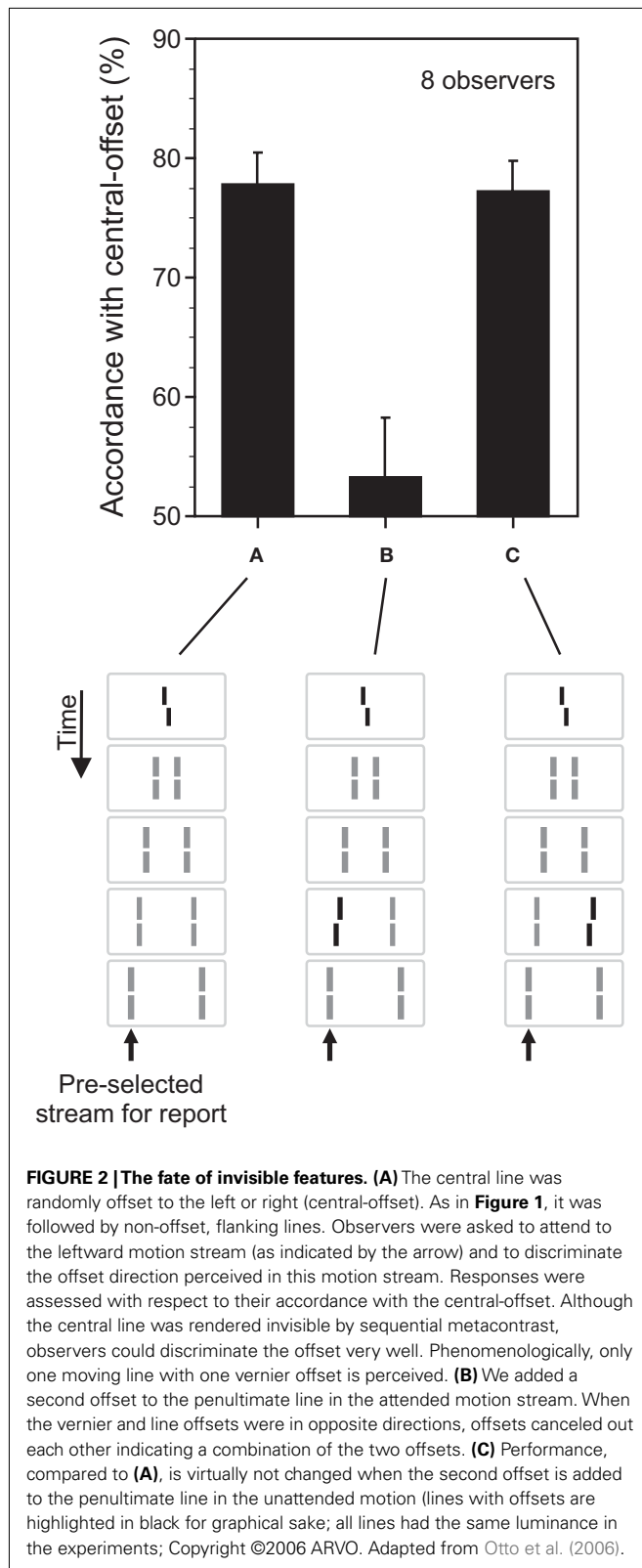
In an extension of the metacontrast masking paradigm called sequential metacontrast (Piéron, 1935; Otto et al., 2006), the central vernier was followed not just by one pair of flanking lines but by three further ISI-line pairs creating the percept of two streams of lines expanding from the center (Figure 1). To verify the very



strong masking effect in sequential metacontrast, we presented the above sequence with (Figure 1B) and without (Figure 1C) the central vernier in a two-interval forced-choice paradigm and asked observers to indicate which interval contained the central vernier stimulus. Performance was close to chance level (Otto et al., 2006).

In the next step, we added a small offset to the vernier, i.e., the lower part of the vernier was offset either to the left or right relative to the upper part (Figure 2A). The first question is what happens to this feature (the vernier offset)? Will it disappear from consciousness altogether along with its carrier stimulus (the central vernier)? Here we define the carrier as the stimulus that contains the feature. Thus, our experiments will determine whether the visibility of the feature can be dissociated from the visibility of its carrier.

To answer these questions, we first asked observers to attend to one of the motion streams and, in a forced-choice task, report



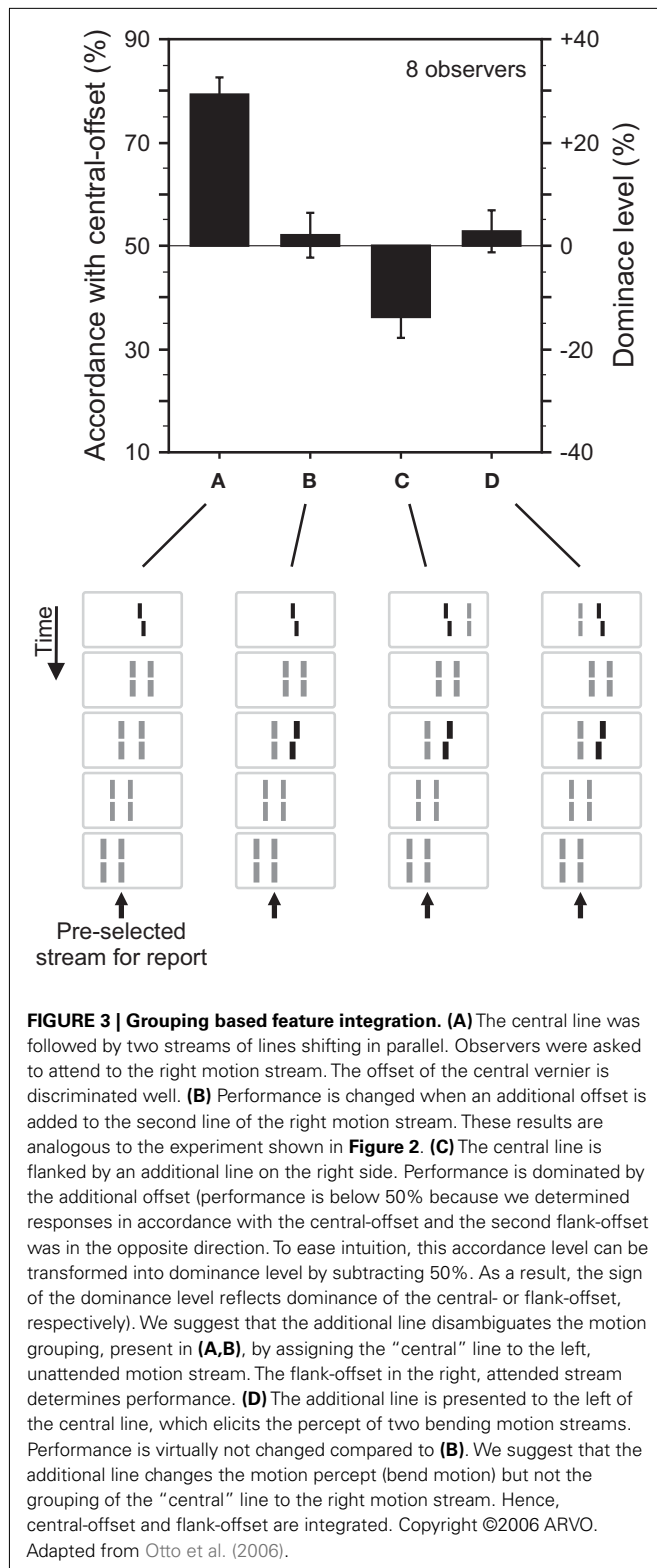
the offset direction of the vernier perceived in that motion stream. We then computed the accordance of their responses with the offset direction of the invisible central vernier. The accordance, also

called dominance, was significantly higher than chance performance (**Figure 2A**) indicating that, even though the retinotopic carrier of the vernier offset was invisible, the vernier offset was perceived as part of the motion stream.

In order to address whether the processing of the vernier offset continues during this binding, in addition to the central vernier, we introduced an additional vernier offset to one of the lines, e.g., the penultimate line in the attended motion stream (**Figure 2B**). If the processing of the vernier continues during the motion stream, it should integrate with other verniers inserted into the motion stream. If not, the two verniers would be perceived as two different features belonging to the same motion stream and, as such, they will not be integrated. Our results show that the processing of verniers within the motion stream continues so that, for example, when the two verniers have opposite offset directions, they cancel each other (**Figure 2B**). In order to assess whether the integration of information is specific to motion streams into which the verniers are bound, we presented the additional vernier offset at the penultimate line in the unattended motion stream (**Figure 2C**). Here, we found no integration (compare **Figure 2A** with **Figure 2C**). Hence, unconscious feature processing and integration is specific to motion streams. The processes uncovered by our stimuli reveal the properties of what Treisman (1996) defined as “location binding” and “temporal binding.” Our results show that feature processing continues during these binding operations. This results in feature integration which is mathematically equivalent to an integration (summation) process. The mathematical integration operation is linear and so is the feature integration we have observed with the vernier offsets. The percentage of dominance for the combined presentation of the vernier and the flank-offset is the sum of the dominance levels when the central and flank vernier are presented alone (Otto et al., 2009). Hence, when the flank-offset is in the same direction as the central vernier offset, performance improves. In general, all offsets within a motion trajectory are linearly summed (within about 500 ms).

For the stimulus shown in **Figure 2**, the central vernier is bound to both motion streams. We argue that the central vernier is attributed to both streams because motion grouping is ambiguous since the vernier is at the center of the expanding motion. To investigate the role of motion grouping on feature integration in sequential metacontrast, we performed an experiment with two parallel motion streams (**Figure 3**). To disambiguate motion grouping, we added a line next to the vernier on the right or left hand side. Now, the vernier in the first frame groups either with the left (**Figure 3C**) or the right (**Figure 3D**) stream according to motion correspondences between the first two frames. Integration of the central- and the flank-offset occurs only when the two offsets are in the same grouped motion stream.

Although the above results clearly show the specificity of vernier processing according to motion streams, one cannot directly infer a perceptual integration. Observers may be perceiving two distinct verniers in the motion stream and, in the forced-choice task, may be combining their offsets cognitively in order to produce a binary response or respond randomly to either one. However, the invisibility of the vernier ensures that only one fused offset is available and the task is well defined. In addition, observers can hardly, if at all, determine whether the central line or the penultimate flanking



line was offset (Otto et al., 2006). Phenomenologically, only one moving line with only one vernier offset is perceived (see for example the animations in Otto et al., 2006). Finally, we have quantified the level of integration between different verniers in a motion

stream by measuring their individual and combined responses. **Figure 4** provides an example where we varied the length of the motion sequence from 4 to 10 flanking lines.

In these experiments, when present, the flanking vernier was always inserted to the penultimate line in the sequence and its offset direction was always the opposite of the central vernier. In order to measure quantitatively the integration between different verniers, we calculated the accordance of observers' responses with respect to the central vernier and subtracted 50% (see also **Figure 3**). As a result, positive and negative values of the dominance level reflect the dominance of central or flank verniers, respectively. We measured the observers responses to the central (C, in **Figure 4B**) and flanking (F, in **Figure 4B**) verniers in isolation, as well as when they were presented together in the motion stream (CF, in **Figure 4B**). We have then calculated the algebraic sum of C and F conditions (C + F in **Figure 4B**) and compared it to the CF condition. As one can see from **Figure 4B**, a linear integration predicts the combined result very well. The experiments showed that this linear integration rule holds in a wide-range of conditions, where we varied the position, the distance, and the orientation of the vernier carrying the flank-offset as well as the magnitude of the offsets (Otto et al., 2009). We believe that this is strong support for automatic integration, since it is not likely that a cognitive strategy would produce such accurate quantitative integration across a broad range of stimulus conditions and configurations. Finally, a fourth line of evidence for automatic integration comes from the experiments discussed in the next section.

THE ROLE OF ATTENTION

In all the experiments reported up to here, observers attended to one pre-determined motion stream and reported the vernier offset that they perceived within this motion stream. Thus, as the attended stream and the stream selected for perceptual report were always the same, the results cannot clarify whether attention plays a role in these binding and integration effects. In order to study the role of attention, we used a cueing paradigm. We modified the experiment shown in **Figure 4** by keeping the length of the sequence to four flanking lines and by introducing an auditory cue (**Figure 5**).

The auditory cue indicated to the observer which stream, left or right, to attend for reporting the perceived vernier offset. The timing between the auditory cue and the visual stimulus ranged from -500 ms to +500 ms relative to the motion sequence onset.

The results for the conditions C and F in **Figure 5** show a slight decay as a function of cue-stimulus onset asynchrony. This decay was also found for single, static stimuli (results not shown; see Otto et al., 2010a). Because the decay is independent of stimulus type or timing, we suggest that it is of central origin. Other than this decay, the cue had little effect on the results, and the algebraic summation rule did apply (**Figure 5B**). Hence, whether attention is distributed to both streams (when the cue was presented after the motion streams) or focused (when the cue was presented before the motion streams) has no effect on the processing and integration of features. These experiments showed that focused selective attention on one stream is not necessary for stream-specific integration.

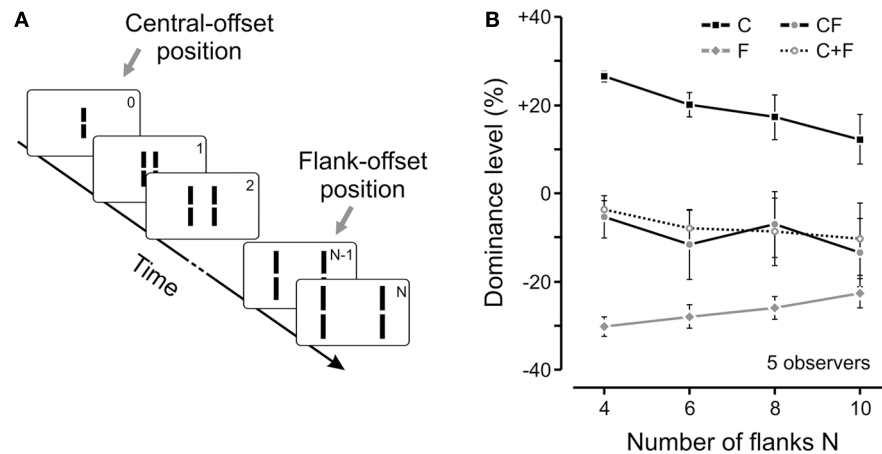


FIGURE 4 | (A) We extended the experiment shown in **Figure 1** by adding more and more flanking lines to the sequence (i.e., sequences with 4, 6, 8, or 10 pairs of flanking lines). The flank-offset was always presented in the penultimate frame (no offset is shown in the illustration). **(B)** We presented only the central-offset (C), only the flank-offset (F), or both offsets together in the attended stream (CF). In general, dominance decreased (as indicated by absolute values closer to 0) for longer lasting sequences, i.e., the more non-offset flanking lines were added. Interestingly, the integration of central- and flank-offset was virtually not

changed as it was always well predicted by the linear sum of performance levels in conditions C and F (see C + F). Notably, in the longest sequence, the distance between the central- and the flank-offset (which was presented in frame 9) was 0.5° with an SOA of 370 ms. Hence, feature integration was not changed during a substantial spatio-temporal window. Copyright ©2009 by the American Psychological Association. Reproduced with permission. The official citation that should be used in referencing this material is Otto et al. (2009). The use of APA information does not imply endorsement by APA.

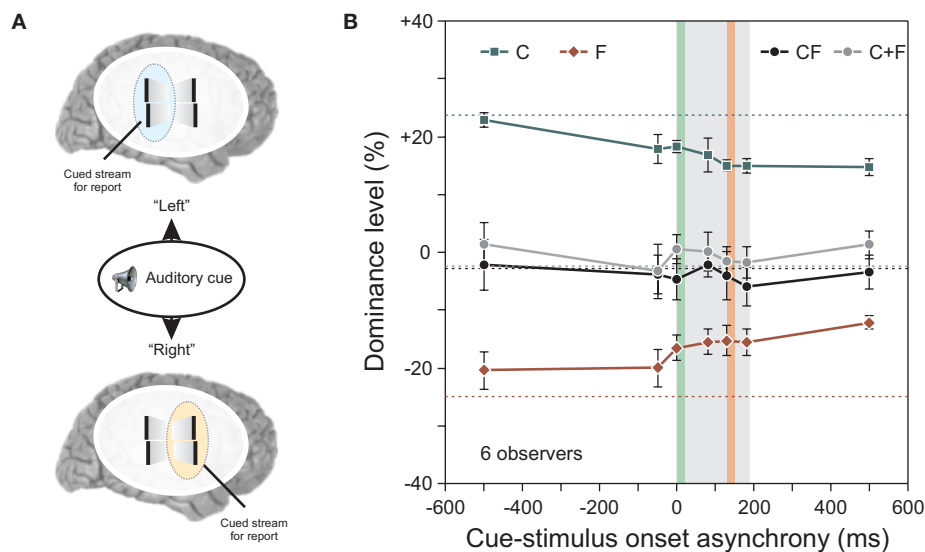


FIGURE 5 | (A) An auditory cue indicated the motion stream, for which the offset should be reported. We varied the cue-stimulus onset asynchrony from -500 to 500 ms. **(B)** Performance in conditions C and F decreased the later the auditory cue was presented (i.e., the absolute value of the dominance level is reduced). Except for this general decay, integration of central- and flank-offset was virtually not changed as it was always well

predicted by the linear sum of performance levels in conditions C and F (see C + F). Dotted lines indicate performance when observers attended to always the same stream without the use of an auditory cue. The grey area indicates the stimulus duration, the vertical green line the onset of the central line, the vertical red line the onset of the offset flank. Copyright ©2010 ARVO. Reproduced from Otto et al. (2010a).

MERGING MOTION STREAMS

The results so far showed that features remain segregated according to motion grouping relations and their processing and integration takes place within each motion stream. As we have mentioned at the beginning of the article, under normal viewing conditions, moving objects overlap and occlude each other. The visual system

needs to decide whether to integrate or segregate overlapping features. To study this problem, we presented two sequential meta-contrast sequences next to each other so that two of the four motion streams merged at a common point (**Figures 6A–C**).

When observers attended to the central line where the two streams merged, vernier information coming from the two streams

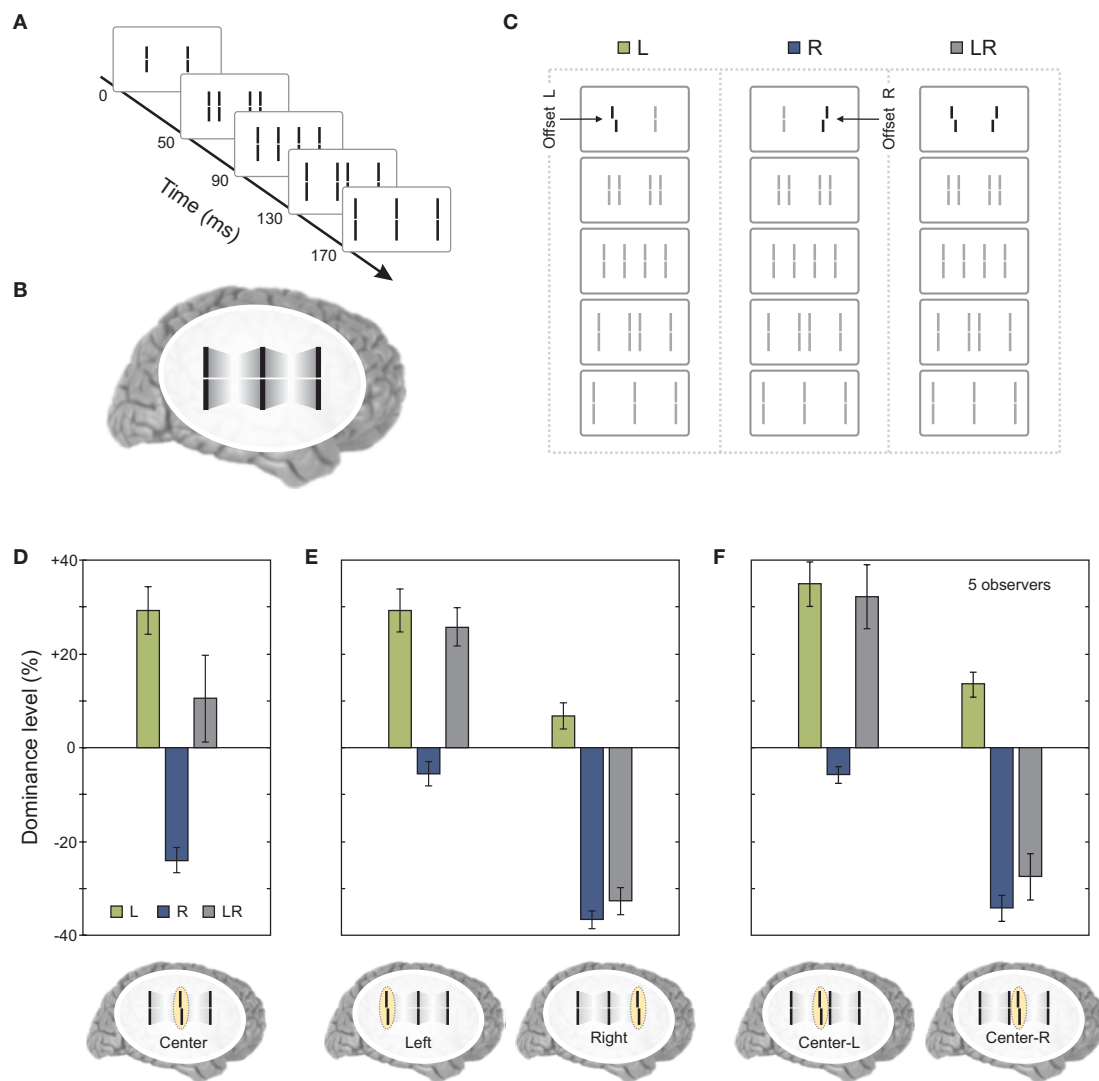


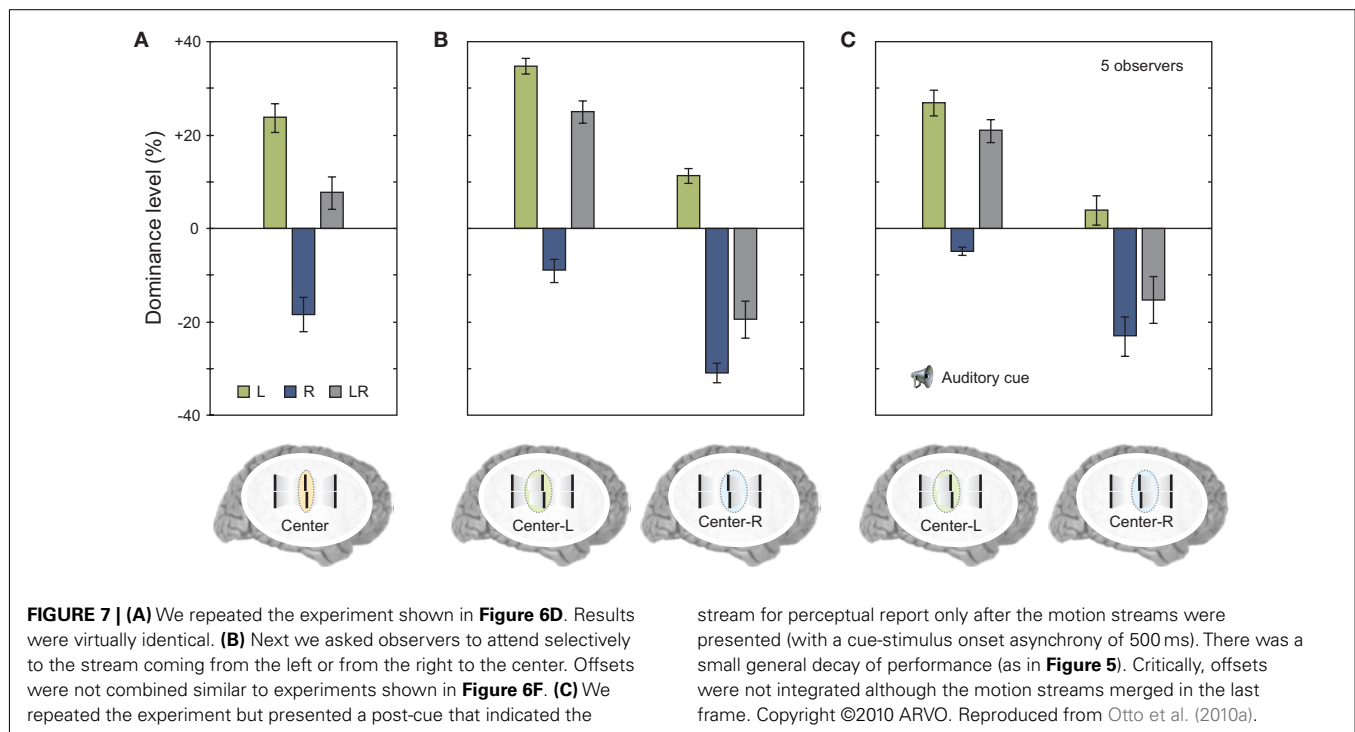
FIGURE 6 | Merging motion streams. (A) We presented to sequential metacontrast sequences (see Figure 1) next to each other so that two motion streams terminated in a common line. (B) The percept of two merging motion streams is elicited. (C) In three conditions, the left, the right, or both lines in the first frame were offset. All flanking lines were non-offset. (D) Offsets from the left and right sequence were combined

(i.e., the left and right offset cancel out each other in condition LR) when the merging motion streams were attended. (E) This effect is not found when the outer left or outer right motion stream was attended. (F) We did not present the last frame [see (A)]. Hence, the central motion streams did not merge in a common line. Offsets were not integrated similar to (E). Copyright ©2010 ARVO. Reproduced from Otto et al. (2010a).

was found to be integrated (Figure 6D). However, this integration did not occur when observers attended to the left or right terminal lines, which produced results replicating the finding that the vernier offset remains specific to its motion stream (Figure 6E). Moreover, the combination of vernier offsets as found in Figure 6D does require the merging of the two streams since, when the last frame was omitted and the observers attended the left or right element in the center, no integration was found (Figure 6F).

Next, we asked observers to report the central line but also selectively attend to one of the motion streams. In this case, there was no integration of verniers coming from different motion streams; the visual system was able to segregate feature information and avoid integration (Figure 7B). The results were similar to the case where

the two streams did not merge (compare Figure 7B to Figure 6F). In order to determine whether this segregation was due to focused and maintained attention on a single stream, we repeated the same experiment with the exception that the task condition (attend center line with left or right stream) was signaled to the observer by an auditory cue delivered 320 ms after the motion streams merged (i.e., with a cue-stimulus onset asynchrony of 500 ms). The results were similar to the case where observers focused their attention on a single stream, i.e., features were segregated and the observers reported the feature associated with the cued stream (compare Figures 7B,C). Thus, in cases where different motion streams merge, the integration of feature information is not mandatory, but flexible. This flexible integration does not necessitate focused and maintained attention.



AN ECOLOGICAL FRAMEWORK: THE PROBLEMS OF MOTION BLUR AND MOVING GHOSTS

The studies outlined above were motivated by the observations that under normal viewing conditions, the visual system needs to compute features at the same time as it binds them. This is because the computation of a feature requires decisions regarding whether transient stimulations generated come from the same or different objects. Our results show that the carrier of a stimulus can be rendered invisible and the corresponding feature can be integrated with features presented at retinotopic locations different than the retinotopic location of its carrier. Why is the perception of the carrier inhibited and why is the feature integrated with other features in a non-retinotopic manner?

Under normal viewing conditions, a briefly presented stimulus can remain visible for more than 100 ms, a phenomenon known as visible persistence (Haber and Standing, 1970; Coltheart, 1980). This should imply that moving objects appear extensively blurred; however, in general we do not experience motion blur (e.g., Ramachandran et al., 1974; Burr, 1980; Hogben and Dillolo, 1985; Farrell et al., 1990; Castet, 1994; Bex et al., 1995; Chen et al., 1995; Westerink and Teunissen, 1995; Bedell and Lott, 1996; Burr and Morgan, 1997; Hammett, 1997). Another problem associated with object motion is the problem of “moving ghosts” (Ögmen, 2007). Since a moving object stimulates each retinotopically localized neuron only for a brief time period, no retinotopic neuron by itself will receive sufficient stimulation to extract features of the stimulus¹. Thus, moving stimuli should appear as “ghosts,” i.e.,

blurred and quasi-uniform in character, devoid of specific featural qualities. This happens when stimuli move at excessively high speeds but not for ecologically observed speeds. We suggest that the visual system solves motion blur and moving ghosts problems by two complementary mechanisms. The carriers and features are first registered in retinotopic representations. The spatial extent of motion blur is curtailed by inhibitory mechanisms that make stimuli, as the central vernier in our displays, invisible on a retinotopic basis (Ögmen, 1993, 2007; Chen et al., 1995; Purushothaman et al., 1998). However, the features of the retinotopically inhibited stimuli are not destroyed; instead, based on prevailing motion grouping relations, they are attributed to motion streams where they are processed and bound (Otto et al., 2006, 2009; Ögmen et al., 2006; Ögmen, 2007; Breitmeyer et al., 2008). This non-retinotopic, motion grouping based feature processing provides the solution to the moving ghosts problem. While features of an object activate retinotopically organized cells momentarily, they remain relatively invariant along the motion path of the object. This allows sufficient time for non-retinotopic mechanisms to receive and process incoming stimuli as they become segregated according to prevailing motion grouping relations. Thus, we suggest that features that become dissociated from their carriers are mapped into non-retinotopic representations following spatio-temporal grouping relations.

When and why are features integrated? Most vision problems are ill-posed (Poggio et al., 1985). For example, the light that shines on a photoreceptor is always the product of the illuminance (e.g., sun light) and the reflectance (properties of the object): $\text{luminance} = \text{illuminance} \times \text{reflectance}$. Hence, the luminance value is not sufficient to determine reflectance. Solving such ill-posed problems can take substantial amounts of time and needs to take contextual information into account, making a short-term retinotopic analysis impossible. Consider the following situation.

¹One may argue that neurons can collect information through their spatio-temporally oriented receptive fields (Burr, 1980; Burr et al., 1986; Pooresmaeili et al., 2012). While this may work for stimuli undergoing simple motion, for natural stimuli it would necessitate a staggering number of pre-wired receptive fields for every imaginable motion trajectory starting from every possible point.

A car drives through a street. Because of shadows and reflecting lights, the car elicits a series of very different luminance and chromacity signals on the retina. For example, the red of the car may be almost invisible when driving through a dark shadow but bright and well visible when in sun light. The brain usually discounts for the illuminance (color constancy). However, for the fast running car, processing time is too short when computed at each retinotopic location. Moreover, it is not necessary to compute the reflectance of the car at each location and instance given the knowledge that car colors do not change. Hence, averaging across the features along a motion trajectory may be a first step toward a good estimate of the car color. Vernier offset integration is just a toy version of such a scenario. For this and other reasons, we would like to argue that most visual processes occur in fact in non-retinotopic frames of reference – including feature processing, binding, and integration. Using a different approach than the sequential metacontrast paradigm, we have shown evidence for non-retinotopic processes of vernier offsets (as used here; Ögmen et al., 2006; Aydin et al., 2011b), motion, form, and attention in visual search (Boi et al., 2009, 2011). In addition, perceptual learning in the sequential metacontrast paradigm occurs within non-retinotopic rather than retinotopic coordinates (Otto et al., 2010b).

Where does feature integration occur? We used high density EEG and inverse solutions. We found that the insula showed enhanced activity when vernier offsets are integrated (Plomp et al., 2009). The insula is one of the areas involved in all sorts of integration processes and consciousness (e.g., Craig, 2009).

IMPLICATIONS FOR MODELS OF BINDING

In classical models of binding by synchrony, features are bound together when their neural representations fire simultaneously or with a common frequency and phase relation (e.g., Singer, 1999). For example, when a red square and a green disk are presented, neurons coding for red and squareness fire synchronously and similarly neurons coding for green and diskness. When the combination of colors and form changes, the synchronization changes accordingly. However, synchronization is not a mechanism *per se* for computing binding but may be a way of communicating information. Therefore, the crucial question that remains is how grouping, feature processing, integration, and binding take place in our stimuli. Synchronization may be an outcome of computational mechanisms underlying these processes; however, it does not provide, in itself, a causal explanation for the outcome. As a result, to test whether synchronization can explain our results necessitates models that would be able to carry out the aforementioned processes and produce synchronization as an emergent property.

Can our results be explained by the association principle and the related convergent coding models? Particularly, averaging of features is a classical property of many models of grandmother cell coding to avoid the curse of dimensionality (Riesenhuber and Poggio, 1999a). The sequential metacontrast paradigm is quite robust to substantial changes, i.e., changes in ISI, spacing between lines, number and orientation of lines, and contrast polarity (see Figure 4; Otto et al., 2009). On the other hand, small spatio-temporal details do matter when they change the grouping

(Figure 3). Hence, it is hard to explain with most convergent coding schemes how for each conceivable motion stream, there are hard wired detectors binding offsets together. Moreover, sequential metacontrast is not limited to vernier offsets; hence, the number of possible motion groups and feature bindings is virtually unlimited (see also Footnote 1).

Often it is proposed that a master map of attention binds features of retinotopic, basic features maps together, particularly, to solve the property binding problem (Treisman, 1998). However, the role of attention in our dynamic stimuli appears to be different. Within a given stream, vernier offset integration occurs automatically without focused attention. When attention is focused on the stream, only the integrated sum of the vernier offsets, rather than individual offsets, can be read-out. On the other hand, attention can play a major role when it comes to combining different, independent motion trajectories into more complex motion structures (Figures 6 and 7).

As a path toward the solution, we propose the following non-retinotopic processing scheme shown in Figure 8 (Ögmen, 2007; Ögmen and Herzog, 2010).

The retinotopic space is depicted at the bottom of the Figure as a two-dimensional plane. A group of dots move rightward (highlighted in red) while another group of dots move upward (highlighted in orange). Based on differences in motion vectors, the two local neighborhoods are mapped into two different non-retinotopic representations; for clarity the figure shows only the non-retinotopic representation for the rightward moving dots. Each feature, visible or not, is attributed to a motion group. The

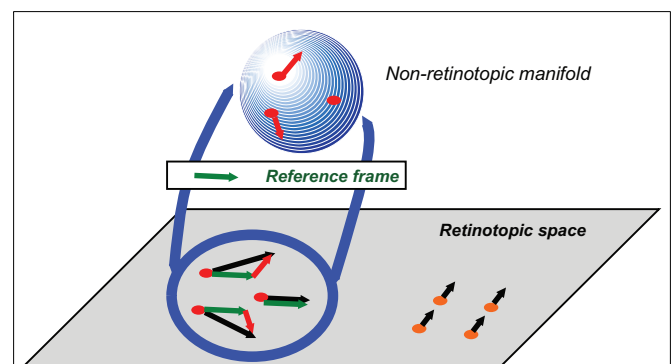


FIGURE 8 | Schematic depiction of the proposed approach to conceptualize non-retinotopic representations wherein feature processing, binding, and integration take place. The two-dimensional plane at the bottom of the figure depicts the retinotopic space in early vision. In this example, a group of dots (shown in red) moves rightward and a second group of dots (shown in orange) moves upward. A fast motion segregation and grouping operation establishes two distinct local neighborhoods, which are mapped into two different non-retinotopic representations (for clarity, the figure shows only the non-retinotopic representation for rightward moving dots). A vector decomposition takes place (e.g., Johansson, 1973) and a common vector for the neighborhood (dashed green vector) serves as the reference frame for the neighborhood. The stimulus in the local neighborhood is mapped on a non-retinotopic manifold (for depiction purposes a sphere is used). This allows the processing and integration of features in a manner that remains invariant to their global motion. Features that are mapped to common manifolds become candidates for binding into groups (from Ögmen and Herzog, 2010).

invisibility of the carrier of the feature indicates the inhibition of its retinotopic activity. A common vector for each neighborhood is determined (dashed green vector) and serves as the reference frame for that neighborhood. All motion vectors are decomposed into a sum of the reference motion and a residual motion vector. The stimulus in the local neighborhood is mapped on a manifold (in **Figure 8**, for depiction purposes a sphere is used), i.e., a geometric structure that preserves local neighborhood relations. However, the surface can be stretched and deformed. The residual motion vectors, or relative motion components with respect to the reference frame, are then applied to the manifold so as to deform it to induce transformations that the shape undergoes during motion. Features that are mapped into this manifold within a pre-determined spatio-temporal window become integrated. Thus, according to this approach, feature processing and binding occurs largely in non-retinotopic representations that are built from ongoing motion grouping relations in the retinotopic space. Two different motion streams are mapped into two different manifolds and remain segregated in agreement with our results. When the streams merge, a common point in the retinotopic space signals occlusion. We suggest that observers can read-out information about different motion streams by accessing their distinct manifold representations and resolve the occlusion in a flexible way by attributing to the common point the feature information associated with the attended stream. This is illustrated in **Figure 9**.

In this example, a square and a triangle move and according to motion grouping relations, a non-retinotopic representation is created for each motion stream. The retinotopic information is conveyed to the appropriate non-retinotopic representations where processing of features takes place. Thus, according to our theory, the first major role of retinotopic processes is to establish grouping relations and convey feature information to non-retinotopic areas according to these grouping relations. Grouping and attention are independent but interactive processes (Aydin et al., 2011a). A second role of retinotopic representations is to resolve depth order and occlusion relations and thereby determine those features that will gain visibility. **Figure 9** shows a time instant when the rectangle and the triangle occlude each other. The reciprocal relationships between retinotopic and non-retinotopic activities reveal occlusion properties and establish visibility based on this information. In the example shown in **Figure 9**, the rectangle is in the foreground and becomes fully visible; only the un-occluded parts of the triangle become visible. However, since the triangle is stored and computed in non-retinotopic representations, the percept is not that of two disjoint segments, but instead a single triangle (amodal completion). Applying this concept to the merging streams, one can see that an observer can access the vernier information of the streams

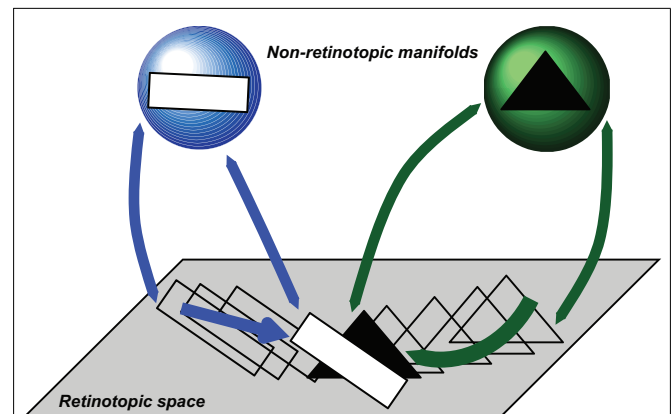


FIGURE 9 | Depiction of how occluded objects are represented and processed. According to this approach, retinotopic areas serve as a relay where features are transferred to non-retinotopic areas according to spatio-temporal grouping relations. A second role of retinotopic areas is to resolve depth order and occlusion relations. While the entire shapes of objects can be accessed from their non-retinotopic representations, visibility of the parts is dictated by retinotopic activities. In this example, observers can recognize a complete triangle (amodal completion) but only those parts that are un-occluded in retinotopic representations become visible.

independently because they are stored in separate representations. The point where the streams merge constitutes an ambiguous occlusion point because, unlike the square-triangle example of **Figure 9**, the shape at the point where the two streams merge (line) can belong to either stream. Thus, based on attentional cueing, the offset of either stream can be attributed to the point of occlusion.

CONCLUSION

In summary, the sequential metacontrast paradigm is a versatile tool to investigate many aspects of vision including consciousness, spatio-temporal grouping, attention, and feature integration. We have shown how features of invisible elements can still become visible at other elements and even integrated with other features. Feature integration occurs only when elements belong to one spatio-temporal group. Our findings show how the human brain integrates even very briefly presented information at a very subtle spatial scale.

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Beyond feature binding: interference from episodic context binding creates the bivalency effect in task-switching

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When switching between different tasks and bivalent stimuli occur only occasionally on one of them, performance is slowed on subsequent univalent trials even if they have no overlapping features with the bivalent stimulus. This phenomenon has been labeled the “bivalency effect.” Recent evidence has revealed that this effect is robust, general, and enduring. Moreover, it challenges current theories of task-switching and cognitive control. Here, we review these theories and propose a new, episodic context binding account. According to this account, binding does not only occur between stimuli, responses, and tasks, but also for the more general context in which the stimuli occur. The result of this binding process is a complex representation that includes each of these components. When bivalent stimuli occur, the resulting conflict is associated with the general context, creating a new conflict-loaded representation. The reactivation of this representation causes interference on subsequent trials, that is, the bivalency effect. We evaluate this account in light of the empirical evidence.

Keywords: cognitive control, binding, anterior cingulate cortex, bivalent stimuli, univalent stimuli

Feature binding is essential for the formation of a coherent representation of an object. In addition, binding processes are involved on further levels of information processing and thus, their occurrence is not restricted to the domain of perception. Binding processes are involved in action planning, sensorimotor coordination, and in memory formation (Hommel, 2004; Mather, 2007; Altmann and Gray, 2008; Verguts and Notebaert, 2009) and all these operations are relevant for cognitive control. Cognitive control is necessary in situations in which the course of action must be shielded against distracting events (Botvinick et al., 2001, 2004). For example, when switching between different tasks, which require responding to bivalent stimuli (i.e., stimuli with features that are relevant to more than one task), control is necessary to select the appropriate task and unselect the inappropriate task. In this example, encountering a conflict (i.e., a bivalent stimulus) triggers an adjustment of cognitive control. Here we focus on the adjustment of cognitive control that is induced by the occasional occurrence of bivalent stimuli.

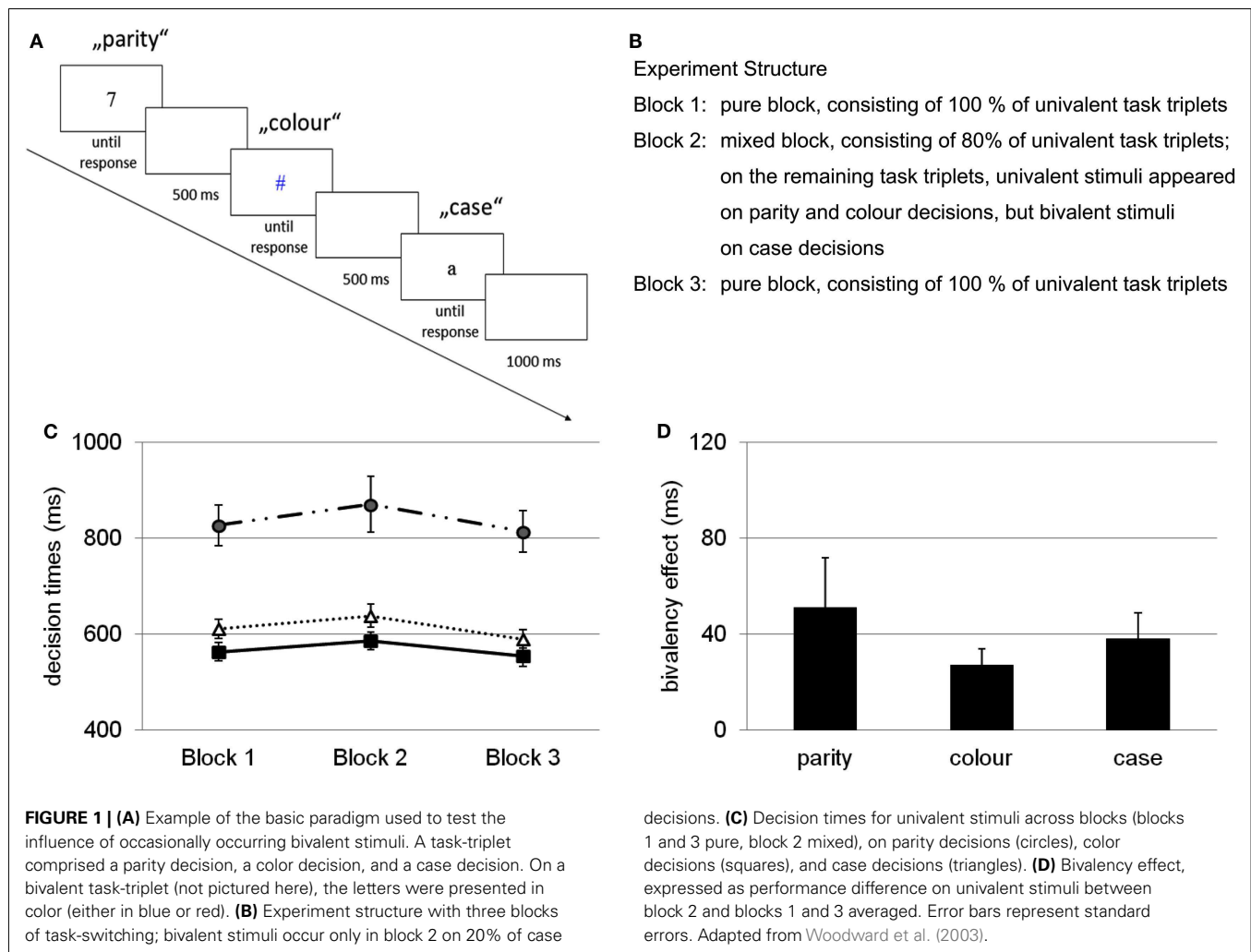
While univalent stimuli trigger one particular task-set, bivalent stimuli trigger two different task-sets and thus can be used to perform two different tasks. In a task-switching environment, examples of univalent stimuli would be black digits presented for a parity decision, black letters presented in uppercase or lowercase for a case decision, or red and blue shapes presented for a color decision. However, when the letters are presented in red and blue color this would turn them into bivalent stimuli. Recent research has demonstrated that when switching among these kinds of tasks even the occasional occurrence of bivalent stimuli results in a general performance slowing that encompasses several subsequent univalent trials. When switching between parity, case, and

color decisions with the stimuli introduced in the above example performance is slowed even on those decisions, which shared no relevant feature with the bivalent stimuli (i.e., the parity decisions). This phenomenon has been labeled the “bivalency effect” (Woodward et al., 2003, 2008; Meier et al., 2009; Rey-Mermet and Meier, 2012a,b).

In this article, we provide a review of the empirical findings on the bivalency effect and we show that it challenges established theories of task-switching and cognitive control. So far, the studies on the bivalency effect were driven by the motivation to test alternative explanations. In the course of this work the theoretical notion of “episodic context binding” has emerged as an explanation for the bivalency effect. One goal of the present paper is to relate this account to established theories, set the stage to enable the design of experiments to critically evaluate this new account and to show how it relates to other findings in the literature.

THE BIVALENCY EFFECT: AN ADJUSTMENT OF COGNITIVE CONTROL IN RESPONSE TO BIVALENT STIMULI

In an initial study, Woodward et al. (2003) used three different binary decision tasks – a parity decision (odd vs. even numerals), a color decision (red vs. blue symbols), and a case decision (uppercase vs. lowercase letters) – and participants were required to repeatedly switch between these tasks, which were always presented in the same fixed order (i.e., parity, color, case). In **Figure 1A**, an example of the procedure is presented; in **Figure 1B** the structure of the experiment, consisting of three experimental blocks, is described. In the first and in the last block (i.e., the pure blocks) all tasks involved only univalent stimuli (i.e., black numerals for the parity decision, colored shapes for the color decision, and black letters for the case decision). In the second block (i.e., the mixed



block), the stimuli were univalent on most of the trials. However, occasionally, on some of the case decisions (i.e., 20%) the letters were presented in color, thus turning them into bivalent stimuli. With this particular set-up, two tasks included stimuli with overlapping features (i.e., color and case decisions) while one task did not include overlapping stimulus features (i.e., parity decisions). A task-switching paradigm with task-triplets is necessary to test for the effect of occasional bivalent stimuli because a paradigm with only two tasks, which is the standard case in task-switching studies, would always involve an overlap of task features.

The results of this study showed that performance was slowed for bivalent stimuli. However, more critical was the comparison between the performance on the univalent task-triplets of the pure block and performance on univalent task-triplets of the mixed block. These results are presented in **Figure 1C**. They revealed a performance slowing for all of the tasks from the mixed block, even for the task that involved stimuli that shared no features with the bivalent stimuli. This slowing was coined the “bivalency effect” and is depicted in **Figure 1D**. Woodward et al. (2003) suggested that these results challenge task-switching theories. These theories have been developed to explain the cost that occurs when

switch and repetition trials are compared. They focus primarily on bottom-up processes, that is, processes initiated and guided by the stimuli and their particular features (e.g., Rogers and Monsell, 1995; Allport and Wylie, 2000; Monsell et al., 2000; Meiran, 2008).

For instance, Allport et al. (Allport et al., 1994; Allport and Wylie, 1999, 2000; Wylie and Allport, 2000) proposed a negative priming account. According to this account, when a bivalent stimulus occurs on a given trial, the task-set for the now-relevant task is activated while the task-set for the irrelevant task is inhibited. If the inhibited task becomes relevant on a subsequent trial, additional time is required to reactivate it (i.e., to overcome task-set inertia). Thus, switch costs are the consequence of exogenously triggered processes to resolve interference. Accordingly, a negative priming account can explain the slowing on tasks with univalent stimuli sharing relevant stimulus features with the bivalent stimuli (i.e., the color and case decisions). However, it cannot explain slowing on tasks with univalent stimuli sharing no relevant stimulus features with the bivalent stimuli (i.e., the parity decision).

Similarly, a task-reconfiguration explanation posits that for processing bivalent stimuli an additional decision is required to determine the relevant task-set and switch cost reflects the time

needed to reconfigure the task-set (e.g., Fagot, 1994; Rogers and Monsell, 1995; Monsell et al., 2000; Rubinstein et al., 2001; Sohn and Anderson, 2001; Meiran et al., 2008; Braverman and Meiran, 2010). According to this account, univalent stimuli, which share stimulus features with the bivalent stimuli, can activate this additional task-decision process. Specifically, with colored letters for case decisions as bivalent stimuli, the stimuli for the color decision would cue the case decision and an additional process would be required to select the color decision task-set. Similarly, the stimuli for the case decision would cue the color decision and an additional process would be required to select the case decision task-set. However, for univalent stimuli with no overlapping stimulus features, such as those for parity decisions, no additional, time-consuming task-decision process would be required. Thus, this account can explain the slowing on tasks with univalent stimuli sharing relevant stimulus features with the bivalent stimuli. However, it cannot explain the slowing on tasks with univalent stimuli sharing no relevant stimulus features with the bivalent stimuli (i.e., non-overlapping univalent stimuli).

In order to explain the slowing on tasks with non-overlapping univalent stimuli, Woodward et al. (2003) argued that top-down processes are necessary in the sense of a more general adjustment of cognitive control rather than a stimulus-specific effect. Specifically, they suggested that a more cautious response style is triggered by bivalent stimuli. This interpretation was further supported by the finding of a speed-accuracy trade-off, that is, the slowing in Block 2 was also accompanied by an increase in accuracy. However, the latter result was not replicated in the follow-up studies and may have been caused by the particular response requirements of the initial study.

TESTING EXPLANATIONS FOR THE BIVALENCY EFFECT

TASK UNCERTAINTY

An alternative interpretation of the initial findings of Woodward et al. (2003) is that rather than an endogenous adoption of a cautious response style, the bivalency effect might represent a process of recovery from task uncertainty elicited by the occasional bivalent stimuli, which would result in a relatively short-lasting effect because only bivalent stimuli induce task uncertainty (Kray and Lindenberger, 2000). To address this possibility, Meier et al. (2009) manipulated the interval between task-triplets and assessed the trajectory of the bivalency effect across task-triplets by presenting bivalent stimuli in the mixed block in regular intervals. They reasoned that the bivalency effect would disappear relatively quickly with longer intervals and across trials with univalent stimuli when it reflects recovery from task uncertainty. In contrast, if the bivalency effect reflects the adoption of a more cautious response style, it should be stable across intervals and should be relatively long-lived.

In three separate experiments with a similar set-up as Woodward et al. (2003), but with variations of the specific tasks, modalities, and bivalent stimuli, Meier et al. (2009) found a consistent bivalency effect across all experiments and experimental conditions. Further, the bivalency effect was not reduced by increasing the interval between task-triplets, and it was still present four task-triplets after the occurrence of a bivalent stimulus. The trajectory of the bivalency effect across task-triplets, averaged across

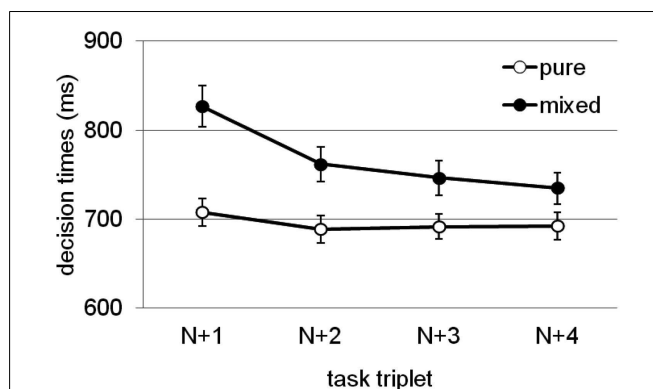


FIGURE 2 | Endurance of the bivalency effect: Mean decision times for task-triplets following a bivalent case decision in the mixed block (closed circles) compared with the corresponding task-triplets in the pure block. Error bars represent standard errors. Task-triplet *N* refers to the task-triplet containing a bivalent stimulus in the mixed block; subsequent task-triplets (represented here) are labeled *N* + 1, *N* + 2, *N* + 3, and *N* + 4, respectively. Results adapted from Meier et al. (2009), averaged across experiments, experimental conditions, and tasks.

experiments, experimental conditions, and tasks, is illustrated in **Figure 2**. It shows that although there is a steady decline in its size, the bivalency effect is characterized by a long-lived slowing. In the condition with the longest inter-trial interval, responding on a task-triplet took on average approximately 8 s (required for making three decisions, each requiring approximately 600 ms, plus two 500 ms inter-stimulus-intervals, plus the 5000 ms interval). Thus, the occasional occurrence of a bivalent stimulus was sufficient to slow down decision making on univalent stimuli for at least half a minute. Meier et al. reasoned that such a long-lasting effect cannot solely be attributed to temporary task uncertainty. **Figure 2** shows that the decline is steepest from first trial following a bivalent stimulus to the second subsequent trial. This may indicate that the bivalency effect involves two separate components. One that is short-lived and related to task uncertainty, or potentially to an orienting response to an infrequent event (cf. Notebaert et al., 2009; Núñez Castellar et al., 2010; Notebaert and Verguts, 2011), and another one that is long-lived and rather related to a persisting adjustment of cognitive control such as the adoption of a more cautious response style.

Meier et al. (2009) noted that the episodic binding of tasks, stimuli, and the experience of trickiness (i.e., episodic context binding) may have contributed to the bivalency effect. They reasoned that a stimulus acquires a history during an experiment, that is, it acquires an association with the context in which it occurs (see Waszak et al., 2003; Hommel, 2004; for similar notions). If episodic binding is not only specific to stimuli and tasks, but also extends to the context in which they occur (i.e., among purely univalent stimuli or among univalent stimuli and occasionally occurring bivalent stimuli), univalent stimuli and tasks are bound to the more demanding context created by bivalent stimuli. Episodic binding would occur whenever a series of events is (co-)registered such as when

performing a task-triplet in the present task-switching experiments. According to this “episodic context binding” explanation, conflict is bound to the context in which bivalent stimuli have been encountered (i.e., a triplet of tasks) and on subsequent univalent trials, this representation is reactivated and slows performance on all of the trials, even on those with no overlapping features.

RESPONSE-SET PRIMING

Another alternative possibility for the occurrence of the bivalency effect is related to the fact that the same responses have been used for each of the three tasks, that is, due to overlapping response-set. According to this explanation, rather than episodic context binding or endogenous adaptation of a cautious response style, the conflict produced by the bivalent stimulus may be bound to the particular response. Because each of the three tasks in a task-triplet shares the same response-set, the conflict associated with a particular key-press in response to a bivalent stimulus can slow down performance when this particular key-press is required on subsequent univalent trials. According to this explanation, the bivalency effect would result from negative priming of bivalent stimulus features via shared response features. This hypothesis is fueled by theoretical and empirical considerations of priming from response features to stimuli (e.g., Deubel and Schneider, 1996; Paprotta et al., 1999; Hommel et al., 2001; Kunde and Kiesel, 2006; Fagioli et al., 2007; Metzker and Dreisbach, 2009).

To test this hypothesis, Rey-Mermet and Meier (2012a) conducted a study in which they contrasted a condition with an overlapping response-set (as in previous studies) and a condition in which responding to each task was mapped on two separate effectors (non-overlapping response-set). They reasoned that if bivalent stimuli prime conflict via response features, then using a non-overlapping response-set would reduce conflict priming, particularly for those tasks that do not share the same responses. In contrast, if the manipulation of response-set does not affect the pattern and magnitude of the bivalency effect, this would rather suggest that the bivalency effect is due to episodic context binding. In two separate experiments, in which the order of tasks was varied, the results showed a consistent bivalency effect that was not affected by the type of response-set (i.e., overlapping vs. non-overlapping). These results, that is, the bivalency effect across response-set conditions, averaged across experiments, are presented in **Figure 3**. It is important to note that despite some non-significant variability between tasks and conditions, a significant bivalency effect was present even for parity decisions in the non-overlapping response-set-condition. Thus, the bivalency effect cannot simply be due to response-set priming.

Rey-Mermet and Meier (2012a) related the findings to results from Waszak and Pholulandeth (2009) who observed that an emotionally arousing picture modulated the episodic binding between a stimulus and a task. They interpreted these results as support for an episodic context binding explanation and suggested that a context does not even need to be emotionally arousing to have an impact on performance. Rather it is sufficient when it triggers a conflict, such as the trickier context caused by occasionally occurring bivalent stimuli (cf. Verguts and Notebaert, 2009, for similar considerations).

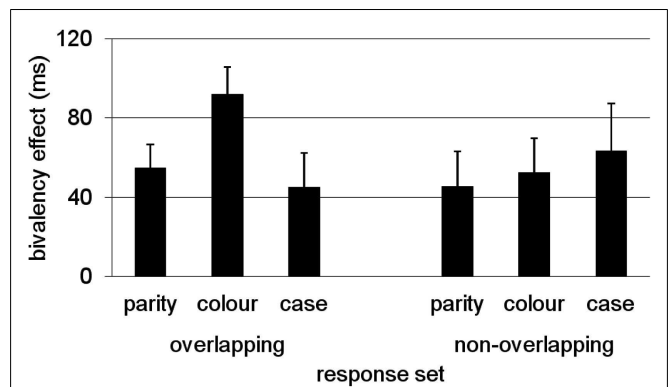


FIGURE 3 | Invariant bivalency effect across response-set conditions depicted as DT difference between univalent stimuli from the mixed block and the average of the pure blocks. Results adapted from Rey-Mermet and Meier (2012a) averaged across experiments.

CONFLICT SPECIFICITY

In the basic paradigm that was used to investigate the bivalency effect, only task-switching trials were present (**Figure 1A**). As switch trials require the inhibition of the previously relevant task and the activation of the newly relevant task, they inherently involve a conflict (Rogers and Monsell, 1995; Allport and Wylie, 2000). Moreover, for some of the trials, a second source of conflict was present due to feature overlap between univalent and bivalent stimuli (cf. Allport and Wylie, 2000; Waszak et al., 2003; Meiran, 2008). So far, the results indicate that the magnitude of the bivalency effect is not dependent on the amount of conflict, that is, from one source such as a switch trial, or from two sources such as a switch trial with features that overlap with the bivalent stimulus. However, it is not clear whether the bivalency effect would occur in the absence of any conflict. To test this question, Rey-Mermet and Meier (2012b) introduced repetition trials into the basic paradigm. Thus, participants were required to perform six rather than only three decisions. Specifically, they were asked to perform repeatedly a series of two size decisions (large vs. small), two parity decisions (even vs. odd), and two letter decisions (vowel vs. consonant), conforming to an AABCC-scheme (where ABC refer to the three different tasks). Across three experiments, the order of the tasks – but not the scheme – was varied. Moreover, in Experiment 1, bivalent stimuli were created by presenting some of the letters for the consonant-vowel decisions either in large or small font; in the other two experiments bivalent stimuli were created by presenting some of the digits either in large or small font for the parity decisions (Experiment 2) or for the size decisions (Experiment 3).

The question whether the bivalency effect would have a differential impact on switch and repetition trials is also important for the interpretation of switch costs (i.e., the slower performance on switch compared to repetition trials). As noted above, one interpretation of switch costs is that they reflect control processes that reconfigure the cognitive system in order to switch tasks (e.g., Rogers and Monsell, 1995; Meiran, 1996). Another interpretation is that they arise from the negative

priming of stimulus and task features (e.g., Allport and Wylie, 2000; Waszak et al., 2003). Both interpretations are concerned with what switch costs represent, making it important to understand which factors affect them in task-switching procedures. Moreover, if the bivalency effect contributes to switch costs, it would reflect a so far neglected component of switch costs.

The results are summarized in **Figure 4**. In **Figure 4A**, the decision times for pure and mixed blocks are presented, in **Figure 4B** the bivalency effect is presented. Overall, the results showed a consistent bivalency effect for all the conditions in which at least one source of conflict was present. However, it was largely reduced and statistically not significant in two of the three experiments for the condition with no conflict, that is, the repetition trials for the parity decision in Experiment 1 and the letter decisions in Experiment 3. Switch costs were affected only for the particular task with no overlapping stimulus features. Thus, for typical task-switching studies that involve two tasks and stimuli with overlapping features by design, the bivalency effect is leveled out by calculating switch costs as the difference between DTs on switch and repetition trials.

Rey-Mermet and Meier (2012b) suggested that the bivalency effect reflects a flexible adjustment of cognitive control, which is sensitive to the presence of conflict, but neither to its amount

nor to its source. The occasional occurrence of bivalent stimuli induces an adjustment of control that is sufficient to deal with situations with an additional source of conflict at no cost. However, it seems to be sensitive to the mere presence of conflict and thus the need for resource allocation is reduced for non-conflict trials (i.e., task repetitions with non-overlapping stimulus features).

The results challenge a prominent hypothesis in cognitive control research, namely that the adjustment of cognitive control is always sensitive to the amount and to the source of conflict (e.g., Botvinick et al., 2001, 2004; Egner, 2008). They also indicate that the bivalency effect does not stem from a general adoption of a more cautious response style. According to this explanation, the presence or absence of conflict on a particular decision should not have affected the magnitude of the bivalency effect. In contrast, an episodic context binding account would suggest that interference is only invoked when a conflict-loaded representation of a task is reactivated. Specifically, the degree of the association between a particular task and its context (i.e., the strength of binding) seems to depend on the presence of conflict (cf. Verguts and Notebaert, 2009). Accordingly, the relationship between presence of conflict and binding is responsible for the reduction of the bivalency for repetition trials.

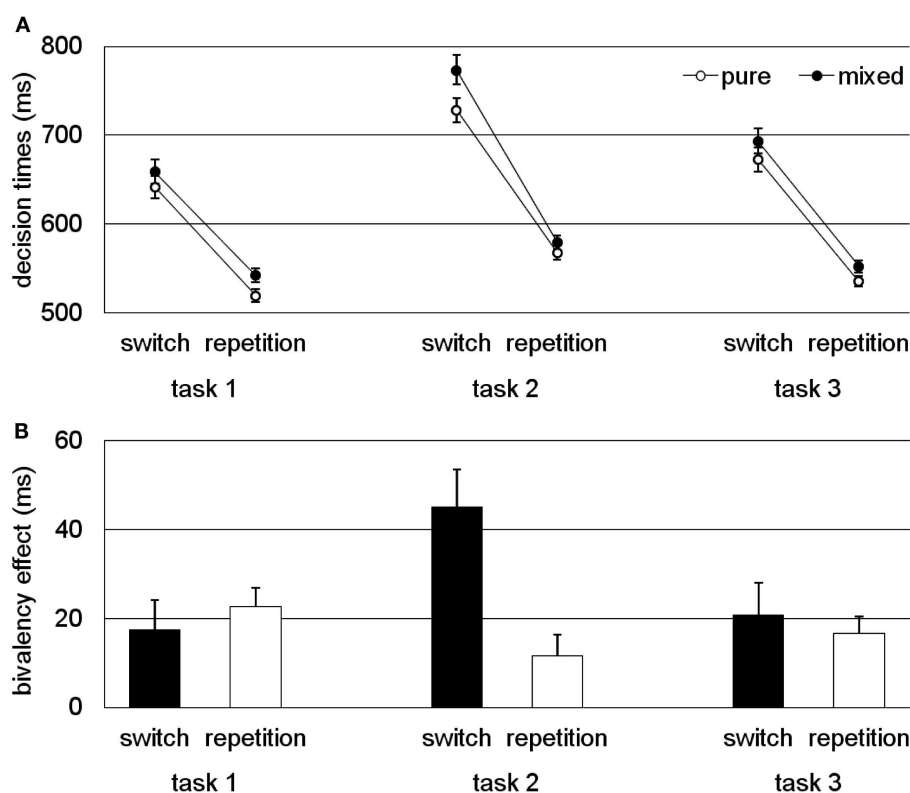


FIGURE 4 | Conflict specificity of the bivalency effect (task 1 refers to the task with overlapping stimulus features, task 2 refers to the task with no overlapping stimulus features, and task 3 refers to the task that occasionally involved bivalent stimuli). (A) Decision time data (i.e.,

performance on univalent stimuli for switch and repetition trials in pure and mixed blocks). **(B)** Bivalency effect (i.e., difference between univalent trials from the pure block and those from the mixed block). Results adapted from Rey-Mermet and Meier (2012b) averaged across experiments and tasks.

THE NEURAL BASIS OF THE BIVALENCY EFFECT

From a neuropsychological view, adjustment of cognitive control in response to conflict is typically associated with increased activation in the dorsal anterior cingulate cortex (dACC, **Figure 5A**). The functions of this brain area include conflict detection, modulation of conflict, and selection between competing mental processes and task-sets (Botvinick et al., 1999; Peterson et al., 1999; Cohen et al., 2000; Holroyd and Coles, 2002; Forstmann et al., 2006; Parriss et al., 2007). As the dACC is involved in situations in which an adjustment of the course of action is necessary to overcome obstacles and to meet the actual goals, one would expect that it is also involved in the bivalency effect. To test this expectation, using an event-related functional resonance imaging (fMRI) design, Woodward et al. (2008) contrasted univalent stimuli from a condition with purely univalent stimuli and univalent stimuli from a condition in which bivalent stimuli were occasionally intermixed on one of the tasks (cf. **Figure 1**). As expected, the results showed that the bivalency effect was associated with activation in the dACC. Similarly, using event-related potentials, Grundy et al. (2011), found amplitude differences at frontal electrodes within time windows of 275–450 and 500–550 ms. They interpreted these modulations as “suppression of processing carried over from irrelevant cues.” Moreover, consistent with the fMRI results, source dipole analyses revealed dipole locations at or close to the dACC.

Thus, there is converging evidence that the bivalency effect is associated with activations in brain areas that signal conflict processing or adjustment of cognitive control. However, it is not clear, what exactly triggers conflict in the absence of bivalent stimuli, that is, when processing purely univalent stimuli. According to the “episodic context binding account” the reactivation of a representation of conflict that has been built up by processing the conflict-loaded task-triplet is a likely explanation. If we consider that binding processes take place on each trial (i.e., stimuli, tasks, and task-triplets acquire a history, cf. Waszak et al., 2003; Meier et al., 2009) then we would also predict memory-related brain activations. However, when contrasting blocks with bivalent stimuli vs. blocks without bivalent stimuli in an fMRI or ERP-study these activations cancel each

other out. Thus, the results from neuroimaging and electrophysiological studies do not contradict the “episodic context binding account.”

However, from these considerations it is clear that we would also expect that memory-related brain areas are necessary for the occurrence of the bivalency effect (in particular the hippocampus, cf. **Figure 5B**). One possibility to investigate this expectation is to test amnesic patients. Amnesic patients have a profound deficit in memory binding, in particular binding an event to a particular context (e.g., Chun and Phelps, 1999; Hannula et al., 2006; Pascalis et al., 2009). Thus, if episodic context binding is involved in the bivalency effect, amnesic patients would be expected to show a considerable reduction in the magnitude of the bivalency effect. In a recent study involving severely memory-impaired amnesic patients, this hypothesis was confirmed (Meier et al., submitted). Although the patients were able to perform the task and they were slowed when processing bivalent stimuli, they did not show a bivalency effect. This result supports the notion that memory-related brain areas are involved in the reactivation of the conflict and that both the hippocampus and the dACC are neural foundations of the bivalency effect.

EPISODIC CONTEXT BINDING AS SOURCE OF INTERFERENCE

The definition of “context” may be at the core of the relation between the proposed “episodic context binding account” and other previous notions of episodic binding (e.g., Waszak et al., 2003; Hommel, 2004; Altmann and Gray, 2008; Verguts and Notebaert, 2009). Given that the basic paradigm used to establish the bivalency effect involves a regular sequence of decision tasks, context is established through the repeated sequential presentation of task-triplets. From the point of view of a participant, a task consists of the whole sequence of the three different decision tasks (e.g., parity – color – case) rather than being composed of three separate tasks. Thus, the representation of a particular decision task includes the context of the whole task-triplet. When a bivalent stimulus is presented on one of these tasks, the conflict that is triggered spreads to the representation of the whole context. For the next task-triplet, this representation is reactivated and performance is slowed for all the stimuli, even for those that have no

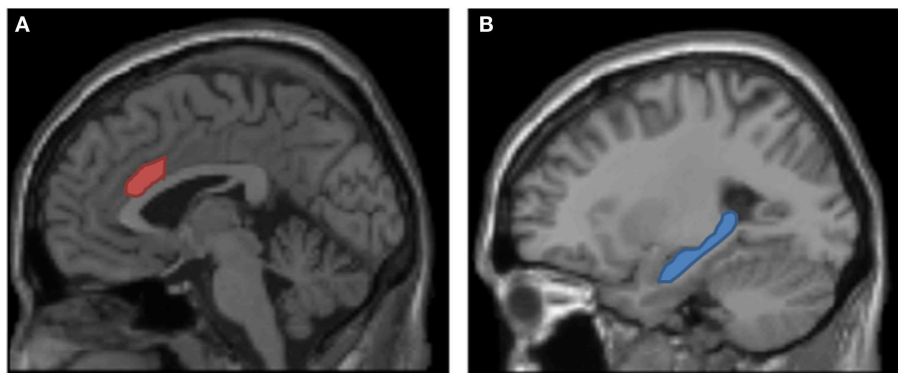


FIGURE 5 | Neural structures underlying the bivalency effect.

(A) Dorsal anterior cingulate cortex signals the requirement to adjust cognitive control (cf. Woodward et al., 2008). (B) Hippocampus (and other

memory-related structures not depicted here) are required for episodic binding and the reactivation of the episodic context (cf. Meier et al., submitted).

overlapping features with the bivalent stimulus. If one considers “context” identical to “task-set,” the current approach would be quite similar to other binding theories of cognitive control. In fact, for example Hommel (2004) acknowledged that “binding takes place across domains, linking relevant, or salient features to the response it is accompanied by and the task-set it is processed in” (p. 498).

To answer the question how exactly the context is established further research is necessary. For example, it would be interesting to address whether the sequential presentation of the tasks is necessary or whether the bivalency effect would occur in a task-cuing context. By switching between task-triplets that involve and triplets that do not involve stimuli that are related to the task-triplets with the bivalent stimuli the specificity of the context binding can be further tested. Moreover, it will be important to see whether the findings generalize to other paradigms such as the Simon- or the Flanker-tasks.

Recent research has suggested that two qualitatively distinct control modes operate to fine tune cognitive control processes, retroactive control, and proactive control (Braver et al., 2007; Braver, 2012). In fact, research on the bivalency effect has been concerned with retroactive control, that is, where resources are recruited in a just-in-time manner when conflict is detected. Defining bivalent stimuli by instructions (e.g., as in prospective memory research) will allow the investigation of conflict anticipation and particularly, to test whether this would produce a similar adjustment of control (cf., Meier and Rey-Mermet, 2012).

A further issue is the definition of binding. It is important to note that the terms “binding” and “association” are closely related. It has been suggested that “binding” rather indicates a “momentary or short-lived coupling of elements in the service of a task,” while association refers to a “long-term coupling of elements” (Vandierendonck et al., 2010, p. 607). However, according to Vandierendonck et al. (2010) binding can also be considered as a “short-term association that may be kept in long-term memory if the elements involved in the binding are not needed in other coupling that could interfere with the already existing association” (Vandierendonck et al., 2010, p. 607). To be consistent we have referred to the critical process as “episodic context binding” rather than to “episodic context association” in our work.

EPISODIC CONTEXT BINDING IN A BROADER CONTEXT

So far, we have focused on the episodic context binding account with respect to the bivalency effect. In this final section we will highlight that it is also related to other findings in the domain of task-switching and cognitive control. Specifically, an episodic context binding account can contribute to the explanation of phenomena such as switch costs, mixing costs, and $N-2$ repetition costs.

SWITCH COST

The bivalency effect may be present in most task-switching studies because these studies typically involve bivalent stimuli throughout. However, as already noted by Woodward et al. (2003), the confounding of switch cost proper and the bivalency effect is probably minimal in task-switching paradigms that involve only two tasks

because switch and repetition trials typically occur within the same block. Similarly, the bivalency effect would also exert a comparable cost when switching between and repeating of multiple tasks is involved, as long as all of these tasks involve bivalent stimuli only. Thus, the bivalency effect would exert a relatively equal influence on both switch and repetition trials and would be canceled out when switch costs are computed (see also Rey-Mermet and Meier, 2012b).

Moreover, the episodic context binding account is also compatible with results from task-switching studies in which task-switching performance on univalent stimuli was compared with task-switching performance on univalent stimuli that appeared intermixed with bivalent stimuli. In the seminal study by Rogers and Monsell (1995), in which the AABBAABB-design was introduced into the literature, they found slower responses to stimuli that appeared intermixed with bivalent stimuli compared to a condition in which task-switching was carried out with univalent stimuli only (Rogers and Monsell, 1995, Experiment 1). However, they did not further discuss this finding. From an episodic context binding view, the performance slowing on univalent stimuli in the intermixed trials can be easily explained by the notion that the typical context, in which the particular task occurred, involved conflict and this conflict was reactivated even on those trials that did not involve bivalent stimuli.

MIXING COSTS

Mixing costs refer to the difference between repetition trials in mixed blocks (consisting of both switch and repetition trials) and single task blocks (i.e., with repetition trials that are univalent by definition) with the typical finding of slower performance on mixed blocks compared to single task blocks. Mixing costs have been considered as a confound in early task-switching studies in which single task repetition blocks and alternating task blocks have been compared to measure switch costs (e.g., Jersild, 1927; Spector and Biederman, 1976). Specifically, the task-switch variable is confounded by working memory demands, attentional requirements, and degree of arousal (Rogers and Monsell, 1995; Meiran, 1996). However, mixing cost can be considered as an important indicator of executive control (Braver et al., 2003; Rubin and Meiran, 2005). For example, Kray and Lindenberger (2000) found that mixing cost was strongly affected by old age, while switch cost was not.

Slower responding has been observed under task repetition conditions when a series of tasks contained regular switch trials (such as in the AABBAABB-design), but also when a series of tasks contained only a few switch trials compared to pure task repetition conditions (De Jong, 2000, Exp. 2; Mayr, 2001; Kray et al., 2002; Exp. 2). De Jong (2000) interpreted these results as the consequence of a control strategy that may reflect a compromise between minimizing control effort and maximizing task performance. Specifically, participants may opt not to fully disengage prior task-sets when they have the expectation that they may become relevant again on subsequent trials. In contrast, according to an episodic context binding account this adjustment may reflect rather the result of memory processes, that is, the association or binding between a task and a conflict-loaded context which is reactivated even in a context that is not conflict-loaded.

N-2 REPETITION COSTS

$N-2$ repetition costs refer to the performance difference between $N-2$ task switches (i.e., a sequence such as CBA) and $N-2$ task repetitions (i.e., sequences such as ABA). Interestingly performance is slowed for an $N-2$ repetition (ABA) compared a non-repetition control condition (CBA). This slowing has been interpreted as a measure of inhibitory processes in the selection of task-sets (Mayr and Keele, 2000; Gade and Koch, 2007, 2012). It is assumed that after having performed task A, task-set A is inhibited in order to successfully perform task B. When encountering task A again, inhibition is still active and overcoming task A inhibition in order to perform task A again requires time, which is reflected in the $N-2$ repetition cost. Typically, the $N-2$ cost is tested with tasks that involve bivalent stimuli. However, in order to test whether the size of the $N-2$ repetition cost is related to the amount of conflict among tasks, a recent study has included some trivalent stimuli (i.e., 25%) amongst the bivalent stimuli (Gade and Koch, 2012). The critical question was whether the presence of a univalent vs. trivalent stimulus on trial $n-1$ would affect performance on $N-2$. The results showed no effect of stimulus valence and thus, Gade and Koch suggested that inhibitory processes are engaged in a rather global manner, which is consistent with an episodic context binding account. Even more interestingly, an additional result was that performance on the intermixed univalent stimuli did not differ from the corresponding bivalent stimuli. Because there was no change in context in which the particular task had been activated previously, this result is exactly what would have been predicted by an episodic context binding account.

Overall, these results show that the episodic context binding account can be used to explain several findings that have occurred as side-effects in the study of switch costs, mixing costs, and $N-2$ costs. Thus, the occurrence of episodic context binding is not

restricted to the bivalency effect and the episodic context account complements and extends existing theories.

CONCLUSION

In this article, we have reviewed the emerging literature on the bivalency effect. The bivalency effect refers to the phenomenon that the occasional occurrence of bivalent amongst univalent stimuli slows performance on subsequent univalent trials, even on those, that share no relevant feature with the bivalent stimulus. From these studies it is evident that this effect challenges current theoretical approaches of task-switching and cognitive control.

Specifically, the slowing observed on stimuli, which share no relevant features with the bivalent stimuli, cannot be accounted for by task-switching theories. However, to be fair it must be noted that these theories have been developed to explain switch costs in the first place. Accordingly, task-switching theories can predict the slowing on those univalent stimuli that have shared properties with the bivalent stimuli. In contrast, the episodic context binding account can explain the slowing on each type of stimulus in terms of binding and reactivation of conflict and context. Thus, it is beyond feature binding. Rather it is related to episodic memory such as establishing an association between tasks and contexts.

However, episodic context binding is engaged flexibly, depending on the presence or absence of conflict (Rey-Mermet and Meier, 2012b). These results challenge the hypothesis that adjustment of cognitive control is always sensitive to the amount and to the source of conflict (e.g., Botvinick et al., 2001, 2004; Egner, 2008). Rather they indicate that the presence of a conflict in univalent trials strengthens binding whereas the absence of conflict weakens it (cf. Verguts and Notebaert, 2009). In summary, considering the general context in which a task occurs informs both theories of task-switching and cognitive control.

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Parallel distractor rejection as a binding mechanism in search

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The relatively common experimental visual search task of finding a red X amongst red O's and green X's (conjunction search) presents the visual system with a binding problem. Illusory conjunctions (ICs) of features across objects must be avoided and only features present in the same object bound together. Correct binding into unique objects by the visual system may be promoted, and ICs minimized, by inhibiting the locations of distractors possessing non-target features (e.g., Treisman and Sato, 1990). Such parallel rejection of interfering distractors leaves the target as the only item competing for selection; thus solving the binding problem. In the present article we explore the theoretical and empirical basis of this process of active distractor inhibition in search. Specific experiments that provide strong evidence for a process of active distractor inhibition in search are highlighted. In the final part of the article we consider how distractor inhibition, as defined here, may be realized at a neurophysiological level (Treisman and Sato, 1990).

Keywords: attention, feature binding, inhibition, visual search, conjunction search

ANALYSIS AND SYNTHESIS IN VISION

Some of the most compelling cases in the neuropsychology of vision are patients who, following brain damage, experience selective loss of particular stimulus qualities. Patients with specific and restricted cortical damage may present with selective deficits for color (achromatopsia see, Zeki, 1990; Bouvier and Engel, 2006), motion (akinetopsia see, Zihl et al., 1983; McLeod et al., 1989; Zeki, 1991), or aspects of form processing (visual form agnosia, see, Riddoch and Humphreys, 1987; Goodale et al., 1991; Riddoch et al., 2008; Karnath et al., 2009). These neuropsychological cases provide convincing evidence that the different features of objects may be processed by brain systems that are at least quasi-independent.

Given that human vision has evolved such an analytic approach, the question naturally arises as to how the multiple features of different objects are properly combined (see Humphreys, 2001, for further discussion). Surely, such an analytic system should be prone to incorrect or illusory conjunctions (ICs) of features? Everyday experience of a seamless perceptual world may mislead us into thinking that “binding” these features of objects together is a trivial problem. However, the kinds of deficits that can occur following brain damage force us to reconsider. Patients suffering bilateral damage to parietal cortex may suffer severe deficits of perception, one aspect of which is frequent incorrect binding of features. Such patients presented with a red X and a green O may erroneously report having seen a red O – an IC (Friedman-Hill et al., 1995; see also Bernstein and Robertson, 1998; Humphreys et al., 2000). Even normal unimpaired observers asked to report relatively brief stimuli under conditions of attentional load may

also report frequent ICs (Treisman and Schmidt, 1982). These ICs arise when the visual system is damaged and/or placed under attentional constraint, and are consistent with an early stage of analysis where the re-combination process is error-prone. The question thus arises as to the nature of the processes that prevent frequent ICs in healthy observers under everyday viewing conditions.

Here we consider some key models of selection and attention with particular emphasis on the mechanisms by which feature binding occurs and ICs are avoided. In particular we explore the role of inhibitory processes in the promotion of correct feature binding and the avoidance of ICs. This question of inhibitory processes was not fully explored by the earliest theories. For instance, one of the earliest and pioneering models of attentional selection was put forward by Broadbent (1957, 1958). Originally developed to account for data in the context of dichotic listening, the theory proposes that, following elementary feature analysis, further processing of information may be limited to stimuli possessing particular features. In Broadbent's framework, a selective filter could be set which allows through only target features, but the fate of the rejected stimuli on this account is unclear. It is not considered whether rejected stimuli are equivalent to all items in the background and simply not subject to further processing, or whether rejected distractors can be inhibited below the background level.

Following our discussion of theoretical approaches below, we critically review some of the key experimental paradigms that have been used to address this question. Finally we suggest some possible neural mechanisms.

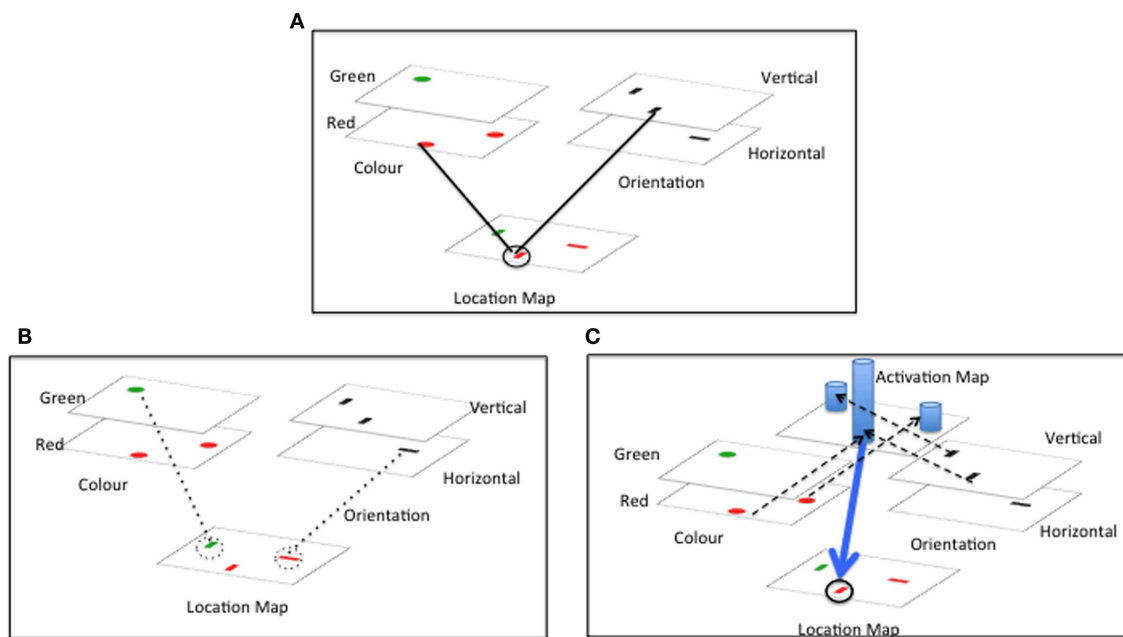


FIGURE 1 | Accounting for conjunction search. Three influential accounts of conjunction search are depicted. In all cases search is for a vertical red bar, amongst vertical green and horizontal red bars. **(A)** Illustrates the basic location based cross referencing scheme that is the core of Feature integration Theory (FIT). **(B)** Illustrates the inhibitory revision of FIT proposed by Treisman and Sato (1990), and **(C)** illustrates the guided search revision proposed by Wolfe et al. (1989). **(A)** FIT: stimuli are decomposed into constituent features. Serial spatial selection

by attention serves to recombine features based on location. **(B)** Feature inhibition revision of FIT: inhibition of distractors with non-target features (dotted lines) leaves target as only remaining uninhibited item. **(C)** Guided search revision of FIT: activation from target features is summed in an activation map. Spatial attention selects location with highest activation. Dotted lines indicate activation of activation map. Blue columns represent activation levels. Blue arrow represents direction of spatial selection by activation.

BINDING BY SELECTION: THEORETICAL APPROACHES

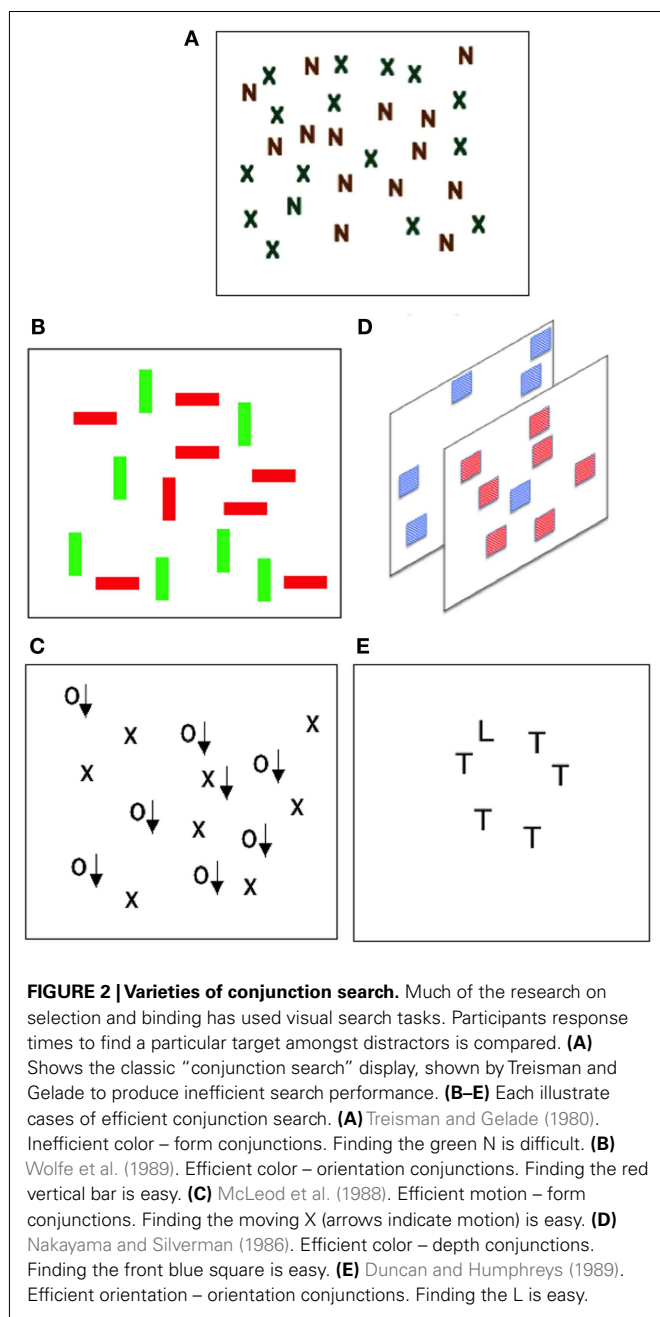
One important hypothesis concerning how features are bound is that spatial selection is key. Feature integration theory (FIT, Treisman and Gelade, 1980; Treisman, 1988; see Quinlan, 2003 for a review) proposes that, in order to properly bind together and represent combinations of features, spatial attention must select a particular location, and by doing so is able to cross-reference multiple features occurring at that location (see **Figure 1A**). Spatial selection of one location at a time can also solve the binding problem by highlighting only features at the attended location and minimizing the impact of other features, which are consequently not available for binding.

However, research shows that sometimes feature binding can be achieved rapidly and without the serial selection of a set of individual locations required by FIT in its unadulterated form. Several cases of efficient search (indicating little need for serial selection) for targets defined by conjunctions of features came to light in the late 1980s (see **Figure 2** for illustration). Nakayama and Silverman (1986) showed that conjunctions of stereoscopic depth and either motion or color could be detected efficiently. Subsequently McLeod et al. (1988) demonstrated that conjunctions of movement and form could also be detected efficiently. Wolfe et al. (1989) returned to the case of color studied earlier by Treisman and Gelade (1980) and showed that conjunctions of color and orientation could be found efficiently given sufficiently large differences in the values of color and orientation used. Duncan and Humphreys

(1989) also reported efficient search for targets distinguished from distractors only by the combination of form elements.

These findings of efficient conjunction search appear to challenge the fundamentals of FIT. Attentional Engagement Theory (AET, e.g., Duncan and Humphreys, 1989, 1992), on the other hand, proposes that feature and conjunction search do not necessarily differ in kind, but merely reflect different similarity relations amongst the stimulus elements. In AET search is directed by a template representing the target features; each item competes for selection with the outcome of this competition determined by the relative “attentional weight” assigned to each item. The attentional weight assigned to a stimulus is increased if it matches the template and decreased if it does not. Importantly, AET postulates that items that group together by sharing features can also change their attentional weights together (a process termed weight linkage). Weight linkage makes it easier for the system to reject groups of items in parallel. Thus in AET search difficulty is understood in terms of the roles of template matching and stimulus grouping enacted not just by positive excitatory changes but also by negative inhibitory changes.

Other authors have suggested ways in which FIT could be supplemented by additional guidance processes in order to account for efficient conjunction search. The Guided Search model (e.g., Wolfe et al., 1989, see **Figure 1C**) posits that search for a known target can be biased by top-down pre-activation of feature maps representing the expected properties of targets. Excitation from the feature



maps is fed forward to a general activation map – where activation at each location is summed across the different incoming features. Values in the activation map dictate the probability that a particular location will be selected for further processing. Provided that the basic feature values are sufficiently discriminable, conjunction targets (with two preactivated features) will receive higher summed activity than distractors (with only one preactivated feature). The net result is efficient guidance of search to conjunction targets.

An issue with the Guided Search model is that the top-down modulation of feature maps will increase the activation of distractors that share features with the target. Increased distractor

activation could lead to distractor features combining incorrectly with other activated features resulting in increased ICs (especially when the target itself is absent). Treisman and Sato, 1990, see also Treisman, 1988) suggested as an alternative a feature inhibition hypothesis in which those items with non-target features would be inhibited together (**Figure 1B**). This parallel inhibition by non-target features, like the suppressive weight linkage proposed by AET leads to reduced competition for selection from distractors, and efficient search. Importantly, selective inhibition by distractor features operates only when target and distractor features are so discriminable that distractor features can be suppressed without affecting target processing. Thus a significant benefit of an inhibitory as opposed to an excitatory bias (e.g., Guided Search), is that ICs are less likely to occur (since distractor features are inhibited). In this paper we seek to assess the feature inhibition hypothesis proposed by AET and suggested by Treisman and Sato (1990), evaluating whether the hypothesis meshes with what is known about visual attention and whether it provides a solution to the binding problem that is adopted by human vision.

There is a further key difference between FIT as proposed by Treisman and Sato (1990) and the AET as proposed by Duncan and Humphreys (1989). According to Treisman and Sato (1990) inhibition for each feature dimension is independent. That is, inhibition of stimuli based on color, would not take into account grouping by orientation. In contrast according to Duncan and Humphreys's AET account, inhibition by different features is not independent, since negative losses of weight accrued to stimuli on the basis of one feature (e.g., color) may spread to other stimuli grouped with these items by other features (e.g., orientation). Under some conditions this can lead to stimuli that group on the basis of their conjunctive relationship (e.g., they differ from other groups only in how the same set of features combine) to be rejected together (see Found, 1998 for a demonstration).

In the next section we review the experimental approaches used to address whether there is suppressive rejection of distractors in general and also specifically in relation to the theories discussed above.

EMPIRICAL EVIDENCE: ATTEMPTS TO EXAMINE DISTRACTOR SUPPRESSION

There have been a number of approaches to testing whether target selection can take place by distractor suppression, and, if it can, how this process might operate. We briefly consider four types of study examining: (i) manipulations of distractor heterogeneity, (ii) trial-by-trial variations in stimulus properties, (iii) effects of stimulus foreknowledge, and (iv) probe-dot detection.

EFFECTS OF DISTRACTOR HETEROGENEITY

Treisman and Sato (1990), Friedman-Hill and Wolfe (1995), McLeod et al. (1991), and Driver et al. (1992) all explored the relative importance of activation and inhibition in search by varying the number of features that characterized to-be-ignored or to-be-attended stimuli. The logic was simple. If participants actively deploy excitatory resources toward known target features, then increasing the number of possible target features should impede performance. In contrast, if participants deploy inhibitory resources toward known distractor features then the opposite

should hold – in this case increasing the number of possible distractor features should impede performance.

Studies employing this method have generated data that support roles for both excitatory and inhibitory mechanisms in search. Treisman and Sato (1990) argued that, in color-form conjunction search, if distractors were added with features even further from the target than the existing distractors, then any mechanism tuned toward target features should be unaffected. In the standard conjunction case participants searched for a green 27° tilted bar amongst green 63° tilted bars and gray 27° tilted bars. The standard condition was compared against a condition where half of the distractors were replaced by green 90° and pink 27° tilted bars. If participants are positively tuned toward green and 27° then they should not be disrupted by the addition of pink and 90° features. The results showed that participants were in fact slower and less efficient when the number of distractor features increased, supporting the presence of inhibitory guidance away from non-targets.

Driver et al. (1992) also used this same logic in the context of search by motion direction. All the items were moving but participants selected items moving in one direction whilst ignoring items moving in another direction. The search items oscillated backward and forward along either a $\pm 45^\circ$ path. Additionally items moving along a particular path did so either coherently (all starting movement from the same point along the path) or incoherently (half of the items starting movement from each end of the path). If the target group moved incoherently there was no disruption to search, but if the non-target group moved incoherently search was disrupted. The greatest decrements to search occurred when both groups were incoherent. This pattern of results is consistent with a contribution from both excitatory and inhibitory processes but with an emphasis on the inhibitory.

On the other hand, similar studies have found no requirement for an inhibitory process. Friedman-Hill and Wolfe (1995) examined the case of selecting by color. Participants searched for an oddly oriented line amongst a color defined subset. Two critical conditions were compared: either participants had to select items of uniform color and reject two different color groups, or participants had to select two colors while rejecting a third possible color. Performance was much poorer when two colors had to be selected, supporting the involvement of excitatory processes that operate more efficiently when excitation can be tuned to a single target feature.

McLeod et al. (1991) asked participants either to select (a) moving and stationary items whilst rejecting items moving in a different direction, or (b) items moving in one direction whilst ignoring stationary items and items moving in different direction. The results clearly showed that the selection of stationary and moving items (condition a) was much more difficult than the selection of one moving direction (rejecting stationary distractors and distractors moving in a different direction, condition b). McLeod et al. interpreted this pattern of findings as evidence in favor of excitatory guidance of attention based on motion direction that may be disrupted by the inclusion of static items in the target group.

Clearly the evidence from studies manipulating distractor heterogeneity is not straightforward. It is difficult to unambiguously attribute changes in performance to attentional tuning (inhibitory

or otherwise) in this task. As a consequence of manipulating the number of features present in the displays the grouping structure of the display also changes (see Duncan, 1995, for discussion); additionally the number of feature contrasts in the display also changes, and this may also alter bottom-up salience (see Julesz, 1986; Nothdurft, 2002). Ideally demonstrations of distractor inhibition should come from studies where display structure is held constant in the critical conditions.

TRIAL-BY-TRIAL EFFECTS

Trial-by-trial priming effects have also been used to make arguments about inhibitory and excitatory guidance in search. Here the logic is that any inhibitory or excitatory effects will carry-over in time to the next trial. Koshino (2001) varied whether the target in a conjunction search on trial n had the same features as either the target or the distractors on trial $n - 1$. The results showed that, when the target was repeated, performance was speeded relative to when the target changed. In addition, there were disruptive effects when the target on the current trial took on the features of distractors on the previous trial (e.g., search for a Red X in Green X and Red N distractors, followed by search for a Green N in Green Vs and Magenta Ns), compared to when the features on the two trials were unrelated. Thus RTs were facilitated when features repeated and impaired when the target took the previous distractor features, consistent with a role for both excitatory and inhibitory processes.

Lamy et al. (2008) also examined trial-by-trial priming in the context of a color feature search. By using a color feature search task, in which participants searched for an odd colored item, they were able to independently manipulate whether the target and distractor features changed to new values, repeated the old values, or switched (previous target features becoming distractor features and vice versa). Relative to when the features changed to new values, there were both benefits of feature repetition and costs for feature switches. Thus performance was slower when the target appeared in the color of the previous distractors, and performance was slower again when the distractors additionally took on the previous target color. The authors interpret these particular effects as evidence for both target activation and distractor inhibition in search. Importantly, this distractor inhibition is reactive in the sense that it is set-up on-line based on whatever feature value the distractors happen to have. The inhibition does not take the form of pre-weighting a particular feature value (e.g., red) since the target and distractor feature values are not known in advance.

One interpretative issue with these studies of carry-over effects, is whether they directly reflect distractor inhibition, or rather the costs that might be involved when features from a past trial have to be re-bound to define the target (see Park and Kanwisher, 1994; Hommel, 2004). The necessity to re-bind the features may disrupt search even if there is no carry-over of the suppression of those features (from distractors onto targets). Therefore, ideally demonstrations of distractor inhibition in search should not rely on trial-by-trial effects alone.

EFFECTS OF FOREKNOWLEDGE

Another method to try to assess the role(s) of inhibitory and excitatory guidance in search is to look at whether providing fore

knowledge of either target or distractor features can lead to costs and benefits to search.

Shih and Sperling (1996) and Moore and Egeth (1998) both investigated the consequences of providing participants with foreknowledge regarding the likely color of an upcoming (feature-defined) target. Shih and Sperling (1996) showed that feature-based knowledge does not allow displays of a particular color to be completely filtered from vision. Participants viewed rapidly alternating displays of two different colors, with one of these displays containing the target. Increasing the probability that the target was a particular color did not modulate performance. Only when the target was a feature singleton in the displays did foreknowledge have an effect, consistent with a role for feature-based knowledge in spatial guidance of attention. Moore and Egeth (1998) used single displays composed of items of different colors, and manipulated the foreknowledge that participants had. The results showed that foreknowledge could change the speed with which targets could be found in time unlimited displays. However, when stimulus quality was degraded (e.g., with brief, masked displays) there was no effect of foreknowledge. The authors argue that had foreknowledge affected fundamental stimulus processing there should have been effects under these degraded conditions. Thus the authors suggest that rather than affecting fundamental feature processing, the effects of foreknowledge operate at a level of guiding attention.

In these tasks it is possible to observe both benefits for valid cues and costs for invalid cues, and at least logically these two effects are dissociable. Take the situation where the target appears 80% of the time in red and 20% of the time in green. Compared to the situation where target color is equiprobable, there can be benefits when the cue is valid, consistent with increased activation of items with likely features. There may also be costs on invalid trials, and these costs are at least consistent with inhibition of items with unlikely features. Relative to the case where the target was equally likely to be one of two possible colors, both Shih and Sperling, and Moore and Egeth reported benefits for validly cued color targets, and costs for trials where the initial target color cue was invalid (i.e., expect red and then the target was green). The presence of both benefits and costs is consistent with both excitatory and inhibitory processes. In particular Shih and Sperling (1996) say the following about participants who exhibit such costs: “they find the location of the odd item and, because it has the not-to-be-attended feature value, they suppress the information from that location – a true cost! . . . it is possible to enhance and also to suppress information from a single location.” (p. 773)

However, the results from manipulations of target foreknowledge are inconclusive. In particular, attentional selection may be understood as the outcome of a competition between different stimuli (e.g., Duncan and Humphreys, 1989). Thus, activating the properties of one stimulus (from an expectation of the target) may itself decrease the *relative* strength of a competing stimulus even though its absolute activation level remains constant. Thus the processing costs seen in these studies could be traced to increased competition from highly activated items in the cued color. In order to circumvent this problem what is needed is a measure of the *relative* loss of competitive strength for distractors that is independent of the search task.

As well as knowledge of the target, some studies have directly investigated the effects of providing knowledge of the distractors. Preview search, for example, presents one set of distractors for a preview period prior to adding a new set of items to the search display. Participants can use their foreknowledge of the distractors to influence their search performance. Under conditions where the preview is sufficiently long, the previewed distractors can have no impact on search – search progresses as efficiently in the preview condition as when only the second set of new items is presented (e.g., Watson and Humphreys, 1997). One striking result is that, if the new target carries features of the old, previewed items, then the target can be very difficult to detect – even when this target is a singleton in the new search display (Olivers and Humphreys, 2003; see also Braithwaite and Humphreys, 2003; Braithwaite et al., 2005 for similar results but with non-singleton displays). This last result is difficult to explain if there is only excitatory guidance of search to the new items with the old items forming a background that does not compete for selection, but it is consistent with the features of the previewed distractors being inhibited. Along with this, though, giving participants explicit foreknowledge of the likely color of the target helps to overcome the negative impact of carry-over from distractor features (Braithwaite and Humphreys, 2003). Again, the evidence is consistent with a role of both excitatory guidance of search to targets and inhibition of distractors.

One other point to note about these data from preview search is that they suggest inhibition not only of the features that will distinguish the previewed distractors from the new search items (e.g., their locations) but also of features carried by the distractors that are irrelevant to the search task. For example, in the studies of Braithwaite, Humphreys and colleagues (Braithwaite and Humphreys, 2003; Braithwaite et al., 2005), the target was defined by its identity and its color was irrelevant. Despite this, there was a negative effect on search when the target carried the distractor's color. Interestingly, recent work has extended the range of conditions under which these effects occur beyond preview search. Thus when search is for a moving target and a group of static distractors are rejected, targets sharing color with the rejected static distractors are difficult to find (see Dent et al., 2011b). This evidence suggests inhibition of the rejected distractors as a group, and rejection of all the properties of the group, rather than just inhibition of the features that segment the target from distractors. This feature non-independence resonates more with the idea of weight linkage and spreading suppression within a distractor group (Duncan and Humphreys, 1989) than with the idea of feature-specific inhibition (Treisman and Sato, 1990).

Studies of target or distractor foreknowledge overall support the existence of both excitatory and inhibitory processes in search. Given that any effects will be due to both the properties of both perceptual processes and to any limitations or strengths of the foreknowledge system, it is important to find converging evidence from other methods as well.

PROBE-DOT STUDIES

The efficiency of processing a probe dot presented at different locations in a display has been used as a tool to explore the allocation of attention in search. The probe-dot task was first coupled with search in order to explore the related phenomenon of inhibition

of return (IOR). IOR refers to the reduction in processing efficiency that follows the withdrawal of spatial attention from a previously attended location (see Posner and Cohen, 1984, for the initial demonstration and Klein, 2000 for a review). Klein (1988) suggested that IOR could be an important mechanism in search allowing examined items to be marked as rejected, acting as a “foraging facilitator,” promoting sampling of new unprocessed stimuli. In order to investigate this link, Klein (1988) had participants carry out a search task and then presented a probe either at the previous location of a distractor or at a previously unoccupied location in the background. He found that probes falling at the locations of earlier distractors were more difficult to detect than probes falling on prior background locations. This difference was increased when the search task was difficult (e.g., involving serial scanning of attention) compared with when it was easy (in feature search tasks) – which is important because it shows that the effect can not be due to masking from an earlier item at the same location. Subsequently Müller and Von Mühlen (2000) and Takeda and Yagi (2000) have shown that these costs for the detection of probes on distractors is stronger again if the search items remain visible when the probe appears. These studies are consistent with the view that, in difficult serial search, distractors can be inhibited below the activation levels associated with the background as a result of IOR.

Whilst important in supporting the general principle of inhibitory processes, the notion of IOR, however, is different from the idea of spreading suppression or the parallel inhibition of distractors with a shared feature. By definition, IOR is applied serially across a display and only to items that have been selected and rejected. In contrast, spreading suppression and feature-based distractor inhibition are proposed to operate during selection – reducing the impact of distractors on target selection and on the chances of their features binding with those of targets. Illustrating this difference, Olivers et al. (2002) tested preview search under conditions where participants had to serially search the previewed distractors prior to searching the new stimuli, which should maximize IOR of the old stimuli. They found people were less, not more, likely to exclude previewed distractors under these conditions and concluded that the rejection of a common set of distractors in preview search took place using mechanisms distinct from IOR.

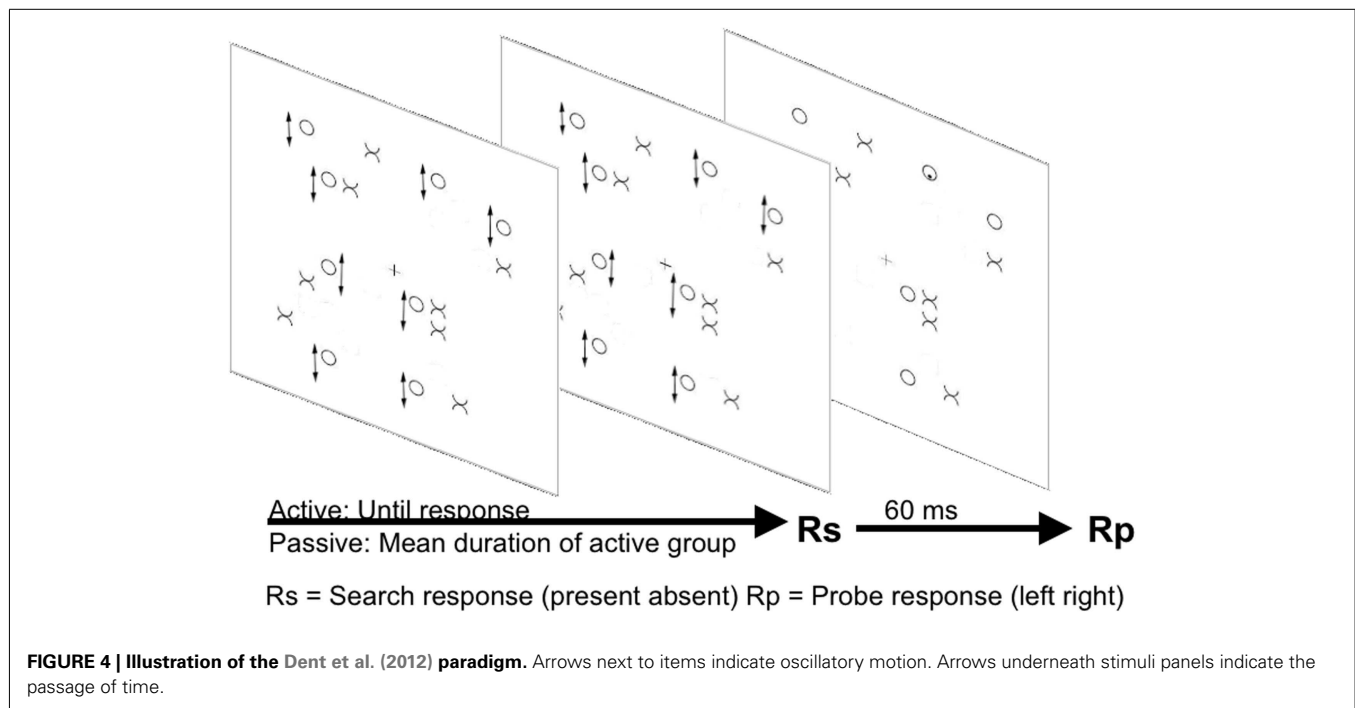
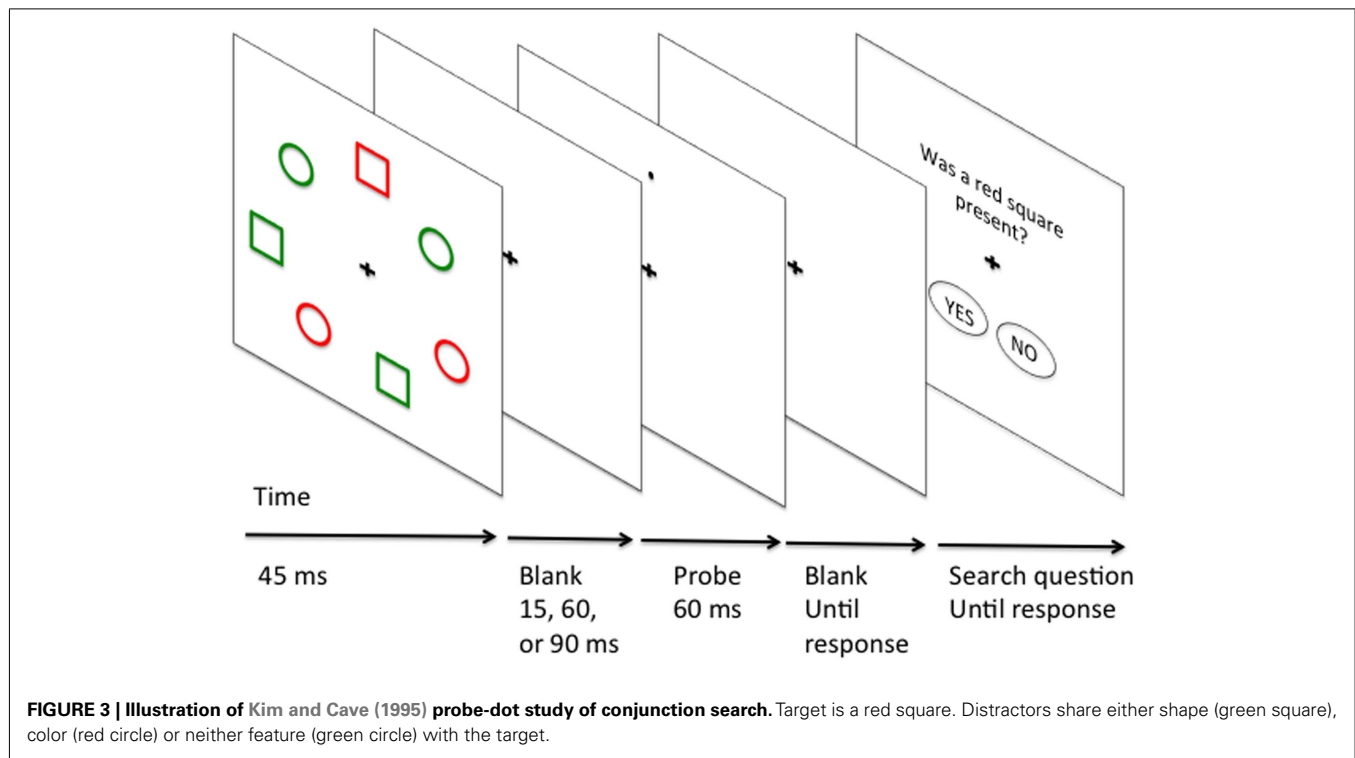
The earlier study of Klein (1988) examined broadly how search difficulty affected subsequent probe detection. However, Klein (1988) and related studies of IOR did not examine tasks where there was an opportunity for feature-based guidance of attention. In these earlier studies the relative excitation or inhibition of distractors possessing different features within a display was not addressed. To address the question of the relative excitation and inhibition of different types of distractors during selection, Kim and Cave (1995) examined probe-dot detection in the context of search for conjunctions of color and form (e.g., find a red square amongst green squares, red circles, and green circles, see **Figure 3** for illustration). Following conjunction search participants responded to the presence of a probe dot (present 25% of the time). The probe dot could appear on the target, or on a distractor. In general RTs were fastest for probes on the target, slower for probes on distractors that shared either color or form, and slowest

of all on distractors that shared neither feature with the target. Unfortunately, probes were never presented on a neutral blank background location, and so it is difficult to judge whether the pattern of results should be attributed to target feature activation, or distractor inhibition.

A subsequent study by Cepeda et al. (1998) addressed the possibility of distractor inhibition by including a neutral baseline condition. Participants searched for a color singleton target and probes were presented either on distractors or in the background. The authors included a structured grid in the background and the elements making up the search items were also made up of the grid – so a probe fell equally far from a grid/distractor contour in the control and experimental conditions, controlling for masking. The results showed suppression of probe detection at distractor locations, even when masking was controlled. Additionally, Cepeda et al. compared the performance of two groups of participants: the active search group searched for the target and then detected the probe, whereas the passive group only detected the probe after viewing the same displays passively. Bottom-up masking is equated for the two groups, thus any effect in the active group, must stem from top-down attentional modulation. The results revealed distractor suppression that was specific to the active group and did not occur for the passive group, consistent with a role for top-down inhibition but only when needed for selection. Müller et al. (2007) reported similar results in the context of an efficient search for an orientation singleton. Müller et al. (2007) also tackled the issue of masking by comparing an active and passive group of participants. The results showed that probes presented on distractors were detected more slowly than probes presented on the background, and this effect was much greater in the active group, supporting a role for top-down inhibition.

Humphreys et al. (2004) applied probe-dot detection to the preview search task, controlling for masking in the manner introduced by Cepeda et al. (1998). They showed that probes presented on old items were more difficult to detect than those presented on the background. Interestingly in their conjunction search task no effects were seen. However it should be noted that the effects in the preview search based on accuracy were small and it may be that effects in the conjunction search were missed. Allen and Humphreys (2007) measured the ability to detect a contrast increment probe on previewed items in a psychophysical paradigm. By measuring the minimum increment that could be reliably be detected on the previewed items, they were able to show that previewed items are effectively reduced in contrast in the visual system. These studies suggest that distractor suppression may be particularly strong under conditions where one irrelevant set of items can be filtered over time.

Recent research from our lab (Dent et al., 2012, see **Figure 4**) has investigated distractor suppression in a further efficient search task, in this case involving target conjunctions defined by movement and form (e.g., McLeod et al., 1988). As described earlier there is disagreement in the literature regarding the mechanisms underlying efficient search for conjunctions of movement and form. Studies manipulating distractor heterogeneity have drawn conflicting conclusions. McLeod et al. (1991) suggested a preeminent role for activation of moving items, whilst Driver et al. (1992)



suggested that distractor inhibition was the more important mechanism. Dent et al. (2012) used the probe-dot task in an attempt to resolve this issue. Dent et al. (2012) showed that, when participants searched for a moving X amongst moving O and static X distractors, there were costs for probes presented on static X distractors consistent with inhibition of the location of the static

items. The inhibition in conjunction search was much larger than any inhibition in any feature search condition. Furthermore this inhibition applied only to a group of participants actively engaged in the search task, and not to a group who viewed the same search displays passively responding only to the probe. Interestingly we found that when the displays were viewed passively responses were

in fact slower to probes presented on moving compared to static items. This static advantage changed into a disadvantage when participants were actively engaged in search. This slowing depending on the participants being actively engaged in search argues against any enhanced masking effect being responsible for probe inhibition under active search conditions.

Results from probe-dot tasks provides strong evidence for inhibition in search. We note that probe-dot studies have significant advantages, for measuring attentional modulation in search, over the other methodological approaches reviewed above. By comparing probe detection at distractor and at blank locations the experiments include an appropriate neutral baseline missing from studies manipulating foreknowledge and target probability. Inclusion of an appropriate neutral baseline is crucial for assessing the polarity of attentional guidance (excitatory or inhibitory) in search.

As noted above, most attempts to examine excitatory and inhibitory contributions to search have manipulated the nature of the search task itself. Here, the experimental observation changes the very nature of the task under scrutiny. The method for measuring inhibition is an integral part of the search task, and is measured with some response to the search display. By changing the nature of the search task the experimenter may also inadvertently change display-wide grouping or bottom-up salience. We argue that the probe-dot task provides a tool that allows the experimenter to measure components of search, without disrupting or changing the nature of the search task under scrutiny. Since the probe task is a tool that is independent of search *per se*, probe detection can be examined as a function of search activity. In other approaches where the search response itself provides the index of attentional priority it becomes difficult to vary the degree of engagement with the search task without also varying the nature of the search stimuli. Additionally, probe detection provides a quite direct and relatively unambiguous measure of attentional priority that by-passes issues related to rebinding of features common to trial-by-trial approaches to measuring distractor activation and inhibition.

In addition to providing evidence for the existence of feature inhibition in search, results from the probe-dot task provide important constraints on the nature of this inhibition. Note that in this task the probe does not necessarily share any features with the distractor on which it is presented apart from location. Thus the probe itself would not be represented in the same feature maps as the search distractors. Thus any disadvantage for probe processing is unlikely to be rooted in inhibition in the feature maps themselves but rather from the coding of priority at the level of a general masters alliance map.

CONCLUSION

Our review so far indicates that there is evidence for the parallel suppression of distractors under conditions in which targets can be efficiently segmented from distractors, with the inhibition across groups of distractors with a common feature not shared by the target. This result is consistent with ideas put forward by both Treisman and Sato (1990), in their modification of FIT, and Duncan and Humphreys (1989), in their AET. The data additionally suggest that the suppression is found not only for the

features distinguishing targets from distractors but also for irrelevant features carried by the rejected distractors. This is consistent with groups of distractors being rejected together (Duncan and Humphreys, 1989) rather than there being suppression of particular feature maps (Treisman and Sato, 1990). On top of this there is evidence that positive expectancies for target features can also bias search, to at least some degree offsetting the influence of spreading inhibition. We conclude that efficient selection of targets, particularly where their features could bind incorrectly with the features of distractors, is based on dual mechanisms of distractor suppression and excitatory guidance of attention to targets (see Braithwaite and Humphreys, 2003, for articulation of a dual attention set hypothesis).

NEURAL MECHANISMS

MacLeod et al. (2003), MacLeod (2007) cautions against the identification of inhibition at the cognitive level with neural inhibition. We endorse this cautious approach as the relationship between cognitive level inhibition and neurophysiology is a complex one and almost certainly a whole network of brain areas will be involved in distractor suppression in search. It is also not necessarily the case that decreased neural activation corresponds to functional inhibition at a cognitive level. For example an fMRI study by Allen et al. (2008) showed that, in preview search when people were ignoring faces and selecting houses or vice versa, activation in stimulus specific processing areas sensitive to the ignored stimuli *increased* rather than decreased (the fusiform face area FFA for faces and parahippocampal place area PPA for houses). Thus when particular features are used to signal inhibition, increases in activation in mid-level feature-specific areas may occur. This might reflect direction of an inhibitory signal itself or the initial allocation of attention to the distractor in order to subsequently inhibit it (see Tsai and Makovski, 2006).

Other recent research using fMRI (e.g., Dent et al., 2011a; Payne and Allen, 2011) has shown that increased efficiency in preview search can be related to decreased activation in V1 when the final search display is present. Similar results have been found when participants know that a target will not appear in a particular location (Serences et al., 2004; Sylvester et al., 2008). One hypothesis might be therefore that location specific feature inhibition could manifest as reduced activation in V1, although this remains to be demonstrated more generally when participants select targets by features rather than using temporal signals (as in preview search). Specifically, in the context of feature inhibition, one may question the suitability of V1 deactivation as a causal mechanism. Reduced activation in V1 may be taken to imply reduced elementary perceptual processing at specific locations or activation of a reduced number of locations. At both a theoretical level (e.g., Wolfe and Horowitz, 2004) as well as an empirical level (e.g., Shih and Sperling, 1996; Moore and Egeth, 1998) there are reasons to prefer the idea that feature inhibition does not completely suppress pre-attentive stimulus processing. Wolfe and Horowitz (2004) point out that if directing attention away from a particular feature results in reduced elementary processing of that feature, then (i) the very basis for the guidance will be undermined over time as the guiding feature is degraded, and (ii) if fundamental stimulus processing is affected then it may be difficult to rapidly

reconfigure the system to accomplish certain tasks, for example deciding if a green object has a red spot. Certainly it remains to be seen if such V1 deactivation is a general phenomenon that can be driven by a range of features or whether it is specific to spatio-temporal cueing.

One way to reconcile the idea that feature inhibition is realized by reductions in V1 activation is to view V1 activity, as revealed by the BOLD signal, as reflecting a salience representation (e.g., Li, 2002), rather than stimulus processing efficiency *per se*. It is certainly possible that the master-map of spatial locations as described by Treisman could be housed in V1, further research is needed to address this question. Clearly other structures including parietal and frontal areas are also involved in directing the deactivation of V1. One possibility is that these areas may code a spatial representation of the to-be-ignored distractors (see Allen et al., 2008) and that this template, in conjunction with frontal areas, can be used to direct changes in the response of V1 neurons. Thus one potential circuit to implement feature inhibition would be that *increased* activation in feature-specific areas (V4, MT, IT, PPA, FFA) signals the to-be ignored feature, and setting of appropriate inhibitory weights to translate feature activation into reduced priority at the master-map level. Subsequently, interactions between feature-specific regions and downstream areas in the parietal cortex and precuneus create a spatial template that is used to coordinate location specific deactivation in V1. There are also other candidate structures that could implement a master salience map. Notably, the temporo-parietal junction has been highlighted as an important neural structure for bottom-up

attentional capture (see Corbetta and Shulman, 2002), and recent computational modeling work suggests important links between salience as implemented in a neuro-computational model and TPJ activity observed in an fMRI study of preview search (Mavritsaki et al., 2010).

SUMMARY AND CONCLUSIONS

Feature inhibition has been hypothesized to play an important role in search, guiding attention away from distractors and preventing ICs. Here we show by exploring the literature, that there is a theoretical niche for such a mechanism. Probe-dot studies are highlighted as being well suited to providing behavioral evidence for this mechanism. Although there is good evidence for inhibitory guidance of attention, there is also good evidence supporting the proposal that the multiple features of objects may not always be independent targets for inhibition, inhibition of one feature of an object may inadvertently lead to the inhibition of other features of the same object. Such feature non-independence of suppressive mechanisms in search is consistent with the AET account (Duncan and Humphreys, 1989), but problematic for guided search models (e.g., Treisman and Sato, 1990; Wolfe et al., 1989) that are rooted in the FIT tradition (Treisman and Gelade, 1980). We suggest that both positive excitatory and negative feature inhibition are necessary to permit efficient selection. We speculate that a brain network involving feature-specific areas V4, MT, FFA, PPA, feature general spatial representations in parietal and precuneus areas, top-down control structures in frontal cortex, and a early sensory regions, e.g., V1 work together to implement feature inhibition.

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Binding “when” and “where” impairs temporal, but not spatial recall in auditory and visual working memory

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Information about where and when events happen seem naturally linked to each other, but only few studies have investigated whether and how they are associated in working memory. We tested whether the location of items and their temporal order are jointly or independently encoded. We also verified if spatio-temporal binding is influenced by the sensory modality of items. Participants were requested to memorize the location and/or the serial order of five items (environmental sounds or pictures sequentially presented from five different locations). Next, they were asked to recall either the item location or their order of presentation within the sequence. Attention during encoding was manipulated by contrasting blocks of trials in which participants were requested to encode only one feature to blocks of trials where they had to encode both features. Results show an interesting interaction between task and attention. Accuracy in serial order recall was affected by the simultaneous encoding of item location, whereas the recall of item location was unaffected by the concurrent encoding of the serial order of items. This asymmetric influence of attention on the two tasks was similar for the auditory and visual modality. Together, these data indicate that item location is processed in a relatively automatic fashion, whereas maintaining serial order is more demanding in terms of attention. The remarkably analogous results for auditory and visual memory performance, suggest that the binding of serial order and location in working memory is not modality-dependent, and may involve common intersensory mechanisms.

Keywords: automatic encoding, attention, localization, serial order, environmental sound

INTRODUCTION

There is ample evidence that different types of information can be associated into integrated multi-dimensional representations in working memory (see Zimmer et al., 2006 for a review). Such integrated representations are ensured by processes of binding, which allow the integration of separate features in correct combinations (Treisman, 1999). Evidence of multi-dimensional binding has had a significant impact on working memory models. A major example is represented by Baddeley's classic working memory model, which has been revised to include an additional component (i.e. the episodic buffer) responsible for integrating different information in short-time multi-dimensional representations (Baddeley, 2000).

Binding processes can involve various categories of stimulus features and take place in different sensory modalities. However, until now some features and modalities have been examined more extensively than others. Specifically, while feature–feature binding (see for example the seminal works of Treisman, 1999; Luck and Vogel, 1997) and feature–location binding (see, among others, Prabhakaran et al., 2000) have been extensively investigated, less attention has been devoted to explore the mechanisms of binding between the serial order and the location of items. Regarding sensory modalities, most binding studies focused on vision and

much less attention has been devoted to the other modalities. In the current study, we focused on serial order–location binding in auditory as well as visual working memory, in order to fully investigate the (dis-)similarities in spatio-temporal binding processes in vision versus audition.

A crucial research question in working memory binding is about the automaticity of feature association. In other words, is overt attention crucial to encode a specific feature, or is it automatically encoded when processing other dimensions of the stimuli? Previous studies in feature-to-location binding have demonstrated that when encoding the identity of the item, we also process its location (Ellis, 1990; Andrade and Meudell, 1993; Köhler et al., 2001). Recently, opposite effects have been reported in the auditory modality by Maybery et al. (2009). They observed that a task irrelevant variation in the identity of the stimuli can affect the recall of auditory locations. They argued that this difference between modalities depends on the fact that location is a crucial feature for vision, whereas it is a subordinate dimension in audition. Few studies specifically focused on the automaticity of serial order–location binding (Dutta and Nairne, 1993; van Asselen et al., 2006). Results so far indicated that the intention to memorize one feature is important for feature encoding. For example, Dutta and Nairne (1993) found a mutual interference

between spatial and temporal information. In their study, participants selectively attended either to spatial or temporal information during a speeded classification task, while ignoring irrelevant variations along the other dimension. They demonstrated that whereas participants can selectively ignore temporal or spatial variations when no recall of the irrelevant dimension is required, they suffer interference when information from both dimensions must be remembered (Dutta and Nairne, 1993). Similar results were found by van Asselen and colleagues. They asked participants to recall either the exact serial order, or the exact individual positions of sequentially presented visual items. In order to investigate the automaticity of spatio-temporal integration, they manipulated attention toward each one of the two dimensions by biasing the expectancy of attending either to a spatial or to a temporal task across different blocks of trials. In two “pure” blocks, participants were exclusively presented with temporal or spatial trials. In two “mixed” blocks, they were presented with the majority of trials (80%) within one dimension (temporal or spatial), and the remaining trials (20%) within the alternative dimension. Higher accuracy was obtained in expected tasks than in the less expected task, both in the spatial and the temporal domains. The authors concluded that attention plays an important role during the encoding of both the spatial and the temporal dimension of visual objects (van Asselen et al., 2006).

In all the above-mentioned order–location binding studies, the existence of bi-directional associations of features is assumed. However, evidence of asymmetric associations has also been observed, in which the encoding of one feature obligatorily implicates the encoding of a second feature, whereas the encoding of the second feature does not imply the encoding of the first one (Jiang et al., 2000; Olson and Marshuetz, 2005; Maybery et al., 2009). In a study conducted in our laboratory, we recently demonstrated asymmetric costs of feature binding in the recall of location and order in the auditory modality (Delogu et al., submitted for publication). In two experiments, participants were presented with sequences of five environmental sounds originating from five different locations in space with the instruction to memorize their location, their serial order, or both. Participants were then asked to recall either sound position or serial order. Results showed that attention in encoding has a stronger effect on the serial order than on the position task. We concluded that, in auditory working memory, serial order, and position are not automatically integrated in a multi-dimensional representation. Moreover, such asymmetric effects of attention lead to the idea that one of the two features is primary and more automatically encoded *per se*, while the other feature is subordinate and/or more demanding in terms of attention. In the specific case of serial order–location binding, our recent findings suggest that in spatio-temporal binding, a primary role is played by item location in auditory working memory. In fact, our results indicated that dual encoding only impairs temporal recall, but not spatial recall (Delogu et al., submitted for publication). By contrast, in van Asselen’s study with visual stimuli, dual encoding impaired both temporal and spatial recall, and no asymmetric effects of attention were found. Such differences in spatio-temporal binding between the visual and the auditory domain can be due to an authentic modality effect, or to the mere effect of the different experimental procedures and designs

adopted in the two studies. A direct intermodal comparison is needed to disentangle the two alternative explanations.

In the current study, we used a within-subject design to directly test the interactions between item modality (i.e. audition versus vision) and the attention in encoding (dual versus single encoding) in serial order–location binding. We presented participants with two blocks of trials that were either exclusively serial or exclusively spatial, and with a third block of trials in which the expectations of recalling the serial and the spatial dimensions were equal. With respect to the latter block, it was reasoned that, as participants did not know which of the two alternative tasks they were going to perform, they were forced to maintain both the serial order and the spatial location of items in their memory.

MATERIALS AND METHODS

PARTICIPANTS

Twenty-four students from Utrecht University [mean age: 21.3 (SD = 3.14), 15 females] participated in the experiment in exchange for course credits or a small amount of money. All participants reported normal hearing and sight, and they were all right handed. Informed consent was obtained from all subjects.

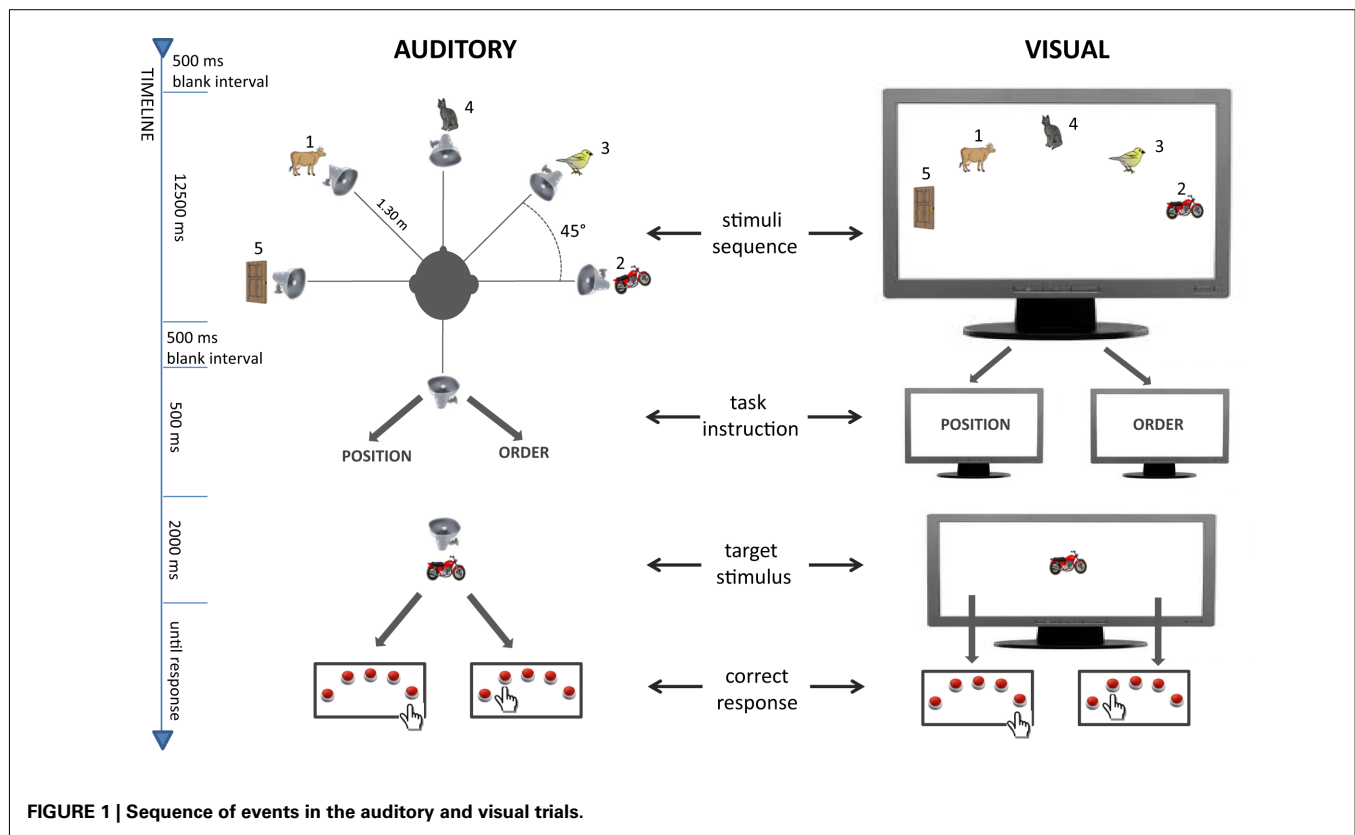
APPARATUS

In the auditory condition, five loudspeakers were placed inside a circular soundproofed room used to present the auditory sequences (see the top-left part of **Figure 1**). They were positioned 45° apart from each other in azimuth, at angles of −90°, −45°, 0°, +45°, +90° (0° corresponds to the position faced by the participant). The loudspeakers were placed at about the head height of the seated participant (1.25 m above the ground), at a distance of 1.35 m from the participant’s head. A sixth loudspeaker (hereafter *test loudspeaker*) was positioned behind the participant (180° angle), at the same height as the other five speakers and 1.35 m behind the participant’s head. Sound absorbing materials were arranged on the walls in order to minimize sound wave reflection. All sounds were presented with an average loudness of 70 dB. A response box was placed in a table in front of the participant for providing responses to stimuli presentation. The position of the keys on the response box was arranged in an ergonomic way in order to reduce muscular tension and fatigue. A 24-channel audio card (MOTU 24 i/o) controlled by a custom script written in MATLAB (The Mathworks, MA, USA) was used for sound presentation. A chinrest was used to prevent head movements during listening.

In the visual condition, five positions in a screen were used to present the visual stimuli (see **Figure 1**, top-right). The visual angle between two subsequent positions was about 7° apart from each other. The screen was placed at about the head height of the seated participant (1.25 m above the ground), at a distance of 1 m from the participant’s head. The same response box used in the auditory condition was also used in the visual condition.

STIMULI AND TASKS

Forty environmental sounds and 40 pictures were used in the study. In order to make visual and auditory presentations as comparable as possible, the semantic category of auditory and visual stimuli were matched (e.g. sound of the telephone and image of a telephone) whenever possible. For images that did not have an



immediate sound correspondence and for sounds with no immediate pictorial representation, we selected pictures and sounds which were correctly named by the 100% of the participants in a pilot study.

The auditory stimuli were sounds of human beings (e.g. baby crying, person coughing), animals (e.g. cat meowing, bird chirping), and inanimate objects (e.g. car engine, telephone ring) selected from a wider set of environmental sounds described in a previous study (Delogu et al., 2009). All stimuli were edited to a duration of 2 s. Sounds were presented in sequences of five sounds, each of them originating from a different loudspeaker. All the sequences contained a semi-random selection of items, with the limitation that a sound which was presented in the last and in the second-to-last sequence could not be presented in the following sequence.

Visual stimuli included pictures of human beings, animals, and objects selected from the database described in Rossion and Pourtois (2004). All stimuli were included in sequences of five pictures and presented on screen for 2 s.

In both the visual and auditory condition, the experiment included three different blocks of trials: two blocks of 10 sequences each (single encoding), in which participants had to perform only one task (either the location memory or the temporal order task) throughout the entire block; one block of 20 sequences each (dual encoding), in which the participants were requested to perform the location memory task in the 50% of trials and the temporal order judgment in the remaining 50%. When attending the mixed block trial, participants did not know if they were going to perform

a spatial or a serial order task. Consequently, they had to encode and maintain both types of information.

PROCEDURE

Participants were first trained to use the five keys to indicate either the position (with the leftmost key indicating the leftmost position and the rightmost key indicating the rightmost position), or to indicate its serial order (with the leftmost key corresponding to the first sound/picture in the sequence and the rightmost key corresponding to the last sound/picture in the sequence). Before starting the experiment, they also performed an auditory localization task in which they were asked to indicate the position of a series of 100 sounds randomly originating from one of the five speakers. Results of the sound localization task showed high accuracy (mean 96%, SD: 3%), indicating a sufficient Azimuthal separation between auditory sources.

Before each block of trials, instructions were given indicating which task the participants were about to perform during the block (i.e. serial order, spatial location, or both). In the dual encoding block, before starting, participants were explicitly told that they could be asked to recall either the position or the order of the items. As participants were told which feature they would have to recall only after the presentation of the stimuli sequence, they were forced to pay attention to both features during the sequence presentation in order to optimize recall performance. For each learning sequence, participants triggered the presentation by pressing a key on the response box. After the learning sequence, the instruction word (either “ORDER” or “POSITION”) indicating

which feature they had to recall was presented for 500 ms from the test loudspeaker in the auditory condition and in the middle of the screen in the visual condition. Then all stimuli of the learning sequence were presented again, one by one in a random order, from the test loudspeaker or in the middle of the screen. After each test item, they recalled either the location or the serial order of the item in the learning sequence (see **Figure 1**). Participants could respond to target items both while items were still displayed and after their presentation. The experiment lasted approximately 1 h. The order of presentation of the visual and the auditory blocks, as well the order of the three blocks within each of the two modalities, was counterbalanced between participants.

ANALYSIS

A three-factor repeated measure ANOVA analysis with the variables *task* (location versus order), *encoding* (single versus dual), and *modality* (auditory versus visual) was performed on the mean percentage of correct responses. For *post-hoc* analyses, Bonferroni correction was applied to pairwise comparisons.

Two participants were excluded from final analysis because their accuracy in one of the experimental blocks was under the group average of more than 2 SD.

RESULTS

The main effects of the factors *task*, *modality*, and *encoding* as well as the interactions between these factors are reported in **Table 1**.

A significant main effect of *task* indicates that the overall across-modalities accuracy in the serial order task (77.6%) was higher compared to accuracy in the location task (72.5%). A significant main effect of *modality* was also found, which shows that the overall accuracy was higher in the visual condition (78%) than in the auditory condition (72%). *Encoding* also yielded a main effect, with higher accuracy in the single encoding trials compared to the dual-encoding trials.

One of the crucial comparisons of our investigation is the two-factor interaction between *task* and *encoding*. This interaction was significant, demonstrating that the effects of attention are significantly higher for the temporal than for the spatial task. Pairwise comparison showed that the influence of attention was significant only for the serial order task. Specifically, while serial order recall is more accurate after dual than after single encoding both in the auditory condition, $t(20) = 5.89$, $p < 0.001$ and in visual condition, $t(20) = 6.69$, $p < 0.001$, location recall does not differ after dual and single encoding neither in the

auditory condition, $t(20) = 1.67$, $p = 0.44$ nor in visual condition, $t(20) = 5.89$, $p = 0.36$.

The two-factor interaction between *task* and *modality* and the interaction between *modality* and *encoding* were both not significant. The three-factor interaction between *task*, *encoding*, and *modality* was also not significant, indicating that the different influence of attention in the spatial and temporal tasks is not modulated by the modality of the stimuli. Accuracy in all conditions is displayed in **Figure 2**.

DISCUSSION

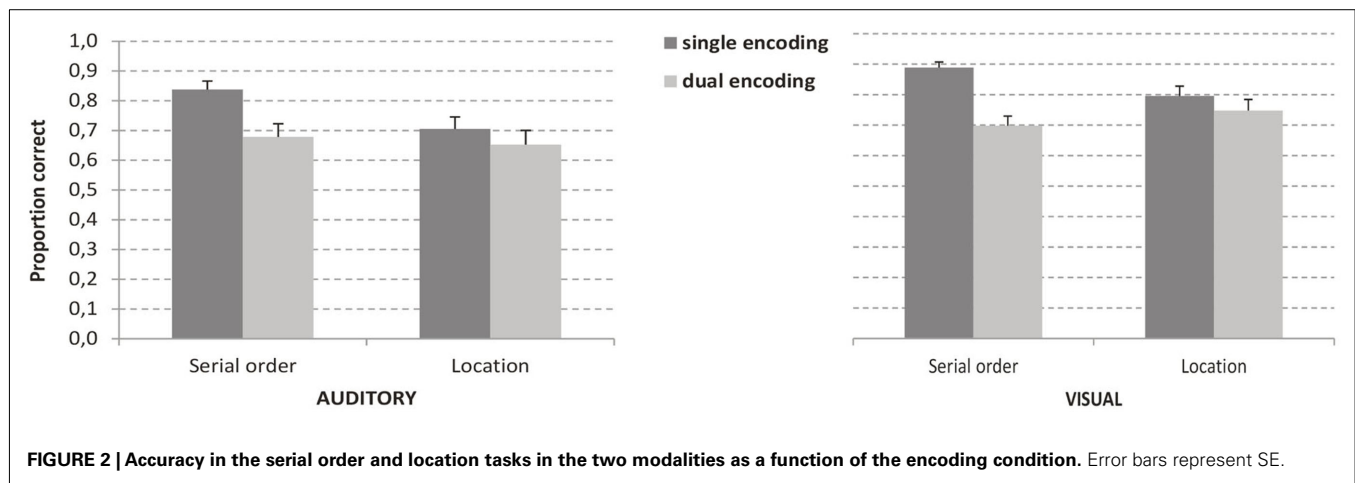
The aim of the current study was to investigate how spatial and serial order features are encoded, both in isolation and under dual encoding conditions, in auditory and visual working memory. We presented sequences of five auditory or visual stimuli originating from five different locations in space, and we asked participants to recall either the position or the serial order of items. Attentional focus during encoding was manipulated by contrasting blocks of trials containing only spatial or temporal trials to mixed blocks containing the same amount of spatial and temporal trials.

Regarding feature processing *per se*, we found that spatial information is more difficult to recall than serial order information. Such difference could be due to different rehearsal mechanisms for serial order and spatial information. We suggest that whereas serial order recall is achieved by mere item rehearsal, location recall is not guaranteed by item identity maintenance. In fact, whereas serial order maintenance is likely to be a mere byproduct of stimuli identity rehearsal (Gmeindl et al., 2011b), location maintenance cannot be accomplished by simply rehearsing item identity and it needs specific spatial additional processing. Concerning the format in which items were rehearsed, it is possible to argue that sounds and pictures were recoded in a verbal format. To establish the influence of verbal recoding in our experiment, an articulatory suppression (AS) condition could have been included. However, for two reasons we decided not to include AS in the experimental design. Firstly, the required tasks already were rather demanding, especially in the dual encoding condition. Therefore, we reasoned that an additional requirement could cause an extreme drop of accuracy and weaken the effects in analysis. Secondly, we argued that the inclusion of AS could cause a greater impairment in the serial order task, since AS has a greater effect on serial order than on spatial encoding (see Dent and Smyth, 2005).

Another possible source of differentiation between the accuracy in the two tasks could be the response method. It is in fact possible that the response device could have caused some benefits for spatial processing. This is because the response buttons were arranged in a horizontal fashion, similarly to item positions, while having a less direct analogy to item serial order. However, considering the higher accuracy in the serial task than in the spatial task, we can assume that serial recall was not severely impaired by the position of the response buttons. By contrast, we think that the use of different spatial configurations for response buttons, for example a spatial arrangement orthogonal to item position, could cause a substantial impairment in spatial recall, which could compromise the emergence of the effects we wanted to scrutinize. Moreover, the use of alternative response devices, like laser pointing, eye tracking or verbal response recording, would have all

Table 1 | Summary of all the ANOVA effects.

Factors and interactions	df	F	p	Part. η^2
Task	20	8.42	0.007	0.30
Modality	20	8.05	0.028	0.29
Encoding	20	42.04	<0.001	0.67
Task × encoding	20	21.68	<0.001	0.51
Task × modality	20	3.19	0.17	0.17
Encoding × modality	20	0.55	0.46	0.03
Task × encoding × modality	20	0.22	0.40	0.03



implied some advantages and raised new problems, but we do not think that they would change the substance of the findings.

Interestingly, an analogous pattern of differences between spatial and temporal tasks was found in the two modalities. This result suggests that, in spite of the obvious perceptual differences between auditory and visual stimuli processing, it could be that the same mechanisms are used in both modalities to maintain serial order (see Depoorter and Vandierendonck, 2009) and location (see Lehnert and Zimmer, 2006) respectively. Concerning memory for item location in particular, previous results suggested that spatial memory is not bound to a specific sensory modality. For example, Baddeley and Lieberman (1980) found that a visuo-spatial main task was impaired by an auditory-spatial secondary task. More recently, Martinkauppi et al. (2000) found a neural substantiation of these findings using imaging techniques. Their data indicated that a common neural network in the human cortex was activated by both auditory and visual stimuli during a working memory task.

Concerning the overall effect of attention, our data showed that participants were more accurate when encoding only the target dimension than when also encoding the second dimension. This suggests that, both in vision and in audition, the integration of serial order and location in working memory is not automatic. This result is consistent with previous findings in both the visual (Dutta and Nairne, 1993; van Asselen et al., 2006) and the auditory (Delogu et al., submitted) domain.

More interestingly, we found that the influence of attention critically depends on the feature to be recalled. In fact, the concurrent encoding of the alternative feature selectively impairs serial order, but does not interfere with item position. As tolerance toward concurrent processing is interpreted as a sign of automaticity (Ellis, 1990; Andrade and Meudell, 1993), we infer that, in dual encoding contexts, spatial encoding is more automatic than serial order encoding. This result confirms, and extends to vision, what we recently found in the auditory modality (Delogu et al., submitted). It is important to underline that the asymmetric influence of attention on the two tasks is remarkably analogous in the two sensory modalities. The absence of modality effects leads to the consideration that some mechanisms of working memory do not depend on the modality of the input, but are more related to the feature to be processed and recalled (e.g., spatial, serial, identity, or

an association of any of them). In particular, the evidence that the dual encoding influence on serial order recall is not dependent on item modality is consistent with previous studies demonstrating the existence of a modality-independent representation of order information in working memory (Jones et al., 1995; Depoorter and Vandierendonck, 2009).

Why is location more resistant to interference than serial order? We may speculate that it depends on different rehearsal mechanisms of spatial and serial information in WM. In serial order rehearsal, which requires remembering the correct sequence of items, the memory of the serial order of each single item is strictly linked with the memory of the other elements in the sequence. In this context, a constant attentional control of item order during rehearsal could be crucial. By contrast, in spatial rehearsal, in which the location of each single item is not linked with the memory of other items' location, maintenance of item location in space could be configurational and not sequential. In this context, a constant attentional control could be less critical for spatial rehearsal, and the encoding of a concurrent feature can be attained without weakening spatial processing. This interpretation is consistent with the notion that the maintenance of dynamic, sequential information is more demanding in terms of attention than static information. In fact, the former draws directly on the central executive, while the latter relies on it to a lesser extent, and only to refresh the image (Logie, 1995; Logie and van der Meulen, 2009).

However, since items are sequentially presented also in the location task, an alternative interpretation is possible. The asymmetric role of attention could be due to the fact that location of the sequence of items, encoded serially, is also rehearsed in a serial fashion, by using the same serial order of the items as in encoding. This way, in dual encoding conditions, when serial order has to be memorized too, there is no impairment in spatial recall. This account is inconsistent with a recent study by Gmeindl et al. (2011b). They found that removing serial order requirements from a location memory task improves spatial performance. They suggested that the position of multiple, serially presented items is not rehearsed serially, but it is simultaneously represented as multi-location configurations (Gmeindl et al., 2011a; see also Jiang et al., 2000). The different results can be caused by the different tasks involved in our and in Gmeindl's study. Whereas their spatial

task required recalling the position of identical squares flashing among distracters (similarly to a Corsi block test, De Renzi and Nichelli, 1975), in our spatial task participants were asked to recall the position of five different meaningful items in five fixed locations (object location memory task). Therefore, it is plausible that object location memory tasks, in which both item identity and position are relevant for the task, requires serial rehearsal. On the other hand, pure spatial tasks, in which only location but not item identity is relevant, can be achieved through a configurational, multi-location rehearsal.

Our findings are also in partial contrast with the findings of van Asselen et al. (2006), who found that not only the serial order task, but also the spatial task is impaired when attention to the target feature is reduced. This contrasting result is likely due to the fact that while we used a dual encoding condition in which the expectation of recall was equally divided between the target and the concurrent feature, they used an unbalanced attentional condition in which the expectation of recalling the target feature was extremely low (20% of the probability of occurrence). This interpretation is supported by the results of our previous study (Delogu et al., submitted) which included an unbalanced attentional condition analogous to the one in van Asselen's study. In such unbalanced attentional condition, we also obtained a significant impairment in

the spatial recall. The comparison between these different studies suggests an attentional threshold model for spatial working memory: as long as a certain amount of attention is allocated to spatial encoding, spatial recall is not influenced by attention. Only when there is an extreme drop in attentional allocation (i.e., in the 20% conditions of van Asselen et al., 2006; Delogu et al., submitted) spatial recall is impaired.

CONCLUSION

This study presents a direct comparison of auditory and visual modalities in the mechanisms of binding between spatial and serial order information.

Although overall accuracy in our experiment was higher in vision than in audition, the effects of attention on the two tasks were not modulated by the sensory modality of the input. We concluded that spatio-temporal binding is not automatic, it is task dependent, and it is not modality dependent.

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Patients with schizophrenia do not preserve automatic grouping when mentally re-grouping figures: shedding light on an ignored difficulty

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Looking at a pair of objects is easy when automatic grouping mechanisms bind these objects together, but visual exploration can also be more flexible. It is possible to mentally “re-group” two objects that are not only separate but belong to different pairs of objects. “Re-grouping” is in conflict with automatic grouping, since it entails a separation of each item from the set it belongs to. This ability appears to be impaired in patients with schizophrenia. Here we check if this impairment is selective, which would suggest a dissociation between grouping and “re-grouping,” or if it impacts on usual, automatic grouping, which would call for a better understanding of the interactions between automatic grouping and “re-grouping.” Sixteen outpatients with schizophrenia and healthy controls had to identify two identical and contiguous target figures within a display of circles and squares alternating around a fixation point. Eye-tracking was used to check central fixation. The target pair could be located in the same or separate hemifields. Identical figures were grouped by a connector (grouped automatically) or not (to be re-grouped). Attention modulation of automatic grouping was tested by manipulating the proportion of connected and unconnected targets, thus prompting subjects to focalize on either connected or unconnected pairs. Both groups were sensitive to automatic grouping in most conditions, but patients were unusually slowed down for connected targets while focalizing on unconnected pairs. In addition, this unusual effect occurred only when targets were presented within the same hemifield. Patients and controls differed on this asymmetry between within- and across-hemifield presentation, suggesting that patients with schizophrenia do not re-group figures in the same way as controls do. We discuss possible implications on how “re-grouping” ties in with ongoing, automatic perception in healthy volunteers.

Keywords: grouping, visual organization, schizophrenia, top-down grouping

INTRODUCTION

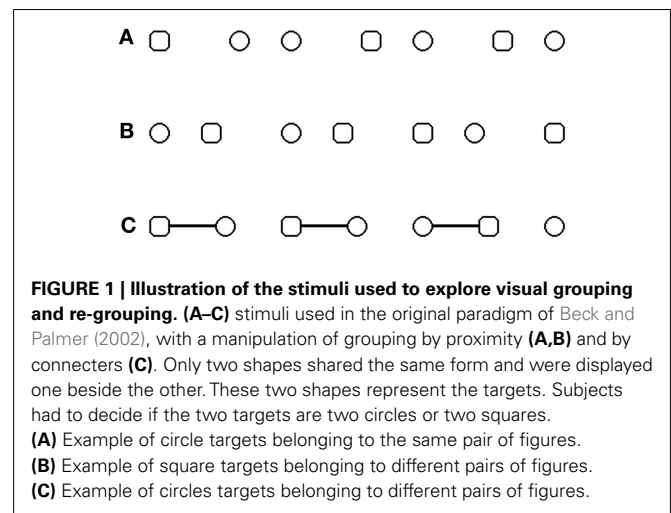
We are able to explore and select information in the environment in a flexible way and usually do not experience any limits or difficulty when doing so. In a cluttered visual scene, we can mentally select and extract visual information and even relate objects that have nothing in common. This ability appears to be impaired in patients with schizophrenia, and may impact on how they adapt to the visual environment. It has been related to a more general difficulty at organizing information that is expressed at a clinical level (Silverstein and Keane, 2011). However, the mechanisms of these impairments are still debated, and especially the relative contribution of automatic grouping mechanisms vs. high-level, top-down mechanisms. Our aim is twofold. Understanding how patients with schizophrenia explore the visual environment should help us to understand the mechanisms underlying their difficulties when attempting to adapt to an ever changing environment. More generally it might contribute to objectify and better define the difficulties of patients at organizing information. Second, patients'

results lead to questions regarding the mechanisms of the mental selection of objects in healthy volunteers and how these mechanisms tie in with automatic grouping. This question is not fully resolved in healthy controls. For this reason we went back and forth from fundamental knowledge to clinically related issues. We explored the ability to mentally relate objects in healthy volunteers, and we use this same paradigm here in patients with schizophrenia. The results will be used to discuss first their significance for patients and second what they reveal about mental selection and visual organization in healthy volunteers.

There is already considerable knowledge regarding visual processing in healthy volunteers. Form processing is known to involve a number of steps, from the extraction of primitives (local orientation, color, luminance, etc.), to the integration of the form contour and surface filling-in that sub-tend object recognition (Boucart et al., 1994; Humphreys, 2003; Grossberg et al., 2007). The integration of contour information involves Gestalt rules like grouping by collinearity, proximity, similarity or common fate,

and the use of segmentation cues in order to correctly separate object parts, objects from the background, and objects from one another (Boucart et al., 1994; Kovács, 1996; Beck and Palmer, 2002; Spillmann, 2006). Similar rules apply when considering the relationship between distinct objects, even though the pathways sub-tending the coding of relations between objects are distinct from those sub-tending the coding of the relations within objects (Humphreys, 1998; Davis, 2001). Grouping between individual items allows to identify global forms that emerge from the way local elements are organized (Kimchi, 2000; Kimchi et al., 2005). Information at the global and local levels are processed by specialized neural pathways, and structure the visual environment in a hierarchical manner (Delis et al., 1986; van Kleeck, 1989; Hübner and Volberg, 2005). A number of studies suggest that grouping mechanisms can occur automatically under conditions of inattention (Driver et al., 2001; Müller et al., 2010). It has been shown also, however, that attention can interact with grouping (Driver et al., 2001), and can be directed either toward the local or the global level (Robertson et al., 1993; Humphreys, 1998).

Here, we question what happens when attention is directed toward object pairs that are unrelated and do not form a global shape. We argue this question is not resolved by usual mechanisms of grouping, and we suspect it might be crucial to understand the impairments in patients with schizophrenia (van Assche and Giersch, 2011). We explore it by using a paradigm designed by Beck and Palmer (2002). Beck and Palmer (2002), see also Palmer and Beck (2007) built visual search tasks with a setting which can be considered as a simplified version of a visual scene. Squares and circles represent simple objects and are displayed on a horizontal row. Squares and circles alternate on the row, except for two shapes sharing the same form and displayed one beside the other (Figures 1A–C). The task of the subjects is to spot these two identical and adjacent shapes, which represent the targets, and to discriminate their form, i.e., to decide whether they are two circles or two squares. An additional manipulation allows us to evaluate the effect of grouping. The objects on the row are grouped by pairs on the basis of classical rules like proximity, or the presence of connectors linking the shapes. As a consequence of this grouping manipulation, the two identical shapes are either part of the same pair of related figures (i.e., grouped by proximity or connectors), or part of different pairs (i.e., unrelated). As can be expected, it is easier for subjects to find the targets if they are part of a pair of related shapes (i.e., grouped), than if they are unrelated and part of different pairs. This effect reflects the advantage provided by grouping. Interestingly, this advantage is modulated by contextual information, i.e., the percentage of related vs. unrelated targets within an experimental block. Beck and Palmer (2002) used three experimental blocks, one with 75% unrelated and 25% related targets, one with equal proportions of unrelated and related targets, and one with 25% unrelated and 75% related targets. The advantage for related targets increases when related targets are the majority, and decreases when they are the minority. This modulation could not be explained by repetition effects, i.e., facilitated search for a target pair when it follows a trial with a pair in the same condition (e.g., related targets following related targets or unrelated targets following unrelated targets). Indeed, Beck and Palmer (2002) observed probability effects for both repeated and non-repeated trials. The



performance modulation rather reflects the prioritization of one type of pairs (related or unrelated) according to the contextual information provided by the frequency of these pairs within a given experimental block. On each trial subjects must process visual information in order to locate the related pairs, and then can direct their attention to the prioritized pairs. Since the prioritization relies on the estimation of a frequency across different trials and is not provided by information in a single trial, it can thus be considered as a top-down effect. This does not mean that subjects provide a conscious effort to prioritize related or unrelated pairs. When subjects are not informed about the proportion modulation and cannot report it after the tasks, the effect is nonetheless identical to the prioritization obtained when subjects are informed (data obtained in unpublished pilot studies). All in all the modulation is considered top-down because it results from a global and automatic probability estimation rather than from a local priming effect.

A top-down modulation of grouping does not imply that unrelated targets can be prioritized, and as a matter of fact, the possibility to prioritize unrelated targets is not straightforward. In the results of Beck and Palmer (2002), the modulation effects for related and unrelated shapes were usually symmetrical. This means that each time performance was improved for related pairs, there was a symmetrical cost for unrelated pairs, and the reverse. Such results can be interpreted as a modulation of the prioritization of connected pairs, and the performance variations for unrelated shapes might be an automatic consequence of the varying prioritization of connected pairs. The more subjects would focus on connected pairs the less they would spend on unrelated shapes. In other words, the results do not imply that unrelated shapes are prioritized selectively. As a matter of fact, the advantage for related over unrelated shapes shows that selecting two unrelated shapes at the same time entails some difficulties (Beck and Palmer, 2002). The literature on multiple object tracking confirms these difficulties, even though it shows it is possible to select distinct shapes. During multiple object tracking tasks, subjects select several unrelated objects efficiently enough to track them when they move in distinct directions among distracters (reviews

in Pylyshyn, 2001; Cavanagh and Alvarez, 2005; Alvarez, 2011). It has been proposed that such ability is sub-tended by goal-directed re-grouping of the separate objects (Yantis, 1992; Alvarez, 2011). However, this ability is severely impacted when the selected objects are automatically grouped with distracters (Scholl et al., 2001; Suganuma and Yokosawa, 2006). This suggests that it is very difficult to select distinct objects when each one is part of a different group. Even with a simpler visual search paradigm and static objects, object-centered attention can be expected to induce difficulties when trying to focus on two shapes that belong to different pairs of objects. Object-centered attention implies that when attention is focused on an element of a group, then attention spreads to the whole group (Duncan, 1984; Egly et al., 1994; Matsukura and Vecera, 2006). This means that when distracters are grouped with target information, attention directed toward the target will spread to distracter information, and attention is not drawn on target information in a selective way anymore. Despite this, is it really the case that we cannot attend selectively to two items when they belong to different sets of objects? In every day life, it can happen that we pick up detail information in different sets of objects and compare them or associate them mentally. In fact, it happens each time information is hierarchical, and we wish to associate mentally details from different hierarchical objects sets (e.g., flowers from different houses, leaves from different trees, fruits from different piles). Yet we are usually able to compare two details from different houses, fruit piles, or trees without experiencing any noticeable difficulty. Our own results (Giersch and Rhein, 2008; van Assche et al., 2012) confirm we can attend to such details and associate them selectively.

We will call “re-grouping” the ability to attend selectively to figures that are not only separate but also part of different sets of objects. We obtained some evidence of “re-grouping” by deriving new paradigms from the one elaborated by Beck and Palmer (2002). We observed in two different studies that healthy volunteers are able to focus selectively on unrelated pairs, even when they belong to different pairs of figures. (Giersch and Rhein, 2008; van Assche et al., 2012). In van Assche et al. (2012), targets were circles and squares like in the original paradigm, but they were arranged in alternation on a circle around a fixation point. Subjects decided whether the two identical shapes located one beside the other were two circles or two squares, as in the typical experiment. The presence of connectors led to the perception of pairs of figures (Figure 2), and as in the previous experiments, targets were either part of the same connected pair, or belonged to two different pairs. We manipulated the frequency of connected and unconnected targets in three different experimental blocks. Contrary to previous experiments however, subjects were instructed to look at the central fixation point throughout the experiment, and this was checked by continuous eye-tracking. In case of an ocular saccade out of central area, the trial was stopped, and was presented again at the end of the experimental block. Hence, subjects could not visually sweep across the stimuli. Because eye movements were not allowed, subjects could not compare nearby figures through ocular exploration, and had to relate them mentally. This might explain why this procedure helped us to evidence “re-grouping” of unrelated figures more easily than previous paradigms. As a matter of fact, the results showed that subjects became

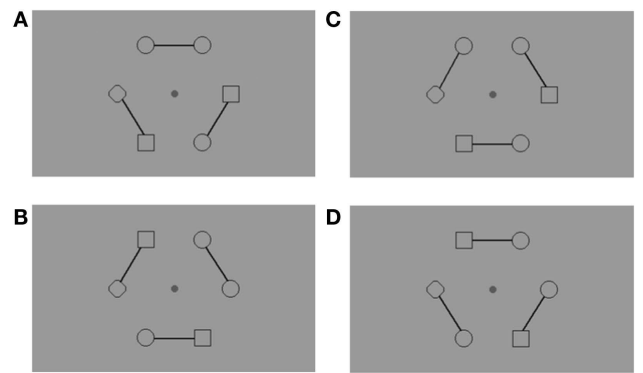


FIGURE 2 | Example of the stimuli used with an arrangement of figures around a central fixation point. Subjects had to fixate the central point throughout the trials, and this was checked with continuous eye-tracking (Cambridge Research System, 50 Hz). Connectors were introduced to link elements in pairs. Consequently, the target pair could be either connected across-hemifields (A), connected within the same hemifield (B), unconnected across-hemifields (C), or unconnected within the same hemifield (D). There was always a diamond (◆) on the horizontal meridian, which remained in the same location during a block of trials, either in the right or the left hemifield. Subjects were informed about the position of the diamond before the experimental block. The diamond ensured that (1) only two adjacent figures were identical, and (2) the target pair was located in equal proportion in the across-hemifield and within-hemifield conditions.

significantly faster (by no less than 123 ms) at finding unconnected targets when those targets were the majority, as compared to the block with an equal proportion of connected and unconnected targets. Despite this large improvement, performance for connected targets remained stable across these two blocks, suggesting that focalization on unconnected targets cannot be explained by an inhibition of connected targets and rather involve a selective “re-grouping” of unconnected targets.

All in all, the results suggest that unrelated stimuli can be isolated and “re-grouped” efficiently, even if they belong to different objects groups. This mechanism bypasses object-centered attention and cannot be accounted for by global/local processing. Local and global information correspond to individual shapes and pairs of related figures, respectively, but the pairs of unrelated figures correspond to neither, and may require higher-level cognitive operations. A late mechanism would be dissociated from usual mechanisms of visual grouping and would rather involve attentional selection mechanisms. It should be noted that our data does not allow us to distinguish between a simultaneous selection of two stimuli and the possibility that each figure is attended to in turn very fast, i.e., that items are selected sequentially rather than simultaneously (Hogendoorn et al., 2010). In the latter case (sequential selection), subjects would not be conscious of alternating between items. Hence, this possibility is beyond the scope of this paper, since both possibilities allow for a selective focalization on the two figures during a period of time. As such, both possibilities, simultaneous selection or fast serial selection, lead to questions regarding object-based attention, and conflict with usual, automatic grouping. We explored this question further by studying to which extent the outputs of automatic grouping and “re-grouping” differ.

Even if the mechanisms underlying this ability are clearly different to the ones underlying classical grouping, one might wonder whether they have comparable end-products.

We used the cost of across-hemifield presentation as a tool to contrast the impact of automatic grouping and “re-grouping.”

We observed that connectors between targets, or physical arrangement leading to automatic grouping, erased the cost of across-hemifield presentation (van Assche et al., 2012). The benefit provided by connectors is akin to what had been described in patients with parietal lesions, who display a difficulty to perceive stimuli in the contra-lesional hemifield (Driver, 1995; Gilchrist et al., 1996; Pavlovskaya et al., 1997; Boutsen and Humphreys, 2000; Brooks et al., 2005). The benefit of grouping contrasted with “re-grouping,” which was without effect on this cost. Even when attention prioritization led to a large improvement of performance for unconnected targets, the cost of across-hemifield presentation remained high. In fact, it was as high as when unconnected targets were the minority. These results suggest that in addition to taking different routes, grouping and “re-grouping” also differ in their output. In other words, outputs for “re-grouping” and automatic grouping would differ. This would sub-tend our subjective experience suggesting that automatic grouping provides background information and that our mental exploration is akin to playing with such information at the foreground. However, as emphasized above, we perceive only one unique outer world, implying that “re-grouping” must be somehow tied in with automatic grouping.

The literature and our own results suggest that understanding the role of “re-grouping” and how it ties in with automatic grouping might be crucial in patients with schizophrenia. Conversely, the results in patients might shed light on this question. A number of studies has shown that patients with schizophrenia have a difficulty to organize visual information (review in Silverstein and Keane, 2011), and our own initial studies suggested a selective difficulty to “re-group” unconnected items (Giersch and Rhein, 2008; van Assche and Giersch, 2011). A selective difficulty at “re-grouping” would be an argument in favor of a complete dissociation between automatic grouping and “re-grouping.” Recently however, we used a working memory task, and results suggested that patients can re-group items when incited to, but then experience a conflict between usual grouping and “re-grouping,” which contrasts with results in controls. This suggests that the difficulty at “re-grouping” also impacts on the ability of the patients to use automatic grouping processes. If grouping and “re-grouping” are found to be competing in patients but not in controls, this would confirm that the usual preservation of automatic grouping is not as straightforward as believed. It would call for explanations on how healthy subjects avoid this competition and make “grouping” and “re-grouping” coexist.

The results to date were obtained in a memory task, however, and the competition between representations of related and unrelated figures might have been specific to this memory task. To test this possibility, we checked whether similar results could be obtained in a perception task.

In order to test the possibility of a competition between grouping and re-grouping in patients with schizophrenia, we used again figures arranged in a circle around a central fixation point, as already described. We chose this arrangement because it had been

particularly efficient in showing the effect of a prioritization of unrelated figures in healthy subjects (van Assche et al., 2012). If patients are unable to re-group items, then we should see no effect of prioritization in patients, i.e., less variation in performance than in controls when the proportion of related and unrelated figures is manipulated. These results would then be similar to those observed in our first study (Giersch and Rhein, 2008). If on the contrary the task is efficient in inciting patients to re-group unrelated figures, then we should observe performance variations across blocks. Most importantly, if patients can maintain the link between related figures while re-grouping information, then performance for related figures should be preserved. If in contrast patients can re-group unrelated figures only at the expense of the link between related figures, as we observed recently (Giersch et al., 2011) then we should observe a cost for related figures that is symmetrical to the gain for unrelated figures. This would indicate a competition between the access to related and unrelated figures in patients, and would reinforce our hypothesis that specific mechanisms are at work to enable the coexistence of the two types of groupings.

In addition, we contrasted within- and across-hemifield presentations, and this was expected to further our understanding of the mechanisms at work, and especially to what extent automatic grouping and “re-grouping” are dissociated. Our previous work has shown that our configuration leads to a large RT cost in case of unconnected targets displayed across-hemifields. Interhemispheric transfer is believed to be impaired in patients (Schwartz et al., 1984; Mohr et al., 2008, but see David, 1993), and we wondered if this explains the difficulties of patients with schizophrenia at “re-grouping.” In that case patients with schizophrenia should be impaired relative to controls mainly in case of across-hemifield presentation. On the other hand, if patients can focus on re-grouped figures, the comparison of the effects of hemifield presentation in patients and controls was expected to give some indications on the mechanisms at work in the two groups. The idea was that early mechanisms of “re-grouping” were expected to be sensitive to the cost of interhemispheric transfer, whereas later and lateralized mechanisms (Kosslyn, 1987; van der Ham et al., 2011; Stevens et al., 2012) would be less sensitive to this cost. Our previous results confirmed that even though the presentation across-hemifields globally slowed down healthy subjects when the targets were unconnected, it was without effect on the prioritization induced by the manipulation of the percentage of connected vs. unconnected figures. If patients with schizophrenia re-group and prioritize pairs the same way as controls, then their pattern of responses should be similar. In contrast, a difference in the effect of across-hemifield presentation might reveal a difference in the mechanisms at work in the two groups.

MATERIALS AND METHODS

PARTICIPANTS

Sixteen outpatients responding to the DSM IV criteria for schizophrenia took part in this study. The diagnosis was based on a semi-structured interview (the *Mini International Neuropsychiatric Interview*) and established by a senior psychiatrist of the University Psychiatry Department. Symptoms were assessed by means of the Positive and Negative Syndrome Scale (PANSS, Kay

et al., 1987). Patients were matched with 16 healthy subjects on age, sex, and education level (**Table 1**). One control subject was discarded from analysis, due to technical problems with the response recording and thus 15 healthy subjects remained.

Subjects had normal or corrected-to-normal visual acuity, and were right-handed according to the Edinburgh inventory (Oldfield, 1971). They had no history of neurological disorder, generalized anesthesia within the past 3 months, drug abuse or benzodiazepines medication. All participants gave written informed consent prior the beginning of the study, consistently with the recommendations of the Declaration of Helsinki. This project was approved by the local ethics committee.

STIMULI

Each display contained six figures ($0.5^\circ \times 0.5^\circ$ of visual angle each). Circles and squares were positioned along a virtual circle (diameter = 6.8°) centered on a central fixation point. Circles and squares were displayed in spatial alternation except for two figures, the target pair, which were identical, and a single diamond. Unlike the circles and squares, the diamond was always in the same location on the horizontal meridian during a block of trials, either in the right or the left hemifield. Subjects were informed about the position of the diamond before the experimental block. This display configuration, and especially the diamond, ensured that (1) only two adjacent figures were identical, and (2) the target pair was located in equal proportion in the across-hemifield and within-hemifield conditions. There were two possible target locations for the across-hemifield location, and two possible target locations for the within-hemifield location, one above and one below the fixation point.

Three solid connectors linked figures by pairs (**Figure 2**). The targets could thus be within the same perceptual group (connected targets) or between two perceptual groups (unconnected targets). In each connected and unconnected condition, targets were displayed equally often in the same hemifield or across different hemifields.

PROCEDURE

Subjects were instructed that they had to look for two target shapes that were identical and displayed one beside the other. Their task

was to identify whether the two targets were two circles or two squares and to answer by pressing on a right (two circles) or left (two squares) response key, respectively. The onset of the display activated the computer clock, which was stopped when the subject pressed a key. Subjects were shown several examples on paper to illustrate the different target locations, and to ensure that they did not ignore unrelated targets. The distinction between related and unrelated targets was not made explicit, however.

Subjects were further told to continuously gaze at the central fixation point throughout the experiment. This ensured that our targets were effectively displayed in the same or different hemifields, and thus processed in the same or in different brain hemispheres, respectively. In addition, central fixation impeded subjects from visually sweeping across the stimulus, forcing them to covertly attend to the figures pairs instead (Moore et al., 2003; Herrington and Assad, 2010). This represents a major difference relative to previous studies with patients with schizophrenia (Giersch and Rhein, 2008; van Assche and Giersch, 2011), but is similar to our previous study in healthy volunteers (van Assche et al., 2012).

EYE-TRACKER

Eye position was recorded throughout the experiment to check constant fixation of the central point (ASL monocular infrared eye-tracker; sampling rate: 50 Hz).

EXPERIMENTAL DESIGN

The experiment was part of a protocol in fMRI; here we focus on two experimental blocks realized inside the scanner and designed to bias subjects toward connected or unconnected targets. For the sake of simplicity we do not present the results of the experimental blocks used to measure brain activation as a function of the target type. In each of the two blocks analyzed here, the proportion of the target types was manipulated. One block biased subjects toward unconnected targets (75% unconnected +25% connected targets) whereas the other block biased subjects toward connected targets (75% connected +25% unconnected targets).

All subjects were first trained extensively outside the scanner to ensure that they would be able to fixate the central fixation point throughout the scanner session, and thus that they would

Table 1 | Demographic and clinical data of the participants.

	Patients (<i>N</i> = 16) mean \pm SD	Controls (<i>N</i> = 15) mean \pm SD	Group comparison
Gender (M/F)	12/4	11/4	
Age	31.8 \pm 6	31.3 \pm 6.3	<i>t</i> (29) < 1, ns
Years of education	12.5 \pm 2.6	12.8 \pm 1.9	<i>t</i> (29) < 1, ns
Age at onset	23.5 \pm 4.8		
Disease duration	8.5 \pm 5.5		
Mean number of hospitalizations	1.7 \pm 1.7		
Medication (typical/atypical/+antiparkinsonian/no medication)	3/11/1/1		
Dose of medication in chlorpromazine equivalent	259 \pm 164		
PANSS total	76.2 \pm 21		
PANSS positive sub-scale	17.4 \pm 4.9		
PANSS negative sub-scale	20.3 \pm 6.4		
PANSS general sub-scale	38.4 \pm 12.2		

search for the targets covertly and not overtly. Our main aim was to examine the impact of the bias toward unconnected targets, and all subjects started with the experimental block with a majority of unconnected targets. The sequence of the two experimental blocks was repeated twice in the same order. The first and second run were identical, except that the location of the diamond differed (in the right vs. left hemifield, the order of the two runs being randomized across participants). Subjects were not told about the manipulation of the proportion of each target type. We checked the impact of the instructions in a preliminary experiment in healthy volunteers, and showed that performance was identical when subjects were told or not about the proportion manipulation. We preferred not to give information about the manipulation in order to avoid a possible difference in the use of this knowledge between groups. As emphasized above, it should be noted that subjects are unable to report the manipulation when asked at the end of the experiment, suggesting that the prioritization does not require a conscious effort. After the fMRI setup up, instructions were displayed on the screen, followed by an eye-tracking calibration. The validity of this calibration was checked before the beginning of the second run. Each trial began with the presentation of a central fixation point for 500 ms. The six figures appeared around this fixation point for 5000 ms, with only two adjacent figures being identical and representing the targets. Inter-trial duration was 500 ms. There were a total of 224 trials. Here we will report only the behavioral data.

BEHAVIORAL DATA ANALYSIS

Median RTs were derived from individual performance. ANOVAs were conducted on RTs and error rates. Trials with error were removed from RTs analysis.

Within-subject factors were the target type (connected vs. unconnected), hemifield presentation (across- vs. within-hemifield) and target type proportion (block with a bias toward unconnected vs. toward connected targets). The group (patients vs. controls) was the between-subjects factor. Data were pooled across the two runs (all interactions between runs – 1st vs. 2nd – and other factors – target type, hemifield presentation, target type proportion and groups: $F_s < 1$; there was no effect of right vs. left presentation).

RESULTS

There was no main effect of group: patients were only slightly slower and less accurate than controls [by 155 ms, $F(1, 29) = 1.030$, $p = 0.318$, partial $\eta^2 = 0.034$, and 3.3%, $F(1, 29) = 2.364$, $p = 0.135$, partial $\eta^2 = 0.075$]. There was however a significant group \times target type \times target type proportion \times hemifield presentation interaction on RTs [$F(1, 29) = 4.459$, $p = 0.043$, partial $\eta^2 = 0.133$], and a target type \times target type proportion \times group interaction on percent errors [$F(1, 29) = 8.555$, $p = 0.006$, partial $\eta^2 = 0.228$]. We first detail RTs (illustrated in **Figure 3**). We then estimate the cost of across-hemifield presentation and summarize data on error rates (**Figure 4**).

Patients and controls differed when targets were in the same hemifield [target type \times target type proportion \times group interaction: $F(1, 29) = 6.353$, $p = 0.017$, partial $\eta^2 = 0.179$]. The interaction between target type and target type proportion was significant in patients [$F(1, 15) = 17.160$, $p = 0.0009$, partial $\eta^2 = 0.533$] but

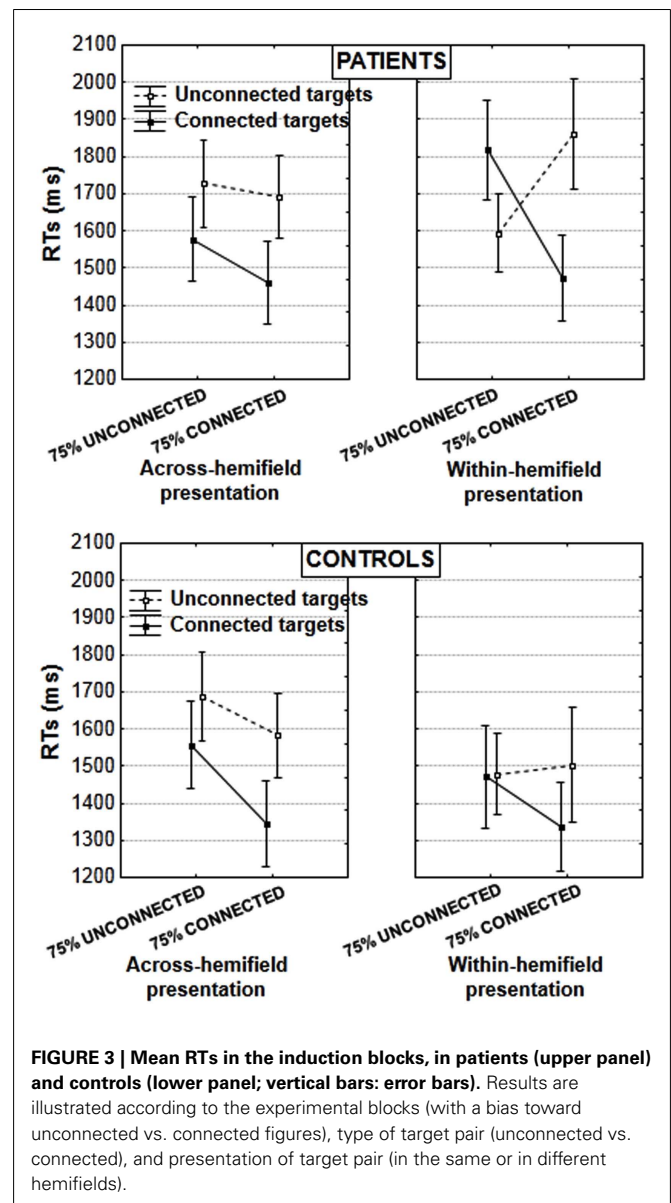
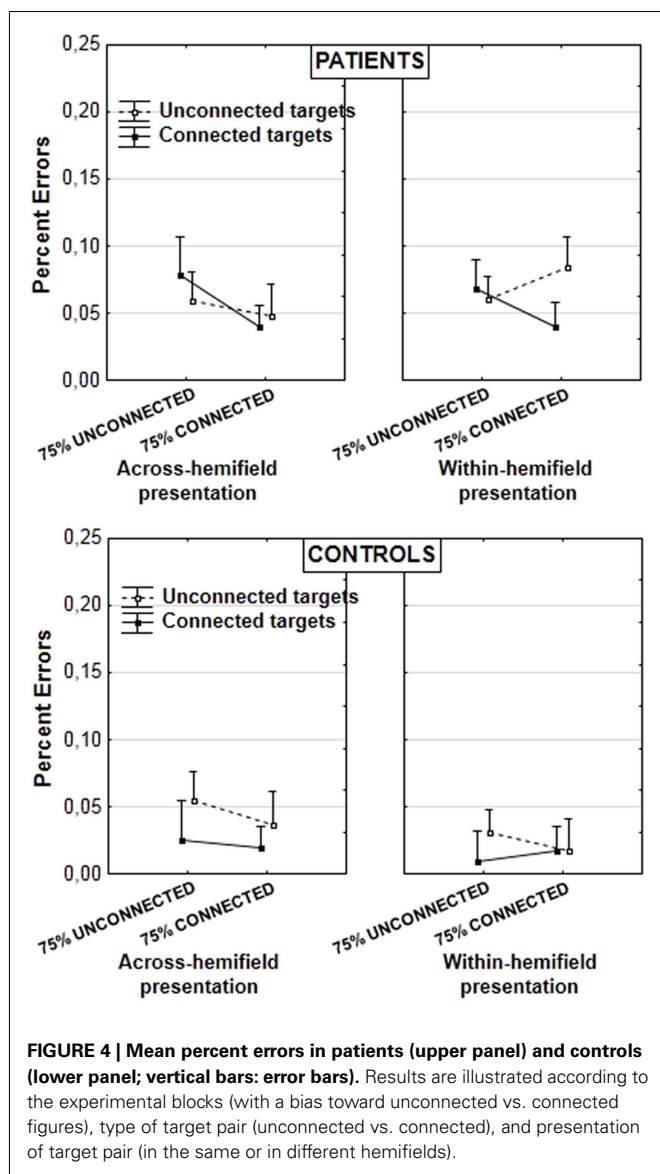


FIGURE 3 | Mean RTs in the induction blocks, in patients (upper panel) and controls (lower panel; vertical bars: error bars). Results are illustrated according to the experimental blocks (with a bias toward unconnected vs. connected figures), type of target pair (unconnected vs. connected), and presentation of target pair (in the same or in different hemifields).

not in controls [$F(1, 14) = 2.518$, $p = 0.135$, partial $\eta^2 = 0.152$]. Patients showed an unusual advantage for unconnected relative to connected targets in the block with a bias toward unconnected figures [by 224 ms, $F(1, 15) = 5.376$, $p = 0.035$, partial $\eta^2 = 0.264$, **Figure 3** rightward upper panel]. This was not the case in controls, who were equally fast for connected and unconnected targets in the block with a bias toward unconnected figures [$F(1, 14) = 0.009$, $p = 0.926$, partial $\eta^2 = 0.0006$]. In contrast in the block with a bias toward connected targets, the advantage for connected over unconnected targets was significant in both patients [390 ms, $F(1, 15) = 10.621$, $p = 0.005$, partial $\eta^2 = 0.414$] and controls [165 ms, $F(1, 14) = 6.649$, $p = 0.022$, partial $\eta^2 = 0.322$; these effects do not differ significantly, $F(1, 29) = 1.525$, $p = 0.227$, partial $\eta^2 = 0.050$]. To summarize, patients showed a significant advantage for unconnected over connected targets when the former were the majority, and vice versa. On the other hand, controls performed equally



for both target types when unconnected targets were the majority, showing that despite the priority toward unconnected targets, they were still efficient in occasional trials with connected targets.

When targets were displayed in different hemifields, there was no interaction with group [target type \times target type proportion \times group interaction: $F(1, 29) = 0.032$, $p = 0.859$, partial $\eta^2 = 0.001$]. Both patients and controls showed the typical advantage for connected over unconnected targets (controls: 184 ms [$F(1, 14) = 22.168$, $p = 0.0003$, partial $\eta^2 = 0.613$], patients: 190 ms [$F(1, 15) = 12.581$, $p = 0.003$, partial $\eta^2 = 0.456$]. This replicates results obtained with another sample of healthy subjects, and shows that connectors linking targets across-hemifields allows to facilitate the comparison of targets that are initially processed in different brain hemispheres (van Assche et al., 2012).

As a result of the performance differences in case of within- and across-hemifield presentation in patients, there was a significant interaction between target type (connected vs. unconnected),

hemifield presentation (across- vs. within-hemifield), and target type proportion (with a bias toward unconnected vs. toward connected targets) in the patients' group: $F(1, 15) = 11.752$, $p = 0.004$, partial $\eta^2 = 0.439$. In controls, there was a global effect of hemifield presentation [with an advantage of 96 ms for within- vs. across-hemifield presentation, $F(1, 14) = 5.453$, $p = 0.035$, partial $\eta^2 = 0.280$] but no interaction with other effects: especially, there was no interaction between target type, target type proportion, and hemifield presentation [$F(1, 14) = 0.119$, $p = 0.734$, partial $\eta^2 = 0.008$].

It should be noted also that the difficulties displayed by patients with schizophrenia in case of a within-hemifield presentation make it difficult to estimate the cost of across-hemifield presentation. Patients with schizophrenia were rather faster in case of across-rather than within-hemifield presentation, by 72 ms, when all results are averaged. This effect was not significant [$F(1, 15) = 1.409$, $p = 0.254$, partial $\eta^2 = 0.086$] but differed significantly from the opposite effect observed in controls [$F(1, 29) = 5.097$, $p = 0.032$, partial $\eta^2 = 0.149$]. To evaluate the cost of across-hemifield presentation more closely, we additionally checked the effect of hemifield presentation for the two conditions yielding the fastest responses in patients when the targets were in the same hemifield. For connected targets in the block with a bias toward connected pairs, there was no significant effect in either group, and no interaction between group and hemifield presentation [$F(1, 29) = 0.110$, $p = 0.732$, partial $\eta^2 = 0.004$]. For unconnected targets, there was a cost of across-hemifield presentation in both groups (209 ms in controls and 133 ms in patients with schizophrenia) and this cost did not differ across groups [$F(1, 29) = 0.489$, $p = 0.490$, partial $\eta^2 = 0.017$]. No effect involving the hemifield presentation was found significant in the analysis on error rates.

In the analysis on error rates, we decomposed the already mentioned interaction target type \times target type proportion \times group [$F(1, 29) = 8.555$, $p = 0.006$, partial $\eta^2 = 0.228$]. A significant interaction between target type and target type proportion was found in patients [$F(1, 15) = 6.212$, $p = 0.025$, partial $\eta^2 = 0.293$]. Further decompositions did not yield significant effects however. Nor was there any significant effect in controls. The effect could thus be attributed to opposite trends of grouping across experimental blocks in patients (Figure 4). The graph suggests it is present mainly when targets are displayed within the same hemifield, but this is not supported by statistical analyses. The lack of randomization across blocks and the lack of significant effects after decomposition of the results mean these results should be taken with caution. They do not contradict the results on RTs, however.

DISCUSSION

The results show that patients can re-group two items which belong to different perceptual groups when incited to do so. Patients improve performance for unconnected targets when those are more frequent, unlike in our previous studies (Giersch and Rhein, 2008; van Assche and Giersch, 2011), suggesting that they can re-group items under specific task conditions. However, this is accompanied by a disadvantage for connected targets in the within-hemifield condition, replicating results with a memory-related paradigm (Giersch et al., 2011). Being slower for

connected than unconnected targets is unusual. We observed this effect once in controls, but only in untrained subjects (van Assche et al., 2012), which was not the case here. All subjects were trained extensively before the test, and in healthy subjects, the results always show a preserved access to connected figures, even when the task incites subjects to prioritize unconnected figures efficiently.

It is as if controls have access to connected targets whatever the attention conditions. In contrast, re-grouping unconnected targets leads patients to temporarily lose the perceptual organization derived from automatic grouping. Several limitations should be discussed first, however.

There is one methodological limitation to this work related to the fact that all subjects started with a block driving them to prioritize unconnected figures. This was done for imaging reasons and prevented us from directly comparing performance variations across blocks. It is to be noted, however, that the opposite effects for connected and unconnected targets across blocks (in case of within-hemifield presentation in patients) cannot be explained by effects of order: for connected targets, performance improves from one block to the other, whereas the opposite is observed for unconnected targets. Most importantly, we base our analysis on performance differences observed within a single experimental block rather than across experimental blocks: the crucial result is the advantage for unconnected over connected targets, and this result was observed within one experimental block. Such an effect has never been observed in trained subjects, whatever the blocks order. Nor was it observed in controls in the present experiment. It can thus be reasonably estimated as being independent of this methodological limitation, especially as it replicates a similar result observed with a different paradigm (Giersch et al., 2011).

It might also be questioned if the loss of perceptual organization observed in patients is specifically related to the need to re-group unconnected items, or whether it reflects a more general weakness in grouping by connectors.

The amplitude of the reversed advantage for unconnected targets in patients shows that the experiment is sensitive enough to reveal a general weakness in automatic grouping. Weakened automatic grouping should have reduced the performance advantage provided by the connectors across all experimental blocks. However, when patients did not prioritize unconnected pairs, they displayed a preserved benefit for connected over unconnected targets. In the present results, this advantage was rather larger in patients than in controls when the prioritization concerned connected pairs. In addition the advantage for connected pairs was preserved in case of across-hemifield presentation. In sum, weakened grouping by connectors appears to result from prior attention focus on unconnected pairs rather than a genuine impairment in automatic grouping, consistent with previous results (Giersch and Rhein, 2008; Giersch et al., 2011; van Assche and Giersch, 2011).

Contrary to controls, however, patients showed significantly different effects in case of within- vs. across-hemifield presentation. Such an effect of hemifield presentation has not been observed in healthy subjects, neither in the present study, nor in our previous study (van Assche et al., 2012). Even when probability effects led to clear performance improvements for unconnected figures in healthy subjects (van Assche et al., 2012), this improvement was similar whatever the position of the targets

(within- or across-hemifields). Importantly this coexisted with a high cost of across-hemifield presentation for unconnected figures, showing that the paradigm was sensitive to the cost of across-hemifield presentation. This pattern of results is in marked contrast with the results of patients in the present study. These results suggest that even if patients “re-group” information, they do not do it in the same way as healthy subjects do. The fact that patients “re-group” efficiently only in case of within-hemifield, and not across-hemifield presentation, might be explained by an involvement of the connectivity between hemispheres. This difference between patients and controls can hardly be explained by a difference in the cost of interhemispheric transfer. There was no evidence of a higher cost of across-hemifield presentation in patients than in controls, and the main difference between the two groups occurred in case of intra-hemifield presentation. The results rather suggest that controls mobilize lateralized mechanisms when prioritizing unconnected figures (Kosslyn, 1987; van der Ham et al., 2011; Stevens et al., 2012), whereas patients use mechanisms requiring an exchange of information between hemispheres, i.e., possibly earlier and more automatic mechanisms. This interpretation requires confirmation. However, whatever the precise explanations for the effects in patients, they suggest that the patients do not re-group items in the same way as controls. In other perception studies (Giersch and Rhein, 2008; van Assche and Giersch, 2011), patients did not show evidence of “re-grouping,” but the results again suggested difficulties with re-grouping. All in all these results confirm that re-grouping requires specific mechanisms and, most importantly, that preserving automatic grouping when re-grouping unconnected figures is not straightforward.

INTEGRATING GROUPING AND “RE-GROUPING”: OUR PROPOSAL

We argue that the results observed in patients with schizophrenia shed light on the difficulties encountered when exploring the visual environment in a flexible way while maintaining a sensation of stability of the outer world. The results in patients emphasize the difficulty arising when relating unconnected items in the environment. Our results show that being able to re-group items is not enough to explore visual information in an optimal way, i.e., without losing access to automatically grouped figures. First, the way re-grouping is performed matters. It is important that grouping and re-grouping are based on distinct mechanisms. Our previous study had already suggested that the two types of grouping are not only based on different pathways, but also lead to different outputs (van Assche et al., 2012). This then raises other questions, however: what is the output of re-grouping, and how prioritizing re-grouping coexists with easy access to automatically grouped items. If the outputs of grouping and re-grouping are distinct and accessed in parallel, there should be some innate priority given to automatic grouping. This way access to items issued from automatic grouping would be preserved even when the subject prioritizes re-grouped items. This might not be enough, however. Additional ties might be necessary between the two types of groupings. Even if “re-grouping” mainly involves high-level cognitive mechanisms, these mechanisms allow us to play with information that is continuously processed by our visual system. For example, when we mentally select two tangerines from different piles and

thus mentally separate them from their piles, we still see these tangerines as belonging to their piles. When having compared the tangerines and made a choice, we need to know from which piles they are issued to take the chosen tangerines. It might thus be proposed that the “re-grouping” of items integrates the links these items have with connected objects. This would mean strong ties between re-grouped items and automatically grouped ones. The literature suggests the possibility of a more integrated representation. As emphasized above, several studies suggest the existence of specialized areas sub-tending the coding of spatial and conceptual relationships between objects (Kosslyn, 1987; van der Ham et al., 2011; Stevens et al., 2012). In line with this specialization, a possibility would be the building of a complex representation integrating the usual links issued from automatic grouping with the links created when mentally “re-grouping” objects. This would allow access to both connected and unconnected items.

Such a representation goes beyond the hierarchical representations involving local and global information. As we have seen, there are pathways specialized in the processing of local and global information and both types of information are first processed through bottom-up, automatic mechanisms. In fact they can be considered as part of the automatic grouping processes. This is not the case for “re-grouping,” however. As already emphasized, “re-grouped” pairs correspond neither to local elements nor to global information. In contrast with local/global processing, the creation of a link between two shapes that belong to different groups thus primarily originates from attention mechanisms, and creating such links is costly. It might be considered as an extension of the coding of independent elements as described by Humphreys (1998). In this work, it was proposed that “visual elements can be selected together provided that the elements activate a single, stored object representation.” In our case, a representation of “re-grouped” items does not pre-exist to the task. We propose however that subjects build this representation as a result of the task at hand. Although this idea clearly requires confirmation, it is supported by several observations. First, results in patients with schizophrenia suggest that patients avoid “re-grouping” when possible (Giersch and Rhein, 2008; van Assche and Giersch, 2011), possibly due to the effort it entails. Second, when patients cannot avoid “re-grouping,” they probably do it differently from controls, and experience a conflict between automatic grouping and “re-grouping,” which suggests that the integration of both types of groupings represents an additional cost. All in all, this might suggest the existence of specific mechanisms in order to integrate the link between “re-grouped” items in the representation of the visual scene. Some kind of relationship must be established between the two types of pairs in order to allow for both a selective focalization on one type of pair and an easy access to both. It is not only the new link between “re-grouped” items that would be coded, but also how they are related with other pairs. An item from a given set that is re-grouped with an other item from another set would be tagged as “re-grouped” but also as being part of a set of objects. Thus, when prioritizing “re-grouped” items, one would select a pair of figures tagged as being part of different groups. This representation is necessarily complex, since it includes the coding of conflicting links between objects. It is probably costly to build such a representation, but once built it enables a flexible exploration of the outer world

while maintaining its stability. This is precisely what seems to be impaired in patients with schizophrenia.

LIMITS AND PERSPECTIVES

Our proposal regarding how “re-grouping” is tied in with automatic grouping clearly requires confirmation. It remains also to be understood how a complex representation integrating outputs of “re-grouping” and automatic grouping fits in with hierarchical representations issued from local and global information. It might be possible that links issued from “re-grouping” represent an additional level of complexity that would be integrated with hierarchical representations through learning, thus leading to the building of the complex representations we propose here. This question is important in order to understand how “re-grouping” impacts on the exploration of visual scenes. It might be possible to study this question by checking to which amount the impairments described here in patients with schizophrenia are at the origin of their reduced span of exploration when spontaneously looking at visual objects or scenes (Gaebel et al., 1987; Kojima et al., 1990; Gordon et al., 1992; Phillips and David, 1997; Loughland et al., 2002; Obayashi et al., 2003; Minassian et al., 2005; Delerue et al., 2010; Delerue and Boucart, 2012). As a rule, patients’ span of exploration is reduced in space and the duration of their fixations is longer (Gaebel et al., 1987; Kojima et al., 1990; Gordon et al., 1992; Phillips and David, 1997; Loughland et al., 2002; Obayashi et al., 2003; Minassian et al., 2005). More often than not, they focus on non-significant details, and explore one part of a stimulus while missing important parts of the faces or objects (Obayashi et al., 2003; Minassian et al., 2005). In order to explore the environment in a coherent way, one needs to be able to go from one object to another without losing the visual scene from sight (Bullier, 2001; Fenske et al., 2006; Huang and Grossberg, 2010; Peyrin et al., 2010). Patients precisely appear to be impaired at relating unconnected items without losing basic links from sight. This might also account for their own complaints (Chapman, 1966): “Everything I see is split up. It’s like a photograph that’s torn in bits and put together again. If somebody moves or speaks, everything I see disappears quickly and I have to put it together again.”

It will be especially of interest to understand how complex representations are used to guide visual exploration. It is known that eye movements are not only automatic responses to retinal inputs but are regulated by a process of target selection involving a variety of complex processes, including attention, perception, memory, and expectation (Henderson and Hollingworth, 2003; Hopp and Fuchs, 2004; Krauzlis, 2005; Iwamoto and Kaku, 2010; Pélisson et al., 2010). It remains to be seen to which amount visual re-grouping is part of these mechanisms and affects endogenously driven visual exploration.

CONCLUSION

Results in patients with schizophrenia and in healthy volunteers suggest that it is possible to mentally re-group items from different sets of objects. This re-grouping conflicts with usual grouping issued from automatic grouping, and requires a cognitive processing that differs from usual grouping and from local vs. global processing. The conflict between the two types of groupings is evidenced in patients with schizophrenia. Trained healthy

volunteers, however, appear to process re-grouped objects while preserving easy access to automatically grouped objects. We propose that easy access to both types of grouping is enabled by the building of a complex representation integrating the relationships between “re-grouped” and grouped objects.

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Inhibition in the dynamics of selective attention: an integrative model for negative priming

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We introduce a computational model of the negative priming (NP) effect that includes perception, memory, attention, decision making, and action. The model is designed to provide a coherent picture across competing theories of NP. The model is formulated in terms of abstract dynamics for the activations of features, their binding into object entities, their semantic categorization as well as related memories and appropriate reactions. The dynamic variables interact in a connectionist network which is shown to be adaptable to a variety of experimental paradigms. We find that selective attention can be modeled by means of inhibitory processes and by a threshold dynamics. From the necessity of quantifying the experimental paradigms, we conclude that the specificity of the experimental paradigm must be taken into account when predicting the nature of the NP effect.

Keywords: selective attention, computational modeling, negative priming, connectionist models

1. INTRODUCTION

Selective attention enables goal-directed behavior despite the large amount of ongoing input to the sensory system. This ability is strongly linked to the problem of how information is ignored. Contradicting an earlier understanding that active attention to some objects requires passively ignoring others, an experiment by Dalrymple-Alford and Budayr (1966) revealed, in a series of Stroop tasks an active nature of the suppression of irrelevant stimuli. While the original Stroop (or Jaensch) test did not use a systematic repetition of color and color words, here the stimulus cards were designed such that the ignored meaning of a color word became the color of the next word shown. This led to slower responses as compared to unrelated stimulus colors. Even if the semantic meaning of the words had been ignored, it must have entered the cognitive system to produce the characteristic interference.

Since then, several standard negative priming (NP) paradigms have emerged featuring various dimensions in which priming can occur, e.g., the identity of stimulus objects (Fox, 1995) or their location on the display (Milliken et al., 1994). The stimulus set has also been varied, e.g., pictures (Tipper and Cranston, 1985), shapes (DeSchepper and Treisman, 1996), words (Grison and Strayer, 2001), letters (Frings and Wühr, 2007), sounds (Mayr and Buchner, 2007), or colored dots (Neill, 1977). All paradigms have in common, stimuli containing targets that are to be attended and distractors that are to be ignored. Experimental conditions depend on Stimulus repetitions, particularly the role of a repeated object as target or distractor in two successive trials. Variations of this basic setting include the manipulation of experimental parameters like the time between two related trials, the number of distractors, and

the saliency of the distractor. The sometimes contradictory results of such variations will be considered in more detail in Section 2.3. Because of the controversial nature of the NP effect, a variety of interpretations have been developed, but so far none of the theories is able to explain all aspects of the effect. Various underlying mechanisms have been proposed to act at different stages of the processing of the stimuli each justified by a certain experimental result. The theories also diverge with respect to the basis of the effect, i.e., whether it is a memory phenomenon or an effect of attention. They all agree, however, on the critical role of temporal processing for an understanding of NP.

We are particularly interested in the neurophysiological mechanisms behind attention and ignoring of perceptual information. Attention is, in principle, a form of guidance of neural activity toward relevant resources. If ignoring of stimuli or stimulus features is an active process, then those resources are subject to suppressive effects of some kind. In principle, these could be maintained by various processes, e.g., elevated thresholds, synaptic depression, or competition involving homeostatic plasticity. However, considering that attention is essentially guided by processes in the prefrontal cortex and the fact that prefrontal feedback is typically given by inhibitory signals (Knight et al., 1999), it seems likely that inhibition plays a key role in the effects of selective attention.

In the model presented here, inhibition serves multiple functions: it not only underlies attention by suppressing irrelevant stimulus components, but is essential in the formation of bound states that represent objects as synchronized set of feature-related activity and is assumed to underlie the selection of action. Corresponding to the multiple uses, inhibition occurs in several forms.

At the sensory level, inhibition is merely a relative advantage of one of the perceived features that is initiated by top-down input. In this case, the model is ignorant to the particular form of suppression, which can be implemented in different but mathematically equivalent forms, e.g., as an adaptive threshold. This indifference is due to the generality of our approach and allows us to express several conflicting theories from the psychological literature by the same formal model component.

In the feature binding component of our model inhibition occurs in a uniquely defined form: object-encoding activations in the binding layer are stabilized by lateral inhibition. Although here also alternatives are mathematically possible, there is no psychological or neurophysiological evidence for a fine-tuned mechanism as proposed by Schrobsdorff et al. (2007a). Finally, inhibition is realized in a more schematic form in action selection which we have included in the model in a form analogous to the perceptual or frontal modules rather than as a realistic representation of the motor system.

A further main contribution of the present study is a single and comprehensive computational model, combining the different theories such that it is able to express the behavior predicted by each of the NP theories¹. To deal with apparent inconsistencies and incompatibilities across the theories, we employ two strategies. First, we choose a dynamical formulation, whose natural mathematical form, allows us to identify similarities that are not obvious from the theoretical conclusions of specific experiments, and whose structure can be directly related to physiological evidence of cognition. Second, we will use a set of configuration parameters that function as weights or semaphores and can scale-down or switch-off a component that is not postulated in a certain theoretical context. In other words, all the model components can work together but often such preselected subsets of components are sufficient to describe a given empirically developed theory. It is crucial to remark that the different roles of inhibition are always present in the variants of the model that are implied by the literature, except for the retrieval module which is not discussed in some accounts. Also generally, the choice of the configuration is unambiguously specified by the psychological account in all major theories of NP. In the present formulation of the general model for negative priming (GMNP) there are seven optional components, but extensions are easily possible, should newer experimental evidence imply additional contributions to the NP effect.

We will describe in detail how a computational model can be constructed along these lines that comprises all potentially relevant processing stages for an NP task. The result is not only a comprehensive model of the theories of NP, but more generally, a framework for perception-based action in natural or artificial cognitive systems. The system is explicit in the sense that the components are mathematically defined. The system is also connectionist, i.e., the interaction between the components represent the task (see **Figure 3**) which is realized either by design or in the wider context by a learning process. Finally, the system is

dynamic, i.e., the activity levels of all components change in time and excite, inhibit or modulate each other. This reflects the importance of the time course in NP as well as in general behavioral contexts.

The paper is organized in the following way. We will first clarify terminology, deepen the discussion on how to concretize psychological theories, present the NP effect, give an overview on the biological background of the model units and finally explain how these enter into the proposed GMNP. The second section thoroughly reviews existing theories of NP. Specifically, we give a historical overview of the development of theories and what additional conclusions were drawn in experimental papers. The quantification of theories and how they are integrated in the framework of the GMNP is followed by a technical chapter that describes the implementation of the model in a way allowing researchers to reproduce the simulations. Finally the behavior of the GMNP in various NP paradigms is shown. The concluding discussion summarizes these results and considers the potential of the model beyond the described target application in NP.

2. MATERIALS AND METHODS

We present an integrative connectionist model of NP. For a thorough description of the model and the necessity of its parts, this section is organized as follows. After defining basic experimental nomenclature we very briefly present a generic NP experiment to introduce the viewpoint of NP research. Next, we summarize the various and diverse modulations of NP when faced with a wide range of experimental variations, thereby showing the sensitivity of the phenomenon and thus the requirement of a rather complex model. Then, we review a number of theoretical accounts that were postulated to explain a certain aspect of NP. Those theories will be incorporated in our model. After an overview of the GMNP, we describe the role of the individual model components in detail, and finally, the rigorous mathematical formulation of the GMNP is presented.

2.1. DEFINITIONS

In the present study we will use the following definition: NP is a slowdown in reaction time in a repetition condition where a former distractor has become target. Because we define the term NP by reaction time differences, we shall not use it to denote the ignored repetition condition. Instead we will label the condition by two (or four) letters that indicate the configuration of stimuli in a trial consisting of a prime and a probe display (see Christie and Klein, 2001). Generally, the first letter contains information about which part of the prime display is repeated in the probe display: the letter D represents the distractor, while T represents the target. The second letter indicates the role the particular object has in the probe display. For example, the string DT refers to the condition in which the prime distractor (first letter D) is repeated in the probe trial as a target (second letter T), which denotes the traditional NP condition. If no stimulus is repeated, the condition is denoted by CO. In case both objects are repeated there is a second pair of letters appended for the second object. Because a target and a distractor are each shown in the prime and the probe display, seven relevant combinations of target-distractor relations are possible, see **Table 1**.

¹The source code containing several paradigm examples is available through the project web site <http://www.bccn-goettingen.de/projects/gmnp>

2.2. A NEGATIVE PRIMING EXPERIMENT

We will now very briefly discuss a prototype NP experiment that we will refer to in the following discussion. The experiment has been adapted from the classic study by Tipper (1985) and is presented in detail in Schrobsdorff et al. (2007b). Subjects are instructed to name the green pictogram as quickly and accurately as possible (see Figure 1). Stimuli are six different objects, represented by hand-drawn pictograms that are either shown in green or in red. We use voice recording together with a sound level threshold to determine the reaction time for every trial. As the experiment is run in German, possible responses are German names of simple objects that begin with a plosive and consist of a single syllable: *Baum* (tree), *Bus* (bus), *Ball* (ball), *Buch* (book), *Bett* (bed), and *Bank* (bench), for a sharp, and thus easily detectable onset of the sound signal. For efficiency reasons, we present the trials continuously, such that every trial primes the subject for the following trial (see Ihrke and Behrendt, 2011, for a discussion of the implications of this procedure). Object presentation is balanced in the different priming conditions as well as in their appearance as target and distractor. Implemented priming

conditions include CO, DT, TT, DDTT, and DTTD, see Table 1 and Figure 1.

A stimulus display consists of two overlapping line drawings, a green target, and a red distractor object. The subject is instructed to name the target objects aloud and ignore the superimposed red objects. They were told to answer as quickly and as accurately as possible. Then, after a blank screen period and the presentation of a fixation cross, the next display is presented. Mean reaction times of the different priming conditions, the standard deviations, and the effect strengths, i.e., the difference to CO trials, are shown in Table 2. For details, see Schrobsdorff (2009). DTTD trials produce the slowest responses, followed by DT and CO trials, whereas the responses to TT trials are faster than control and DDTT trials produce the fastest responses.

The experiment shows how the repetition of stimuli can influence reaction times in a NP paradigm. A repetition of relevant stimuli leads to prominent speedups (TT, DDTT conditions), whereas a presentation of formerly irrelevant stimuli as the current target results in slowed reaction times (DT and DTTD conditions) as compared to the control condition.

Table 1 | The priming conditions of a paradigm with one target and one distractor in each of the prime and probe display.

	Prime display		Probe display		
	Target	Distractor	Target	Distractor	
TT	A	B	A	C	Target(<i>n</i> + 1) = target(<i>n</i>)
DT	A	B	B	C	Target(<i>n</i> + 1) = distractor(<i>n</i>)
TD	A	B	C	A	Distractor(<i>n</i> + 1) = target(<i>n</i>)
DD	A	B	C	B	Distractor(<i>n</i> + 1) = distractor(<i>n</i>)
DDTT	A	B	A	B	Target and distractor are repeated
DTTD	A	B	B	A	Target and distractor are swapped
CO	A	B	C	D	Two new stimuli

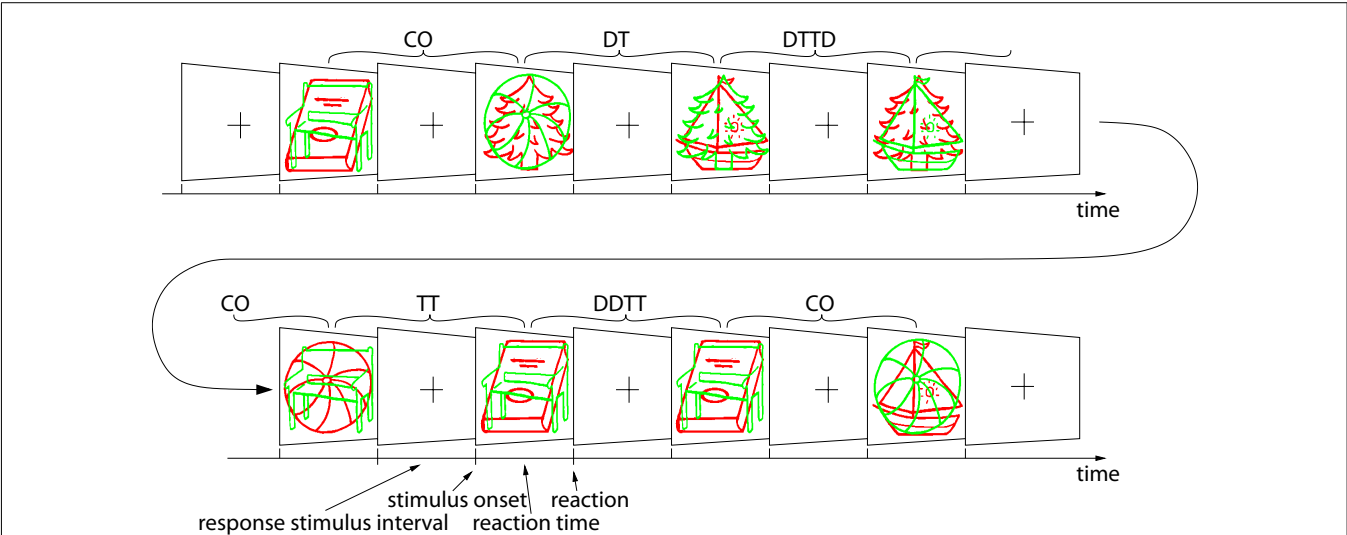


FIGURE 1 | Example of a sequence of stimuli. Consecutive screens are shown. Either stimuli or a blank screen followed by a fixation cross is displayed. Acronyms are explained in Table 1.

2.3. CHARACTERISTICS OF THE NEGATIVE PRIMING EFFECT

Negative priming has been found in a wide variety of experimental contexts (for reviews, see Fox, 1995; May et al., 1995; Tipper, 2001; Mayr and Buchner, 2007). For example, NP has been elicited using different stimuli such as line drawings (Tipper and Cranston, 1985), letters (Neill and Valdes, 1992; Neill et al., 1992), words (Grisson and Strayer, 2001), auditory stimuli (Banks et al., 1995; Buchner and Steffens, 2001; Mayr and Buchner, 2006), and nonsense shapes (DeSchepper and Treisman, 1996). NP has been found in various tasks including naming (Tipper, 1985), same-different matching (DeSchepper and Treisman, 1996), Stroop-like tasks (Neill, 1977), and spatial localization (Milliken et al., 1994; Park and Kanwisher, 1994; May et al., 1995; Kabisch, 2003), see Figure 2 for four example paradigms.

The NP effect is sensitive to a large number of parameters. Most paradigms show a particular aspect of NP, but no global pattern of results exists (Fox, 1995). It has been shown that NP can depend on the length of the response stimulus interval (RSI) between prime and probe (Neill et al., 1992; Kabisch, 2003; Frings and Eder, 2009). However, there are also studies reporting a constant NP effect for varied RSIs (Hasher et al., 1991, 1996; Tipper et al., 1991). Surprisingly, for very short RSIs, a DT condition can produce a facilitatory (Lowe, 1985), or hampering effect (Frings and Wühr, 2007). At the other extreme, an experiment revealed NP after a month using nonsense shapes which are very unlikely to be seen in other circumstances (DeSchepper and Treisman, 1996). For continuous presentation of trials, the proportion of preprime RSI and current RSI influences NP (Neill and Valdes, 1992; Mayr and Buchner, 2006), but not reliably (Hasher et al., 1996; Conway,

1999). In the absence of distractors in the probe trial during a DT condition, NP vanishes or even reverses to facilitation (Allport et al., 1985; Lowe, 1985; Tipper and Cranston, 1985; Moore, 1994). A more salient prime distractor increases the magnitude of the NP effect in DT conditions (Grisson and Strayer, 2001; Tipper, 2001). NP is reduced or even reversed to facilitation when the emphasis is put on speed rather than accuracy (Neumann and Deschepper, 1992). Increasing the perceptual load, e.g., by raising the number of distractors presented in a single trial, leads to less NP (Lavie et al., 2004). In other settings a higher number of prime distractors causes an increase of NP (Neumann and Deschepper, 1992; Fox, 1995). The inclusion of TT trials or single target trials in the presentation sequence enhances NP (Neill and Westberry, 1987; Titz et al., 2008). A short presentation time of prime and probe stimuli attenuates NP (Gibbons and Rammsayer, 2004). NP vanishes if the target is presented a bit earlier than the distractor in the prime trial. On the other hand, if the prime distractor is shown simultaneously with the prime target but blanked after a short time, NP is observed (Moore, 1994). If the prime display contains a single stimulus that is masked, subjects reporting awareness of the prime object show positive priming, while subjects not aware of the object show a NP effect (Wentura and Frings, 2005). In subliminally primed trials the presence of a distractor in the probe leads to negative priming, whereas the absence of a probe distractor leads to a positive priming effect (Neill and Kahan, 1999).

2.4. THEORIES OF NEGATIVE PRIMING

Because of the sensitivity of the NP effect to numerous factors, a variety of theories have been proposed to explain the disparate experimental facts. None of the present theoretical descriptions, however, explains all observation related to the NP effect, cf. Section 2.3. In the present section we will give an overview on the most relevant approaches.

2.4.1. Distractor inhibition theory

In the first attempt to explain NP, the inhibition hypothesis (Neill, 1977; Neill et al., 1990) inhibition plays a central role. Later, this hypothesis branched into distractor inhibition theory (Tipper, 1985, 2001; Tipper and Baylis, 1987; Tipper et al., 1988, 1991, 2002; Tipper and McLaren, 1990; Houghton and Tipper, 1994, 1996), and episodic-retrieval theory (Neill and Valdes, 1992, see Section 2.4.2).

Table 2 | Reaction times, standard deviation, and priming effects, i.e., the differences of control (CO) reaction time and reaction time of the according condition (DT, DTTD, TT, TDDT).

	(RT) (ms) (SD)	Effect (ms)
CO	660.22 (62.85)	–
DT	681.57 (69.65)	–21.36
DTTD	685.92 (78.04)	–25.70
TT	625.02 (65.29)	35.20
DDTT	600.69 (70.56)	59.53

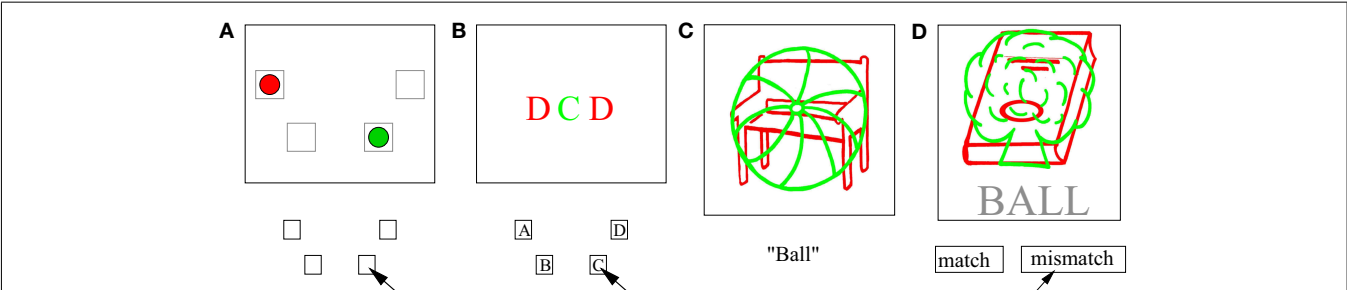
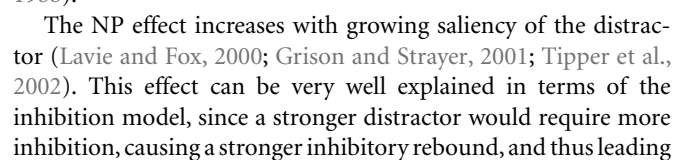


FIGURE 2 | Four different paradigms for NP. (A) The location priming paradigm reveals NP in the encoding of space. (B) The flanker task implements a stimulus response mapping. (C) Responses are given as vocalization in the

voicekey paradigm. (D) The word-picture comparison paradigm has the advantage of a disentanglement of target identity and response. The examples have been adapted such that green always defines the target.



to a more prolonged reaction time. Distractor inhibition theory can explain the larger NP effect by a stronger activation and thus more inhibition for distractors (Craik and Lockhart, 1972; Craik, 2002). Therefore, more deeply processed stimuli produce larger NP effects.

Opposingly, distractor inhibition theory fails to explain the experimentally observed dependency of NP on the RSI: if the representation of a distractor object is inhibited, the impact of inhibition should be strongest immediately after the selection, because the inhibition is assumed to decay with time. Although there is a general trend of NP to decay with increasing time between prime and probe (Neill and Valdes, 1992), no NP is observed in several studies when the RSI is very short or non-existent (Lowe, 1985; Houghton et al., 1996).

2.4.2. Episodic-retrieval theory

Proposed by Neill and Valdes (1992), episodic-retrieval theory supposes that if a task is executed over and over again, memories of past trials are more and more used in the current trial. NP is then assumed to be the result of automatic retrieval of the prime episode during probe processing causing a hampering interference. It is argued that the retrieval is triggered by the similarity of prime and probe episodes. As the information from the retrieved episode in a DT trial is inconsistent with the current role of the repeated object as a target, retrieved and perceived information are in conflict. Resolving the conflict is time consuming and results in the slowdown of the reaction time.

According to later extensions by Neill (1997), the main determinants of the strength of retrieval are the recency of the memory trace and the strength of the memory representation of the former trial. Recency as a relevant factor receives empirical support from studies that show a negative correlation between RSI and NP effect (Neill and Valdes, 1992).

A facilitated response at very short RSIs (Lowe, 1985) is difficult to explain in terms of the episodic-retrieval framework. Another weakness of this approach is the empirically found effect of semantic NP (e.g., Waszak et al., 2005): the absence of perceptual similarity should prevent any retrieval to occur thus predicting the absence of any priming effects.

2.4.3. Response-retrieval theory

A relatively recent version of the episodic-retrieval theory focuses on the encoding and retrieval of processing operations that have been carried out during trial processing – in particular the response (Rothermund et al., 2005). The theory builds on results from the research on event-files (Hommel, 1998, 2004, 2005), which investigates the encoding and retrieval of perception-action bindings. Since the retrieved response conflicts with the response required by the task in DT trials when a naming task is implemented, NP is explained as an interference between the retrieved and the currently required response. One particular merit of this response-retrieval theory is therefore that it points to the inherent confounding of the priming condition and the response relation in most NP paradigms: usually DT trials are accompanied by a response switch, whereas TT trials require the same response. The response-retrieval approach postulates that every reaction time difference in priming paradigms is explained by the retrieval of

a past response depending on the perceptual similarity between the two displays. In their initial study, a letter-matching task initially developed by Neill et al. (1990) was adapted in order to orthogonally vary repetition or non-repetition of the response and priming conditions (Rothermund et al., 2005). Since the proposition of response-retrieval theory, many studies have found empirical support for it (e.g., Mayr and Buchner, 2006; Ihrke et al., 2011).

2.4.4. Temporal discrimination theory

Temporal discrimination assumes a classification of stimuli as *old*, where a response can be retrieved from memory, or *new*, where a response has to be generated from scratch (Milliken et al., 1998). The classification consumes time depending non-monotonically on the similarity between the current stimulus and a memory trace: the classification as *new* is fast when prime and probe stimuli are very dissimilar. The classification as *old* is fast when the displays are identical. Intermediate similarities, however, such as in DT trials where the prime distractor is repeated but not in the same color, the decision whether the display is *old* or *new* takes longer (see also Neill and Kahan, 1999; Healy and Burt, 2003). Hence, both NP and positive priming effects can be explained with this mechanism.

Temporal discrimination and episodic-retrieval theories are quite similar in structure. Most criticism toward temporal discrimination relies on the equivalence of processing time after the *old/new*-classification. Temporal discrimination tacitly assumes that the direct computation of a response is completely different from a retrieval of the answer from memory. Thus no statement exists that these processes take an equal amount of time. Another weak point of temporal discrimination theory is the assumption that classification and retrieval or direct generation of a response is processed serially. Most processes in the brain work in parallel, and therefore a simultaneous computation (at least partly) of the *old/new* signal together with a directly computed answer and the retrieval of past episodes is more plausible.

2.4.5. Dual mechanism theory

Since there is evidence in support of both inhibitory and episodic-retrieval processes, several authors have proposed that both mechanisms should be active. This notion has been termed dual mechanism theory. Originally, May et al. (1995) proposed that inhibition as well as memory retrieval can be the source of NP and the experimental context specifies which of the two mechanisms is expected to operate. Tipper (2001) argued that it is important to note that distractor inhibition and episodic-retrieval theories are not mutually exclusive, and both inhibitory and retrieval processes could be involved in the emergence of NP. Although retrieval processes can be responsible for producing NP effects, inhibitory processes are still required in selecting information for goal-directed behavior. In most tasks, NP will supposedly be caused by a mixture of contributions from persisting inhibition and interference from retrieval. Because these processes may sometimes oppose each other, it is difficult to distinguish them by means of behavioral measures like reaction times and error rates (Gibbons, 2006). However, depending on the context and other experimental factors, the contributions of inhibitory and retrieval processes might vary considerably (Kane et al., 1997; Tipper, 2001). Nevertheless,

Gamboz et al. (2002) revealed in a meta-analysis that there is no significant evidence for a paradigm to produce patterns of results favoring either inhibition or retrieval theories, pointing to simultaneous presence of inhibition and retrieval. Such a conclusion supports the general framework adopted in the GMNP, presented in this paper.

2.4.6. Global threshold theory

Kabisch (2003) developed the imago-semantic action model (ISAM) with the hypothesis of a threshold variable whose value decides to which items the system will respond from perceptual input. The threshold adapts according to the current average activation of representations of objects. Additionally, a forced decay of activation is assumed in the model if residual activity is partly overwritten by perceptual input of a new stimulus. The ISAM can account for positive as well as NP as shown by computer simulations (Schrobsdorff et al., 2007b). It differs from distractor inhibition theory (Section 2.4.1) by postulating only facilitative input and passive decay in the absence of input.

The ISAM gives a comprehensive account of action selection. The presented objects are assumed to undergo pre-attentive processing and a perception stage, resulting in an abstract cognitive representation of the objects. Formally, the decision between target and distractor is determined by the task instruction, which is made accessible to the model via a semantic feedback loop. In contrast to the early visual processes, the decision is guided by attention and a conscious application of the task instruction. The semantic object representations are assumed to be initially processed automatically according to a relevance rating based on low-level features such as motion or color. If more than one or no option for suprathreshold actions exist, the threshold adapts until only one option remains. The relative relevance of stimuli can be affected in a posterior rating. According to the dual-code hypothesis of Krause et al. (1997), assigning modified relevance values to the object representation happens in a semantic space. The activation corresponding to a target is further amplified by a top-down feedback loop informed of the task, such that even if low-level perceptual features result in a higher input to the distractor, the target representation eventually becomes significantly stronger than that of the distractor.

2.5. A GENERAL MODEL FOR NEGATIVE PRIMING

The existing theories of NP have pointed to several mechanisms that are likely to play a role in producing NP. However, it is very important to keep in mind that fundamental research in psychology uses statistical properties of experimental data in order to interpret human behavior. On the one hand, behavioral experiments tend to produce largely varying results which reflect the complexity of the involved systems and the sensitivity of the effect. On the other hand, the interpretation of results is usually not unambiguous. Both aspects provide a base for the arduous and controversial discourse that is necessary for a clarification of the psychological phenomenon.

2.5.1. Computational modeling of negative priming

Theories explaining NP can be categorized roughly into memory-based and activation-based approaches. The first group assumes the memorization of a trial and eventually a retrieval of the information in the next trial. The latter group assumes NP to be caused

by interference of trial processing with persistent activation from former trials. Within both groups a number of variants were produced, many of which were created to explain a specific pattern of results. Comparability is nevertheless an issue that calls for a more comprehensive approach.

It seems reasonable to focus on the interaction of underlying processes rather than on *ad hoc* definition of data features. However, a substantial reduction of complexity is already achieved by the careful design of experiments and all theoretical explanations are based on the assumption that the complexity of experimental data can be further reduced by identifying repeating patterns in the data. A crucial point in the specification of mechanisms producing NP seems to be the exact time course of processing in a trial where a previously ignored stimulus has to be attended in comparison with the processing of an unprimed stimulus.

In order to tackle the diverse paradigms and the incomparability of the theories, we designed a computational framework for perception-based action selection in the NP paradigm by means of physiologically justified building blocks, each showing biologically plausible dynamics. The general architecture is a dynamical implementation and generalization of the model studied in Hommel (2004). The simple thresholding mechanism responsible for the creation of perception-action bindings in Hommel's model is generalized using dynamic and weighted bindings. The obtained implementation inherits freedom of interpretation from the underlying theory. Additionally, the implementation adds further degrees of freedom by the introduction of a number of technically implied parameters. The benefits of an implementation are, nevertheless, obvious. The computational model reduces the risk of misinterpretation if the source code is available to other research groups for an independent reproduction of the results.

In order to reproduce observed results, most models have to undergo a precise fitting of model parameters, which is often a very subjective process. Therefore, great care has to be taken of the distinction between results due to parameter fits and predictions generated by the internal dynamics of the model without further fitting. A different way to benefit from a computational model is to analyze the structural result after fitting, which carries a formalized version of the fitted data. We build a computational model comprising most of the mechanisms suspected to play a role in the neural processing in NP. The outcome is not only a meta-model for NP, termed GMNP, but in itself a simplified model of the brain as a framework for action selection based on perception. We addressed the tradeoff between biological realism and understandability by implementing all mechanisms as separate blocks keeping the internal dynamics simple by implementing the exponential dynamics previously developed in Schrobsdorff et al. (2007b).

2.5.2. Different paradigms

A common explanation for the divergent results of NP studies is the difference of the conducted experiments. Each paradigm has special aspects concerning trial processing beginning from perceptual pathways up to the response modalities. Differences in the task are assumed to affect the involvement of memory and inhibitory

modulations. Thus it is important to build a GMNP that is flexible enough to evaluate a variety of paradigms, i.e., not only to computationally reproduce interesting priming experiments, but also to quantify the difference of paradigms. Such a formulation contributes directly to the clarification of the debate about the influences of experimental design on NP. Most importantly, the model has to accept different stimuli and to produce distinct forms of responses. In addition, a mechanism formalizing the actual task for a paradigm is necessary.

A computational implementation (Houghton and Tipper, 1994) of an artificial neural network qualitatively explains NP by an inhibitory rebound naturally emerging from the network connections between excitatory and inhibitory cells homeostatically balancing the state of a so-called property unit. Perception is assumed to be split into the detection of single features which are bound into object representations by hardwired connections. The model has a very general connection scheme to be able to describe selective attention in a variety of situations.

This connectionist implementation of distractor inhibition theory is designed to deal with diverse perceptual inputs. Stimuli are decomposed into their features and recognized by specialized feature units. Then the object identity is realized by a flexible feature binding mechanism (Treisman, 1996). The GMNP implements a binding mechanism for feature representations by means of persistent spiking activity (Schrobsdorff et al., 2007a) that is similar to the abstraction of population activity in a neural network leading to the exponential dynamics (Section 2.7.1). Different response modalities are included in two separate layers for semantic representations and response actions. Between the two layers, a central executive implements a mapping to account for different tasks (e.g., comparison). The central executive also provides information about which feature instance codes for the target and distractor, and which feature dimension is relevant for the response (see Section 2.6.5). Before presenting a formal version of the GMNP (Section 2.7) we will specify the model components based on the discussion above.

2.6. MODEL COMPONENTS

The GMNP is formulated in a distributed way in which several specialized layers interact according to the flow of information in the brain during perception-based action selection tasks. An overview of the model structure is shown in **Figure 3**. Information is mostly fed from top (perceptual input) to bottom (action execution), except modulating layers like the binding layer, episodic memory, and the central executive. Perceptual input is fed into various feature layers, each representing a certain aspect of the presented stimuli. The object entity is represented in a feature binding layer which forms a link between all features of one object. Depending on the task, the model implements a mapping of relevant features into a semantic layer, which is equipped with a decision mechanism to sort out the semantic representation relevant for an accurate response to the task. The winning information is passed to the action layer, which chooses between different possible responses on the basis of the available information. Aside from the above pathway, is a memory layer which stores the network state from former episodes and feeds this information back when helpful for a quick response.

2.6.1. Feature layers and feature binding

In the visual pathway the information from the retina is decomposed into low-level features which are represented by different subsets of neurons (Van Essen et al., 1992). Later, the low-level representations are recombined to form higher-order features of objects from visual input (Prinzmetal, 1995). Feature decomposition entails the disadvantage that the distributed information about an object needs to be bound together for the recognition of objects as entities, a concept known as feature binding (Treisman, 1996). The neural implementation of such bindings is still under discussion (Hommel, 2004) but synchronization is likely to play a role (Singer, 1995). In the GMNP, we implement this mechanism in terms of a feature binding model on the basis of localized excitations in a spiking neural network (Schrobsdorff et al., 2007a).

In order to cover the paradigms featuring visual stimuli, we equip the current implementation of the GMNP with feature layers to detect color, shape, location, and word(-shape). A visual stimulus is recognized by particular activation in each of the corresponding feature layers and a binding between them. Binding of the features of a certain object is realized as a set of features, and a binding strength which specifies both the importance of the object to working memory and also the effectiveness of activation exchange between the features of the corresponding object. The GMNP is able to keep a small number of such bindings active at a time.

In the formation of binding, attention seems to form a crucial role, as neuromodulators associated with attention are essential for the formation but not for the maintenance of bindings (Botly and De Rosa, 2007). In terms of the GMNP this means that objects from currently perceived stimuli are bound, and the binding can survive the vanishing of the perceptual input. Bindings are stable against stimulus changes up to the point where the limited resources are in use, i.e., the maximum number of bindings is reached.

2.6.2. Semantic representations

Some NP paradigms require stimulus evaluation on a semantic level, e.g., the word-picture comparison task: the specialized Stroop cards which are the origin of NP research (Dalrymple-Alford and Budayr, 1966); or the naming of pictograms in the experimental paradigm introduced in Section 2.3. Semantic representations are closely related to language processing (Demb et al., 1995), which is distributed over the entire cortex. Despite the distributed nature of semantic processing (Bookheimer, 2002; Devlin et al., 2002), the GMNP includes only one layer holding the strengths of the semantic representation of a given stimulus (similar to the description in Schrobsdorff et al., 2007b). The GMNP also inherits the attention mechanism, i.e., an adaptive threshold relying on activations in the semantic layer. The threshold controls information propagation to the response layer.

2.6.3. Episodic memory

Episodic-retrieval theory, assumes that previously processed stimuli are stored in episodic memory. In most NP paradigms, the memorized sequence of trials is assumed not to extend beyond the directly preceding trial. The interference of memory with behavior is assumed to depend only on the time elapsed and the stimuli

encountered in the meantime. We prefer naming the memory processes relevant in NP as *episodic memory*.

Physiologically, memory encoding is related to activity in the left prefrontal cortex, whereas retrieval is more associated with right prefrontal cortex (Tulving et al., 1994; Fletcher et al., 1997). This is conjectured to be due to different control mechanisms on the two tasks (Craik, 2002). We solve the stability-plasticity problem that memories have to be formed reliably and instantly but have to persist for some time even in the presence of interfering input (Norman et al., 2005; Suzuki, 2006), by implementing a limited number of memory slots that hold the entire state of the system at a certain point in time. Such a memory is assigned a strength which decays with time. Individual instances are the only forms of experience that are represented neurologically, as (Logan, 1988) postulates.

2.6.4. Memory retrieval

Memory research distinguishes between involuntary retrieval and voluntary recollection (Yonelinas, 2002). The so-called familiarity signal is physiologically measurable, and becomes visible in the EEG 300 ms after stimulus onset. Familiarity is assumed to trigger further retrieval, as a spontaneous recognition can lead to recollection (Zimmer et al., 2006; Ecker et al., 2007). Context monitoring means the evaluation of the appropriateness of a retrieved episode (Egner and Hirsch, 2005). Topography, latency, and polarity of the familiarity signal in EEG-data bears resemblance to the *old/new* effect related to episodic memory retrieval (Rugg and Nagy, 1989).

The two approaches, episodic retrieval and temporal discrimination theory, predict differing mechanisms controlling the strength of memory retrieval. The first theory assumes that involuntary retrieval is positively correlated with perceptual similarity of the two trials. The latter postulates another perception-based classification of the encountered episode as *old* or *new*. When significant evidence for an old stimulus display is accumulated, full retrieval is triggered, while simultaneously suppressing the direct response generation.

The GMNP performs the computation of a familiarity signal by comparing the current percept with the memorized one. Depending on model parameters emphasizing either episodic-retrieval theory or temporal discrimination, this familiarity can influence further processing in two ways. First, the strength of retrieval can be determined directly, i.e., familiar stimuli cause stronger retrieval-related activity, while unfamiliar stimuli still produce a positive activity. Secondly, the system holds a template time course of a familiarity signal separating the time courses of the familiarity signal while encountering a perfect match of stimulus displays and a pair of subsequent displays that vary in a single feature. Greater familiarity indicates an identical stimulus configuration, while lower familiarity is considered as being produced by a new display. The uncertainty of the signal early in the trial is implemented by the GMNP by a shrinking margin around a template familiarity curve for a nearly identical stimulus, in which the evidence of the display being *old* or *new* is not yet significant.

2.6.5. Central executive

The GMNP aims at a compromise of evidence-based complexity and computational simplicity. Instead of providing mechanisms

for the adaptation to different paradigms, we rather map the paradigms to appropriate parameter configurations. The corresponding component of the GMNP is called the central executive (Cowan, 1988) and is understood as an emergent property of interacting subsystems (Barnard, 1985; Teasdale and Barnard, 1993; Bressler and Kelso, 2001). Even if there is no consensus on the necessity of a central executive in memory functions (Baddeley, 1998; Johnson, 2007), we will use the term in order to describe the sudden change in system behavior if it is presented a new task. In this way the GMNP receives information about the task demands, i.e., about a specific paradigm, including the top-down input modulating target or distractor activation and mappings describing the determination of the input to the action layer.

2.6.6. Representing theories of negative priming

The comparison of the different theoretical approaches is one of the major reasons for the design of the GMNP. In order to be able to directly compare the respective impact of each mechanism, the main components of each theory need to be precisely formulated within a common language. In the following, we outline how each of the theoretical approaches is realized in the GMNP.

Distractor inhibition theory is expressed in a straightforward way. The distractor object, i.e., the feature that specifies the distractor, is subject to inhibition. Simultaneously, dynamic activations below baseline are included to model the inhibitory rebound (this constitutes a deviation from the model developed in Schrobsdorff et al., 2007b). Correspondingly, inhibition in the semantic layer is indirectly achieved via the binding between feature and semantic layers.

Episodic-retrieval theory requires explicit modeling of memory and retrieval processes. Therefore, we included short-term memory by adding a dedicated layer that is able to store a snapshot of the state of the dynamic system and that is subject to decay over time. This memory layer is also capable of computing the strength of retrieval determined by the similarity of the current percept and the memory content. Retrieval is modeled by partially restoring former system variables. Memory is updated at the most prominent point in a trial, i.e., when the decision takes place. Response retrieval manifests itself in the GMNP as a simplification of episodic retrieval. Only the system variables of the action layer are restored during retrieval. The retrieval strength is still determined by the similarity of current and stored percept.

Temporal discrimination theory acts on the same episodic memory layer as episodic retrieval. The probability that a stimulus display was just presented can be computed by looking at the similarity between current and memorized percept as described above. This value is highest when both configurations match exactly. The similarity slowly rises from zero to its final value. The current similarity is compared to a prototype similarity signal in order to determine whether the current percept is old or new. In order to be robust against initial fluctuations in the similarity stemming from residual activation of the last trial, the computed difference has to surpass a threshold that is large at trial onset but shrinks with time. If a display is rather similar to the memorized one, the similarity value will stay within the uncertainty interval the longest, preventing an old–new-classification. When the classification is accomplished, temporal discrimination theory assumes

the information flow to be affected: in the presence of new stimuli, retrieval is blocked, and direct computation is facilitated. For old stimuli the direct computation is dropped and retrieval will be performed. This is included in the GMNP in terms of a modulation of the transmission strengths between the corresponding layers: from semantic to action for direct computation and from episodic memory to action layer for retrieval.

The spirit of the dual mechanism hypothesis is inherent to the GMNP, because it accounts for all theories at once. By tuning the model parameters, the behavior predicted by each theory can be generated. According to the above discussion it is evident that the mechanisms postulated by inhibition and threshold theory are located in the more sensory part of the system whereas retrieval, even though affecting the entire system, only becomes apparent in later parts, i.e., in the semantic and action layer. As the two mechanisms are implemented at distinct parts of the GMNP, coexistence of the mechanisms is achieved trivially.

2.7. MODEL DYNAMICS

After the examination of the processes involved in an NP task in the previous section, we will now mathematically describe the model. The level of description results from a compromise between the explicitness of the formulas and the complexity of the full system. The basic architecture of the model is simple. Perceptual input enters the system in the feature layers, which passes information to the semantic and action layer. Finally, we describe the behavior of the memory variables.

Activations of feature and object representations follow an exponential fixed-point dynamics (Schrobsdorff et al., 2007b), i.e., the difference of a state variable and a given fixed-point determines the change of that variable while the rate of change is governed by a time constant. This dynamics can be derived from firing rate considerations of a network of spiking neurons, as we show in the following section.

The model has a number of meta-parameters that act as *weights* or “setscrews” (see Section 3.1). In this way the model represents the particular assumptions in each of the theories in Section 2.4. We will not consider a graded likelihood of the assumptions and therefore choose the weights to be either 1 or 0. In this way the GMNP yields quantitative comparisons between the theoretical accounts while continuous weights would result in new theories.

2.7.1. Determining a simple intrinsic dynamics

For the GMNP, we will subsume the mental representation of each cognitive object, e.g., a perceived feature or a semantic category, under a single variable which corresponds neurophysiologically to the activation level in an assembly of neurons. The firing behavior of this assembly is driven by external excitatory input which, for simplicity, is assumed to be constant while the sensory object is present.

We consider a cluster of all-to-all coupled integrate and fire neurons. We average the firing rate of the network over many input presentations and analyze the shape of rise and decay of the overall firing rate. In each time step, the membrane potential h_i of neuron $i = 1, \dots, N$ receives additive external input $I_i(t)$ and excitation via recurrent connections with synaptic strength w_{ij} every

time neuron j spikes, i.e., n_{sp}^j , see equation (1).

$$h_{i,n+1} = h_{i,n} + I_{i,n} + \sum_{j=1}^N w_{ij} \delta(n - n_{sp}^j) \quad (1)$$

where $\delta(x) = 0$ for $x \neq 0$ and $\delta(0) = 1$. For continuous-time systems the time step becomes infinitesimally small and changes are expressed by a derivative dh_i/dt . The dynamics can be described by a differential equation (2).

$$\frac{dh_i}{dt} = I_i(t) + \sum_{j=1}^N w_{ij} \delta(t - t_{sp}^j) \quad (2)$$

If h_i reaches the firing threshold $\theta = 1$, it delivers a spike to its postsynaptic neurons and is reset by the threshold value $h_i^{\text{post-spike}} = h_i^{\text{pre-spike}} - \theta$. The external input $I_i(t)$ is drawn independently in each time step from a Gaussian distribution with a mean chosen such that a single neuron receives on average input equal to the difference of threshold and resting potential $\theta - h^0$. Without the recurrent coupling, a neuron would thus on average fire once during stimulus presentation.

We simulated a network of $N = 1000$ neurons. A stimulus was shown for 1s, and the inter-stimulus interval was 1s (we are using 50 time steps per second). The total output of a neuron, i.e., the sum of all outgoing weights, was fixed to $\alpha = \sum_{i=1}^N w_{ij} = 0.87 \forall j$. The stochasticity of the input and the sensitivity of the network for fluctuations result in rather random single trial firing. However, on average a coherent behavior emerges. For the results shown in **Figure 4**, we averaged 10,000 trials to obtain a good estimation of the firing rate over time.

In order to derive a computationally simple dynamics for the representation variables of the GMNP, we are interested in the shape of the time course of rise and decay of the firing rate. A good candidate to describe the observed dynamics seems to be a set of coupled non-linear Langevin equations (Risken, 1996) of the basic form equation (3).

$$\frac{dx}{dt} = h(x, t) + g(x, t) \Gamma(t) \quad (3)$$

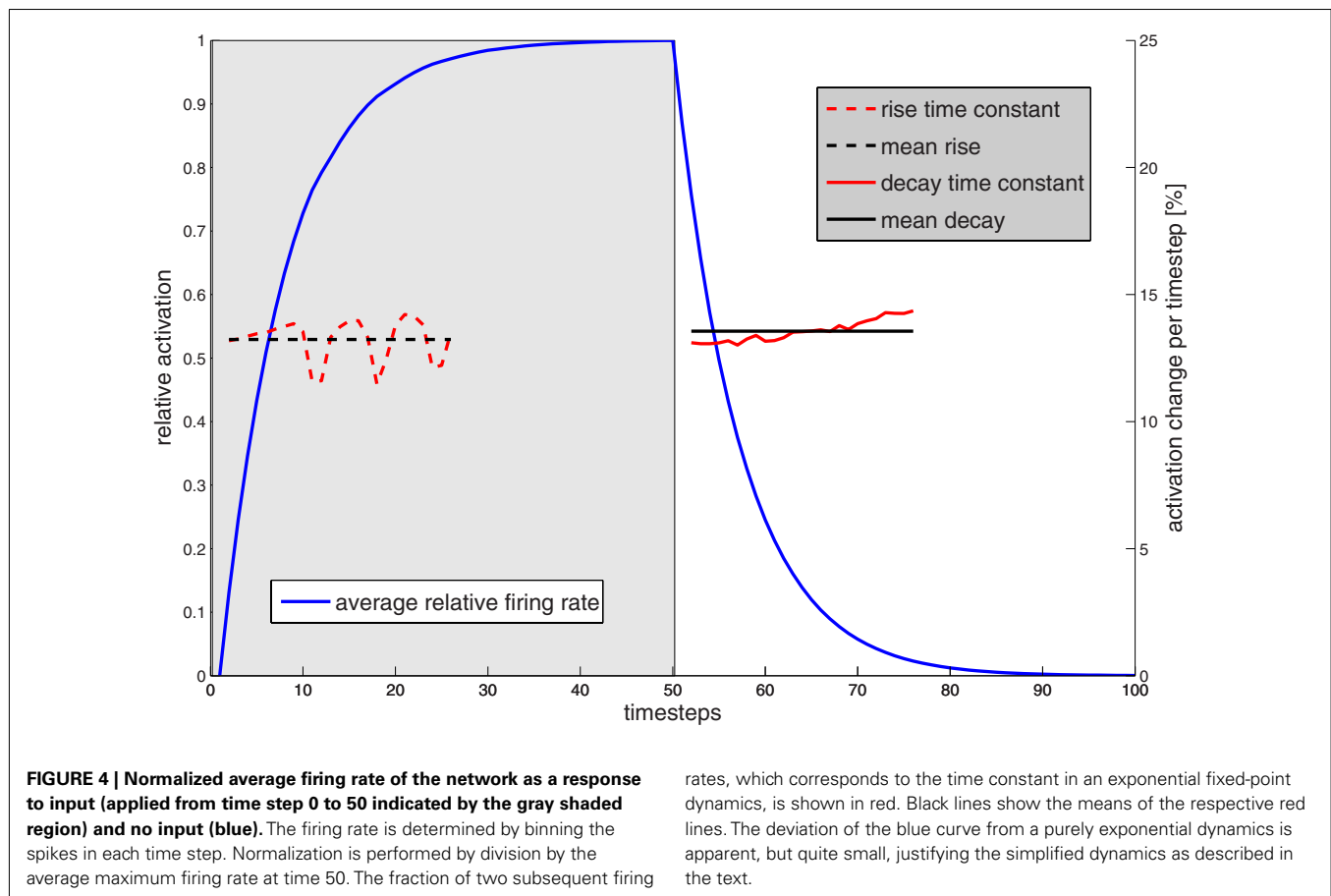
The state of the system is \mathbf{x} , t is time, h is a function that describes drift forces that depend on the actual state and time and $\Gamma(t)$ is a Gaussian diffusion term with zero mean $\langle \Gamma(t) \rangle_t = 0$ and no correlation $\langle \Gamma(t) \Gamma(t') \rangle_t = 2\delta(t - t')$.

Since theories of NP do not make any statements about noise influences, our strategy of aiming at a minimal model also suggests that we exclude noise effects in the model. The result is an exponential fixed-point dynamics with time constant τ .

$$x_{n+1} = x_n + \tau \cdot (I - x_n) \quad (4)$$

$$\frac{dx}{dt} = \tau \cdot (I - x) \quad (5)$$

In **Figure 4** we show the averaged firing rate f and plot the relative change $(f_{n+1} - f_n)/f_n$ between two time steps in reference to



rates, which corresponds to the time constant in an exponential fixed-point dynamics, is shown in red. Black lines show the means of the respective red lines. The deviation of the blue curve from a purely exponential dynamics is apparent, but quite small, justifying the simplified dynamics as described in the text.

the actual fixed-point, i.e., maximum firing rate 1 in case of input or 0 in the absence of input. The observed time constants are sufficiently constant to justify the simplified dynamics of equation (4) we used for the implementation of the GMNP.

The small periodicity of the rise time constant, even after averaging over a large number of runs, can be explained by the model structure. **Figure 5** shows the distribution of membrane potentials averaged over 10,000 trials as shown in **Figure 4**. During input, all neurons are shifted in their membrane potential such that small potentials become improbable, to the benefit of superthreshold potentials. Most potential bins have a relative frequency of 0.0098 and 0.0115, which is near a uniform distribution. However, there is some structure that survives the averaging process. In the beginning, all units receive only external input. They are shifted upwards, leaving a gap which propagates through the entire range of potentials. Neurons that spiked are not reset to zero but lowered in their normalized potential by 1. Since they additionally receive recurrent as well as external input, virtually no neurons have membrane potentials between 0 and 0.15. As recurrent input tends toward a fixed-point, there is a trend of jumping into the band between 0.18 and 0.28 after spiking. This band is now shifted upwards by the same amount of activation. In every time step, a neuron jumps from one band to the next one. After the offset of input only decaying recurrent excitation is present.

2.7.2. Feature variables

In the GMNP, all objects from input space are represented by tuples of feature activations. The number of relevant features can vary according to the paradigm. Information about a perceived object Ω is decomposed into its constituent features and then passed to the appropriate layers of the GMNP. Perceptual features drive feature detection variables of the system, whereas the information about the combination of all features to one object entity is governed by the binding layer. This defines the dynamic synaptic interaction between the feature variables of the object.

Feature variables f_i^j represent whether a feature i , e.g., color, shape, or word shape, has the value j , e.g., green, etc. True information enters the system by the corresponding external input F_i^j . The dynamics of a feature variable is determined by several driving forces that act simultaneously, see equation (6). The first one is an exponential drift toward F_i^j . The time constant τ_f of the drift equals either ρ_f if the feature variable is lower than the input and rises by an active drive, or δ_f if the input variable is lower than the current activation and the feature variable passively decays. F_i^j is defined by constant unit input \hat{F} in the presence of the respective feature in the display configuration. If the particular feature instance defines the object to be target or distractor, an additional input, excitatory or inhibitory, respectively, is applied to the corresponding feature variable. In case of feature perception, F_i^j is set to a generic input strength \hat{F} plus the current value of the

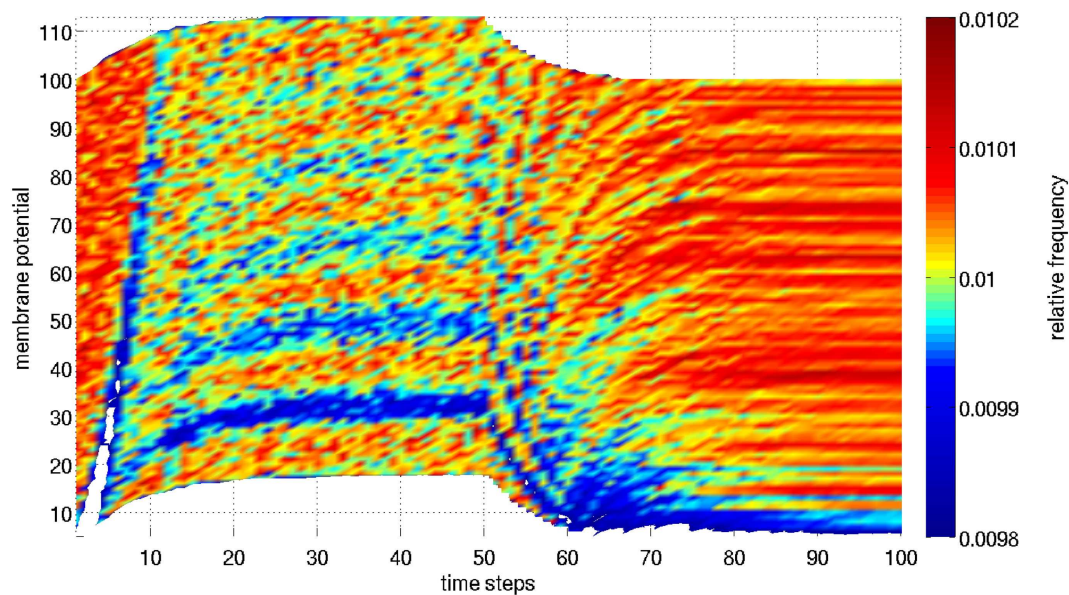


FIGURE 5 | Distribution of membrane potentials averaged over 10,000 trials. Note that the potentials are mostly uniformly distributed, as the color map only covers values from 0.0098 to 0.0115. Nevertheless, the fine grained plot reveals the processes generating the firing rates analyzed in **Figure 4**: initially all neurons are pushed toward higher membrane potential by the

input, leaving a relative gap that is propagated upwards. Then, assemblies of neurons that are characterized by increased membrane potentials form when the recurrent input builds up. Finally, the system relaxes and the less regular spikes rebuild a more equally distributed picture until no further spikes are generated.

variable accounting for the reception of input by only a subset of neurons in one assembly, similar to residual activations introduced in Schrobsdorff et al. (2007b). The residual overshoot of the input decays to the maximum input in the same way that would feature activation. In the case of feature absence, the input is set to the activation baseline value of \hat{F} , which is not necessarily zero.

$$F_i^j = \begin{cases} \hat{F} + f_i^j & \text{at display onset, if instance } j \text{ of feature } i \text{ is present} \\ \delta_f (\hat{F} - F_i^j) & \text{during stimulus perception, as long as } F_i^j > \hat{F} \\ \hat{F} & \text{at display offset} \end{cases} \quad (6)$$

Both target selection mechanisms, target amplification and distractor inhibition add to the corresponding feature input F_i^j resulting in the overall input F_i^j , see equation (7). Target amplification A is linearly increasing until a response is given and set to zero afterward, see equation (8). Distractor inhibition I is said to persist for some time, as it has to be retrenched after a response was given. Therefore, inhibition I increases linearly with slope k during perception and fades linearly after the decision was made, see equation (9).

$$F_i^j = \begin{cases} F_i^j + A & \text{if } \{i, j\} \text{ defines the target} \\ F_i^j + I & \text{if } \{i, j\} \text{ defines the distractor} \\ F_i^j & \text{otherwise} \end{cases} \quad (7)$$

$$\begin{aligned} \frac{dA}{dt} &= \alpha & \text{during stimulus presentation} \\ A &= 0 & \text{no stimulus present} \end{aligned} \quad (8)$$

$$\frac{dI}{dt} = \begin{cases} k & \text{during external input} \\ -k & \text{after the offset of input until } I = 0 \end{cases} \quad (9)$$

The second term governing the dynamics of features is the loss of feature specificity in the absence of input defined by a broadening of activation with time constant β , within one feature toward the feature mean $\langle f_i^j \rangle_i$, without lowering the total activation of the respective feature layer. Additionally, feature activation is passed via existing bindings to the other feature instances belonging to the same object. If, e.g., the feature tuple {color, green}{shape, ball}{location, bottom} defining a green ball shown at the bottom of the visual scene is held by the binding variable $b_{\{\text{color, green}\}\{\text{shape, ball}\}\{\text{location, bottom}\}}$, its value defines the amount of activation interchange between the variables $f_{\text{color}}^{\text{green}}$, $f_{\text{shape}}^{\text{ball}}$, and $f_{\text{location}}^{\text{bottom}}$ such that they all approach the object mean. There exists only one feature variable for green. Therefore multiple green objects experience a natural connection, as they share this variable. The last term that drives feature variables is the back projection of memorized episodes into the feature layer. Weighted by the matching value r_k of the actual percept and the k th last memorized episode and the strength e_k of the respective memory trace, the value of the feature variable at the respective response moment e_k^j is fed back to the variable.

In total, the change of feature activation f_i^j is the sum of four exponential drifts, given in equation (10). First, an adaptation toward input strength F_i^j with time constant τ_f . Second, an adaptation toward the mean of all activations in the particular feature layer $\langle f_i^j \rangle_i$ with time constant β . Third, an adaptation toward the

mean of the other features of each object Ω the current feature belongs to with time constant b_Ω , i.e., the current binding strength of that object. And finally, fourth, an adaptation toward the memorized value of the current variable e_k^j with time constant $r_k e_k$, i.e., the product of the retrieval strength, the match between the percept and the k th memorized episode, and the current memory strength.

$$\frac{df_i^j}{dt} = \tau_f \left(F_i^j - f_i^j \right) + \beta \left(\langle f_i^j \rangle_i - f_i^j \right) + \sum_{\Omega \ni f_i^j} b_\Omega \left(\langle f_i^m \rangle_{f_i^m \in \Omega} - f_i^j \right) + \sum_k r_k e_k \left(e_k^j - f_i^j \right) \quad (10)$$

where

$$\tau_f = \begin{cases} \rho_f & \text{if } F_i^j > f_i^j \\ \delta_f & \text{if } F_i^j < f_i^j \end{cases}$$

2.7.3. Feature binding mechanism

The bindings are dynamic variables themselves that encode feature combinations within an object. Because the underlying structure (Schrobsdorff et al., 2007a) is a flexible but resource-constrained layer, the number of such binding variables is limited. When an object appears in stimulus space the feedback activation from the binding layer indicates whether the current object is already represented. This would correspond to an immediate recognition of the identity of the object. If the object is not yet represented, the weakest binding variable that is not subject to current input is overwritten, deleting the respective object from working memory. If an object is shown, the respective binding variable is driven with time constant ρ_b toward a maximum strength \hat{b} . If the percept of an object is gone, the respective binding variable passively decays with time constant δ_b to zero, see equation (11).

$$\frac{db_{\{i_k, j_k\}k}}{dt} = \begin{cases} \rho_b (\hat{b} - b_{\{i_k, j_k\}k}) & \text{if an object with the respective} \\ & \text{feature combination is perceived} \\ -\delta_b b_{\{i_k, j_k\}k} & \text{if the percept is switched off} \end{cases} \quad (11)$$

If the binding slot is overwritten, we have $b_{\{i_k, j_k\}k} = 0$, i.e., object $\{i_k, j_k\}k$ is not shown and is held by the weakest binding when a new display is uncovered containing a non-bound object $\{i_l, j_l\}l$.

2.7.4. Short-term modulation of connectivity

The GMNP directs the information flow such that it achieves a decision whether a response will be computed anew from the perceptual input or will be retrieved from episodic memory. For this purpose, synaptic connections between the layers are either blocked or facilitated, depending on the old-new signal o_k that is generated by comparing the k th last episode to the current percept. A blocking variable σ_{block} approaches o_k with time constant τ_{block} , see equation (13). The limiting value is set to 1, 1/2, or 0 depending on whether the signal is old, unclassified or new, respectively. This is applied if the model behavior is tuned to represent the temporal

discrimination theory. The synaptic strength is scaled according to σ_{block} between a minimum synaptic strength $\check{\sigma}_{f \rightarrow s}$ and an entirely open channel of $\sigma_{f \rightarrow s} = 1$, see equation (12).

$$\sigma_{f \rightarrow s} = (1 - \check{\sigma}_{f \rightarrow s}) + \check{\sigma}_{f \rightarrow s} \sigma_{\text{block}} \quad (12)$$

with

$$\frac{d\sigma_{\text{block}}}{dt} = \tau_{\text{block}} (o_k - \sigma_{\text{block}}) \quad (13)$$

2.7.5. Semantic variables

The role of the variables in the semantic layer is assigned by the central executive, depending on task demands. Therefore, a fixed description of the dynamics of semantic variables is not possible. We assume that after a hypothetical training phase that introduces a new task, the central executive has produced a reasonable gating function $S(f)$ of feature activations to the semantic layer. In the case of a naming paradigm this mapping can be as simple as the identity map from object shapes to semantic object category. The function $S(f)$ determines the fixed-point, which the semantic activation approaches at a rate ρ_s or δ_s , for an actively driven rise or a passive decay, respectively, see equation (15). Again the variables are subject to retrieval of former episodes analogous to feature variables. Additionally, the information flow is modulated by the connection factor $\sigma_{f \rightarrow s}$, see equation (14).

$$\frac{ds^j}{dt} = \sigma_{f \rightarrow s} \tau_s \left(S^j(f) - s^j \right) + \sum_k r_k e_k \left(e_k^{s^j} - s^j \right) \quad (14)$$

where

$$\tau_s = \begin{cases} \rho_s & \text{if } S^j > s^j \\ \delta_s & \text{if } S^j < s^j \end{cases} \quad (15)$$

Actions of the GMNP are based on the most prominent activation of the semantic layer. We chose an adaptive-threshold mechanism to single out the highest activation. Only activations surpassing the threshold s^θ are eligible to be passed on to the action layer.

2.7.6. The adaptive-threshold in the semantic layer

As a decision mechanism for comparison tasks, the semantic layer is equipped with an adaptive-threshold s^θ . The threshold variable itself obeys an exponential fixed-point dynamics on the basis of a scaled average of activation in the semantic layer. This is done similarly to the threshold behavior in Schrobsdorff et al. (2007b). The scaling of the average v_{s^θ} is dependent on the paradigm and should be set such that the fixed-point of the threshold is between the highest two semantic activations. As a consequence, the baseline activation \check{F} which is considered a virtual zero in the process has to be accounted for by only considering the difference to \check{F} , see equation (16).

$$\frac{1}{\tau_{s^\theta}} \frac{ds^\theta}{dt} = v_{s^\theta} \sum_j \left(s^j - \check{F} \right) - \left(s^\theta - \check{F} \right) \quad (16)$$

2.7.7. Action representations

The action layer behaves similarly as the semantic layer, see equation (17). Action activation variables are driven toward an external input $A(s, f)$ that is computed from semantic and feature representations according to the task, i.e., given by a mapping function from the central executive. Depending on whether the adaptation is an actively driven rise or a passive decay, two respective time constants ρ_a , δ_a apply. An aspect that is easily overseen is the option not to respond, for example in cases where no target object is shown. This is represented by the formal action a^0 . $A^j(s, f, \sigma_{f \rightarrow a})$ is designed such that whenever there is no target stimulus shown, e.g., between two trials, $A^0(s, f, \sigma_{f \rightarrow a})$ equals 1. In case of stimuli triggering a response $A^0(s, f, \sigma_{f \rightarrow a})$ equals 0. The variable $\sigma_{f \rightarrow a}$ is the current synaptic strength between both feature and semantic layer toward the action layer.

$$\frac{da^j}{dt} = \tau_a \left(A^j(s, f, \sigma_{f \rightarrow a}) - a^j \right) + r_a \sum_k r_k e_k \left(e_k^{aj} - a^j \right) \quad (17)$$

where

$$\tau_a = \begin{cases} \rho_a & \text{if } A^j(s, f) > a^j \\ \delta_a & \text{if } A^j(s, f) < a^j \end{cases}$$

The relative retrieval of action representations r_a is modulated contrary to the synaptic transmission to the action layer $\sigma_{f \rightarrow a}$ reflecting the facilitation of action retrieval by an old-c an old episode which can be answered by retrieving a former response. Also, the modulation of information flow can decrease the retrieval of a response if a new episode is classified, see equation (18).

$$r_a = (1 + \max(\check{\sigma}_{f \rightarrow a}, \check{\sigma}_{f \rightarrow s})) - 2 \max(\check{\sigma}_{f \rightarrow a}, \check{\sigma}_{f \rightarrow s}) \sigma_{\text{block}} \quad (18)$$

where

$$\sigma_{f \rightarrow a} = (1 - \check{\sigma}_{f \rightarrow a}) + \check{\sigma}_{f \rightarrow a} \sigma_{\text{block}}$$

In order to model the decision making process in the action layer where a single action has to be chosen for execution, we introduce a threshold level analogous to the semantic layer described in Section 2.7.6, see equation (19). As input to the action layer ranges from 0 to 1, we do not have to care about baseline activation here.

$$\frac{1}{\tau_{a^\theta}} \frac{da^\theta}{dt} = v_{a^\theta} \sum_j a^j - a^\theta \quad (19)$$

Suprathreshold activations $a^j > a^\theta$ define the space of possible actions the system can take. If there is only one action that is suprathreshold, the corresponding action is executed. In case of $a^0 > a^\theta$, the system does not do anything.

2.7.8. Memory processes

Memory processes are modeled in a simple way. At points in time that mark the closure of an episode, in the present paradigm when an action has been performed, the entire state of the model is

written down as one episode. The stored values are used to compute similarities between past episodes and a current percept, the retrieval strength r_k . This similarity signal triggers an automatic retrieval of the former episodes. The greater the similarity, the stronger the memorized values drive the respective variables. Additionally, to account for memory decay with time, the presence of memorized episodes is set to a certain initial value \hat{e} when the episode is written down, and then freely decays to zero with time constant δ_e , see equation (20).

$$\begin{aligned} e_k &= \hat{e} & \text{if episode } k \text{ is memorized} \\ \frac{de_k}{dt} &= -\delta_e e_k & \text{otherwise} \end{aligned} \quad (20)$$

If a new episode is memorized, the k th last episode becomes the $(k+1)$ th last one, see equation (21).

$$\left. \begin{aligned} e_{k+1}^v &= e_k^v \\ e_1^v &= v \in \{f_i^j, b_{\{j_k, i_k\}_k}, s^j, a^j\} \end{aligned} \right\} \text{ when an action is taken} \quad (21)$$

To account for the classification, postulated, e.g., in temporal discrimination theory, we need a reliable old-new signal which is rather hard to get from only internal values, i.e., information that is accessible by the system itself. The current percept can only be assessed through the extracted feature. The intention is to have a value that is higher for a higher degree of similarity between the current percept and a memorized one. In other words, the difference of a current feature or binding value and the corresponding memory trace should be minimal, e.g., $(f_i^j - e_k^{f_i^j})$. This is best achieved by the inverse of the sum of all differences. Still, there is a normalization problem, due to the varying stimulus displays. As the system is trained for the present task, it has some knowledge about the expected number of objects n in the display. However, the current objects can only be guessed by looking at the n strongest bindings. Therefore, we apply a normalization by the significance of a percept given by the sum over all currently perceived feature variables, divided by the number of features relevant to the task, see equation (22).

$$r_k = \frac{\sum_{i,j} f_i^j}{\#_f} \left(\sum_{\{i,j\}_l} \left(\left| f_i^j - e_k^{f_i^j} \right| + \frac{1}{\hat{b}} \left| b_{\{i,j\}_l} - e_k^{b_{\{i,j\}_l}} \right| \right) \right)^{-1} \quad (22)$$

where $\{i, j\}_l$ denotes a subjective percept, i.e., one of the objects being held by the n strongest bindings, n being the number of objects in one display.

2.7.9. Connectivity modulation

Information gating is modeled by the dynamic opening or closing of synaptic transmissions between the different layers as well as the retrieval channel to the action layer. This modulation is governed by an old-new signal o_k comparing the k th last episode to the current percept. The comparison process is modeled by locating the k th retrieval signal r_k below, in between, or above a deviation u from a prototype time course for an intermediate resemblance of displays given by an exponential adaptation from an initial value \check{d} with time constant τ_d toward a retrieval level \check{d} dividing old from

new displays, see equation (23). In order to account for a greater uncertainty after the beginning of a trial, u shrinks exponentially with time constant τ_u , see equation (24).

$$o_k = \begin{cases} 0 & \text{if } r_k > d + u \\ 1 & \text{if } r_k < d - u \\ \frac{1}{2} & \text{otherwise} \end{cases} \quad (23)$$

$$\frac{du}{dt} = -\tau_u u \quad (24)$$

where $d = \check{d}$ and $u = \check{u}$ at display onset, $d = 0$ and $u = 0$ at display offset, while the stimulus is present the following dynamics is observed, see equation (25).

$$\frac{dd}{dt} = \tau_d (\hat{d} - d) \quad (25)$$

3. RESULTS

Even though the most important aspect of the GMNP is the possibility to quantitatively compare different priming theories, the current contribution is not intended to establish the conditions and perform a thorough comparison, but the main result we are presenting is a framework which is general enough to quantify all theories of NP in a common language. Therefore, the current section is meant as a proof of concept to demonstrate the way the GMNP works.

3.1. DEFINING MODEL PARAMETERS

In order to analyze the consequences of a theory, we define weights Ξ that switch on or off the effect of particular assumptions in a theory. These weights are meta-parameters insofar as they introduce constraints on the low-level parameters of the model that reflect the impact of a specific theoretical mechanism at a behavioral level. We label these variables according to the corresponding theory, see **Table 3**: Ξ_{er} , episodic retrieval; Ξ_{rr} , response retrieval; Ξ_{ib} , inhibition vs. boost; Ξ_{gt} , global threshold; Ξ_{fsb} , feature-semantic block; Ξ_{sab} , semantic action block; Ξ_{td} , temporal discrimination.

Retrieval is controlled by adjusting the initial strength of a memory trace as it linearly determines the impact of retrieval. The

modulation factor Ξ_{er} scales the maximum memory strength \hat{e} . If Ξ_{er} is 0, no memory is written down, and therefore retrieval has no effect on the system behavior. If $\Xi_{er} = 1$, memories are stored initially with the maximum strength \hat{e} and retrieval provides the input to the system described in Section 2.7.8.

The question whether the entire system state is retrieved or only the prime response, separates episodic retrieval from response-retrieval theory. These two assumptions are mutually exclusive. Therefore the weight Ξ_{rr} gradually shuts down the retrieval of activations in layers other than the action layer. If $\Xi_{rr} = 1$ the entire episode is retrieved, whereas, if $\Xi_{rr} = 0$, only the action layer receives memory input.

Distractor inhibition theory and the global threshold theory conflict with each other by either assuming inhibition of the distractor or a target boost, respectively. The weight Ξ_{ib} modulates input to the feature instance that identifies target and distractor. If $\Xi_{ib} = 0$, only the distractor receives inhibiting input, i.e., $\alpha = 0$. If $\Xi_{ib} = 1$ only the target feature receives excitation, i.e., $k = 0$. Ξ_{ib} additionally adjusts the baseline activation level from 1/2 in the distractor inhibition case to 0 with target boost, where no sub-baseline activation is assumed.

At this point, a major gap in the retrieval accounts becomes obvious. They do not make any statements on what the direct computation of a trial may look like. The GMNP thus needs some decision making mechanism. In order to have the least effect of the decision making mechanism on priming effects in the case where we consider retrieval based mechanisms, we chose to have a pure target boost in the feature layers. Forced decay as well as activation broadening as inherent features of the global threshold theory will thus be controlled independently. Ξ_{gt} linearly controls the broadening of activation β and the strength of the forced decay if two concepts compete for a feature instance.

Both temporal discrimination and episodic-retrieval theory postulate a decision of the system as to whether the current response should be generated directly from the input, or retrieved from memory. The corresponding modulation in the general model is done via the weight Ξ_{fsb} . If $\Xi_{fsb} = 0$, there is a competition between direct computation and retrieval in the system. If $\Xi_{fsb} = 1$, the strength of retrieval, i.e., the similarity signal, triggers a shutdown of the synapses between features and semantic layer, modeling a decision of the system to only retrieve the response and drop the direct determination of the right answer.

In an excursion into episodic retrieval (Tipper and Cranston, 1985) argued in favor of blocking of the information flow in the episodic retrieval context right before the action selection state. This manifests in the general model as a blocking similar to Ξ_{fsb} described in the last paragraph. However, the block acts between the semantic and the action layer. The corresponding weight is Ξ_{sab} .

A final weight is given by Ξ_{td} which controls the evaluation of a stimulus being old or new before retrieval is initiated. In the case $\Xi_{td} = 0$, the similarity signal determines the retrieval strength from the beginning of a trial, whereas if $\Xi_{td} = 1$ there is no retrieval unless the similarity signal surmounts the uncertainty region around the prototype similarity signal, as explained in Section 2.7.8.

Table 3 | Weights controlling the strength of the implementation of a theoretical account into the GMNP.

	Model behavior for $\Xi = 0$	Model behavior for $\Xi = 1$
Ξ_{er}	No retrieval at all	Maximum retrieval
Ξ_{rr}	Only retrieval of response	Total retrieval
Ξ_{ib}	Distractor inhibition	Target boost
Ξ_{gt}	No activation interference	Forced decay and activation broadening
Ξ_{fsb}	Full propagation	Retrieval blocks features semantic synapses
Ξ_{sab}	Full propagation	Retrieval blocks semantic action synapses
Ξ_{td}	Classical episodic retrieval	Old/new evaluation

Their range is continuously between 0 and 1.

Table 4 summarizes the values of the weights if the impact of a single theoretical account is to be evaluated. Note that some mechanisms are inherent to the GMNP such as activation propagation

via the feature bindings. Therefore, these settings do not give a minimal computational model of the respective theory. Rather, we keep the unspecified mechanisms constant across all simulations.

Table 4 | Weight settings required by various theories.

	Ξ_{er}	Ξ_{rr}	Ξ_{ib}	Ξ_{gt}	Ξ_{fsb}	Ξ_{sab}	Ξ_{td}
Distractor inhibition	0	0	0	0	0	0	0
Global threshold	0	0	1	1	0	0	0
Episodic retrieval	1	1	1	0	0	0	0
Response retrieval	1	0	1	0	0	0	0
Temporal discrimination	1	1	1	0	1	1	1

3.2. VOICEKEY PARADIGM

The following section will show an example of the GMNP in a voicekey paradigm, see Section 2.2. To show the internal dynamics of the GMNP, all relevant variables are plotted over nine trials including all five conditions in **Figure 6**. The weights are tuned to episodic retrieval, i.e., there are no activation interferences in the feature layers. In response to the perceptual input, the target color green is boosted and activation exchanged via the bindings. In addition, activation is retrieved from memory.

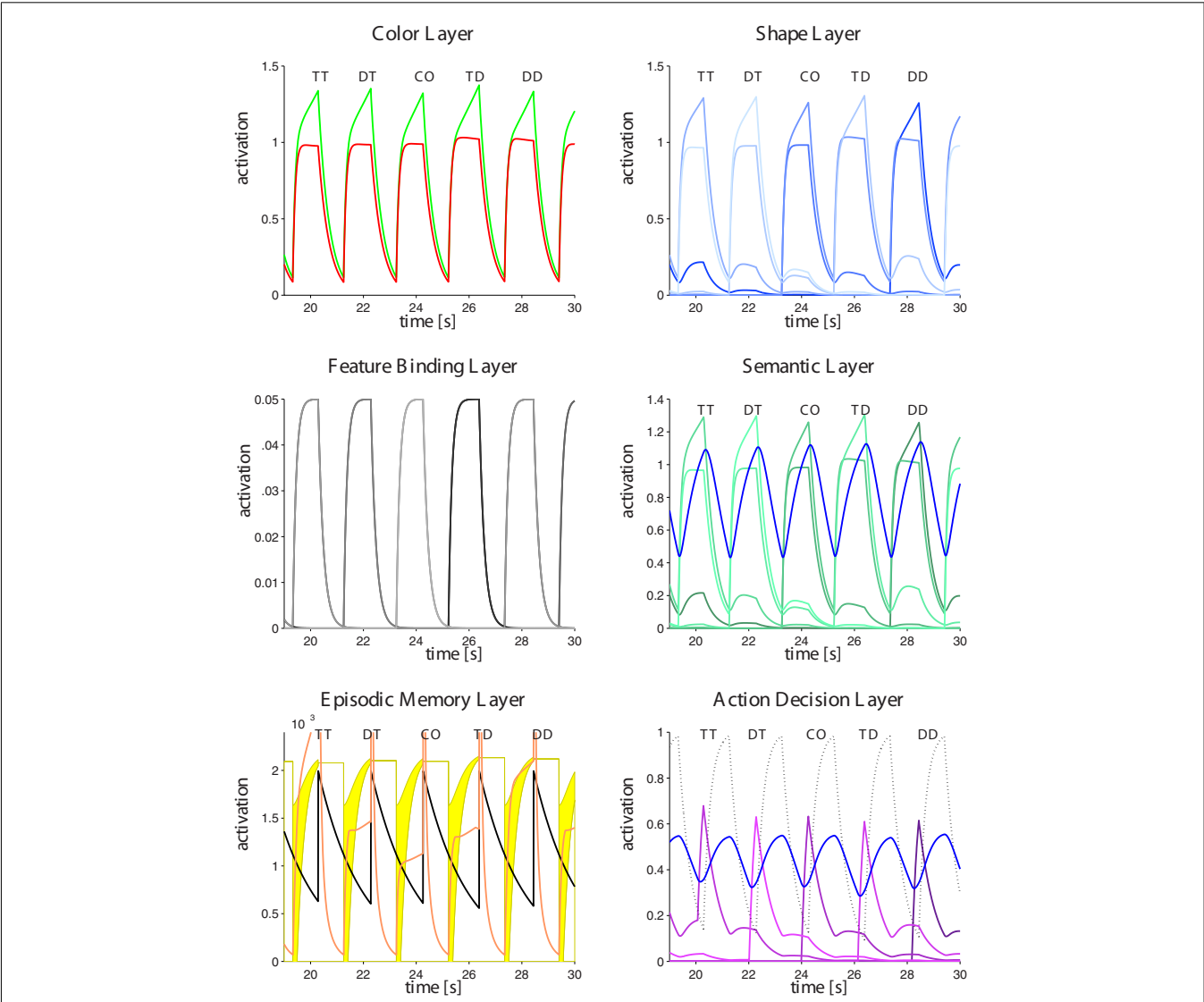


FIGURE 6 | Activation traces over time in the different layers of the GMNP in the voicekey paradigm described in Section 2.2. Different colors correspond to different variables in the respective layer. A few traces are to be highlighted: solid blue lines in both the semantic and the action layer correspond to the respective threshold variable, black in the episodic memory

layer denotes the strength of the memory trace, yellow is the uncertainty region for the old-new signal which is drawn in orange. The model is in classical episodic-retrieval mode, see Section 3.1. Targets are boosted and the entire episode retrieved. Retrieval is apparent in the plots by the re-rise of formerly active variables.

The presentation of a red and a green pictogram drives the two color and the two shape representations in the respective layers. The central executive delivers additional input to green which augments the activity of the target object's shape via the bindings. The semantic representations are fed by a one-to-one mapping from the shape layer, i.e., $S(f) = \mathbb{I}$. The plot of the episodic memory layer shows the memory strength in black which decays with time from a fixed value at memory initialization which takes place at the point a response is given. In orange, the plot shows the similarity signal which linearly modulates the retrieval of a former trial. The signal is highest for the TT trial, intermediate for DT, TD, and DD in ascending order. In the action layer, the black dotted trace is for the no-action response, see Section 2.7.7. The selection of the target in the semantic layer, i.e., the object surpassing the semantic threshold, is fed forward to the action layer.

The present simulation was run with the following values of the relevant parameters: $\Xi_{er} = 1$, $\Xi_{rr} = 1$, $\Xi_{ib} = 1$, $\Xi_{gt} = 0$, $\Xi_{fsb} = 0$, $\Xi_{sab} = 0$, $\Xi_{td} = 0$, $\alpha = 0.0005$, $\check{F} = 1$, $t_{\text{recognition}} = 50$, $t_{\text{afterimage}} = 30$, $t_{\text{motor}} = 80$, $\rho_f = 0.01$, $\delta_f = 0.003$, $\hat{b} = 0.05$, $\#_b = 7$, $\rho_b = 0.008$, $\delta_b = 0.005$, $\tau_{s^\theta} = 0.002$, $v_{s^\theta} = 0.51$, $\rho_a = 0.004$, $\delta_a = 0.002$, $\tau_{a^\theta} = 0.002$, $v_{a^\theta} = 0.5$, $\hat{e} = 0.002$, $\delta_e = 0.003$.

Negative priming in DT trials and positive priming in TT trials are with 24 and 53 ms at rather realistic scales (see Table 5). The present example together with three other realizations is part of the GMNP-software bundle.

3.3. ANALYSIS OF THE WORD-PICTURE PARADIGM

As a showcase example of how to exploit the capabilities of the GMNP to gain more insight in the interaction of the different processes that are involved in NP, we now present a detailed analysis of the GMNP when faced with a word-picture comparison task as it is described in Ihrke et al. (2011). This particular paradigm has a second factor besides priming condition, which is response repetition. Therefore, the labels of the experimental conditions receive an additional suffix, i.e., *s* for response switch and *r* for response repetition. By a parallel implementation, we are able to perform a gradient descent on the parameter set, while keeping the theory semaphores adjusted to each of the settings described in Table 4. Thereby, we obtain information about which of the theoretical assumptions implemented in the GMNP is able to reproduce the experimental results to which degree. Although we optimized the model for the DT and TT conditions, we provide the results for the other conditions that were present in the corresponding experiment as well, which can be regarded as parameter-free predictions.

Table 5 | Mean reaction time and effect strength for the priming conditions CO, DT, TT produced by the GMNP in episodic-retrieval mode as described in Section 3.2.

	(RT) [ms] (SD)	Effect [ms]
CO	976 (7)	–
DT	1000 (10)	–24
TT	923 (22)	53
TD	1134 (11)	–73
DD	1049 (9)	–158

These predictions are there to provide the reader with an idea of how the model can inform further experimental work.

After convergence, the root mean squared error between experimental and simulated effects and control reaction time of the GMNP instance set to distractor inhibition behavior is the lowest (see Table 6). The obtained parameters in that case are: $\Xi_{er} = \Xi_{rr} = \Xi_{ib} = \Xi_{gt} = \Xi_{fsb} = \Xi_{sab} = \Xi_{td} = 0$, $\iota = 0.000001$, $\beta = 0.00155$, $\phi = 0.00011$, $\alpha = 0.0005$, $\check{F} = 1$, $t_{\text{recognition}} = 50$, $t_{\text{afterimage}} = 30$, $t_{\text{motor}} = 80$, $\rho_f = 0.009$, $\delta_f = 0.003$, $\hat{b} = 0.05$, $\#_b = 7$, $\rho_b = 0.0096$, $\delta_b = 0.005$, $\tau_{s^\theta} = 0.002$, $v_{s^\theta} = 0.4131$, $\sigma_{\text{shape} \rightarrow s} = 0.1$, $\sigma_{\text{word} \rightarrow s} = 0.12$, $\sigma_{s \rightarrow a} = 1$, $\rho_a = 0.0036$, $\delta_a = 0.002$, $\tau_{a^\theta} = 0.002$, $v_{a^\theta} = 0.6$, $\hat{e} = 0.002$, $\delta_e = 0.003$.

The corresponding reaction times, given in Table 7, show a very good reproduction. The interaction between response relation and priming condition gave rise to response-retrieval theory, as distractor inhibition theory *per se* is not able to explain it, although

Table 6 | Root mean squared error (RMSE) after a converged gradient descent fit to the absolute reaction time of a control trial (COs and CO_r) and the priming effects of DTs, DT_r, and TTs and TT_r while keeping the theory weights fixed.

	RMSE
Distractor inhibition	14.0
Temporal discrimination	22.5
Episodic retrieval	34.6
Response retrieval	38.1
Global threshold	39.1

Table 7 | Simulated reaction times and effects by the GMNP in distractor inhibition mode compared to experimental results from Ihrke et al. (2011), after fitting model parameters to minimize the RMSE in control RT and the effect sizes for TT and DT conditions.

	GMNP RT [ms]	Experimental RT [ms]
COs	825.5	821.2
DTs	829.8	842.0
TTs	840.4	835.8
TDs	830.5	814.9
TTs	819.8	817.6
CO _r	835.5	838.4
DT _r	826.3	829.5
TT _r	814.3	816.7
TD _r	815.4	840.7
DD _r	836.2	824.4
EFFECTS		
DTs	–4.2	–20.8
TTs	–14.8	–14.6
TDs	–5.0	6.3
DDs	5.7	3.6
DT _r	9.1	8.9
TT _r	21.2	21.7
TD _r	20.1	–2.3
DD _r	–0.7	14.0

it is remarkable that distractor inhibition, as it is implemented in the GMNP, seems to best explain the experimental data. There are several aspects to discuss in that context. First, the GMNP does not reduce to the original implementation of distractor inhibition theory with one on- and one off-cell, controlling recognition of objects. The framework of the GMNP, i.e., its layer structure, the feature decomposition, and the dedicated action layer offer a flexibility that the original theory did not have. Second, the inability of the GMNP in distractor inhibition mode to perfectly fit both DTs and DTr simultaneously may point to the limitations of a pure inhibitory account and toward the necessity of retrieval mechanisms to fully explain the interaction as postulated in Rothermund et al. (2005), for a graphical comparison of DTs and DTr trials see Figure 7.

When encountering apparent contradictions to the original formulation of a theory, another great advantage of computational modeling becomes important: it is very easy to extract detailed information about the conditions that are responsible for unattended behavior, thus providing quick and definite explanations for it. In the described example it seems like distractor inhibition theory is not well implemented in the GMNP as the corresponding setting produces the best fit for an interaction of response relation and priming condition, one of the known weak points of distractor inhibition as it cannot explain these results. But when examining the behavior of the GMNP in detail, the effect is solely present in the action layer, which has not been taken into account by the original distractor inhibition theory. The RMSE

between DTs and DTr is less than a tenth of the difference in the action layer when averaged over one trial. Further, this numerical experiment shows that the postulate that response repetition interaction with priming is incompatible with distractor inhibition seems too strict. Obviously, adding a response mechanism with slowly decaying response activation is sufficient to enable a distractor inhibition model to show such an interaction, even if it is admittedly imperfect.

4. DISCUSSION

Combining experimental evidence from behavioral experiments with basic system neuroscientific mechanisms, we present a GMNP that incorporates all presently relevant theories of the phenomenon. The model clearly identifies differences of experimental conditions and is thus able to resolve existing inconsistencies among the important theories. The model is tested in a number of standard scenarios and is shown to be easily extendable to non-standard versions of priming experiments.

The GMNP gives a unified framework to quantify each of the theories for NP, allowing, for the first time, a quantitative comparison of the impact of the proposed mechanisms. The identification of weights for the different accounts makes it convenient to compare the different predictions in a particular setting.

Negative priming presents itself as a complex phenomenon which has been accounted for by different theoretical descriptions focusing on specific experimental paradigms. A computational

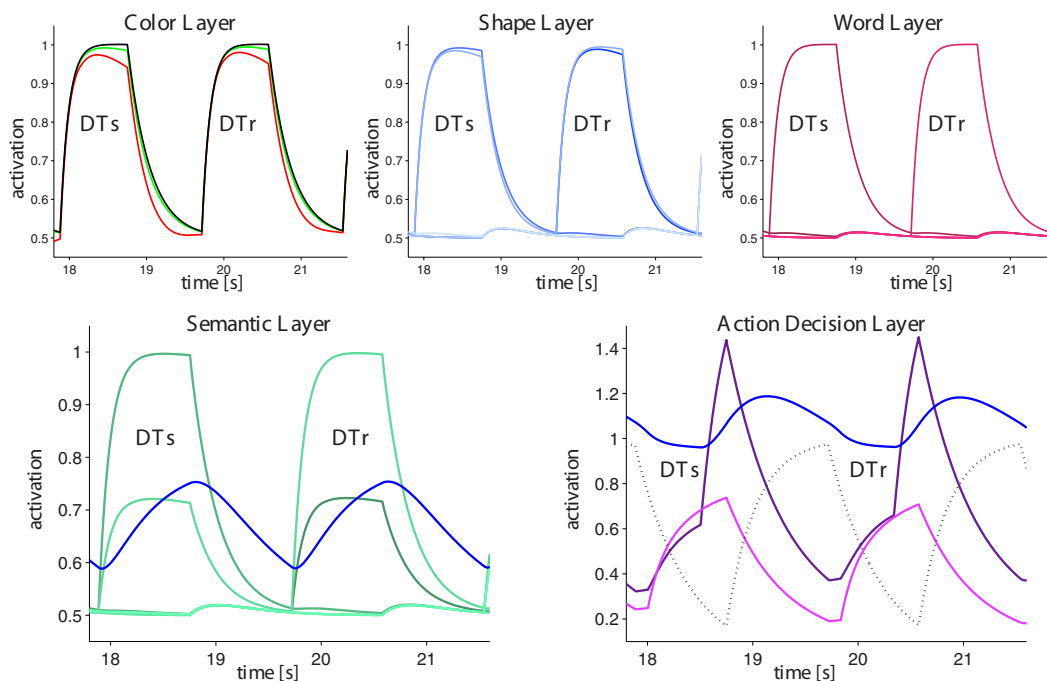


FIGURE 7 | Activation traces over time in the relevant layers of the GMNP in the comparison paradigm. For coloring see Figure 6. The model is tuned to distractor inhibition mode, see Section 3.1. Two different conditions are shown: DTs, the former target becomes the current target and the reaction switches (from no to yes in this case); and DTr, again the former distractor becomes the current target but now the reaction does not switch (yes in both

prime and probe trial). This plot illustrates the difficulty of comparing theories that are developed in a different context. Distractor inhibition theory itself is not able to explain a reaction time difference between the two conditions, as it is only formulated on a semantic level. Indeed GMNP does not show a difference in the traces except in the action layer, where persistent activation and relative inhibition causes the observed effects.

theory can provide a comprehensive framework under these conditions if it is both sufficiently abstract and flexible to reveal similarity and to describe the differences between the aspects of the phenomenon under consideration. Interestingly, the adaptation of the computational model by means of weights (see **Table 4**) gives a straightforward recipe for generating predictions. In principle there are $2^7 = 128$ possible configurations for the values of the weights, only five of which related to experimental and theoretical studies investigated so far in the current literature. Obviously not all configurations are interesting or even meaningful, but a few more studies can be easily suggested that would provide insight into the necessity of the model's components while so far we can only judge whether they are sufficient.

The simulated reaction times in Section 3.2 and the other examples featured in the provided code, show that the behavior of the GMNP is far from being robust against even small parameter changes. Even though a stable model is much more convenient from a theoretical point of view, we consider this instability necessary in order to account for the multitude of different findings in connection with NP. However, we have to face the question of whether the model is able to fit any pattern of experimentally recorded data with just the right parameter settings. Due to the high dimensionality of the parameter space and the sensitivity of the GMNP, this question cannot be answered conclusively by the means of parameter scanning techniques. In fact, an important next step for the GMNP is parameter reduction by determining as many values as possible by comparisons with trusted experimental results, e.g., for the availability of afterimages, decay times of feature bindings, etc. The detail of the GMNP is also easily capable of showing partial reaction times as described in Ihrke et al. (2012) and Schrobsdorff et al. (2012). Therefore, a good way to limit the range of the parameter space would be to have a series of time-marker experiments specially designed to reveal processing stages that are measurable in the GMNP. Till that time the GMNP can only be a basis on which a concrete discussion on the nature of NP theories and paradigms can be made.

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Besides the direct computation of reaction times, the structure of GMNP allows for numerical fitting via a multitude of algorithms. As an example we showed a gradient descent search for an optimal parameter set, keeping the theory weights fixed in order to compare the different theories in terms of flexibility to fit a given set of experimental results. Although a pure gradient descent may not be suitable for such a complex and huge parameter space, the numerical experiments in Section 3.3 already showed a surprising result: expanding the distractor inhibition model by only a reaction mechanism with a threshold and persistent activation as well as relative inhibition, provides a context which is able to produce the interaction of response relation and priming condition, which is otherwise considered to be the weakest point of distractor inhibition theory.

Another promising extension follows from the abstract formulation of relations among mechanisms that are involved in NP. Just as NP theories are formulated using concepts such as memory or central executive which are borrowed from other areas in psychology, the computational implementation of relations among these concepts also has a wider applicability than NP. The main components of the GMNP qualify it already as a *cognitive architecture* similar, e.g., to ACT-R (Anderson et al., 1997) or SOAR (Laird et al., 1987). Beyond this, it would be interesting to discuss the ensuing perspectives for design of artificial cognitive systems, such as for the control of an autonomous robot.

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When the ignored gets bound: sequential effects in the flanker task

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Recent research on attentional control processes in the Eriksen flanker task has focused on the so-called congruency sequence effect a.k.a. the Gratton effect, which is the observation of a smaller flanker interference effect after incongruent than after congruent trials. There is growing support for the view that in this paradigm, the congruency sequence effect is due to repetition of the target or response across trials. Here, results from two experiments are presented that separate the contributions of target, flanker, and response repetition. The results suggest that neither response repetition alone nor conflict is necessary to produce the effect. Instead, the data reveal that only flanker repetition is sufficient to produce congruency sequence effects. In other words, information that is associated with a response irrespective whether it is relevant for the current trial is bound to response representations. An account is presented in which the fleeting event files are the activated part of the task set in which flankers, targets, and response representations are associatively linked and updated through conflict-modulated reinforcement learning.

Keywords: flanker task, cognitive control, conflict monitoring, sequential dependencies, associative learning, episodic binding

INTRODUCTION

Cognitive psychological research has shown that when a participant is instructed to make a response to a target stimulus, he or she is typically slower and less accurate when distractors are present. This is even the case despite receiving instructions to ignore these distractors and having had extensive practice on trials with targets and distractors. Theorists who address this distractor interference effect generally refer to these tasks as conflict or congruency tasks. However, there is great disagreement about how participants exert cognitive control in these tasks. Although some theories have been presented in great detail, by using computational methods, ambiguities still remain. One such computational theory of cognitive control in conflict tasks (Botvinick et al., 2001) has had such a substantial impact on the field that it spawned a plethora of investigations focusing on the precise neurocognitive mechanisms underlying conflict-modulated cognitive control and questioning the sufficiency and necessity of conflict to observe cognitive control.

Research has largely focused on three types of conflict tasks. In the Stroop (1935) task (for a review see MacLeod, 1991), participants are instructed to name the color of a word as quickly and accurately as possible. The word itself refers to a color, allowing the creation of congruent words, such as the word “green” in green font color, and incongruent words, such as the word “blue” in red font color. The second task is the Simon or spatial compatibility task (Simon and Rudell, 1967), in which a stimulus (letter, word, or symbol) is presented on the left or right side of the computer screen. The participant is required to press a left or right button based on the stimulus content while ignoring the stimulus location. For example, a congruent trial could be the word LEFT presented on the left side of the screen and an incongruent trial

could be the word LEFT on the right side of the screen. Finally, in the flanker task (Eriksen and Eriksen, 1974), a central target character is flanked by distractors. There are more distractors than targets and the distractors may be identical to the target (congruent trial) or different than the target. In response-incongruent (RI) trials, the identity of the distractors is associated with the opposite response as the target.

These three tasks have largely been treated as identical in terms of the control processes involved, which has led to theorists making inferences and predictions about one task based on published findings in another task. In fact, the influence of stimulus repetitions differs greatly between the Stroop and flanker tasks (Mayr et al., 2003). In addition, the comparisons of response time distributions are fundamentally different (Spieler et al., 2000; Pratte et al., 2010), which may reflect differences in perceptual, response, and control processes. Thus, even though much of the research on conflict processing has used the Stroop and Simon tasks, those results can not readily be assumed to hold for flanker tasks. As it turns out, the flanker task is the odd one out when it comes to the effects of repetition of stimuli across trials (as will be discussed below) and is the only task that consistently falsified a necessary prediction of the conflict/control-loop model (Botvinick et al., 2001). This has led to a number of new models of conflict-modulated cognitive control that appeal to additional control processes (Blais et al., 2007; Verguts and Notebaert, 2008; Davelaar and Stevens, 2009). This paper continues this approach and addresses the relative influence of distractors on congruency sequence effects in the flanker task.

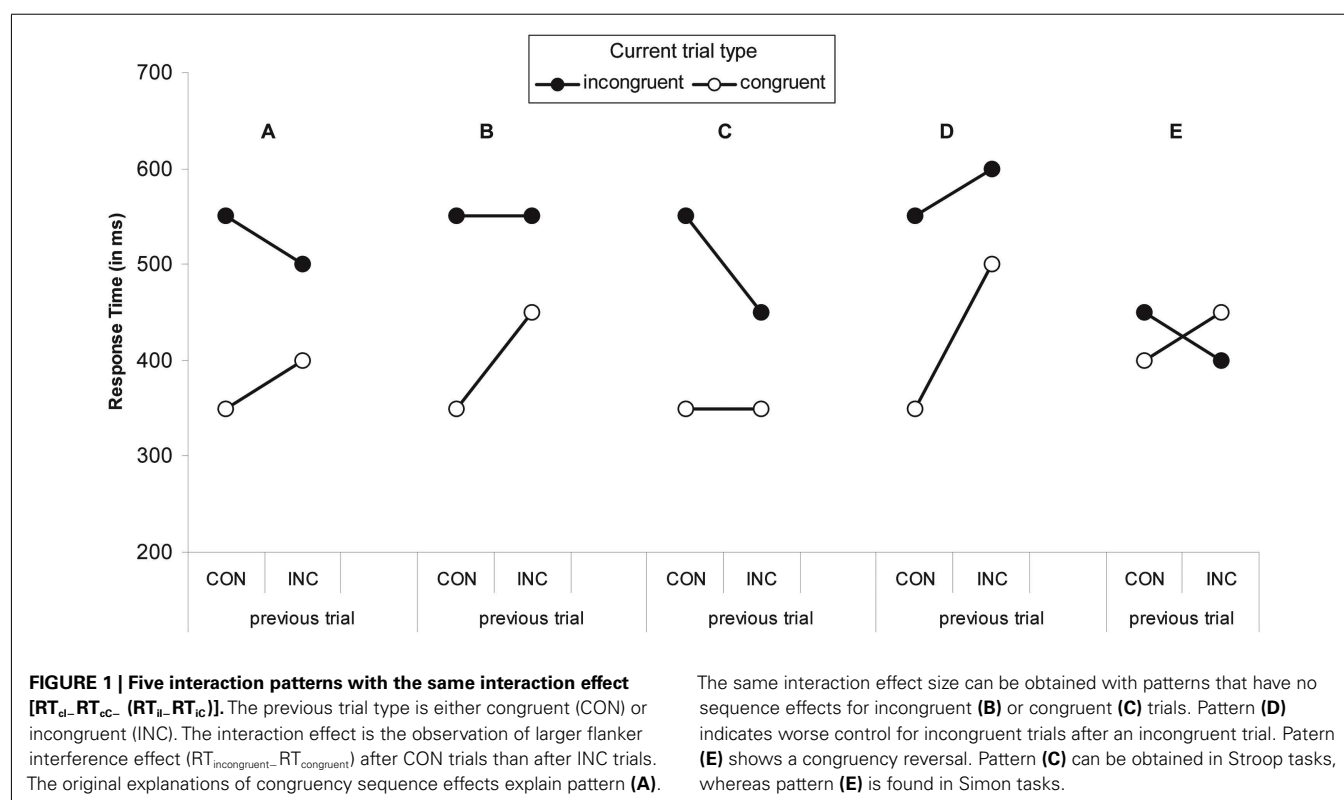
Our starting point is the work by Botvinick et al. (1999, 2001); Kerns et al., 2004; see also Davelaar, 2008a). In several studies using the Stroop and flanker tasks, they observed that the anterior

cingulate cortex (ACC), a frontal brain structure, is more activated in response to processing incongruent than congruent stimuli. Their theoretical innovation was that the ACC may be monitoring the amount of conflict in a trial and at the system level this measured conflict is used to enhance the amount of control on the next trial. Thus, the more conflict on trial n , the more control on trial $n + 1$. This would lead to a particular interaction called the congruency sequence effect or the Gratton effect, which has been interpreted as a signature of cognitive control in conflict tasks. The congruency sequence effect (Gratton et al., 1992) is the finding of a lower interference effect after an incongruent trial compared to the effect after a congruent trial (see **Figure 1A**). Congruent trials after an incongruent or congruent trial are referred to as iC and cC trials, respectively, whereas incongruent trials after an incongruent or congruent trial are referred to as iI and cI trials. The Botvinick-model explains congruency sequence effects as follows. On trial n , the incongruent stimulus leads to an increase in conflict, which is detected by the ACC. On trial $n + 1$, this increased conflict leads to more control, causing distracting information to be ignored more efficiently. Thus, incongruent (iI) and congruent (iC) trials will be responded to more quickly and more slowly, respectively. Although this pattern is observed in all three conflict tasks, several unresolved issues remain.

The first unresolved issue is that not all interactions between the previous and current trial type are created equal. **Figures 1B,C** show examples of an interaction pattern with the same interaction effect (100 ms). In **Figure 1B**, there is no control over incongruent trials, whereas in **Figure 1C**, the congruent trials are unaffected (cf., Kerns et al., 2004). **Figure 1D** has the same interaction effect,

but would not fit the theoretical description of a Gratton effect. Finally, **Figure 1E** presents another interaction with the same effect size, but in this case there is a reversed interference effect after incongruent trials. This pattern is impossible to obtain with the Botvinick-model, as the theoretical limit is the complete absence (or perfectly ignoring) of distractors, which would lead to equal response times for iI and iC trials.

The reversal depicted in **Figure 1E** is most often found in the Simon task (Hommel et al., 2004) and is readily explained within the feature-integration account of sequential effects in the Simon task (Hommel et al., 2004). Specifically, the account assumes that stimulus and response representations on a trial get bound into a single representation called an event file. When part of the stimulus-response ensemble is repeated the remaining parts are reactivated. In the original account, subsequent trials that involve stimuli that partially match (and partially mismatch) the content of the event file lead to confusion and thus longer response times. Response times to stimuli that completely match or completely mismatch are assumed not to differ. Applied to the flanker task, the following is expected based on the feature-integration account. Assume that the stimuli are left- and right-pointing arrows, such as <<<<< and >>>>> as congruent trials and <<<<< and >><>> as incongruent trials. To distinguish between <<<<< followed by <<<<< and <<<<< followed by >>>>>, the reference to the trials include whether the response repeats (e.g., cCr) or alternates (e.g., cCn; “n” for non-repetition). When the response repeats across trials, iI and cCr trials are complete repetitions and will lead to faster response times compared to cI and iCr trials. Dependent on the overall flanker interference effect,



the final pattern will either resemble **Figures 1A,E**. The pattern is the same when the response alternates across trials. For example, iIn and cCn trials are complete mismatches whereas iCn and cIn are incomplete mismatches. Evidence in favor of the feature-integration account comes predominantly from studies employing the Simon task (Hommel et al., 2004) and supports the claim that specialized conflict-related processes (as assumed in the Botvinick-model) are not necessary to explain the congruency sequence effect.

Despite the success of the feature-integration account, both it and the conflict/control-loop hypothesis require further extensions in order to explain the pattern of sequential effects in the flanker task, which constitutes the second unresolved issue. Specifically, in the flanker task, the two-way interaction that resembles **Figure 1A** is found only when the response/target repeats across trials. When the response/target changes, the interaction is absent with the effects of the previous and current trial on response times being completely additive (i.e., parallel lines; Mayr et al., 2003; Nieuwenhuis et al., 2006; Bugg, 2008; Davelaar and Stevens, 2009)¹. Interestingly, the original results reported in Gratton et al. (1992) reveals the same three-way interaction, but this was not analyzed. There is some variation across experiments with the effect of previous trial congruency with iCn and iIn being (equally) slower than cCn and cIn, respectively, which is due to an increase in the response threshold after a conflict trial (Davelaar, 2009).

To date, despite the introduction of new models of the flanker task (Hübner et al., 2010; White et al., 2011; see for debate, Hübner and Töbel, 2012) no computational theory has been put forward that accounts for this three-way interaction pattern. However, variations on the Botvinick-model with and without some elements of the feature-integration account have been proposed to address Stroop and Simon tasks (Blais et al., 2007; Verguts and Notebaert, 2008). These were then falsely assumed to also account for findings in the flanker task. An account that would be able to capture the three-way interaction pattern was given by Davelaar and Stevens (2009) and is essentially a weaker version of the feature-integration account. In particular, the assumption is that only complete matches lead to faster response times, whereas complete mismatches are equal to incomplete matches.

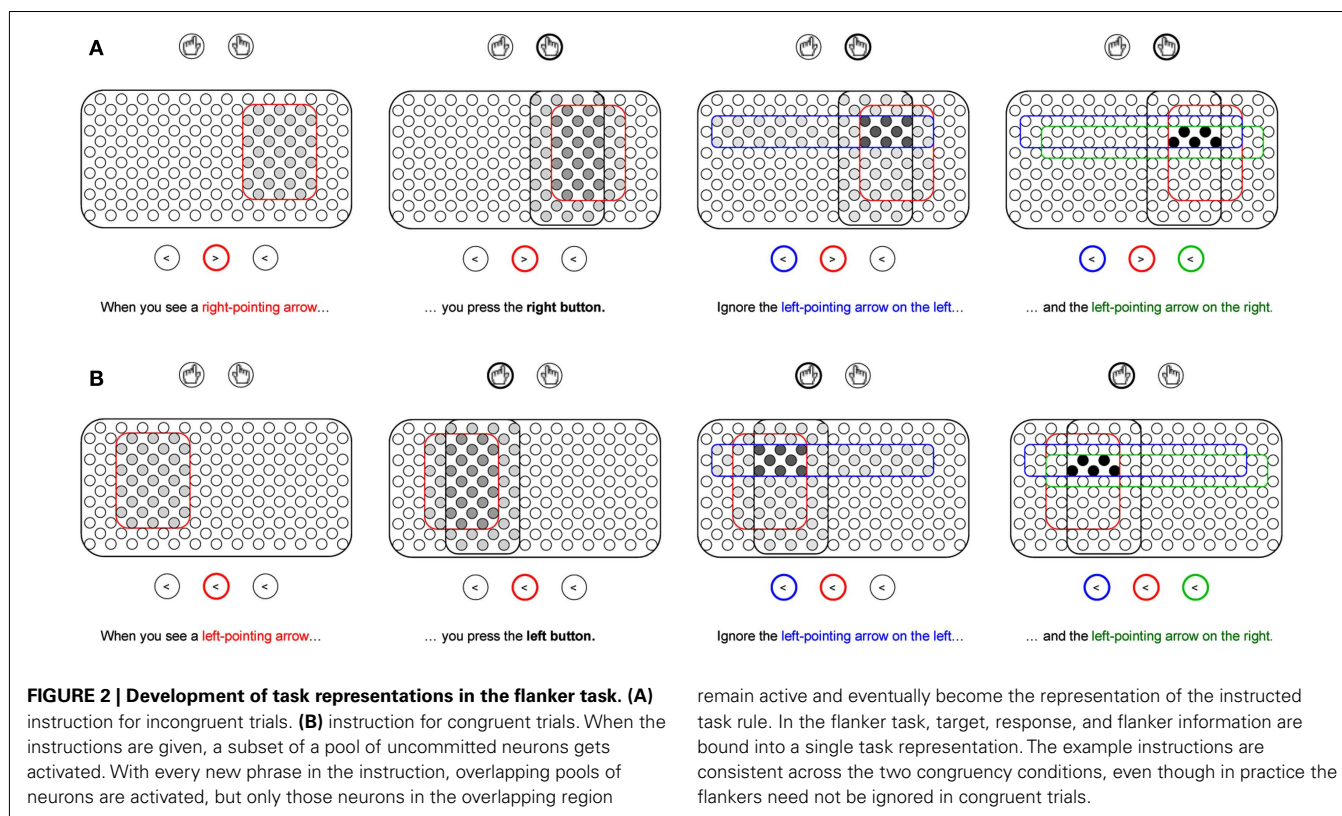
Even though the account put forward by Davelaar and Stevens (2009) captures the three-way interaction, it does not specify the relative importance of repeating the target, response, and flankers. In other words, in the feature-integration account relevant features are bound into an event file, but Davelaar and Stevens (2009) did not state what does and what does not get bound. At first blush,

one would assume that the relevant features are the target and the response, but this would merely produce faster responses when the target/response repeats. Clearly, the flankers, despite being destined to be ignored, are included in the event files. The fact that they are not at all ignored is obvious from the existence of the flanker interference effect. What is not obvious is how the flankers are bound in the event file and what role they play in congruency sequence effects. To address this, we need a detailed account of how the task set or task instructions get represented by a participant. As will become clear in the next section, a very specific interpretation of the term “event file” is used together with a feature binding account of task representations.

A FEATURE BINDING ACCOUNT OF TASK SET REPRESENTATIONS

In typical laboratory settings, experimental paradigms present the participant with novel combinations of stimuli and responses. In order for the participant to follow the instructions required for the experimental task, an internal representation of the task is required in the form of task goals or task sets. These representations encode the task rules and can thus be assumed to correspond to a set of IF-THEN statements. Initially, these rules are maintained in declarative memory until the task becomes well-practiced and transferred to procedural memory. According to Davelaar (2011), goal representations are bindings of representations related to the stimuli and responses. The representation that binds the various subcomponents can be likened to an event file. However, the process by which the event file is formed may require two levels of associative learning. **Figure 2** illustrates the creation of two rules that are employed in the flanker task, using the analogy of neurons in a brain area, presumably the prefrontal cortex (Dehaene et al., 1998). A pool of non-specific neurons exist that have the latent ability to form connections with other intra-pool neurons and with extra-pool representations, such as motor representations (indicated by circles with hands) and location-specific stimulus representations (indicated by circles with arrows). Let us assume that weak random connections exist from every extra-pool representation to the neuronal pool. When an instruction is given, extra-pool representations activate the units in the pool that happen (by chance) to be connected to them. In the example, the sentence phrase “When you see a right-pointing arrow...” activated the 31 units within the red enclosure. The next sentence phrase “...you press the right button” activated the units in the black enclosure. Importantly, only the units that were activated both during the first and second phrase will remain active and have pre-existing, albeit weak, connections with the extra-pool representations of the middle right-pointing arrow and the right motor program. The instructions also mention ignoring the left-pointing arrows on the left and the right. Instead of excluding these from the final representation of 5 units, they are integral to development of the goal representation. The 5 units will be strongly active, which lead to strengthening of the associative connections among them (see **Figure 2**; first level of associative learning) and with the extra-pool representations (second level of associative learning). The newly formed representation needs both levels of associative learning to be effective as a task representation. The intra-pool connectivity leads to a process of pattern completion: whenever

¹ Some studies still reported an interaction when the target/response does not repeat across trials (Ullsperger et al., 2005; Notebaert and Verguts, 2006; Verbruggen et al., 2006). However, these studies used different methodologies (e.g., very short presentation durations or using a large set of numbers instead of two arrows) than the studies listed. Egner et al. (2010) observed an inverse correlation between the congruency sequence effect and the temporal separation between consecutive trials. This highlights the impact of seemingly arbitrary methodological choices, such as timing and stimulus material. The current work aims to address explicitly what underlies the three-way interaction between previous trial type, current trial type, and target/response repetition by using methods that are known to give rise to the three-way interaction. Future work could investigate why some studies failed to replicate this three-way interaction effect.



one of the units becomes active, the entire assembly becomes active.

The initial fragile new representation will continue to strengthen during the practice trials and be sensitive to reinforcement signals. Computational theories of instruction learning and task goal representations typically use slow reinforcement-based learning algorithms (Dehaene et al., 1998; Sutton and Barto, 1998; Doll et al., 2009) and are thus only applicable at stages after initial creation of the task representation. This includes conflict-modulated learning (Davelaar, 2009). By using the pool of uncommitted neurons, a novel task representation can easily be created and kick-start the development of a more stable representation that eventually will lead to automatization of the task. As the stimuli differ in the amount of conflict they trigger, an asymmetry is expected whereby the task representations of incongruent stimuli compared to congruent stimuli undergo more changes in connectivity. The fate of distracting information is interesting, as it is associated with a response, but contextualized via the target. In the example, left-pointing distractors are included in both the top and bottom representations, but are associated with different responses (right and left, respectively). This perspective contrasts with views that ignored flankers would be associated with a “do-not-respond” tag as assumed in some theories of in negative priming (Neill et al., 1992; see for reviews, Mayr and Buchner, 2007; Schrobsdorff et al., 2012). The issue of putative negative priming in the flanker task will be discussed in the discussion.

In the account put forward here, the verbal instructions give rise to task representations, which through associative learning become

strengthened further. This particular representation remains available during the entire experiment and increases in internal and external connectivity. Thus, this is a weight-based representation that stabilizes over protracted time. This contrasts with the fleeting event file referred to by Hommel and colleagues. According to their view, the event file resulting from feature-integration processes is of a transient nature (Colzato et al., 2006; Hommel and Colzato, 2009). These approaches are not incompatible. In fact, they form part of a continuum of various binding processes (cf. Colzato et al., 2006) that operate over different time-scales. In particular, one could consider the possibility that the transient event file could be the activated part of the task set and other salient activations. In other words, the transient event file may be the activated task representation. This distinction between a short-lasting activation-based representation and a longer-lasting weight-based representation has a long history in the memory literature (e.g., James, 1890; Norman, 1968; Shiffrin, 1976; Cowan, 1988) and computational theories (e.g., Davelaar et al., 2006) have explicated the interactions between these levels.

In the current study, the focus is on the presence of flanker information in the task representation and therefore flanker information will be present in the fleeting event file which influences responses in subsequent trials. This leads to two predictions. First, repeating flankers across trials should contribute to response repetition effects irrespective of whether the target repeats across trials. The flankers will continue to activate the previous task representation, which should facilitate complete reactivation. This is investigated in Experiment 1. Second, in the absence of responses on the

previous trial, flankers should still prime the task representations, resulting in response facilitation on the following trial. This is investigated in Experiment 2 and is a consequence of the asymmetry in connection strength for incongruent and congruent task representations. Finding such a pattern of results supports the view that flankers are bound together with target and response information into a unique task representation and that this task representation is sensitive to cross-trial reactivations. This view is congruent with the findings that associative learning processes (as involved in creating the intra- and extra-pool connections) and the binding processes underlying event file creation (activation level of task representations) are different (Colzato et al., 2006).

SEQUENTIAL EFFECTS: WHAT NEEDS TO BE REPEATED?

The Eriksen flanker paradigm has provided critical insights into the spatiotemporal processes involved in visuospatial attention (Eriksen and Eriksen, 1974). Yet, the observation of cross-trial dependencies has attracted a lot of attention. This may be partly due to the explicit detail in prominent conflict/control theories (Botvinick et al., 2001) and partly due to leading contender theories (Hommel et al., 2004) that challenge core assumptions about the need to invoke conflict-related processes. The three-way interaction observed by Mayr et al. (2003) suggested that stimulus/response repetition was all that was needed to account for the pattern without recourse to conflict control processes. The early version of the repetition view was silent with regard to whether the target or the response needs to be repeated to obtain a congruency sequence effect. Take for example the arrow-flanker task used by Mayr et al. (2003). The transition <<>><< to <<>><< repeats the response, the target character and the flankers. Is it necessary to repeat all elements or is one or a combination of two (e.g., target and response) sufficient? To address this question one needs a flanker paradigm in which the target, flankers, and response can be manipulated independently. In the first experiment, a letter-flanker task is used, in which a consonant/vowel categorization is to be made on the central letter and has three types of stimuli: stimuli in which flankers (i.e., the distractors) are identical to the target (e.g., AAAAA: congruent; CO), different from the target but from the same category (e.g., EEAE: stimulus-incongruent; SI), or are from a different category than the target (e.g., KKAKK: RI). The general finding is that RI-trials are slower than either CO- and SI-trials (Eriksen and Eriksen, 1974; Miller, 1991). The first experiment will make use of this task. The second experiment will use arrows instead of characters. In this arrow-flanker task, congruent, and incongruent trials are those in which the flanking arrows point in the same (e.g., <<<<<, >>>>>) or different (e.g., <<>><<, >><>>) directions than the central target arrow. In the arrow-flanker task, the incongruent trials are both SI- and RI.

Using a letter-flanker task, response- and target-repetitions can be disentangled. It is possible that merely repeating the response is sufficient to speed up responding to a RI-stimulus after a RI-trial (e.g., KKAKK followed by BBEBB) compared to the same RI-stimulus after a CO-trial (e.g., AAAAA followed by BBEBB). Davelaar and Stevens (2009) reported an analysis from a study using a consonant/vowel categorization task, showing that the two-way interaction effect (previous x current trial type) was

only observed when the target and flankers repeated across trials. Although this supports the view that the entire stimulus array needs to be repeated across trials to observe facilitation, it is also consistent with the view that flankers need to be repeated (Frings et al., 2007) together with the response. If a two-way interaction is found when flankers repeat while targets change (e.g., KKEKK followed by KKAKK), the repetition view needs to be updated to include the possibility that the flankers, despite being irrelevant (cf. Jaswal, 2012), are bound in episodic memory (i.e., activates the task representation) and can drive the sequential effects.

In a study that obtained the Gratton effect (i.e., the two-way interaction between previous and current trial type) when stimuli do not repeat across trials, Notebaert and Verguts (2006) proposed that stimulus conflict could contribute to the effect. Stimulus conflict is present when the flankers and target are different characters that are associated with the same response. Their study employed a numerical flanker task, which differs conceptually from the arrow-flanker task used in the original study by Mayr et al. (2003). The consonant/vowel categorization variant, as used here in Experiment 1, is conceptually closer due to the small set size (four letters versus two arrows versus ten digits) and a direct manipulation of stimulus conflict. It is possible that stimulus conflict, which is also present in RI-trials, underlies the conflict-modulated effect, as suggested by Verbruggen et al. (2006). This is yet unknown for a flanker paradigm using letters instead of numbers (Notebaert and Verguts, 2006), or colors (Verbruggen et al., 2006).

Finally, several researchers have suggested computational accounts in which monitored conflict modulates associative strengths (Blais et al., 2007; Verguts and Notebaert, 2008; Davelaar, 2009; Davelaar and Stevens, 2009). Evidence supporting this view comes from finding a larger speed up for repeated RI stimuli than for repeated CO stimuli (Davelaar and Stevens, 2009). Comparing RI- with CO-trials necessarily confounds stimulus-conflict with response conflict. The consonant/vowel variant of the flanker task deconfounds these factors and allows an assessment of the relation between type of conflict and the priming effect.

The present investigation aims to contribute to the literature by addressing the following questions. First, can the three-way interaction that supported the original repetition view by Mayr et al. (2003) be replicated in a consonant/vowel flanker paradigm? Second, what type of repetition (target, flanker, response, or a combination) is needed to obtain the two-way interaction between previous and current trial type? Answers to these questions provide critical boundary conditions for models of cognitive control and those that focus on the flanker task in particular. Specifically, knowing what type of information needs to be repeated will force the theorist to develop models that explicitly process this information. To preview the results, the observation that repeating the flankers and response are necessary suggests that flankers are not simply ignored, but form an integral part of any ensuing control process. Experiment 1 uses the letter-flanker task, while Experiment 2 uses an arrow-flanker task that singles out a critical pattern found in Experiment 1 and is predicted by the feature binding account of task representations.

EXPERIMENT 1

MATERIALS AND METHODS

Participants

Twelve participants (six women, mean age = 26) from the University of London were tested individually and received a remuneration of £7 for their time.

Stimuli and procedure

Stimuli consisted of five horizontally arranged capital letters. The letters used were: A, E, B, and K. The letters were arranged to create three types of stimuli: congruent (CO: AAAAA, EEEEE, KKKKK, BBBB), stimulus-incongruent (SI: EEAE, AAEEA, KKBKK, BBKBB), and RI (RI: BBABB, KKAKK, BBEBB, KKEKK, AABAA, EEBEE, AAKAA, EEKEE). To avoid biases in expecting a subset of stimulus transitions, all possible stimulus transitions were included. Stimuli were presented in black font on a white background. Participants were instructed to respond to the central target letter by pressing the “z” or “/”-key on the keyboard when the letter is a consonant or a vowel. The category-response mapping was counterbalanced across participants. The instruction was followed by a practice block of 48 trials (16 trials per condition). Each trial started with five dashes in gray font for 1,000 ms followed by the flanker stimulus presented for a maximum of 1,500 ms. Following the practice, participants completed 12 experimental blocks testing each condition 32 times. All blocks were followed by feedback regarding the accuracy and average response time. Participants were instructed to aim for an average response time of less than 1 s and to maintain accuracy above 80% correct.

RESULTS

Across participants and conditions, accuracy varied between 88 and 99%. There was a main effect of condition in both accuracy [$F(2,22) = 14.33$, $MSE < 0.001$, $p < 0.001$, $\eta^2 = 0.56$] and correct RTs [$F(2,22) = 66.63$, $MSE = 55.77$, $p < 0.001$, $\eta^2 = 0.86$]. Accuracy was lowest (92%) and correct RTs were slowest (518 ms) in

the RI condition. Accuracy (95 vs. 96%) and correct RT (486 vs. 490 ms) did not differ between CO and SI conditions (all $ps > 0.08$). In addressing the two questions set out in the introduction, repeated measures ANOVAs were conducted on the accuracies and the RTs conditioned on the previous and current trial being correct (a standard procedure in this literature). As the various repetition effects do not allow a full factorial analysis, analyses were focused on the relevant parts of the data that address the questions. **Table 1** presents correct RTs and error rates for all conditions (see **Table 2** for examples). For correct RTs, an overall 3 (previous trial type) \times 3 (current trial type) \times 3 (repetition status) factorial ANOVA that included trials with flanker repetitions revealed main effects of current trial type [$F(2,22) = 39.45$, $MSE = 650.89$, $p < 0.001$, $\eta^2 = 0.78$] and repetition [$F(2,22) = 62.81$, $MSE = 2087.41$, $p < 0.001$, $\eta^2 = 0.85$], a two-way interaction between previous and current trial type [$F(4,44) = 7.83$, $MSE = 357.31$, $p < 0.001$, $\eta^2 = 0.42$], and a three-way interaction [$F(8,88) = 4.33$, $MSE = 425.49$, $p < 0.001$, $\eta^2 = 0.28$]. For error rates, there were main effects of previous trial type [$F(2,22) = 6.05$, $MSE = 0.001$, $p < 0.01$, $\eta^2 = 0.36$], current trial type [$F(2,22) = 14.66$, $MSE = 0.001$, $p < 0.001$, $\eta^2 = 0.57$], and repetition [$F(2,22) = 20.35$, $MSE = 0.004$, $p < 0.001$, $\eta^2 = 0.65$], but no three-way interaction. The interactions in the RT data can be understood through addressing the questions, to which we turn now.

Question 1: Is there a three-way interaction?

Figure 3A presents the correct RTs across the CO/RI conditions for which the transitions involve both response and target-repetitions. These conditions constitute the typical conditions used in previous experiments and involve response conflict and stimulus conflict. Replicating previous results, the two-way interaction is present for CO- and RI-trials, when the target and the response repeat, but is absent when there is no repetition. A repeated measures ANOVA crossing the factors current trial (CO vs. RI), previous trial (CO vs. RI), and repetition (no repetition vs. full repetition, including

Table 1 | Mean correct response times (in ms) and error rates (in brackets), separated by flanker repetition.

Transition	Previous trial type								
	No repetition			Response repetition			Target + response repetition		
	CO	SI	RI	CO	SI	RI	CO	SI	RI
RI	541 (0.06)	544 (0.09)	546 (0.11) ^b	518 (0.11)	516 (0.10)	528 (0.07)	475 (0.03) ^b	469 (0.02)	462 (0.04) ^b
RI-repeat ^a	524 (0.08) ^{bd}	527 (0.04) ^d	536 (0.07) ^f			489 (0.05) ^e			437 (0.03) ^e
SI	504 (0.05) ^c	505 (0.05) ^c	506 (0.05)		479 (0.05)	486 (0.03)	458 (0.03) ^c		452 (0.01)
SI-repeat ^a			511 (0.09) ^d	495 (0.04)				433 (0.02) ^c	
CO	503 (0.06) ^{bc}	501 (0.04) ^c	506 (0.06)	473 (0.05)	471 (0.04)	491 (0.06)		430 (0.01) ^c	437 (0.02) ^b
CO-repeat ^a			506 (0.11) ^{bd}				418 (0.01) ^{bc}		

CO, congruent; SI, stimulus-incongruent; RI, response-incongruent.

^aX-repeat refers to the X-condition in which the flankers repeat from the previous trial. ^bThese eight conditions are used in the analysis in question 1 on response conflict. ^cThese eight conditions are used in the analysis in question 1 on stimulus conflict. ^dThe effect of flanker repetition on RTs was not significant ($p > 0.09$ for all pairwise comparisons). ^eThe effect of flanker repetition on RTs was significant ($p < 0.05$ for all pairwise comparisons). ^fThis trial is a RI–RI transition in which the flankers do not become the target. The difference with the corresponding negative priming type transition was not significant ($p > 0.55$).

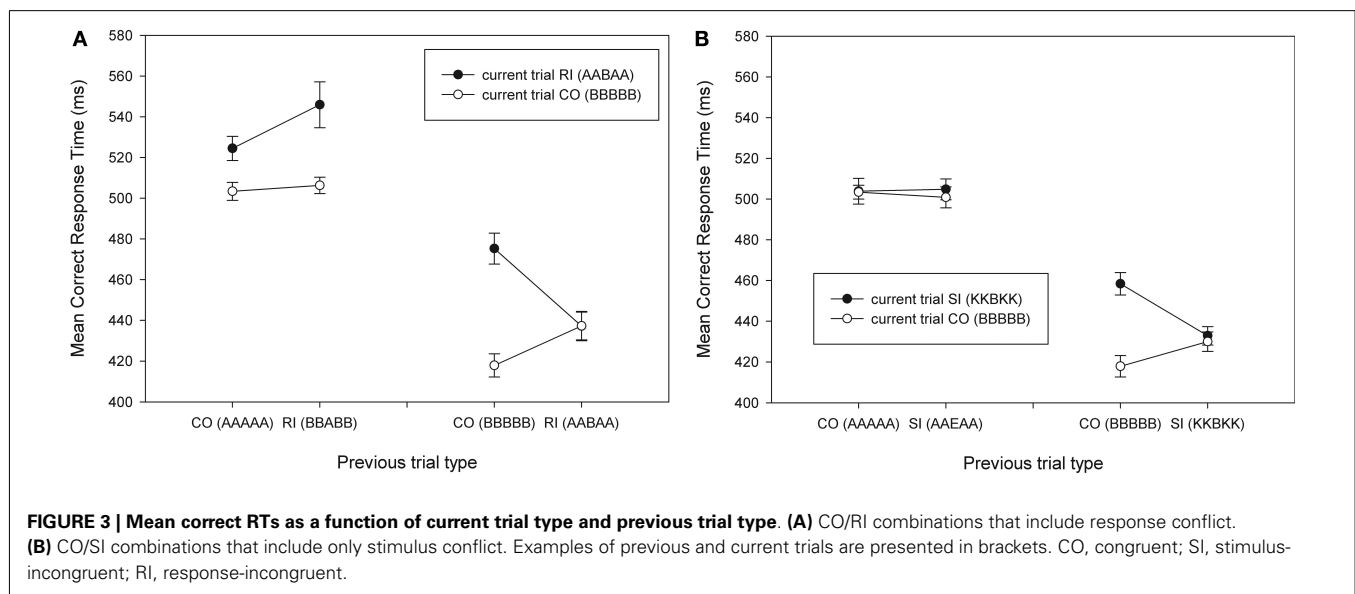
The bold values feature in the target vs. flanker repetition analysis.

Table 2 | Examples of stimuli used in Experiment 1 by condition.

Transition	Previous trial type								
	No repetition			Response repetition			Target + response repetition		
	CO BBBB	SI BBKB	RI AABAA	CO EEEEE	SI AAEEA	RI BBEBB	CO AAAAA	SI EEAE	RI BBABB
RI	KKAKK	KKAKK	BBABB ^b	BBABB	BBABB	KKAKK	BBABB ^b	BBABB	KKAKK ^b
RI-repeat ^a	BBABB ^b	BBABB	BBEBB ^d			BBABB			BBABB
SI	EEAEE ^c	EEAEE ^c	EEAEE		EEAEE	EEAEE	EEAEE ^c		EEAEE
SI-repeat ^a			AAEEA	EEAEE				EEAEE ^c	
CO	AAAAA ^{bc}	AAAAA ^c	EEEE	AAAAA	AAAAA	AAAAA		AAAAA ^c	AAAAA ^b
CO-repeat ^a			AAAAA ^b				AAAAA ^{bc}		

CO, congruent; SI, stimulus-incongruent; RI, response-incongruent.

^aX-repeat refers to the X-condition in which the flankers repeat from the previous trial. ^bThese eight conditions are used in the analysis in question 1 on response conflict. ^cThese eight conditions are used in the analysis in question 1 on stimulus conflict. ^dThis trial is a RI–RI transition in which the flankers do not become the target.



flankers) revealed a significant three-way interaction in the RT data [$F(1,11) = 11.82$, $MSE = 731.31$, $p < 0.01$, $\eta^2 = 0.52$]. As expected this three-way interaction was due to a previous \times current trial type interaction when target/response repeated [$F(1,11) = 34.90$, $MSE = 283.01$, $p < 0.001$, $\eta^2 = 0.76$], which was absent when repetition was absent [$p = 0.21$, $\eta^2 = 0.14$]. This replicates the three-way interaction previously reported in experiments using arrows as stimuli.

The remaining analyses take advantage of the task mapping two letters onto a single response, i.e., the SI conditions and flanker-non-repetitions.

Figure 3B presents the correct RTs across the CO/SI conditions for which the transitions involve both response and target-repetitions. These conditions do not involve any response conflict, but do have stimulus conflict. A similar repeated measures ANOVA using these CO and SI-trials revealed a three-way interaction [$F(1,11) = 14.14$, $MSE = 179.05$, $p < 0.005$, $\eta^2 = 0.56$], which

was due to a previous \times current trial type interaction when target/response repeats [$F(1,11) = 22.62$, $MSE = 187.74$, $p < 0.01$, $\eta^2 = 0.67$], but not when the target/response changes [$p = 0.67$, $\eta^2 = 0.02$]. In other words, the data reveals a previous \times current trial type interaction effect in the absence of response conflict.

Question 2: What type of repetition is needed to obtain the Gratton effect?

In both analyses focusing on response and stimulus conflict, both the target and response repeated across trials. In addition, the repeated CO–CO, SI–SI, and RI–RI transitions also repeated the flankers from one trial to the next. To address question 2, the focus is on **Figure 4**, which contains transitions that do not repeat the flankers. We conducted a 2×2 ANOVA on the data (with CO and RI as previous trial types) with the RI–RI transition that includes flanker repetition (e.g., BBEBB followed by BBABB) and one that includes flanker change (e.g., BBEBB followed by KKAKK). There

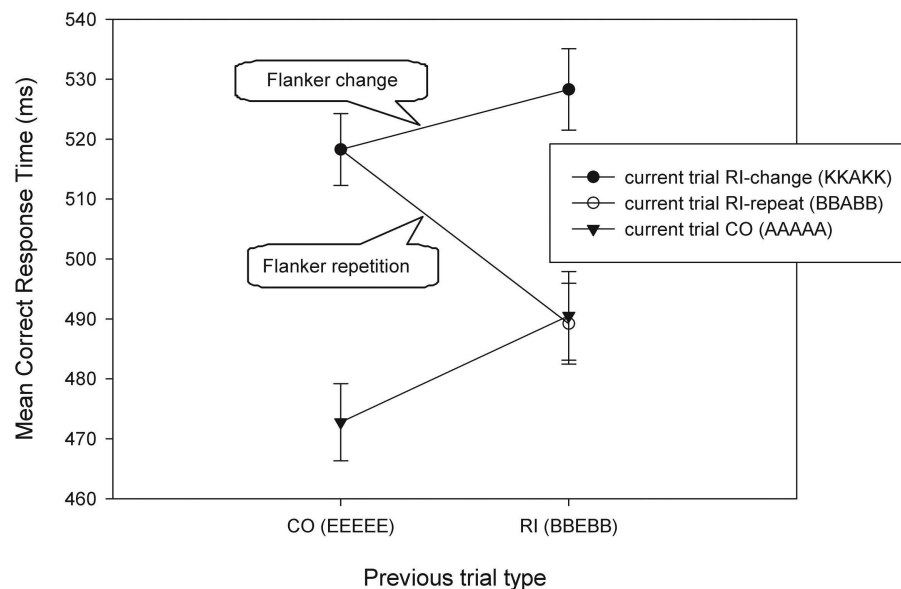


FIGURE 4 | Mean correct RTs as a function of current trial type and previous trial type for trial sequences that have response repetition, but no target repetition. The RI–RI transitions can be split into trials that have

flanker repetition (BBEBB followed by BBABB) and trials that have not (BBEBB followed by KKAKK). Examples of previous and current trials are presented in brackets. CO: congruent; RI: response-incongruent.

was no previous \times current trial type interaction effect when the flankers changed (RI–RI transition = 528 ms; $p = 0.68$, $\eta^2 = 0.02$), but there was with flanker repetition (RI–RI transition = 489 ms) [$F(1,11) = 9.4$, $MSE = 698.76$, $p < 0.05$, $\eta^2 = 0.46$].

No flanker repetition effects were found when the target and response change across trials (all $ps > 0.09$). With regard to the priming effects following different types of conflict, the RI-priming effect is numerically larger than the SI-priming effect (38 ms vs. 25 ms), but the sizes are not statistically different ($p > 0.10$).

DISCUSSION

The results can be summarized as follows. There are four effects in the data: an overall flanker interference effect (EEEE vs. BBEBB), a response repetition effect (EEEE followed by BBBB vs. EEEEE followed by AAAA), a combined target and response repetition effect (KKEKK followed by BBABB vs. KKEKK followed by BBEBB), and a flanker repetition effect (KKEKK followed by BBABB vs. KKEKK followed by KKAKK). Whereas none of these effects are controversial, the combination of these produces the three-way interaction effect between previous trial, current trial, and target/response repetition that has been discussed in the cognitive control literature (Mayr et al., 2003; Nieuwenhuis et al., 2006; Davelaar and Stevens, 2009). Importantly, the current experiment used a methodology involving letters, a non-spatial categorical judgment, and multiple target characters mapping onto a single response. Thus, the three-way interaction can not be attributed to the use of arrows as stimuli and confounding target repetition with response repetition.

We set out to address two questions. First, can the three-way interaction be replicated in a consonant-vowel flanker paradigm? Second, what type of repetition (target, flanker, response, or a

combination) is needed to obtain the Gratton effect? The answer to the first question is unequivocally “Yes!.” In addition, the results show for the first time that this three-way interaction is present in both CO/RI combinations and CO/SI combinations. Therefore, the interaction is not dependent on response conflict. However, this description in terms of response and stimulus conflict is qualified by the findings to the second question. The analyses revealed that when nothing repeats across trials, the two-way interaction between current and previous trial type, which defines the Gratton effect, is absent. The interaction is also absent when only the response repeats. To obtain the two-way interaction at least the flankers and the response need to be repeated across trials. This finding supports the view that flanker repetition (in the absence of target repetition) contributes to the Gratton effect. Previously, the flanker benefit has been demonstrated by Frings et al. (2007) using a negative priming paradigm. Here, flankers are shown to critically contribute to congruency sequence effects that were previously attributed to global attentional control processes.

In relation to the conflict monitoring theory (Botvinick et al., 2001), the results revealed that conflict by itself does not produce a Gratton effect and that stimulus repetition seems to govern its presence. The experiment did not show a Gratton effect after RI and SI conflict when nothing repeats across trials. In one study, Verbruggen et al. (2006) found a marginal interaction effect between previous trial type (CO vs. SI) and current trial type (CO vs. SI), but did not report any statistics or effect sizes. In following Davelaar and Stevens (2009), the size of the RI-priming effect ($RT_{EEEE} \text{ followed by } KKEKK - RT_{KKEKK} \text{ followed by } KKEKK$) was larger than the SI-priming effect ($RT_{EEEE} \text{ followed by } AAEEA - RT_{AAEEA} \text{ followed by } AAEEA$). Within the associative learning theory that uses conflict-modulated learning (Davelaar and Stevens, 2009; see also Blais et al., 2007; Verguts and Notebaert, 2008) this could

be interpreted to mean that response conflict is a stronger learning signal than stimulus conflict. However, the statistics did not support the numerical difference. This aspect would benefit from further research.

EXPERIMENT 2

In the first experiment, flanker repetition contributed to the previous \times current trial type interaction when the response also repeated. This is consistent with a theoretical view in which traces are formed in episodic memory during the instruction phase and contain information about the flankers and the response. Target information would also be stored in the trace. These episodic traces are different, but related, to what Hommel (1998; Hommel et al., 2004) refers to as event files. At the current stage in the theoretical development, it is assumed that these episodic traces form the task representations and that short-lived event files are the activations of these representations. In other words, the relation between event files and task representation is analogous to the relation between short-term memory and long-term memory within the activation-based approach (e.g., James, 1890; Norman, 1968; Shiffrin, 1976; Cowan, 1988). This reinterpretation of event files allows for integration with the literature on memory and executive function (Davelaar et al., 2005; Davelaar, 2011) and underscores the breadth of binding processes proposed (Colzato et al., 2006). Whether the activation-based approach can be distinguished from Hommel's event files depends on the definitions and characteristics attributed to them. Nevertheless, in the current incarnation as activated task representations, any bound element, including flankers, could lead to congruency sequence effects.

To truly assess whether flanker repetition contributes to the congruency sequence effect, only flanker information should be presented. In Experiment 2 some of the trials are preceded only by flankers. As there is no target, no response is needed. If the task representation includes flanker information, then merely presenting flankers should lead to (partial) reactivation of those representations and subsequently to (pseudo)repetition effects. This prediction follows from the observation that task rules are activated despite being unnecessary for a given trial (see Hommel et al., 2004, for a review). Congruency sequence effects have been observed when no response on the previous trial was made (Hommel et al., 2004, experiment 3), indicating that features presenting in a preceding trial can activate task rules that have their influence on subsequent trials.

Critical in the current theorizing is the assumption that the strengthening of the intra- and extra-pool connections is modulated by reinforcement and conflict signals. Thus the more conflict, the larger the change in connection strength (Davelaar, 2009). This leads to an asymmetry, whereby the task representations for incongruent stimuli have stronger connections than those for congruent stimuli. This means that flankers tend to activate the incongruent task representation more than the congruent one.

Consider the four possible scenarios: $\gg \gg$ followed by $\gg \gg \gg$, $\gg \gg$ followed by $\gg \langle \gg \rangle$, $\gg \gg$ followed by $\langle \langle \langle \langle \rangle \rangle$, and $\gg \gg$ followed by $\langle \langle \rangle \langle \rangle$. The flankers $\gg \gg$ do not predict the stimulus on the following trial, but this set of flankers has stronger connections with the task representation "IF $\gg \langle \gg \rangle$ THEN left button" than with "IF $\gg \gg \gg$

THEN right button." This produces a competitive advantage that leads to faster responses when the stimulus $\gg \langle \gg \rangle$ is presented. Thus, even though no target or response has occurred on the previous trial, the content of the event file includes the activated task representation, which in turn facilitates responses on the next trial when a stimulus matches that representation. This is tested in Experiment 2.

MATERIALS AND METHODS

Participants

Eighteen participants (12 women, mean age = 29 years) for the University of London were tested in individually and received a remuneration of £8 for their time.

Stimuli and procedure

Stimuli consisted of five horizontally arranged arrowheads, making up congruent ($\langle \langle \langle \langle \langle \rangle \rangle \rangle \rangle \rangle$ and $\gg \gg \gg \gg \gg$) and incongruent ($\langle \langle \rangle \langle \rangle \langle \rangle \langle \rangle \langle \rangle$ and $\gg \gg \langle \gg \rangle \gg$) trials. Stimuli were presented in black font on a white background. Participants were instructed to respond to the central target arrowhead by pressing the "z" or "/"-key on the keyboard when the arrow pointed to the left or the right, respectively. On 25% of the trials the target would be absent (blank space) and participants should withhold responding for 1,000 ms. This produced four new sequences: incongruent and congruent trials that were preceded by similar or different flankers. The instruction was followed by a practice block of 64 pairs of trials. Each pair of trials started with a blank interval for 1,000 ms followed by the first flanker stimulus, presented for a maximum of 1,500 ms, followed by another blank interval and finally the second flanker stimulus. From the viewpoint of the participant, each block consisted of 128 independent trials. Feedback on accuracy and reaction time was given after the practice block and after each experimental block. Participants were instructed to aim for an average response time of less than 1 s and to maintain accuracy above 80%. After the practice block, participants completed eight experimental blocks, testing each unique responding condition 32 times and each of the sequences with flankers only trials 64 times.

RESULTS

A $2 \times 2 \times 2$ within-subject ANOVA with previous trial type (repeating response versus non-repeating response), current trial type, and target/response repetition as factors was conducted, followed by a 2×2 ANOVA on the no response flanker repetition trials. The results are presented in **Table 3** and **Figure 5**. Incongruent trials were slower and less accurate than congruent trials [RT: $F(1,17) = 142.41$, $MSE = 1565.81$, $p < 0.001$, $\eta^2 = 0.150$; error: $F(1,17) = 22.39$, $MSE = 0.005$, $p < 0.001$, $\eta^2 = 0.568$]. There was a main effect of previous trial type on error rates [$F(1,17) = 13.36$, $MSE = 0.002$, $p < 0.005$, $\eta^2 = 0.440$], but not on RTs ($p > 0.10$) and a main effect of repetition for RTs [$F(1,17) = 17.41$, $MSE = 656.11$, $p = 0.001$, $\eta^2 = 0.506$], but not for error rates ($p = 0.612$). All two-way interactions for error rates were significant [previous \times current: $F(1,17) = 110.03$, $MSE = 0.001$, $p < 0.01$, $\eta^2 = 0.371$; previous \times repetition: $F(1,17) = 6.05$, $MSE = 0.003$, $p < 0.05$, $\eta^2 = 0.263$; current \times repetition: $F(1,17) = 10.22$, $MSE =$

Table 3 | Mean correct response times (in ms) and error rates (in brackets), separated by previous trial type, current trial type, repetition, and flanker only trials.

Current trial type	Previous trial type					
	No repetition		Target/response repetition		Flankers only	
	Congruent	Incongruent	Congruent	Incongruent	Change	Repeat
Incongruent	511 (0.05)	522 (0.06)	528 (0.12)	476 (0.03)	535 (0.07)	506 (0.04)
Congruent	434 (0.02)	448 (0.01)	416 (0)	424 (0)	436 (0.01)	436 (0.01)

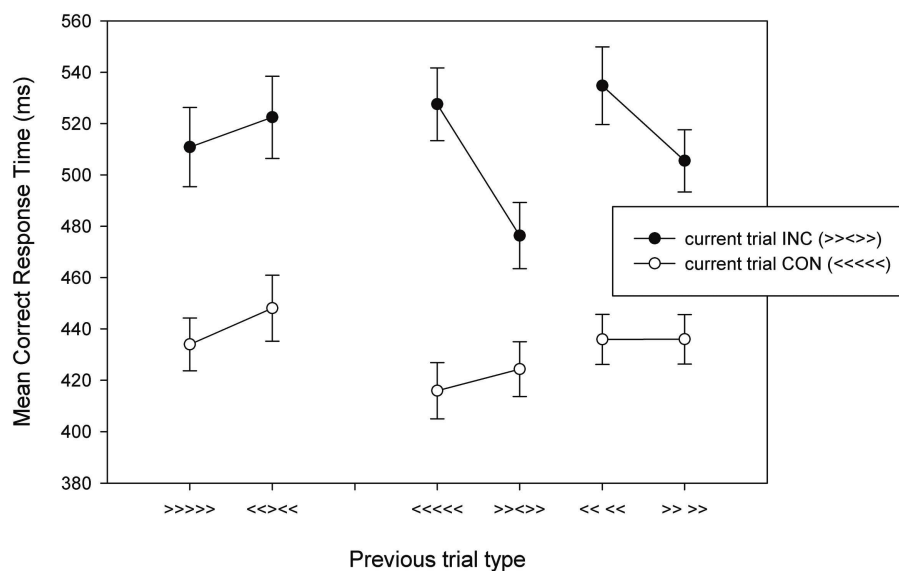


FIGURE 5 | Mean correct RTs as a function of current trial type and previous trial type for Experiment 2. Examples of previous and current trials are presented in brackets. INC, incongruent; CON, congruent.

0.001, $p = 0.005$, $\eta^2 = 0.375$], and all but the current trial type \times repetition interaction for RTs [previous \times current: $F(1,17) = 26.13$, $MSE = 331.35$, $p < 0.001$, $\eta^2 = 0.606$; previous \times repetition: $F(1,17) = 25.42$, $MSE = 414.32$, $p < 0.001$, $\eta^2 = 0.599$; current \times repetition: $p = 0.287$]. These interactions were qualified by significant three-way interaction in both the RTs [$F(1,17) = 20.41$, $MSE = 359.31$, $p < 0.001$, $\eta^2 = 0.546$] and error rates [$F(1,17) = 11.85$, $MSE = 0.002$, $p < 0.005$, $\eta^2 = 0.411$]. These three-way interactions are due to the presence of a previous \times current trial type interaction when the target/response repeats [RT: $F(1,17) = 40.42$, $MSE = 394.90$, $p < 0.001$, $\eta^2 = 0.704$; error rate: $F(1,17) = 14.41$, $MSE = 0.003$, $p = 0.001$, $\eta^2 = 0.459$], but not when it changes ($ps > 0.37$). These results replicate the basic pattern presented in previous reports (Mayr et al., 2003; Nieuwenhuis et al., 2006; Davelaar and Stevens, 2009).

In this experiment, the trials that were preceded by flankers only and did not require any response are the main focus. A 2×2 ANOVA revealed a significant effect of current trial type [$F(1,17) = 134.14$, $MSE = 950.30$, $p < 0.001$, $\eta^2 = 0.888$] and an effect of flanker repetition [$F(1,17) = 26.69$, $MSE = 133.69$, $p < 0.001$, $\eta^2 = 0.628$]. Importantly, these main

effects were qualified by a significant interaction [$F(1,17) = 27.38$, $MSE = 141.18$, $p < 0.001$, $\eta^2 = 0.617$], which was due to an effect of flanker repetition on incongruent trials [$t(17) = 5.93$, $p < 0.001$], but not on congruent trials ($p > 0.98$).

The final statistical comparison that tests the view that the three-way interaction is due to flanker repetition is to correlate the two-way interaction in repetition trials ($M = 58.9$, $SD = 9.6$) with the flanker repetition effect in the incongruent trials ($M = 25.1$, $SD = 2.7$). This correlation was significant ($r = 0.63$, $p < 0.01$) and suggested that 40% of the variance in the two-way interaction is accounted for by flanker repetition in the incongruent trials. In order to put this finding in perspective, all four pairwise effects (flanker effect in flanker change and flanker repetition trials and flanker repetition effect in congruent and incongruent trials) were entered as predictors for the critical two-way interaction effect. The overall multiple regression was significant [$F(3,13) = 4.68$, $MSE = 988.84$, $p < 0.05$, $R^2 = 0.52$]. Of the predictors, only the flanker repetition effect in incongruent trials remained significant [$t(13) = 2.60$, $p < 0.05$] and accounted uniquely for 34.1% of the variance in the two-way interaction effect. The other predictors were not significant ($ps > 0.23$). As a final check, when a two-way ANOVA was run with factors previous trial type and current

trial type for the repetition only trials (iCr, iIr, cCr, cIr) with the flanker repetition effect in incongruent trials entered as a covariate, the two-way interaction was not significant [$F(1,15) = 0.015$, $MSE = 269.10$, $p = 0.905$, $\eta^2 = 0.001$].

DISCUSSION

Experiment 2 provides strong evidence for the view that repetitions of flankers partially drive the previous \times current trial type interaction. First, it shows that there is no need to make a response or even to see a target in order to get an interaction. Importantly, the non-necessity of a response and a target on the preceding trial shows that response conflict and stimulus conflict are not necessary to observe a speed up in response times in incongruent trials. Second, it places the locus of the effect squarely on processing of incongruent trials. Theories that attribute the congruency sequence effect only to conflict-related processing will have difficulties accommodating these findings unless other mechanisms are included.

One such mechanism, as suggested by one reviewer, could be negative priming, which is known to influence response times on subsequent trials in the absence of responding on a preceding trial or trial frame. Presenting the flankers on the first trial will help the participant learn about their irrelevance and thereby tagging them as such in a “conventional” event file that binds the flankers to an internal “ignore” response. Of course this scenario implies that feature bindings in an event file can include representations that are neither stimulus-related nor response-related, but are “cognition”-related. That is, event files may include bindings to cognitive states. Extending the breadth of what is bound in an event file is one direction of current research efforts (Colzato et al., 2006; Hommel and Colzato, 2009), but even this version fails to capture the entire data set. In particular, if an internal “ignore” response is bound to the flankers, the presentation of a stimulus with target and flankers constitutes a partial match. According to the feature-integration account, the sequences with flanker only trials with flanker repetitions should be slower than those with flanker change, which constitute complete mismatches. If we make a different arbitrary assumption that “ignore” responses do not contribute to mismatch calculations, but lead to actually ignoring the flankers in the subsequent trial, incongruent trials should become faster and congruent trial become slower. Although this is an interaction that matches **Figure 1A**, it is not the interaction found in the experiment, which matches **Figure 1C**.

It is not inconceivable that a specific feature-integration account can be given for this particular finding, but the scenario put forward here is the following. The assumption is that flankers are part of task representations that include response information. Therefore when $>>>>$ is presented both the “IF $>>>>$ THEN right button” and the “IF $>><>>$ THEN left button” task representations are activated with a competitive advantage for the latter. Only when flankers repeat is the corresponding response (i.e., pressing the left button) in the most active task representation facilitated. This results in an interaction between flanker repetition and congruency that is entirely driven by flanker repetition in incongruent trials. In addition, this facilitation underlies the congruency sequence effect in the sequences with complete stimuli, as shown by the regression analyses.

GENERAL DISCUSSION

The current experiments addressed the question whether flankers, despite the requirement to be ignored, are influencing cross-trial congruency effects, as manifest by an interaction between previous and current trial type: the congruency sequence a.k.a. the Gratton effect. In Experiment 1, the Gratton effect was observed when only flankers and responses were repeated across trials. This finding demonstrated the necessity of flanker repetition, together with the non-necessity of target repetition and response conflict. Experiment 2 further revealed that flanker repetition alone is sufficient to produce congruency sequence-like effects, suggesting that no conflict (stimulus or response) or an actual response is needed to produce the effect. Moreover, using regression analyses, it was shown that the congruency sequence effect is fully accounted for by this flanker repetition effect. This is not to say that the conflict-related mechanisms suggested in the literature do not play a role. Statistically, there is another 65.9% of the variance to be accounted for, but with 34.1% only due to flanker repetition this can not be ignored. However, given that the congruency sequence effect disappeared when controlling for the interaction due to flanker repetition, the current hypothesis is that conflict does not contribute directly to the effect.

The experiments put important constraints on current theorizing. Egner (2007) reviewed the literature on conflict tasks and addressed the two leading alternative explanations: conflict adaptation and feature-integration. Both of these theories are able to account for the two-way interaction, but for different reasons. In the former, the interaction is due to conflict-triggered adjustment of attentional focus. In the latter, the interaction is due to speed up of complete matches and mismatches. As mentioned in the introduction, the data shows that the target/response repetition is a modulating factor. Neither theory accounts for this modulating effect, but a minimal extension to the feature-integration account suffices. For example, facilitation could be assumed to occur only for complete matches and not for complete mismatches. Although this would capture the data, it would not explain why in the flanker task complete mismatches do not lead to facilitation, whereas in the Simon task they do.

The theoretical view put forward here assumes that task representations are formed at the beginning of the experiment and are activated during the experiment when stimuli are presented. The activation of the task representation persists after a trial is terminated, setting up a bias, or expectation for the required response in the next trial. Response times in the next trial are facilitated when the stimulus matches the active task representation. The strength of the associative connections within the task representation and with the stimulus and response representations increase with continued use according to the associative learning rules, which are sensitive to reward and conflict. According to this view merely repeating the flankers is sufficient to activate the task representations and thereby set up expectations about the required response on the next trial. The experiments presented here question the role of conflict of any type in congruency sequence effects. Instead, the proposal is that conflict has an indirect influence by being used as a learning signal in ongoing stabilization and proceduralization of task representations. Other pathways through which conflict indirectly

influence cognitive control are outlined elsewhere (Davelaar, 2009).

A recurrent critique to associative learning accounts of the Gratton effect is that the RI–RI transition in the no repetition situation (e.g., BBABB followed by AABAA) promotes negative priming (Ullsperger et al., 2005; Bugg, 2008). Bugg (2008) compared the critical trials against a neutral baseline and found slower RTs for the RI–RI transition, which was interpreted to provide support for a negative priming effect counteracting the expected conflict-induced speed up. However, two types of evidence argue against this interpretation. First, in a similar experiment, no such increase in RT was found (Davelaar and Stevens, 2009). Second and more importantly, “a similar magnitude of slowing was also observed” (Bugg, 2008; p. 1221) on RI–RI and RI–CO transitions (in the letter notation that would be: BBABB followed by BBBB) relative to the neutral conditions. Clearly, if negative priming is evident for the RI–RI transition, the same influence of the previous flankers should produce positive priming for the RI–CO transition. Such a pattern was never observed in the literature that focuses on sequential effects in the Eriksen flanker task (see figures in: Mayr et al., 2003; Ullsperger et al., 2005; Nieuwenhuis et al., 2006; Verbruggen et al., 2006; Bugg, 2008; Davelaar, 2009; Davelaar and Stevens, 2009). This is not to say that negative priming can never be found with a flanker paradigm. Quite the opposite. Stadler and Hogan (1996) obtained negative and positive priming effects in a numerical flanker task. The main discrepancy between their findings and the aforementioned literature is that Stadler and Hogan (1996) exclusively employed stimuli in which the target and the flankers were associated with different responses. In other words, they only used RI-trials, which may trigger a stronger requirement and reliance on attentionally deselecting the flankers, producing negative priming effects. To date, there is no report showing evidence of negative priming in a binary flanker task that includes incongruent and congruent trials. Even in Experiment 1, which

contained four types of RI–RI transitions, there was no evidence for slower RTs for transitions where the flankers became the target compared to transitions where flankers changed across trials (all p s > 0.5).

Another recurrent comment is that as a whole, the Stroop and Simon tasks do not show the three-way interaction and therefore the original conflict model need not require modification. This comment falsely implies that all three congruency tasks are equal. Several recent reports have documented differences in response time distributions. For example, Spieler et al. (2000) showed that the RT distributions of incongruent Stroop, but not flanker trials have a longer tail than the corresponding congruent trials. Pratte et al. (2010) contrasted the Stroop and Simon tasks, revealing that the Stroop effect increases with increasing quantiles of the RT distribution, whereas the Simon effect decreases with increasing quantiles. Davelaar (2008b) showed that RT distributions in the flanker task are sensitive to stimulus repetition, such that the flanker interference effect increases with increasing quantiles of the RT distribution, unless an incongruent stimulus repeats. Together these studies question the extent with which findings from one task can be assumed to be obtained in another.

In conclusion, the experiments presented here adds to the body of literature by demonstrating the considerable impact of flanker repetition in a phenomenon previously attributed to general attentional control processes. Despite the requirement of being ignored, the flankers reactivate task representations and thereby prime certain responses on the subsequent trial. Thus, flankers are bound in the representations that drive congruency sequence effects. In the flanker paradigm, monitored conflict might only have a modulatory role in adjusting associative connections of task representations. Future research, using the flanker task, could explore the boundary conditions of the repetition effects with regard to the nature of event files, the influence of task representations, and the process of conflict-modulated (indirect) control.

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