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AFTEREFFECTS IN FACE PROCESSING

Topic Editor
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AFTEREFFECTS IN FACE PROCESSING

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This image is primarily associated with Walton & Hills. It is an example of the distortions employed in aftereffects studies: Focus on the right hand image for about 30 seconds, then look to the left hand image and it will appear distorted in the opposite direction.

Aftereffects are the psychophysists microelectrode (Frisby, 1979) and can allow for an exploration of the neural representation of particular stimuli (Li, Tzen, Yadgarova, & Zaidi, 2008) including faces. Two distinct forms of aftereffect have been identified in face perception: the face-distortion aftereffect (FDAE) and the face-identity aftereffect (FIAE). In both cases, prolonged exposure to the adaptor face causes a test face to take on the "opposite" characteristics (e.g., a normal face will appear compressed following adaptation to an expanded face, Webster & MacLin, 1999).

Leopold, O'Toole, Vetter, & Blanz (2001) demonstrated that identification of a particular face was facilitated by adaptation to an anti-face (opposite in terms of Euclidean geometry). Theoretically, it has been proposed that adaptation shifts the perceived face norm toward the adaptor face (Anderson & Wilson, 2005), making the opposite face easier to identify (Rhodes, Robbins, Jaquet, McKone, Jeffery, & Clifford, 2005). Aftereffects do not readily transfer across faces of different gender (Little, DeBruine, Jones, & Waitt, 2008), race (Jaquet, Rhodes, & Hayward, 2007), or orientation (Rhodes, Jeffery, Watson, Jaquet, Winkler, & Clifford, 2004), indicating populations of neurons representing certain classes of faces (Rhodes, et al., 2004). Aftereffects do, however, transfer across viewpoints (Jiang, Blanz, & O'Toole, 2006) and image size (Zhao & Chubb, 2001), but to a significantly lesser degree than within-view and within-size adaptation for unfamiliar faces. The transfer across viewpoints is more robust for familiar faces (Hole, 2010) and there is cross-modality transference for familiar faces (e.g., adaptation to voices caused aftereffects in faces, Hills, Elward, & Lewis, 2010). Evidently, adaptation effects are greater when there is greater perceptual similarity between the adaptor and the test stimulus.

Face aftereffects have also been shown to depend on exposure and test timings. The magnitude of the FIAE is greater when the duration of the adaptor is long and the duration of the test stimulus is short (Rhodes, Jeffery, Clifford, & Leopold, 2007). For unfamiliar faces, the FIAE is short-lived, lasting about five seconds. However, for familiar faces, aftereffects are long-lasting, lasting about 80 minutes (Carbon & Leder, 2005) or more (Hills & Lewis, in preparation). For long-term effects, participants received visual input, including faces, between adaptation and the test. Nevertheless, these aftereffects persisted, suggesting some sort of learning or neural change had occurred. Indeed, this highlights important and underexplored aspects of face aftereffects: the effect of familiarity and the neural and brain correlates of adaptation and aftereffects, although Jacques, d'Arripe, & Rossion (2007) have demonstrated that repeated presentations of a face reduced the magnitude of the ERP N170 (see also, Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2008).

This Research Topic, thus, has a broad scope for exploring the FIAE using behavioural, electrophysiological, neuroimaging, and eye-tracking research.

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EDITORIAL
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Aftereffects in face processing

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Keywords: face identity aftereffects, face distortion aftereffects, familiarity, adaptation, psychological, expression

The original aim of this special issue was to use aftereffects to highlight the different cognitive, perceptual, and neural representations of unfamiliar and familiar faces. Face aftereffects occur due to prolonged exposure to an adaptor face that causes a test face to take on the "opposite" characteristics (e.g., a normal face will appear compressed following adaptation to an expanded face, Webster and MacLin, 1999). The resulting papers went beyond this aim and have demonstrated the extensive potential for theoretical advancement that research on aftereffects can create.

Within the papers contained in this research topic is a highly informative review article. Strobach and Carbon (2013) have highlighted three dimensions that can be used as a framework to consider face aftereffects: adapting information (the type of adapting feature); temporal facets (including the duration that the aftereffect lasts); and transferability (across images and viewpoints). This framework necessarily implies the face distortion aftereffect (FDAE) and the face identity aftereffect (FIAE) are based same recalibration mechanism (Hills and Lewis, 2012). I will use this framework to guide this editorial.

By manipulating different facial features for adaptation, researchers have gone some way to understand the mechanismsof the adaptation process both specifically (in expressions) and in general. Dickinson and Badcock (2013) have shown that aftereffects in the perception of expressive faces (happy) is due to the angle of the mouth. Their novel conclusion is that aftereffects in expressions are due to the misperception of the orientation of the mouth due to the tilt aftereffect. This highlights the importance of ruling out lower-level explanations when considering face aftereffects, especially since aftereffects can occur at any level of the visual pathway (Thillman and Webster, 2012). More generally, Little et al. (2012) have shown that the FIAE is primarily based on face shape information rather than color information.

In one of the most inovative studies in face aftereffects, Vakli et al. (2012) have shown that the FDAE can be caused by gray stimuli with white dots in the triangular configuration of the internal facial features. This indicates that higher-level visual areas involved in the processing of facial configurations mediate the FDAE. Further evidence for the higher-level nature of facial aftereffects comes from evidence that shows there is residual sensitivity in the fusiform gyrus and the occipital face area in participants with acquired prosopagnosia (Fox et al., 2013). Furthermore, human bodies can adapt orientation-independent face representations (Kessler et al., 2013) further indicating the multi-modal nature of face aftereffects (see e.g., Hills et al., 2010).

In the current research topic, Carbon and Ditye (2012) were the only authors who explored the effects of temporal factors on the face aftereffects. They provided further evidence for the long-lasting effects of FIAEs in famous faces. These effects lasted 7 days and were observed even if the participant was tested in a different context to where they were adapted.

In terms of the transferability of the face aftereffects, Keefe et al. (2013) have shown that trustworthy aftereffects transfer across different face identities and to opposite gender faces. This result, coupled with data suggesting that there is some degree of selectivity of aftereffects (Juricevic and Webster, 2012; Rooney et al., 2012), indicates that there are likely to be many face prototypes: one for every trait that can be adapted to.

A series of studies in this research topic also explored the differences in aftereffects between faces of different levels of familiarity. Both Walton and Hills (2012) and Rooney et al. (2012) showed that aftereffects transferred across faces of different levels of facial familiarity. Specifically, aftereffects transferred from unfamiliar and famous faces to personally familiar faces, but not between famous and unfamiliar faces. This indicates that the representation of unfamiliar faces is distinct to famous faces, but both share some similiarities with the representation of personally familiar and self faces. Finally, aftereffects in famous faces transfer across viewpoint and photographic negation but not across orientation (Hills and Lewis, 2012; Vakli et al., 2012) indicating the representation of familiar faces is more robust than unfamiliar faces.

This research topic has also identified a number of practical advances in the study of face aftereffects. Little et al. (2012) have shown that these aftereffects are equivalent for laboratory based studies and studies conducted on the internet. These authors also noted that the aftereffects were stronger during the earlier trials during the post-adaptation test.

Several of the studies reported in this research topic show that the face aftereffect is in part carried by low-level mechanisms, in which aftereffects are twice as large when the adaptor and test image match than when the images do not match (Hills and Lewis, 2012; Juricevic and Webster, 2012). However, beyond this low-level effects, there are aftereffects in expressions, trustworthiness, identity, and distortion demonstrated in this research topic. The advancements made by the studies in the research topic have reiterated Frisby's (1979) comment that aftereffects are the psychophysists microelectrode.

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Face adaptation effects: reviewing the impact of adapting information, time, and transfer

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The ability to adapt is essential to live and survive in an ever-changing environment such as the human ecosystem. Here we review the literature on adaptation effects of face stimuli to give an overview of existing findings in this area, highlight gaps in its research literature, initiate new directions in face adaptation research, and help to design future adaptation studies. Furthermore, this review should lead to better understanding of the processing characteristics as well as the mental representations of face-relevant information. The review systematizes studies at a behavioral level in respect of a framework which includes three dimensions representing the major characteristics of studies in this field of research. These dimensions comprise (1) the specificity of adapting face information, e.g., identity, gender, or age aspects of the material to be adapted to (2) aspects of timing (e.g., the sustainability of adaptation effects) and (3) transfer relations between face images presented during adaptation and adaptation tests (e.g., images of the same or different identities). The review concludes with options for how to combine findings across different dimensions to demonstrate the relevance of our framework for future studies.

Keywords: face adaptation, figural adaptation effects, memory representation, learning, plasticity, perception, transfer, delay

The term *adaptation* refers to the ability to adjust to novel information and experiences. This ability to adapt is essential for living and surviving in an ever-changing environment such as the human ecosystem (Carbon and Ditye, 2012). Visual adaptation in particular is an effect of the processes by which the visual system encodes and represents information, and includes a process by which the visual system (passively or actively) alters its function in response to the lack of fit between mental representations and perceived objects (e.g., Clifford et al., 2000; Clifford and Rhodes, 2005). Such responses result in adaptation effects. In experimental situations, such adaptation effects are typically assessed in an adaptation test phase after an adaptation phase. Intensive investigations of these adaptation effects provides an excellent opportunity for an exploration and deeper understanding of the processing architecture as well as the representation of particular stimuli (Li et al., 2008a; Webster, 2011).

The present paper includes a systematic review about the literature on adaptation effects of face stimuli[1]: which areas does this review on face adaptation cover and which areas does it negotiate? This review focuses on empirical studies that investigate face adaptation effects on a behavioral level; this is typically realized by an overt categorization of face stimuli in a test phase. In fact, we focus on adaptation under optimal conditions in a fully developed and (more or less) optimally functioning cognitive system; i.e., we review findings of studies typically investigating adaptation effects in younger adults possessing face recognition skills that are particularly impressive, for instance the fact that normal persons can discriminate thousands of faces (Jeffery and Rhodes, 2011) when they reach so-called "face expertise" (Schwaninger et al., 2003). This focus on complex objects of the face category is realized in an exclusive and extensive way; that is, we do not relate findings in the area of face adaptation effects to other visual coding mechanisms such as color coding as realized in previous work (Webster, 2011; Webster and MacLeod, 2011). By reviewing face issues exclusively, we assume to provide the main aim of this review most efficiently: we aim to clearly highlight and systematize existing findings as well as gaps in the research literature in the area of face adaptation effects. This systematization should stimulate new directions in face adaptation research and help to design future adaptation studies. In contrast to what we provide, we do not include results about the adaptation of neural processes to face stimuli: for instance, studies on modulations of the N170 as a result of prior adaptation (e.g., Kovács et al., 2006; Kloth et al., 2010) as questions regarding this area of research refer to further dimensions and use different theoretical frameworks, mostly based on specific brain processes and structures. In addition, we omit research from developmental and evolutionary perspectives on face adaptation effects as they were already the major aim of recent alternative review papers (Leopold and Rhodes, 2010; Jeffery and Rhodes, 2011).

We start this review by presenting a framework that enables a systematic organization of findings in the field of face adaptation

[1]We refer to face adaptation effects as aftereffects (Köhler and Wallach, 1944) at higher perceptual and cognitive levels (Carbon and Ditye, 2011).

effects. This framework includes dimensions representing the major characteristics of studies (i.e., experimental manipulations) or operational parameters in this field. As discussed in detail in a later section, the dimensions enable a categorization of the (1) various adapting face information (2) timing characteristics of adaptation effects (e.g., the delay between adaptation and adaptation test phases), and (3) transfer relations between face images presented during these phases (e.g., images of the same or different identities). In the main section of the present review, we discuss the research literature specifically toward each of the framework's dimensions. Finally, we present options for how to combine findings across different dimensions to demonstrate the relevance of our framework for future studies.

Investigations on adaptation effects in faces are very relevant for the progress of cognitive research, since these effects offer a window into the processes and dynamics of highly complex object processing. First of all, faces are arguably the most important social stimuli since they are the primary means by which we perceive identity information, emotional information, etc. (see below). This expertise and its investigation in adaptation effects provide an essential tool or window for dissecting different levels of neural code and the visual pathway in face processing. This latter fact is also the motivation for a close look at timing and additionally the transfer characteristics of adaptation effects in faces. As research on adaptation effects in faces is moreover a broad and elaborated field today, represented by a great number of adaptation studies employing different procedures and aiming at different research questions, this research field also offers an excellent opportunity for taking a more general perspective on the found effects in the form of a review.

FRAMEWORK TO CONCEPTUALIZE RESEARCH ON FACE ADAPTATION EFFECTS

As illustrated in **Figure 1** and in **Table 1**, we integrate findings in the field of face adaptation research into a conceptual framework that includes three dimensions. The first dimension of this framework represents different types of potential facial information which are susceptible to adaptation; we call this dimension *adapting information.* Instances of adapting information are identity information (e.g., Leopold et al., 2001; Jiang et al., 2006), configural information (e.g., Carbon et al., 2007b; Little et al., 2008), gaze information (e.g., Jenkins et al., 2006), emotional information (e.g., Webster et al., 2004; Ng et al., 2008; Adams et al., 2010), age information (e.g., Schweinberger et al., 2010), gender information (e.g., Kovács et al., 2007; Bestelmeyer et al., 2008), ethnicity information (e.g., Jaquet et al., 2008; Ng et al., 2008), attractiveness information

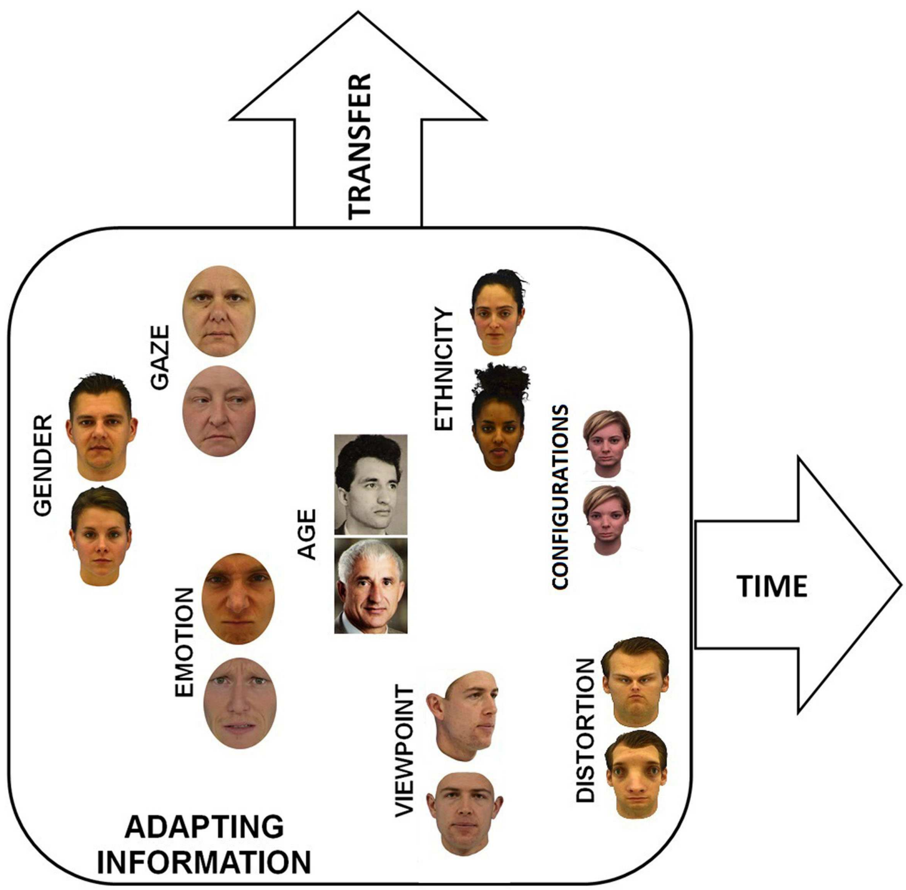


FIGURE 1 | Framework to review face adaptation effects including dimensions for different types of adapting information, transfer effects, and timing between adaptation and adaptation test phases.

Table 1 | Overview of types of adapting face information and related references.

Adapting face information	Reference
Age information	O'Neil and Webster (2011), Schweinberger et al. (2010)
Attractiveness information	Anzures et al. (2009), Carbon et al. (2007a), MacLin and Webster (2001), Rhodes et al. (2003), Rhodes et al. (2009b), Webster and MacLin (1999)
Configural information	Carbon and Ditye (2011), Carbon and Leder (2005), Carbon et al. (2007b), Little et al. (2005), Little et al. (2008), McKone et al. (2005), Strobach et al. (2011)
Emotion information	Adams et al. (2010), Benton and Burgess (2008), Fox and Barton (2007), Ng et al. (2008), Webster et al. (2004)
Ethnicity information	Jaquet and Rhodes (2008), Ng et al. (2008), Rhodes et al. (2010), Webster et al. (2004)
Figural (distortion) information	Burkhardt et al. (2010), Hills et al. (2010), Jaquet and Rhodes (2008), Jaquet et al. (2007, 2008), Jeffery et al. (2006, 2007), Morikawa (2005), Robbins et al. (2007), Webster and MacLin (1999), Yamashita et al. (2005), Zhao and Chubb (2001)
Gaze information	Jenkins et al. (2006), Schweinberger et al. (2007)
Gender information	Bestelmeyer et al. (2008), Buckingham et al. (2006), Kovács et al. (2007), Ng et al. (2008), Ng et al. (2006), Webster et al. (2004), Yang et al. (2011)
Identity information	Anderson and Wilson (2005), Hurlbert (2001), Jiang et al. (2006), Leopold et al. (2001), Leopold et al. (2005), Palermo et al. (2011), Rhodes et al. (2009a), Rhodes et al. (2011), Rhodes and Jeffery (2006), Rhodes et al. (2010)
Viewpoint information	Chen et al. (2010), Fang et al. (2007)

(e.g., Anzures et al., 2009), or viewpoint information (e.g., Chen et al., 2010). The present list of adapting information is completed by face information investigated in the context of face distortion aftereffects (FDAEs; e.g., Webster and MacLin, 1999). This method of manipulating faces may affect types of facial information that are listed above (e.g., configural information, age, identity, gender; please see also later sections). However, FDAEs are realized by unique manipulation algorithms (i.e., distortions by expanding or contracting the frontal-view original face image relative to a midpoint on the nose). Further, these algorithms relax the controlling of which specific information types are affected. For example, manipulating faces in the context of FDAEs affect facial features (e.g., eyes, mouth, etc.) while manipulations of configural information (i.e., spatial distances between these features) rather leave these features unaffected. Generally, these different types of instances of adapting information realize different levels of ecological validity. While differences in age, viewpoint, gaze, or emotion are plausible and realistic in an ecological context, manipulations of identity or configural information have less validity since such changes do not typically occur in the ecosystem.

The second dimension of the present framework, *time*, orders adaptation effects according to different types of temporal information. The first information type, *delay*, is related to the robustness and sustainability of adaptation effects; basically, the time interval between an adaptation and an adaptation test phase. Delays range from milliseconds (e.g., Leopold et al., 2001; Rhodes et al., 2003) to minutes (e.g., Carbon and Leder, 2006; Kloth and Schweinberger, 2008), but also include days and even weeks under typical laboratory (e.g., Carbon et al., 2007b; Carbon and Ditye, 2011) as well as ecologically more valid test contexts (Carbon and Ditye, 2012). The delay characteristics of adaptation effects are essential for providing useful information about the decay of adaptation effects and thus the "recalibration" and "readaptation" abilities of the visual system (Carbon and Ditye, 2011). Furthermore, they allow inferences about the robustness and consistency of perceptual information in general. In parallel to the "time" information *delay*, we focus on *adaptation duration*, the time span during which the adapting stimulus is presented (e.g., Strobach et al., 2011). Adaptation duration information provides insights into how this time span can modulate the adaptation effect size or the adaptability of faces. Moreover, this type of time information was compared with simple adaptation effects (e.g., with tilt information; Leopold et al., 2005; Rhodes et al., 2007) to explore the dynamics of adaptation effects at different levels of cortical visual hierarchy. Finally, we focus on "time" information of the *test duration* type, establishing the time span during which the test stimulus is presented (e.g., Rhodes et al., 2007). Similar to the adaptation duration, test duration can give insights into to the dynamics of adaptation in face stimuli in contrast to simple adaptation effects.

The third dimension in the present framework is associated with the transfer of adaptation effects. This *transfer* dimension reflects the range and limits of adaptation transfer effects providing important inferences about the nature of processing being linked with specific adapted stimuli or being of more general quality. In this way, the investigation of adaptation is a tool (rather than a topic) for localizing the plasticity and pointing out common coding principles of various levels of visual processing (from retinotopic to high and possibly face-specific levels of visual processing; Webster, 2011; Webster and MacLeod, 2011). There exists two systems of structuring transfer effects: transferring between different (manipulated) image versions of the identical identity during adaptation and test phases (e.g., variations in size or orientation) enables exclusive low-level perceptual effects of adaptation (e.g., on a retinal level; Zhao and Chubb, 2001) to be excluded.

Additionally, as proposed by Carbon et al. (2007b), adaptation transfer can be systematically tested with face images used in the adaptation and test phases showing the same images of the same identity vs. different images of the same identity vs. different images of different identities[2].

The approach can be extended by investigating transfer effects, *inter alia*, across family members, gender, and/or ethnicity.

As will be seen later, not all studies in the field of face adaptation research allow a localization of its research in all dimensions of the applied framework. For example, many studies apply sets of face images of different identities during adaption and the identical set of images during a following test phase (e.g., Buckingham et al., 2006; Chen et al., 2010). Such a procedure prevents conclusions about the transferability of adaptation effects, since potential effects in an adaptation test phase may originate from the presentation of the identical image and/or the presentation of other identities' images during the adaptation phase.

INVESTIGATING THE ADAPTATION EFFECTS OF DIFFERENT TYPES OF FACE INFORMATION – THE ADAPTING INFORMATION DIMENSION

Basically, the result patterns in studies on adaptation effects showed an *adaptation bias* and were thus consistent in the following way: values of adaptation test ratings tend toward the (typically extreme) values of adapting information presented during the adaptation phase; in other words, average or neutral faces are perceptually biased away from the adapting face. After introducing findings in the context of FDAEs, we show findings of facial information loosely ordered with increasing abstractedness.

FACE DISTORTION AFTEREFFECTS

Webster and MacLin (1999) investigated FDAEs within face images of a single identity by presenting adaptation images that were distorted by expanding or contracting the frontal-view original face image relative to a midpoint on the nose. After viewing distorted faces during adaptation (e.g., contracted face images), original faces appear distorted in the direction opposite to the distraction (e.g., expanded face images). In contrast to this effect after adaptations to distorted faces, no such adaptation effect followed the presentation of original face images (i.e., distorted faces still appeared distorted). In this way, Webster and MacLin provided among the first evidence for adaptation effects in complex, natural objects, suggesting that adaptation may play an important normalizing role in face perception and adaptation effects may strongly influence form perception (see also Zhao and Chubb, 2001; Morikawa, 2005; Yamashita et al., 2005; Jeffery et al., 2006, 2007; Jaquet et al., 2007, 2008; Robbins et al., 2007; Jaquet and Rhodes, 2008; Burkhardt et al., 2010; Hills et al., 2010); such a "complex" adaptation phenomenon was recently transferred to animals, trees, or every-day objects (e.g., light bulb; Daelli et al., 2010).

However, the FDAE enables no specification of which types of facial information are precisely involved in face adaptation. For example, the usage of FDAEs simultaneously affects feature information such as mouth, eyes, or eyebrows (e.g., Tanaka and Sengco, 1997; Cabeza and Kato, 2000), configural information such as nose-mouth distance (Young et al., 1987; Rhodes, 1988; Leder and Carbon, 2006), as well as holistic information referring to face processing "as a whole" (e.g., Tanaka and Farah, 1993; Leder and Carbon, 2005). As a consequence, it is essential to systematically vary distinct face information between adaptation and test phases in order to generate precise conclusions about the mechanisms of face adaptation effects, a fact that is not necessarily granted in the context of FDAEs.

CONFIGURAL INFORMATION

Carbon and colleagues (Carbon and Leder, 2005; Carbon et al., 2007b; Carbon and Ditye, 2011; Strobach et al., 2011) aimed instead at investigating adaptation effects of distorted configural information on subsequent adaptation tests. Participants were either presented face images during adaptation of familiar identities with decreased eyes-mouth distance or face images with increased eyes-mouth distance relative to the original. In a subsequent test phase participants were asked to select the veridical version (1) out of a series of versions of gradually altered eyes-mouth distances, or (2) from one original and one slightly altered version (e.g., slightly decreased or increased eyes-mouth distance). The results showed a bias in participants' selections in the direction of the respective manipulations, e.g., after viewing face images with extremely decreased eyes-mouth distance there was an increased likelihood of selecting a version with slightly decreased distances (for similar results with exclusive shifting the eyes in the vertical axis, see Walton and Hills, 2012). Thus, these studies demonstrated adaptation effects of configural information. Similar results are demonstrated by Little et al. (2005, 2008) following the inspection of manipulated eyes-spacing: inspecting faces with extreme narrow or wide eye distances resulted in increased normality rating for subsequently presented face images with moderately manipulated distances. These latter findings demonstrate the generalization of adaptation effects after exposure to manipulated configural information.

GAZE AND VIEWPOINT INFORMATION

Adaptation to a consistent leftward or rightward gaze produces ratings that demonstrate an elimination of observers' perception of the gaze in the adapted direction (Jenkins et al., 2006; Schweinberger et al., 2007). That is, a gaze to the adapted side was subsequently seen as pointing straight. Leftward and rightward viewpoint adaptation resulted in similar adaptation effects (Fang et al., 2007; Chen et al., 2010); thus, a face turned to the adapted side was subsequently seen as pointing straight. Again, these effects can be interpreted as a recalibration mechanism: probably the best heuristic to use if one constantly lacks a straight viewpoint is to retune the processing of gaze direction or viewpoint.

EMOTIONAL AND ATTRACTIVENESS INFORMATION

Another example for testing adaptation effects is represented by investigations on the effects of different facial expressions. For instance, after perceiving a happy face, a previously ambiguous happy-angry face appeared distinctly angry, and thus the boundary between happy and angry faces was shifted toward the happy

[2] In the present work, we define that different facial images can originate from the same identity. For example, the same identity can produce face images differing in emotionality. In contrast, the same facial image of the same identity can produce different versions that vary in size or orientation.

expression (Webster et al., 2004; Fox and Barton, 2007; Juricevic and Webster, 2012). Such shifted emotion categorization was even evident with adapting stimuli having been suppressed from awareness (Benton and Burgess, 2008; Adams et al., 2010) illustrating the fast and automatic processing of such expressions. Attractiveness adaptation effects demonstrated that viewing consistently distorted faces shifts attractiveness preferences toward the adapting stimuli; for instance, contracted face images (Webster and MacLin, 1999) appeared more attractive after adapting to contracted faces than after adapting to expanded faces (MacLin and Webster, 2001; Rhodes et al., 2003; Carbon et al., 2007a; Anzures et al., 2009). Similarly, faces with left-right asymmetries appeared more attractive when asymmetrical faces were presented during adaptation (Rhodes et al., 2009b).

GENDER INFORMATION

Adaptation to either masculine or feminine faces increases preferences for novel faces that are (gender-wise) similar to those that were recently seen (Buckingham et al., 2006), as well as increasing the femininity and masculinity ratings of test faces, respectively (see also Webster et al., 2004; Ng et al., 2006, 2008; Kovács et al., 2007). An alternative measurement of gender-adaptation effects demonstrated that adapting to a male/female face selectively enhances discrimination for male/female faces (Yang et al., 2011).

AGE AND ETHNICITY INFORMATION

When participants viewed young or old adult faces (i.e., adults of different ages), their "young/old boundary" was biased toward the age of the adapting face (O'Neil and Webster, 2011). Consistently, test faces appeared older or younger when the adapting faces were young or old, respectively (Schweinberger et al., 2010). Therefore, there is evidence for an adaptation bias for facial age as well (see also Lai et al., 2012). An analog bias also exists for face ethnicity, exemplarily shown for Caucasian vs. Asian faces: adaptation to an average Asian or Caucasian face reduced identification thresholds for faces from the adapted relative to the unadapted ethnicity (Webster et al., 2004; Rhodes et al., 2010).

IDENTITY INFORMATION

Leopold et al. (2001) provided evidence for increased sensitivity for particular face identities after adaptation, as investigated in the context of face identity aftereffects (FIAEs). Based on the ideas of a "face space" (e.g., a multidimensional representation of faces as their distance to a prototypical "center" face, Valentine, 2001), the authors were able to explain the effect in the theoretical framework of a computationally derived mental representation (**Figure 2**). After perceiving an "anti-face" (located opposite an original face of an identity, on a trajectory crossing this original face and a face-space average), adaptation specifically shifted perception along a trajectory passing through the adapting anti-face and average face away from the original face, selectively facilitating recognition of a test face lying on this trajectory. Such adaptation effects on the identity level were replicated in a number of studies and variations (Hurlbert, 2001; Anderson and Wilson, 2005; Leopold et al., 2005; Rhodes and Jeffery, 2006; Rhodes et al., 2009a, 2010, 2011; Palermo et al., 2011) and are often explicitly referred to as changes of the face space.

In sum, this section demonstrates adaptation effects of numerous facial attributes. To our knowledge there are no attributes that don't show any such effects in the research literature, which indicates that adult face coding systems are more flexible than was previously thought (Bruce, 1994). At this point it is essential to stress again, that the class of faces is the only object class that allows investigating and reviewing this large number of information types.

INVESTIGATING TEMPORAL CHARACTERISTICS OF ADAPTATION EFFECTS – THE TIME DIMENSION

DELAY

Face adaptation effects are typically tested with a delay interval of only a few seconds or even less (Webster and MacLin, 1999; Leopold et al., 2001; Rhodes et al., 2003; Benton and Burgess, 2008; Bestelmeyer et al., 2008; Carbon and Ditye, 2011). Given these constraints, the studies mainly show that (A) adapting face information such as face identity occurs on a perceptual level, and (B) there is no recalibration of the visual system after this delay. In sum, they allow conclusions about neither adaptation effects on the representational level nor on the robustness of visual system recalibration. One of the first systematic investigations of adaptation effects and their delay characteristics focused on gaze information (Kloth and Schweinberger, 2008); **Table 2** gives an overview of studies testing adaptation effects with short and long delays. This study demonstrated a decrease in the gaze adaptation effect over time but this effect was still measureable up to 385 s after the end of the adaptation phase. This is evidence for the idea that adaptation effects are not completely perceptually-based. Also it suggests that there is no complete "return to normal" ("recalibration," see Carbon and Ditye, 2011) of the visual system, associated to gaze processing, within this time range of more than 6 min. Consequently, adaptation effects are "stickier" than many of the traditional low-level adaptation effects (e.g., Köhler and Wallach, 1944) and can be initially interpreted as evidence of representation-based effects.

Carbon and colleagues systematically extended research on effects of adaptation to manipulated configural information of famous faces. These studies demonstrated adaptation effects after 5 min (Carbon and Leder, 2005; Carbon et al., 2007b; Strobach et al., 2011), 80 min (Carbon and Leder, 2006), 24 h (Carbon et al., 2007b; Carbon and Ditye, 2011; Strobach et al., 2011), and even 1 week (Carbon and Ditye, 2011). Therefore, adaptation seems to be very robust and refers to effects on the functional level of representations. According to Carbon et al.'s research, it takes at least 1 week for the visual system to return to its original state before adaptation (i.e., to recalibrate to its pre-adaptation state), at least in terms of adaptation effects for configural facial information.

To sum up, regarding the delay dimension, a series of recent experiments revealed relatively long-lasting adaptation effects. This evidence is related to face attributes of gaze information (Kloth and Schweinberger, 2008), and configural information (e.g., Carbon et al., 2007b). It illustrates aspects of face processing that are related to an increased participation of representations and do not only rely on simple iconic traces or simple visual aftereffects (Carbon et al., 2007b). To learn about mental representations, these findings of long-lasting adaptation effects demonstrate that

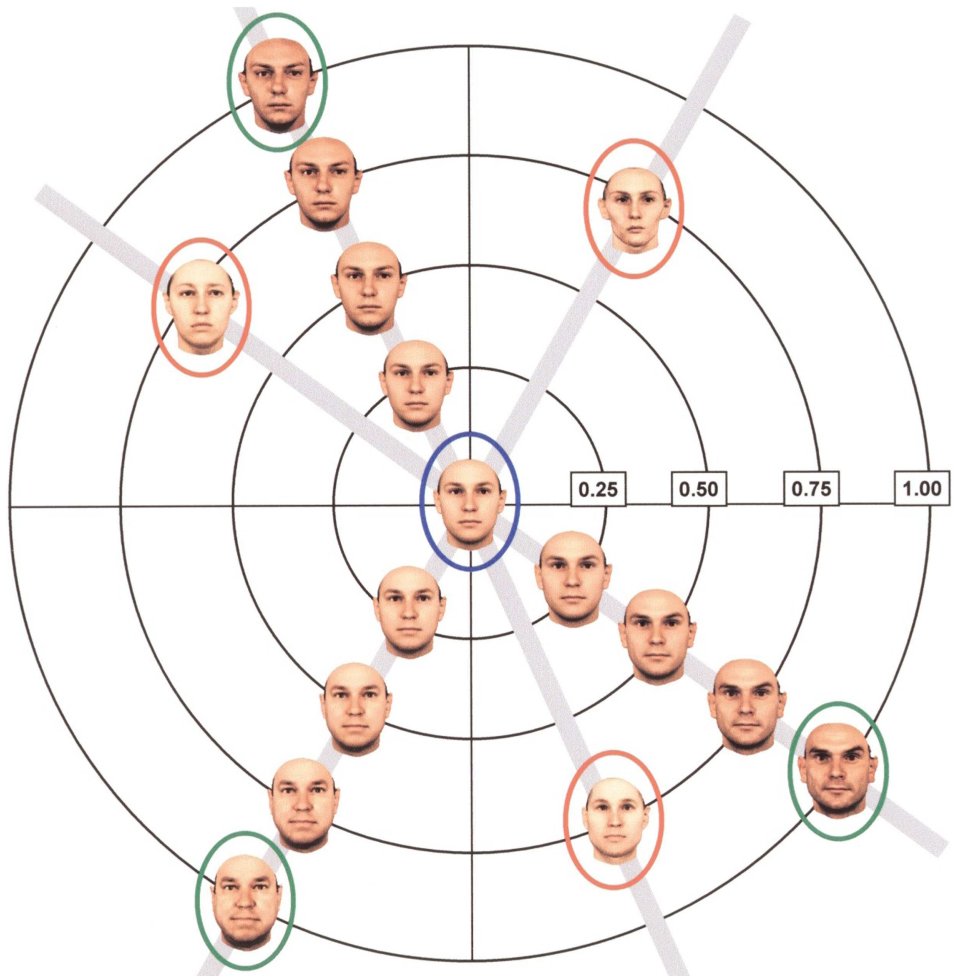


FIGURE 2 | Computationally derived face space in which the stimuli were generated to investigate face identity adaptation effects (FIAE). The original faces (green ellipses) are connected to the average face (blue ellipse) by an "identity trajectory." Numbers refer to the "identity strength" possessed by the given face (taken from Leopold et al., 2001).

the investigated types of facial information (i.e., gaze information, configural information) are not exclusively processed and coded at a perceptual level. One may speculate that such processing and coding involves long-term memory functions. However, there are no investigations of "delay" effects on facial information aspects of age, attractiveness, emotion, ethnicity, gender, FIAEs, or viewpoint information. Such investigations are essential to assess the functional level (representation level and/or perceptual level), the robustness/sustainability and the time needed for recalibrations of adaptation effects of these types of information. We will come back to this immense gap in the adaptation literature in a later section.

ADAPTATION DURATION

The increase in the time interval for presenting visual adaptation material typically results in an increase of simple perceptual adaptation effects demonstrating the adaptability of tilt, motion, or shape information (Rhodes et al., 2007). In fact, this relation is characterized by a logarithmic function between adaptation duration and effect size. A comparable relation was found in faces. Rhodes, Leopold, Jeffery and colleagues (Leopold et al., 2005; Rhodes et al., 2007) tested the FDAEs as well as FIAEs after varying presentation times of adapting face stimuli; in fact, test stimuli appeared immediately after adaptation material was presented between 1,000 and 16,000 ms. Independent of size relations between adaptation and test faces, FDAEs and FIAEs increased with adaptation time. The relationship between adaptation duration and effect is thus comparable in simple perceptual information as well as complex face objects, illustrating common coding principles at different levels of cortical visual hierarchy.

There were however no, or very short, time delays between adaptation and test phases in these prior studies (Leopold et al., 2005; Rhodes et al., 2007) and thus it is likely that adaptation effects were investigated at the perceptual level only. In contrast, Carbon et al. (2007b) introduced delays of 5 min to 24 h between these phases, allowing investigation of the effects of adaptation

Table 2 | Overview of examples of face adaptation studies and their delays between adaptation and test phases.

Study	Delay
Barrett and O'Toole (2009)	100 ms
Benton and Burgess (2008)	500 ms
Bestelmeyer et al. (2008)	Not available
Carbon and Ditye (2011)	24 h, 1 week
Carbon and Ditye (2012)	1 week
Carbon and Leder (2005)	4,000 ms; 5 min
Carbon and Leder (2006)	80 min
Carbon et al. (2007b)	5 min; 24 h
Fang et al. (2007)	1,000 ms
Hills et al. (2010)	5,000 ms
Hole (2011)	≤2 min
Kloth and Schweinberger (2008)	0–6 min
Kovács et al. (2007)	500 ms
Leopold et al. (2005)	Not available
Leopold et al. (2001)	150; 300; 600; 1,200; 2,400 ms
McKone et al. (2005)	15 min
Rhodes et al. (2007)	1,000 ms
Rhodes et al. (2003)	500 ms
Strobach et al. (2011)	5 min; 24 h
Webster et al. (2004)	250 ms
Webster and MacLin (1999)	Not available

delay on the adaptation of memory face representations (in this case, the adapting information was configural information). On the basis of this argument, Strobach et al. (2011) performed multiple regression analyses on the individual adaptation duration and their adaptation effects after both 5 min and 24 h. Positive relations between both measures (i.e., longer presentation times of adaptation faces resulted in increased adaptation effects) demonstrated an impact of the adaptation time on the effect size, extending findings on the perceptual level to findings demonstrating mechanisms instead on a memory level.

There is a lack of studies that explicitly investigate the effects of adaptation time for facial attributes other than FDAEs, FIAEs, and configural information – e.g., for age, gender, and attractiveness. Such investigations would provide elaborated knowledge about the coding principles of face-specific and simple visual information.

TEST DURATION

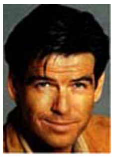
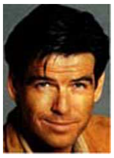
Similarly to changes in the magnitude of adaptation effects following variability in adaptation duration, the time span of presenting a test stimulus modulates the magnitude of these effects (Leopold et al., 2005; Rhodes et al., 2007). In fact, test faces were presented for 100, 200, 400, 800, or 1,600 ms and the adaptation effects, as measured in paradigms of FDAEs and FIAEs, reduced with increasing test time. Since similar effects are evident with simple aftereffects, face and simple perceptual information (i.e., tilt, orientation) illustrate common coding principles at different levels of cortical visual hierarchy. However, what is clearly lacking in this domain is research on the question of whether the test duration has an effect when adaptation effects are tested on a memory rather than on a perceptual level. That is to say, it is an open issue in the literature whether the negative relation of test duration and adaptation effect (e.g., increasing test duration and decreasing adaptation effects) is evident after a delay of minutes, hours, or days. Furthermore, this negative relationship was established for FDAEs and FIAEs. However, it is lacking for alternative facial information and such tests should be attempted in future studies. They are essential to establish a more elaborate knowledge of the coding principles of face-specific types of information.

INVESTIGATING THE TRANSFERABILITY OF ADAPTATION EFFECTS – THE TRANSFER DIMENSION

After reviewing adaptation effects of different face information and time characteristics (e.g., the sustainability of adaptation effects), it is essential to review the relationship between the adapting and test face images; i.e., to test transfers of adaptation effects to new face images (or new image versions) not presented during adaptation. Here, we review findings that investigated transfer effects between the same image of one identity (identical images or images differing in viewpoint, orientation, or size between adapting and test images) and different images of the same identity. Additionally, we also discuss adaptation transfer effects between images of different identities. As illustrated in **Table 3**, we test these transfer effects at the *pictorial level* (identical face image during adaptation and test), *identity level* (different face images of the same identity during adaptation and test), and *novel level* (different face images of different identities during adaptation and test, Carbon and Ditye, 2011). In the following section, we primarily discuss types of adapting face information that demonstrate transfer effects. We followed this strategy because, for the remaining types of face information (e.g., gaze, emotion), there was (A) no investigation of transfer effects and/or (B) no conclusive evidence for such effects.

When focusing on FIAEs, Hole (2011) demonstrated adaptation effects with identical face images during adaptation and testing which also transfer onto new image versions changed in viewpoints, orientation, and vertically stretched versions from the adapting face images when using familiar; this confirmed Jiang et al.'s (2006) finding of viewpoint invariance of FIAEs who also added evidence of their transfers across shape and surface reflectance information. Anderson and Wilson (2005) supported Hole's finding of size independent transfer with unfamiliar, synthetic faces while their study provided no support of a viewpoint-invariant FIAE for this face type. Guo et al. (2009) revealed limits to the transferability of the FIAEs by showing that this effect exclusively works from upright to inverted orientation, but not vice versa with unfamiliar faces. With familiar faces, however, Hole showed that the FIAE produced by inverted adaptation faces and upright test faces was similar to that produced by upright adapting faces. Furthermore, this type of adaptation effect seems to be gender-specific since there is an effect from adaptation to test faces when these faces are related via a gender-specific prototype, whereas there was no such effect with an androgynous face (i.e., combined male and female prototype; Rhodes et al., 2011). Leopold et al. (2001, 2005) showed that relations between a facial prototype and the individual faces in face space

Table 3 | Different transfer levels of adaptation effects as realized in studies of Carbon and colleagues (Carbon et al., 2007b; Carbon and Ditye, 2011, 2012; Strobach et al., 2011).

	Transfer of the adaptation effect		
	Picture level	**Identity level**	**Novel level**
Adaptation phase			
Test phase			

could be manipulated by face adaptations of different identities. In other words, this manipulation includes face images during adaptation that are not located on a trajectory crossing an original face and a face-space average (similar to **Figure 1**); thus, there is evidence for FIAEs on the *novel level.* This conclusion is consistent with the fact that FIAEs are rather high-level perceptual effects: composite faces (different views of a composite face comprised of the top half of a famous face and the bottom half of a non-famous face) either did or did not produce a FIAE depending on whether or not the famous face is explicitly recognized before the post-adaptation test phase (Laurence and Hole, 2012).

Conversely, adaptation to facial expressions (i.e., emotional information) was partly independent from the represented identities. That is, adaptation effects with a focus on facial expressions were transferred to different faces and thus include at least portions of novel-level processing (Fox and Barton, 2007). Interestingly, the above discussed FIAE is not affected by expressional information. That is, FIAEs were not modulated by congruency of facial expression during adaptation and test phases (i.e., same expression vs. different expression; Fox et al., 2008). Thus, expressional adaptation and FIAEs tend toward asymmetry with impact of identity information on expression adaptation, but there is no reverse effect.

For facial gender, Yang et al. (2011) demonstrated that gender discrimination enhancement induced by face adaptation can transfer across a substantial change in three-dimensional facial orientation. Additionally, gender-adaptation effects are position invariant effects (Kovács et al., 2007). These effects also seem to be age-independent, since Barrett and O'Toole (2009) demonstrated an effect of gender adaptation within sets of children's and adults' faces and also between these sets of faces. These age-independent effects also demonstrate that gender-adaptation effects may work on a *novel level* since adaptation and test faces were derived from different identities. However, this novel level is limited to the orientation of faces; that is, adaptation effects work independently with upright and inverted face presentations (Watson and Clifford, 2006). Alternatively, the limitation of emotion adaptation effects is set at race boundaries: adapting to one type of emotion in, for instance, a Caucasian face, affects the later processing of an alternative Caucasian face but not that of an alternative ethnicity (i.e., black faces; Otten and Banaji, 2012).

The adaptation effect realized in the form of viewpoint adaptation (i.e., adaptation to left or right-turned faces) occurs at the *novel level* as demonstrated by transfer effects across different identities, different gender, and different vertical orientations (Fang et al., 2007). In the case of face normality ratings and their adaptation effects, there exists evidence for at least orientation-transferable adaptation effects, i.e., between upright and inverted orientations of face images (Rhodes et al., 2003).

Transfer effects of adapting configural information are not only in action at the *pictorial* and *identity* levels, but also at the *novel* level (i.e., different face images of different identities during adaptation and test; Carbon et al., 2007b; Carbon and Ditye, 2011); even though the effect was slightly reduced compared with pictorial and identity conditions. This was demonstrated by the transfer effects of adapting configural information in combinations of identical adaptation and test facial images, of different adaptation and test facial images from the same identity and transfers to new identities, i.e., transfers to test face images of identities not presented during prior adaptation (Walton and Hills, 2012, for comparable results with exclusive eyes shifts in the vertical axis). Little et al. (2008) assumed that such transfer effects are gender-specific. FDAEs are not transferable to images mirrored after the adaptation phase (Morikawa, 2005), but there is evidence of the transfer of such effects to different ethnicities (Jaquet et al., 2007), between different viewpoints (Jeffery et al., 2006, 2007), different orientations of upright and inverted faces (e.g., adapting face is oriented 45° from vertically upright and the test face 45° in the opposite direction; Watson and Clifford, 2003) between different identities and orientations (Webster and MacLin, 1999) as well as different facial image sizes (Zhao and Chubb, 2001; Yamashita et al., 2005). Consequently, FDAEs occur up to the *novel level.* Consistently, adaptation effects of facial age on a *novel level* are demonstrated by transfers between different genders (O'Neil and Webster, 2011) and identities (Schweinberger et al., 2010).

In sum, there is clear evidence for adaptation effects across different identities for a first set of face information (e.g., gender, age, configural information), i.e., transfer effects on a *novel level.* Adaptation of this set of information seems to affect the high-order visual system and/or memory representations. In contrast to these transferable adaptation effects, there is no clear evidence of transfer effects for other face information, such as attractiveness. Furthermore, there is evidence that some face information is only transferable between different identities when the specific subgroups are not changed simultaneously (e.g., FDAE transfers are gender-specific). To learn about processing characteristics and mental representations of faces, this section indicates that face coding is hierarchically structured with an orchestration of common underlying structures. This common structure was demonstrated at the novel level and maybe theoretically represented in a prototype in face space (Valentine, 2001). However, the processing of some facial aspects is characterized by and related to specific modules (e.g., gender-specific modules of FDAEs) potentially working in parallel to a general face-space prototype.

FUTURE INVESTIGATIONS OF FACE ADAPTATION EFFECTS

A summarizing overview of existing and lacking research in the field of face adaptation effects is illustrated in **Table 4**. Future studies may apply the present framework's dimensions or operational parameters (adapting information, time, and transfer) for a systematic continuation of investigating face adaptation effects. For instance, for a number of adapting information types (e.g., emotion, age, attractiveness, gender) there exists no test for the robustness of adaptation effects; that is, adaptation effects of these types of face information are demonstrated after short delays between adaptation and adaptation test phases. However, there are no studies that test these adaptation effects after long delays and their decay over time. To present one specific example, in accordance with time intervals applied by Carbon and colleagues (Carbon et al., 2007b; Carbon and Ditye, 2011), the adaptation effect of facial age should be tested after time intervals of 5 min, 24 h, and 1 week in order to cover a broad range of time periods and to test the robustness of the age adaptation effect. Likewise, testing the impact of adaptation and test time should be extended to forms of facial information beyond phenomena investigated in the context of FDAEs (Leopold et al., 2005; Rhodes et al., 2007). As illustrated, a first extension of investigations on adaptation time occurs in the context of adaptation of configural information (Strobach et al., 2011), but other contexts are definitely needed to generate a broader picture of timing aspects in face adaptation. In this way, our framework is able to characterize gaps in the adaptation research literature while combining findings along the dimension adaptation information and delay.

Similarly, such an expansion of tests should also be performed on the transfer dimension since this type of test is essential for investigating the functional level of adaptation effects and increasing the ecological validity of these studies. While transfer tests on the same face image of the same identity (e.g., varying orientation or context during adaptation and test; Carbon and Ditye, 2012) enable investigations on picture or "iconic" processing (Carbon, 2008), and thus not necessarily on face processing *per se*, transfer tests on different face images of the same identity as well as different identities' face images allow for conclusions about the characteristics of face representations. So far, these two types of transfer tests [i.e., (1) different face images of the same identity, (2) different face images of different identities] were separately conducted in most studies. Future studies may combine these two transfer types.

An additional way to continue face adaptation research, in terms of gaining knowledge on the basis of adaptation effects, is to combine aspects (i.e., our framework's dimensions) of time and transfer. For instance, future studies should systemically investigate the effects of manipulating face information across different

Table 4 | Overview of existing and lacking research in the field of face adaptation effects: what types of face information does this research include? What types are neglected?

Dimension	Existing investigations on	Lacking investigations on
Adapting information	FDAE	Distinctiveness
	Configural information	Eye color
	Gaze information	
	Viewpoint information	
	Emotional information	
	Attractiveness information	
	Gender information	
	Age information	
	Ethnicity information	
	FIAE	
Time		
Delay	Gaze information	Alternative types of information
	Configural information	
Adaptation duration	FDAE	Alternative types of information
	FIAE	Various delays between adaptation and adaptation test phase
Test duration	FDAE	Alternative types of information
	FIAE	Various delays between adaptation and adaptation test phase
Transfer	Configural information	Alternative types of information
	Gender information	Temporal characteristics (i.e., delay, adaptation duration, test duration)
	Emotional information	
	Viewpoint information	
	Attractiveness information	
	FIAE	

delays between adaptation and test phases, combined with tests for the different transfer levels between adaptation and test faces. Additionally, the effects of gender adaptation can be investigated after relatively short and long delays between faces of the same or different age groups, ethnicities, or gaze points. A related investigation focused on transfer effects between different emotional expressions and gender in the context of FDAEs (Tillman and Webster, 2012). This systematic investigation of the interplay of delay and transfer may provide conclusions about the range of adaptation effects and their origin from similar or different methods of neural coding.

Additionally, future studies should relate investigations on the functional level of face adaptation effects to concepts applied to other types of processes or skills. One option might be in relation to improved skills acquired during cognitive training (e.g., working memory training) and their range of transferability. Existing studies on this issue (Li et al., 2008b; Karbach and Kray, 2009; Strobach et al., 2012a,b) categorize the range of skill transfer into near transfer (transfer between situations with common basic characteristics) and far transfer (transfer between situations with structural differences). Conversely, near transfer tests could investigate the adaptation effects of facial images on other facial images, while far transfer tests investigate adaptation effects on facial images after prior adaptation to specific properties of cars (Carbon, 2010) or adaptations to mental sets due to the presentation of gender-typical objects (e.g., lipstick vs. motor bike, Javadi and Wee, 2012). For instance, one could test whether there is a transfer of adaptation effects of configural information (i.e., spatial relations between features) from face stimuli to car stimuli (i.e., far transfer). In particular, front views of cars with a similar setting of parts as can be found in faces are favorable for performing such transfer tests (see Windhager et al., 2010). In fact, this type of future transfer study would cross boundaries between different types of visual objects and may show similarities and differences in these general object characteristics.

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Face distortion aftereffects evoked by featureless first-order stimulus configurations

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After prolonged exposure to a distorted face with expanded or contracted inner features, a subsequently presented normal face appears distorted toward the opposite direction. This phenomenon, termed as face distortion aftereffect (FDAE), is thought to occur as a result of changes in the mechanisms involved in higher order visual processing. However, the extent to which FDAE is mediated by face-specific configural processing is less known. In the present study, we investigated whether similar aftereffects can be induced by stimuli lacking all the typical characteristics of a human face except for its first-order configural properties. We found a significant FDAE after adaptation to a stimulus consisting of three white dots arranged in a triangular fashion and placed in a gray oval. FDAEs occurred also when the adapting and test stimuli differed in size or when the contrast polarity of the adaptor image was changed. However, the inversion of the adapting image as well as the reduction of its contrast abolished the aftereffect entirely. Taken together, our results suggest that higher-level visual areas, which are involved in the processing of facial configurations, mediate the FDAE. Further, while adaptation seems to be largely invariant to contrast polarity, it appears sensitive to orientation and to lower level manipulations that affect the saliency of the inner features.

Keywords: face distortion aftereffect, first-order relations, second-order relations, configural processing, contrast polarity

INTRODUCTION

In the course of the last decade, several studies have demonstrated that the way we perceive faces is systematically biased by the characteristics of a previously presented face, a phenomenon commonly referred to as the face adaptation aftereffect (FAE). A prime example of such face – related aftereffects is the so-called face distortion aftereffect (FDAE): following adaptation to a distorted face, a subsequently presented normal face appears distorted in the opposite way (O'Leary and McMahon, 1991; Webster and MacLin, 1999; MacLin and Webster, 2001). For example, an undistorted face seems expanded after viewing a face with features compressed toward the midline. Besides distortion, FAEs have been observed for a number of natural facial properties including identity (Leopold et al., 2001), gender (Webster et al., 2004), age (Schweinberger et al., 2010), ethnicity (Webster et al., 2004) as well as more dynamic facial features such as emotional expression (Webster et al., 2004; Fox and Barton, 2007), eye-gaze direction (Jenkins et al., 2006; Seyama and Nagayama, 2006), and lip angle (Jones et al., 2010).

Such perceptual aftereffects enable researchers to link changes in perception to changes in the underlying neural mechanisms and thus provide information about the representation of complex visual patterns in the brain. One fundamental question about FAEs is the extent to which they reflect the recalibration of neural populations engaged in high-level visual processing. Since the rationale behind adaptation is that the same or overlapping neural populations process the adaptor and test stimuli, the tolerance of FAEs toward physical differences between the adaptor and test images provides important clues about the neural locus of the aftereffects. For example, it has been shown that although the magnitude of the FDAE is the greatest when the images are of the same size, the aftereffect survives a two-octave difference in size between adaptor and test faces (Zhao and Chubb, 2001). Aftereffects for facial identity are also tolerant to differences in image size (Leopold et al., 2001; Anderson and Wilson, 2005), and the size-invariance of the face identity aftereffect can be observed in younger age as well (Pimperton et al., 2009). These results are in line with data from monkey single-cell recordings (Perrett et al., 1982; Rolls and Baylis, 1986) and functional brain imaging studies in humans (Andrews and Ewbank, 2004) demonstrating a largely size-invariant neural representation of faces in the ventral regions of the temporal lobe.

FAEs have also been shown to transfer across different retinal positions (Leopold et al., 2001; Fang and He, 2005), albeit they are not entirely position-invariant (Kovács et al., 2005), and the magnitude of the aftereffect decreases with increasing distance between the adaptor and test stimuli (Afraz and Cavanagh, 2008). To date, the results regarding the position-sensitivity of FAEs have been controversial, with studies emphasizing the contribution either of spatiotopic (Melcher, 2005; van Boxtel et al., 2008) or of retinotopic coding (Afraz and Cavanagh, 2009). These inconsistencies may result from the different adaptation protocols (identity-specific versus gender-specific) employed in the above-mentioned studies, which are thought to tap different cortical processing sites (see Zimmer and Kovács, 2011b for a review). In addition, the duration of the adaptation period is a critical factor that determines the position-sensitivity of the aftereffect, since varying the time course of adaptation allows one to selectively adapt position-sensitive and position-invariant neural populations along the ventral visual pathway (Kovács et al., 2007, 2008).

Besides position, FAEs also tolerate remarkable differences in picture plane orientation and viewpoint between the adaptor and test faces. For example, Watson and Clifford (2003) have shown that the FDAE rotates with the test face in the picture plane, suggesting that the distortion is coded in an object-based reference frame. In relation to three-dimensional orientation, it has been shown that FAEs induced in one viewpoint transfer to other viewpoints, although this transfer is limited in a sense that the aftereffect decreases as the angular difference between the adaptor and test views increases (Benton et al., 2006, 2007; Jeffery et al., 2006). This finding can be explained in terms of viewpoint-specific coding, subserved by face-selective areas in the ventral visual cortex, which show viewpoint-sensitive fMRI adaptation as well (Fang et al., 2007).

Taken together, these results suggest that FAEs reflect the adaptation of neural populations at higher-levels of the visual processing stream that tolerate substantial changes in several low-level attributes of the stimulus, such as retinal size, position, and viewpoint. This notion is further supported by studies showing that aftereffects of identity are not affected by differences in facial expression between the adaptor and test stimuli (Fox et al., 2008), or the distortion of the adaptor face by vertical stretching (Hole, 2011), which implies that the adaptation affects a rather abstract representation of facial identity (Hole, 2011). On the other hand, the extent to which these aftereffects are mediated by processing sites that are sensitive to the configural properties of faces is a matter of further inquiry. The term "configural processing" in the face perception literature refers to the encoding of the exact relations among the constituent elements of the face (Maurer et al., 2002). This process involves the detection of the basic configuration that all faces share, that is, the relative position of the eyes, nose, and mouth (first-order relations) as well as the encoding of the precise metric distances among the features (second-order relations – Diamond and Carey, 1986; Maurer et al., 2002). A related phenomenon that is often used interchangeably with configural processing is "holistic processing," which refers to the integration of the features as well as their spatial relations in a single unified representation that makes the processing of individual features rather difficult (Young et al., 1987; Tanaka and Farah, 1993, for a recent review, see Tanaka and Gordon, 2011). The contribution of configural/holistic processing to face perception can be demonstrated for example by the face inversion effect – the disproportionate detriment in our ability to recognize faces as opposed to objects when they are presented upside-down (Yin, 1969). Since inversion affects face recognition more than the recognition of objects, it is thought to tamper with perceptual mechanisms that are unique to face processing. Indeed, impoverished recognition of inverted faces is attributed to the diminished performance in detecting fine-scale differences in the metric distances among facial features (e.g., Sergent, 1984; Searcy and Bartlett, 1996; Freire et al., 2000), which is thought to be in connection with the inability to integrate distant elements of the face into a unified percept (Rossion, 2008, 2009, however, there is an alternative view according to which inversion disrupts the coding of individual features as well, as long as featural information is defined in terms of variations in shape, see McKone and Yovel, 2009 for a review).

Therefore, the face inversion effect is a useful behavioral marker of configural/holistic processing, which operates normally when the visual system is presented with an upright face, but breaks down when the face is turned upside-done. It follows from this that if FAEs reflect the adaptation of neural populations engaged in such mechanisms, they should also be sensitive to inversion. However, in many cases, the aftereffects observed with both the adaptor and test faces turned upside-down are of the same magnitude as those reported when the adaptor and test faces are upright. (Webster and MacLin, 1999; Leopold et al., 2001; Zhao and Chubb, 2001; Watson and Clifford, 2003, 2006; Guo et al., 2009; but see Rhodes et al., 2009a). On the other hand, aftereffects do not transfer fully between faces in opposite orientations (Webster and MacLin, 1999), and this is especially true when the adaptor face is inverted and the test face remains upright (Watson and Clifford, 2003, 2006; Guo et al., 2009). One possible explanation for this asymmetry is that aftereffects following adaptation to upright and inverted faces arise at different stages of the visual system – adaptation to upright faces affect both face-specific configural/holistic representations and non-specific part-based representations, whereas adaptation to inverted faces affects only the later (Watson and Clifford, 2003, 2006). The assumption that adaptation to upright and inverted faces tap into different representations finds support from orientation-contingent aftereffects, that is, opposite aftereffects are induced for upright and inverted faces at the same time (Rhodes et al., 2004). A related notion is that upright face aftereffects reflect partly, while inverted aftereffects reflect entirely the recalibration of high-level generic shape-coding mechanisms (Susilo et al., 2010). Susilo et al. (2010) found that aftereffects for eye-height show a partial transfer between T-shapes and real faces. For example, adaptation to upright T-shapes resulted in an aftereffect in eye-height judgments of upright real faces, but this aftereffect was smaller than the one obtained by real face adaptors. In contrast, there was a complete transfer between the two stimulus classes when they were presented upside-down. These findings can be taken as evidence that a shape-generic component can partly account for upright face aftereffects. Another factor that appears to modulate the transfer of aftereffects between adaptor and test faces of opposite orientation is familiarity. Hills and Lewis (2012) found that identity aftereffects for famous faces showed greater transfer from inverted adaptors to upright images than vice versa. This pattern is the exact opposite of the ones observed in FDAEs and face gender aftereffects with unfamiliar faces (Watson and Clifford, 2003, 2006). Since the FDAE and the identity aftereffects are usually assumed to reflect the operation of the same mechanisms (Hurlbert, 2001; Webster and MacLeod, 2011), the above discrepancy is rather attributable to the effect of familiarity than to the different types of aftereffects examined in these studies (Hills and Lewis, 2012).

Turning to the role of basic facial configuration (first-order spatial relations) in FAEs, it has been shown that an adaptor with a preserved whole-face configuration is crucial for identity aftereffects (Pichler et al., 2012), but not for aftereffects of facial affect (Butler et al., 2008). However, the latter can also be induced with adaptors consisting of non-facial elements, provided that they are arranged in a face-like fashion (Butler et al., 2008). Thus, it seems that in both cases, the locus of adaptation is sensitive to the basic geometrical structure of the face. In addition, the identity aftereffect showed a significant decrease in magnitude when the adaptor and test faces differed in the metric distances between their features (Pichler et al., 2012).

The above results emphasize the role of first- and second-order spatial relations in upright face aftereffects of facial identity and emotion. Previous studies examining the effect of inversion on FAEs (see above) suggested that these facial properties might also be important for aftereffects of gender and distortion. In case of distortion, a recent study has shown that the FDAE is contingent on emotional expression and gender, which might indicate that the underlying processing sites are sensitive to configural changes that differentiate between faces varying along these dimensions (Tillman and Webster, 2012). However, as the authors note, these results can be explained by the adaptation of processing sites engaged in more generic visual processing, and do not necessarily involve face-specific response changes. Therefore, unraveling the precise nature of the representations underlying these aftereffects requires further investigation. In the present study, our aim was to investigate the role of basic facial configuration in the FDAE. We used schematic face-like images as adaptor stimuli that preserve the basic configural properties of a face (the first-order spatial relations of the major parts) but only consist of simple geometric shapes and therefore lack the typical features that describe a real human face (**Figure 1**). Previous studies have shown that newborns orient preferentially to such stimuli (Johnson et al., 1991) and that in adults, schematic faces activate a face-selective cortical area, the fusiform face area (FFA – Kanwisher et al., 1997) more strongly than non-face objects, albeit less strongly than real faces do (Tong et al., 2000; Liu et al., 2009). Photographs of real faces of famous celebrities with different degrees of distortion (expansion and contraction) served as target stimuli in our experiments. We argued that if the processing sites underlying the FDAE are sensitive to the basic configural properties of a face, then they should be activated by the schematic face-like adaptors. If this were so, then prolonged exposure to these adaptors with variations in the metric distances between their components (expanded or contracted face-like stimuli) would bias the perception of the subsequently presented real faces, resulting in a systematic aftereffect. In other words, we tested whether the FDAE can be induced with simple geometric shapes arranged in a face-like pattern (Experiment 1). We also assessed whether such an aftereffect reflects the adaptation of a high-level processing sites by manipulating several low-level features of the adaptor stimuli, such as size (Experiment 2), orientation (Experiment 3), contrast polarity (Experiment 4),

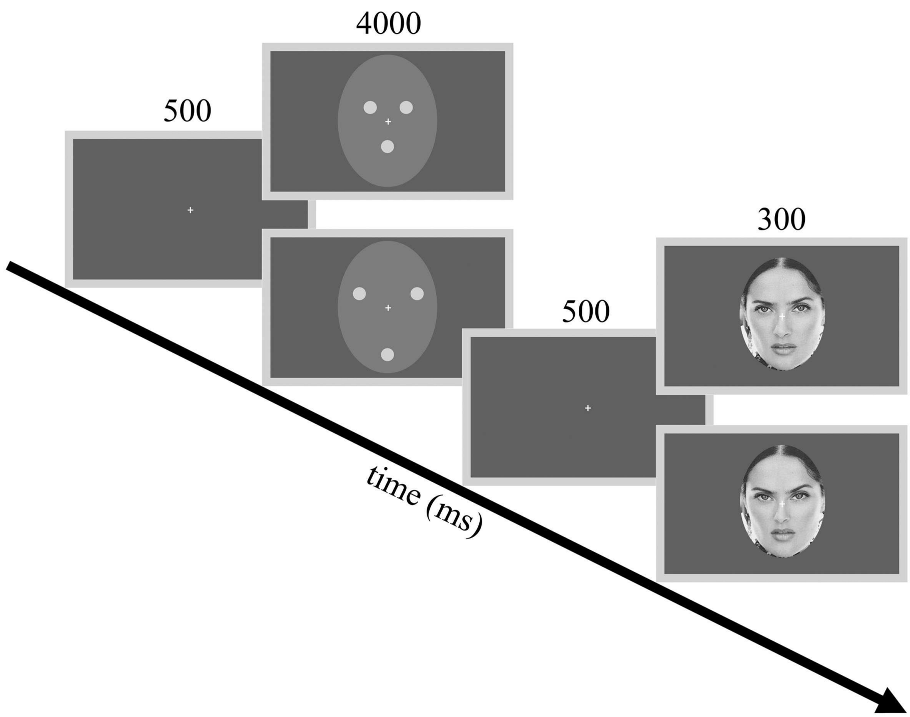

FIGURE 1 | Procedures and example stimuli. The flowchart illustrates the adaptor stimuli used in Experiment 1 and one of the three test faces used during the experiments as an example. Adaptor stimuli from top to down: contracted (CONT) and expanded (EXP) white dots. Test stimuli from top to down: −10% (expanded) and +10% (contracted) distorted faces.

and the effect of replacing the constituent elements with visual noise (Experiment 5).

EXPERIMENT 1

MATERIALS AND METHODS

Participants

Thirteen naive, healthy volunteers (six females) participated in the experiment (mean age: 26 ± 3 years). All the participants had normal or corrected-to-normal vision and gave written informed consent. We conform to the protocols approved by the Ethical Committee of the University of Regensburg.

Stimuli

We used the full-front gray-scale face images of three famous persons (Angelina Jolie, Nicole Kidman, and Salma Hayek) as test faces. These faces were compressed and expanded using the Adobe Photoshop 6.0 "Pinch" option. We applied four different expansion (−20%, −15%, −10%, −5%) and four different contraction (5%, 10%, 15%, 20%) levels to the face images. These distortions affected the shape of the internal features of the face as well as their exact spatial relations while the outer contour of the face and the overall shape of the head remained the same (Zimmer and Kovács, 2011a). The three undistorted celebrity faces and their four expanded and four contracted versions (corresponding to the distortion levels described above) were used as test faces. Thus, there were a total of 27 face images that served as test stimuli in the present experiment and in all the other experiments reported in this paper.

Two different adaptation conditions were presented in separate blocks. In both conditions, the adaptor image consisted of three white dots (luminance: 64 cd/m^2), arranged in a triangular fashion. The dots were placed according to the location of the eyes and mouth and were embedded in a light gray elliptic surround (luminance: 13 cd/m^2, Michelson contrast = 0.66). The elliptic surround subtended a visual angle of 9°× 11 under a viewing distance of 70 cm. In the contracted adaptor condition (CONT), the distance between the individual dots was 2.1°. In the expanded adaptor condition (EXP), the space between the dots was increased to 3.9° (**Figure 1**). Stimuli were presented in the center of the screen on a uniform gray background using a 17″ monitor (1024 × 768 pixel resolution, 75 Hz vertical refresh rate). Participants were tested individually in a dimly lit room. All software was written in MATLAB 6.5 (MathWorks, Inc.) using PsychToolbox 2.45 for Windows.

Procedure

Before the beginning of the test phase, participants were familiarized with each celebrity whose images were used as target stimuli in the test phase. During this "familiarization phase," participants were presented with the veridical, 20% contracted and 20% expanded images of each of the three celebrities and they were asked to note the differences between the original and the distorted images, as well as to recognize these persons and recall their names.

The testing phase followed a course that was similar to that of Zimmer and Kovács (2011a). In the beginning of each trial, a blank screen appeared for 500 ms followed by the adaptor image, which was presented for 4000 ms. Following the adaptor image there was a 500 ms gap, after which the test stimulus was presented for 300 ms. Participants were instructed to fixate on a white crosshair presented centrally on the screen and to press a button whenever they perceived the test face expanded or another button if the test face appeared contracted compared to the veridical, undistorted face of the given celebrity. Contracted and expanded adaptor conditions of all the three celebrities were given in two separate blocks, with a short break between the two. The order of the blocks was randomized across participants. Each block consisted of 135 trials – 9 (number of distortion levels) x 3 (number of celebrities) × 5 (number of repetitions of a given test stimulus) – in a random order. Experimental sessions lasted approximately 30 min.

Data analysis

Psychophysical data were modeled by the Weibull psychometric function, using the Psignifit toolbox (Version 2.5.6.) for MATLAB (Wichmann and Hill, 2001). In order to determine whether adaptation to contracted or expanded dot patterns results in a bias in face distortion discrimination of the subsequently presented target stimuli, we conducted a two-way repeated measures analysis of variance (ANOVA) with type of adaptor (2) and distortion level (9) as within-subject factors.

RESULTS AND COMMENT

Participants' contraction ratings varied with different levels of distortion, indicating that they perceived the negative and positive distortions of the target faces [main effect of distortion level: $F(8, 96) = 34.21$, $p < 0.0001$, $\eta_p^2 = 0.74$]. Another observable tendency is that on average, participants perceived the test faces to be more expanded than contracted. Specifically, at 0% distortion (veridical face), the percentage of "contracted" ratings is slightly less than 50%, even in the expanded adaptor condition. One factor that might have contributed to this effect is the sensitivity to different directions of distortion, namely that people are more sensitive to inwards than outwards shifts of the eyes (Haig, 1984). This might have counteracted the aftereffect to the extent that the veridical face was reported somewhat more often as "expanded" than "contracted."

More importantly, adaptation to the dot patterns biased the perception of the target faces, causing a significant aftereffect: test faces were judged more contracted following adaption to an expanded, than to a contracted dot pattern [main effect of adaptor type: $F(1, 12) = 38.92$, $p < 0.0001$, $\eta_p^2 = 0.76$, no interaction between adaptor type and distortion level: $F(8, 96) = 0.43$, $p = 0.9$, $\eta_p^2 = 0.03$, **Figure 2**]. This indicates that perceptual aftereffects for faces can be induced by using relatively simple adaptor stimuli, such as three dots arranged in a face-like fashion. Moreover, the pattern of results suggests that these aftereffects are similar in nature to those reported in previous studies demonstrating that prolonged viewing of a distorted face biases the perception of a subsequently presented face in a way that is opposite to the distortion of the adaptor image (Webster and MacLin, 1999; Zhao and Chubb, 2001; Watson and Clifford, 2003; Yamashita et al., 2005; Zimmer and Kovács, 2011a). The obvious differences in terms of physical characteristics between the adaptor and the test stimuli

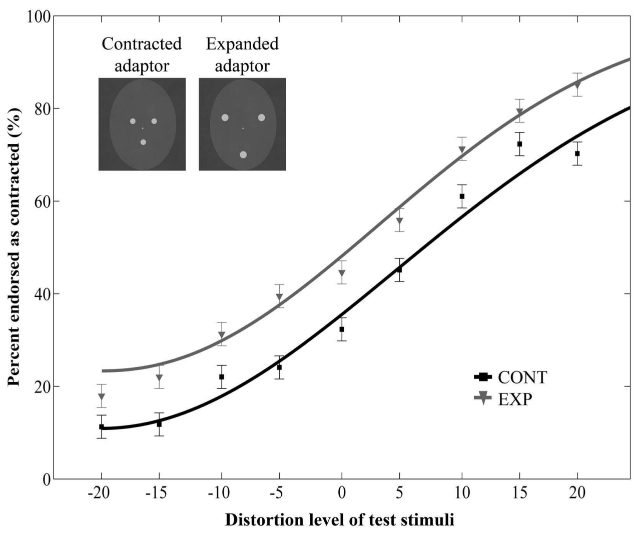

FIGURE 2 | Mean ratio of stimuli endorsed as contracted as a function of distortion level (% distorted). Negative and positive distortion levels correspond to expanded and contracted target faces respectively. Results obtained by using contracted (CONT) and expanded (EXP) white dots as adaptor stimuli. The inset illustrates the adaptor stimuli. Data are modeled by a Weibull psychometric function.

used in the present experiment suggest that the neural mechanisms of this aftereffect are not engaged in image-based, but rather in higher-level visual processing. To investigate the contribution of such high-level adaptation, we developed another experiment in which the adaptor and test stimuli differed in size. Since there is considerable evidence for a size-invariant neural representation of faces in both monkeys (Perrett et al., 1982; Rolls and Baylis, 1986) as well as in humans (Andrews and Ewbank, 2004), we hypothesized that if the aftereffect is indeed mediated by high-level visual areas, then it would occur despite a remarkable difference in size between the adaptor and test images (Leopold et al., 2001; Zhao and Chubb, 2001; Anderson and Wilson, 2005; Pimperton et al., 2009).

EXPERIMENT 2 – SIZE

MATERIALS AND METHODS

A new group of 11 naive, healthy participants (five females, mean age: 26 ± 4 years) with normal or corrected-to-normal vision participated in the experiment and gave written informed consent. In this experiment, the adaptor and test images were identical to those of Experiment 1 except that the adaptor stimuli were 30% larger than the test faces. To compare the results of the present experiment to those of Experiment 1, we analyzed the data from both experiments together in a three-way mixed-design ANOVA with size (2; same/different) as a between-subject factor and adaptor type (2) and distortion level (9) as within-subject factors.

RESULTS AND COMMENT

Prolonged exposure to the dot pattern resulted in an aftereffect: adaptation to a dot pattern distorted in one way caused the subsequent test faces to appear distorted in the opposite way [main effect of adaptor type: $F(1, 22) = 29.18$, $p < 0.0001$, $\eta_p^2 = 0.57$, main effect of distortion level: $F(8, 176) = 72.83$, $p < 0.0001$, $\eta_p^2 = 0.77$, no interaction between adaptor type and morph level: $F(8, 176) = 1.2$, $p = 0.3$, $\eta_p^2 = 0.05$]. Crucially, the main effect of size was not significant [$F(1, 22) = 0.6$, $p = 0.45$, $\eta_p^2 = 0.03$], and there was no interaction between size and adaptor type [$F(1, 22) = 1.62$, $p = 0.22$, $\eta_p^2 = 0.07$]. The three-way interaction was also not significant [$F(8, 176) = 0.7$, $p = 0.69$, $\eta_p^2 = 0.03$]. These results suggest that aftereffects occur also when the schematic face-like adaptors and the test faces differ in size.

Additionally, we ran a separate two-way repeated measures ANOVA on the data of the Experiment 2 with adaptor type (2) and distortion level (9) as within-subject factors. This analysis yielded a significant main effect of adaptor type [$F(1, 10) = 5.43$, $p = 0.04$, $\eta_p^2 = 0.35$] and distortion level [$F(8, 80) = 39.36$, $p < 0.0001$, $\eta_p^2 = 0.8$, no interaction between adaptor type and distortion level: $F(8, 80) = 1.34$, $p = 0.24$, $\eta_p^2 = 0.12$, **Figure 3**]. Taken together, these results show that the aftereffect tolerates remarkable size differences between the adaptor and test images.

The fact that the aftereffect is, to a great extent, size-invariant suggests that it is mediated by higher processing levels of the visual system. However, the degree to which the aftereffect is due to the adaptation of a neural population involved in face-specific configural processing requires further investigation. To this end, we conducted an additional experiment in which the dot pattern was inverted while the orientation of the test images remained upright. It is well known that turning a face upside-down deteriorates its recognition greatly (Yin, 1969). This so-called "face inversion effect" is believed to arise due to the disruption of coding the spatial relations between face elements and thus regarded as the hallmark of configural processing (Maurer et al., 2002; Rossion and Gauthier, 2002; see Introduction). Thus, inverting the dot pattern presumably renders it more difficult to encode its face-like configural properties. Therefore we hypothesized that if face-sensitive processing sites account for the aftereffects observed in Experiment 1 and 2, then the inversion of the adaptor image should reduce or even eliminate the aftereffect.

EXPERIMENT 3 – ORIENTATION

MATERIALS AND METHODS

A new group of 10 participants (nine females, mean age: 22 ± 3 years) with normal or corrected-to-normal vision was recruited for the experiment and gave written informed consent. Task instructions, adaptor and test stimuli were the same as in Experiment 1, except that the adaptor images were turned upside-down. To compare the results of the present experiment to those of Experiment 1, we analyzed the data from both experiments together in a three-way mixed-design ANOVA with orientation (2; upright/inverted) as a between-subject factor and adaptor type (2) and distortion level (9) as within-subject factors.

RESULTS AND COMMENT

The main effect of adaptor type was significant [$F(1, 21) = 20.22$, $p = 0.0002$, $\eta_p^2 = 0.49$] but it was qualified by a significant interaction between adaptor type and orientation [$F(1, 21) = 8.75$,

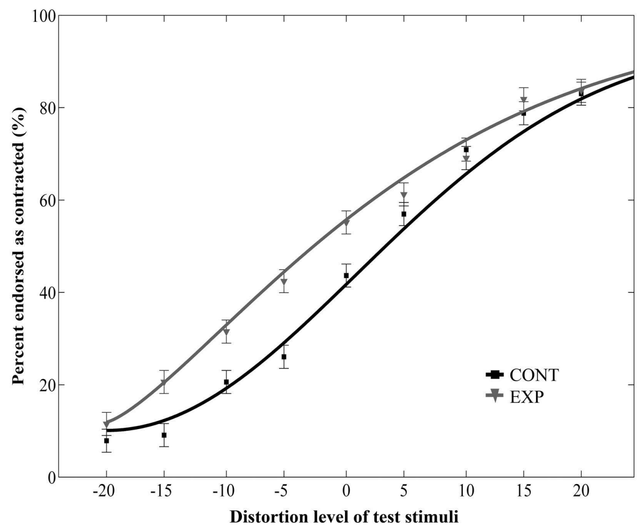

FIGURE 3 | Mean ratio of stimuli endorsed as contracted as a function of distortion level (% distorted) when the relative size of adaptor and target was varied. Negative and positive distortion levels correspond to expanded and contracted target faces respectively. Results obtained by using versions of contracted (CONT) and expanded (EXP) white dot adaptors that differed in size from the target stimuli.

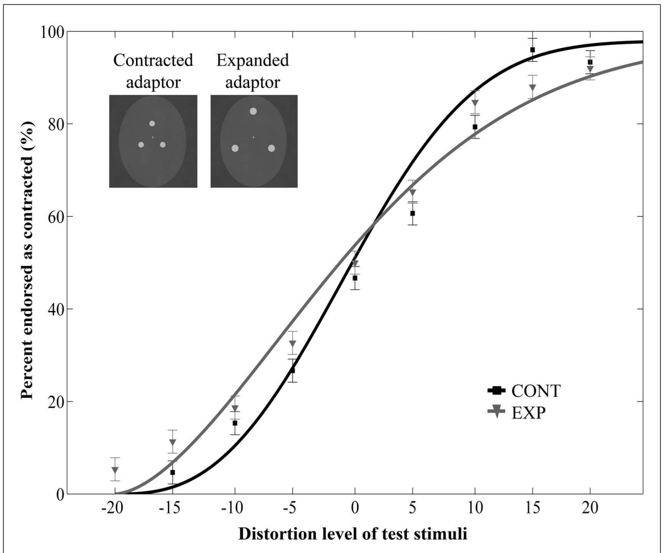

FIGURE 4 | Mean ratio of stimuli endorsed as contracted as a function of distortion level (% distorted) when the adaptor images were upside-down. Negative and positive distortion levels correspond to expanded and contracted target faces respectively. Results obtained by using the inverted versions of contracted (CONT) and expanded (EXP) white dots as adaptors.

$p = 0.007$, $\eta_p^2 = 0.29$]. *Post hoc* tests (Fisher's Least Significant Difference test) revealed that contracted ratings significantly differed between CONT and EXP conditions in case of upright adaptors ($p < 0.0001$), whereas there was no such difference in case of inverted adaptors ($p = 0.32$). The main effect of orientation [$F(1, 21) = 1.45$, $p = 0.24$, $\eta_p^2 = 0.06$] and the three-way interaction [$F(8, 168) = 1.45$, $p = 0.93$, $\eta_p^2 = 0.02$] were not significant. Thus, while aftereffects were observed with upright adaptors, the inversion of the adaptor stimuli eliminated the aftereffect. We also observed a main effect of distortion level [$F(8, 168) = 113.05$, $p < 0.0001$, $\eta_p^2 = 0.84$] and an interaction between distortion level and orientation [$F(8, 168) = 4.29$, $p = 0.0001$, $\eta_p^2 = 0.17$], but no interaction between distortion level and adaptor type [$F(8, 168) = 0.82$, $p = 0.59$, $\eta_p^2 = 0.04$].

Additionally, we ran a separate two-way repeated measures ANOVA on the data of Experiment 3 with adaptor type (2) and distortion level (9) as within-subject factors. This analysis yielded to no significant effect of adaptor type [$F(1, 9) = 0.85$, $p = 0.38$, $\eta_p^2 = 0.09$ with a significant main effect of distortion: $F(8, 72) = 110$, $p < 0.0001$, $\eta_p^2 = 0.92$ and to no interaction of adaptor type and distortion: $F(8, 72) = 0.71$, $p = 0.68$, $\eta_p^2 = 0.07$, **Figure 4**]. Thus, prolonged viewing of inverted dot patterns did not bias the perception of test faces.

This result implies that the exact configuration of the dot pattern applied in Experiment 1 – three dots arranged in a triangular fashion – is crucial to evoke the aftereffect. Since this arrangement mimics the first-order configural properties of a face, the lack of aftereffect when the dot pattern is inverted suggests the involvement of face-sensitive configural processing sites. Whether these processing sites represent faces based solely on configural information, or whether they are sensitive to low-level cues remains an open issue. Hence, we conducted an additional experiment to test the role of low-level features in which the contrast polarity of the adaptor image was varied by presenting either white dots on a black background or black dots on a white background. We reasoned that if the adapting sites are sensitive solely to configural properties, then aftereffects should be obtained irrespective of the actual contrast polarity of the adaptor images.

EXPERIMENT 4 – CONTRAST REVERSAL

MATERIALS AND METHODS

Ten participants (six females, mean age: 29 ± 8 years) with normal or corrected-to-normal vision participated in the experiment and gave written informed consent. Task instructions, test stimuli, and overall procedures were identical to those of Experiment 1. The adaptors either consisted of white dots on a black oval, or black dots on a white oval. In both cases, the contrast between the dots and the oval was the same (Michelson contrast = 0.95). Both types of adaptors appeared in two forms: expanded and contracted to the same extent as in Experiment 1. Thus, there were a total of four conditions (expanded and contracted white dot adaptors; expanded and contracted black dot adaptors). Each participant was tested with all four adaptors with the order of the conditions randomized across participants. A three-way repeated measures ANOVA was employed to determine the effects of adaptation on the distortion discrimination of the test faces, with contrast polarity (2), adaptor type (2) and distortion level (9) as within-subject factors.

RESULTS AND COMMENT

The main effect of adaptor type was significant [$F(1, 9) = 6{,}76$, $p = 0.029$, $\eta_p^2 = 0.43$], showing that adaptation to the dot patterns resulted in a perceptual aftereffect. However, neither the main effect of polarity [$F(1, 9) = 0.06$, $p = 0.82$, $\eta_p^2 = 0.006$], nor the interaction between polarity and adaptor type [$F(1, 9) = 0.33$, $p = 0.58$, $\eta_p^2 = 0.04$] was significant. The three-way interaction between polarity, adaptor type and distortion level was also not significant [$F(8, 72) = 0.75$, $p = 0.65$, $\eta_p^2 = 0.08$]. Finally, there was a significant main effect of distortion level [$F(8, 72) = 42.86$, $p < 0.0001$, $\eta_p^2 = 0.83$], while every other effect was non-significant (p values above 0.16, **Figure 5**).

These results show that prolonged viewing of contracted and expanded adaptors results in a perceptual aftereffect similarly to the findings of Experiment 1 and 2. The results also show that when the internal elements of the adaptor image are matched in contrast (hence in perceptual saliency), this effect does not depend on the contrast polarity of the adaptor image. These findings indicate that the underlying processing sites represent the structural properties of the image largely independently of contrast polarity.

However, it is possible that the adaptation sites are sensitive to other low-level manipulations that affect the saliency of the internal features of the adaptor. Hence we investigated to role of low-level image properties in a further experiment in which we used the upright contracted and expanded adaptor images with their constituent dots replaced by equiluminant visual noise patterns, reducing the contrast between the dots and their background strongly. We reasoned that if the locus of adaptation is sensitive to the contrast of the constituent elements, then replacing these elements with visual noise should also reduce or eliminate the aftereffect.

EXPERIMENT 5 – LOW-CONTRAST

MATERIALS AND METHODS

Eleven participants (10 females, mean age: 27 ± 4 years) with normal and corrected-to-normal vision participated in the experiment and gave written informed consent. Task instructions, test stimuli and overall procedure were the same as in Experiment 1. Adaptor images had the same configuration as those in Experiment 1 but their constituent elements were replaced by visual noise. First, Fourier phase-randomization was applied to the original versions of the three celebrity faces. Second, the resulting images were equated in luminance (13 cd/m^2) and were resized to match the size of the dots of the adaptor stimulus. Finally, the three noise patterns were placed on a gray oval (luminance: 8 cd/m^2) at the locations corresponding to the eyes and mouth of a face, as in the previous experiments. The contrast between the dots and the oval background was reduced strongly (Michelson contrast = 0.24) when compared to the previous experiments. To compare the results of the present experiment to those of Experiment 1, we analyzed the data from both experiments together in a three-way mixed-design ANOVA with dot quality (2; white dots/noise) as a between-subject factor and adaptor type (2) and distortion level (9) as within-subject factors.

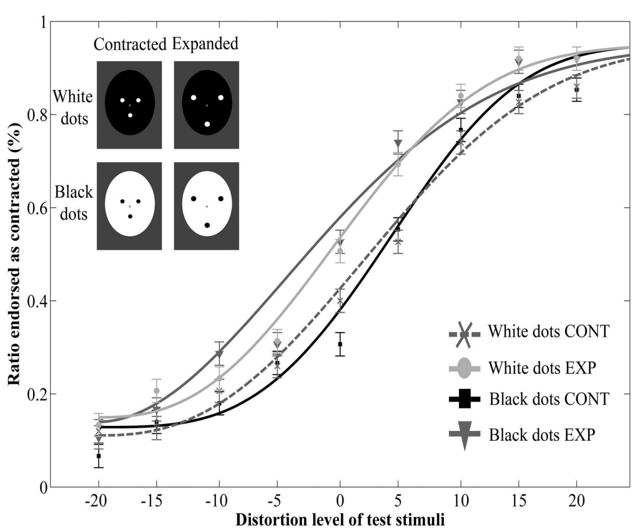

FIGURE 5 | Mean ratio of stimuli endorsed as contracted as a function of distortion level (% distorted) with adaptors of opposite contrast polarity. Negative and positive distortion levels correspond to expanded and contracted target faces respectively. Results obtained by using white dots on a black oval (White dots CONT and White dots EXP) and black dots on a white oval (Black dots CONT and Black dots EXP).

RESULTS AND COMMENT

The main effect of adaptor type was significant [$F(1, 22) = 16.43$, $p = 0.0005$, $\eta_p^2 = 0.43$], showing that adaptation to the dot patterns resulted in a perceptual aftereffect. However, neither the main effect of dot quality [$F(1, 22) = 1.52$, $p = 0.23$, $\eta_p^2 = 0.06$], nor the interaction between dot quality and adaptor type [$F(1, 22) = 1.11$, $p = 0.3$, $\eta_p^2 = 0.05$] was significant. The three-way interaction between polarity, adaptor type and distortion level was also not significant [$F(8, 176) = 0.37$, $p = 0.94$, $\eta_p^2 = 0.02$]. These results suggest that the aftereffects are not affected strongly by the low-level properties of the constituent elements of the adaptor image. Finally, there was a significant main effect of distortion level [$F(8, 176) = 103.61$, $p < 0.0001$, $\eta_p^2 = 0.82$], and a significant interaction between distortion level and dot quality [$F(8, 176) = 2.14$, $p = 0.03$, $\eta_p^2 = 0.09$], but no interaction between distortion level and adaptor type [$F(8, 176) = 0.88$, $p = 0.53$, $\eta_p^2 = 0.04$].

However, the separate two-way repeated measures ANOVA on the data of Experiment 5 [with adaptor type (2) and distortion level (9) as within-subject factors] showed only a mild tendency of adaptor type effect [$F(1, 10) = 2.36$, $p = 0.16$, $\eta_p^2 = 0.19$; main effect of distortion level: $F(8, 80) = 88.73$, $p < 0.0001$, $\eta_p^2 = 0.9$, no interaction between adaptor type and distortion level: $F(8, 80) = 0.79$, $p = 0.61$, $\eta_p^2 = 0.07$, **Figure 6**]. The lack of significant main effect of adaptor type in the present experiment shows that lowering the contrast of the adaptor image reduces the amount of the aftereffect somewhat, even when the elements of the adaptor images are placed according to the basic face configuration. This result implies that the adaptation site is sensitive to changes affecting the low-level image properties, that is, the disruption of homogeneous brighter regions corresponding to eyes and mouth. The absence of any significant aftereffect in the separate ANOVA might be the consequence of the lower contrast between the brighter dots and the darker background, a possibility in line with the results of a previous study which showed that high-contrast faces generate stronger FDAEs than low-contrast ones (Yamashita et al., 2005).

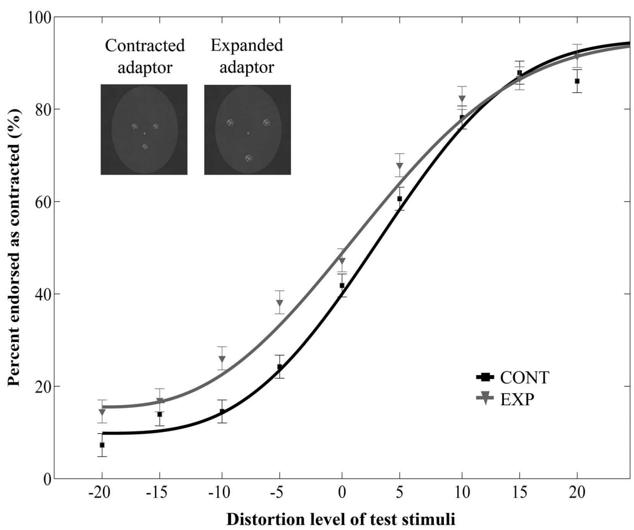

FIGURE 6 | Mean ratio of stimuli endorsed as contracted as a function of distortion level (% distorted) with low-contrast adaptor features consisting of visual noise. Negative and positive distortion levels correspond to expanded and contracted target faces respectively. Results obtained by using the contracted (CONT) and expanded (EXP) dots consisting of visual noise.

DISCUSSION

In the present study, we demonstrated that FDAEs could be evoked by stimuli consisting of three dots arranged in a triangular position, corresponding to the position of usual facial features. This suggests that the processing sites underlying the FDAE are sensitive to the basic facial configuration and the fine spatial arrangement of the elements of the face (second-order relations) as well, even in the absence of realistic face parts.

One of the main questions is whether the aftereffect is due to the adaptation of low- or high-level visual areas, or both. One possibility is that the aftereffects originate from the early stages of visual processing, which are sensitive to the low-level visual properties of the image. A related assumption is that adaptation to the face-like patterns biased the response of low-level areas, and this bias propagated up the visual processing hierarchy, affecting the response of higher-level visual areas to the subsequently presented face-stimuli. Such "cross-level" (Xu et al., 2008) adaptation has been found previously with simple curved lines as adaptors, which not only affected the curvature judgments of target lines (low-level aftereffect) but the emotional expression decisions in real faces as well (high-level aftereffect; Xu et al., 2008). In case of low-level adaptation, however, due to the smaller receptive field sizes of the neurons we would expect the aftereffect to be sensitive to image size, whereas in Experiment 2 a significant aftereffect was observed in spite of the size difference between the adaptor and test stimuli. This result is in line with the previous finding that the FDAE tolerates large size differences between the adaptor and test images (Zhao and Chubb, 2001), and suggests the role of higher-level visual areas engaged in non-retinotopic visual processing and having a large degree of size-invariance.

However, these processing sites need not necessary be face-selective (Rhodes and Leopold, 2011). High-level, non-retinotopic aftereffects have been observed for general shape properties such as taper and aspect ratio (Suzuki and Cavanagh, 1998; Suzuki, 2005), which might have contributed to the aftereffects observed in the present study as well. On the other hand, in Experiment 3, we found that inverting the schematic face-like adaptor image eliminated the aftereffect entirely. Inverting a face is thought to interfere with face-specific configural processing mechanisms (see Introduction). Accordingly, a previous study showed that the inversion of the adaptor face (with the test face retaining its upright orientation) reduces the magnitude of the FDAE compared to any other combination of adaptor and test orientations (Watson and Clifford, 2003). Although the absence of aftereffect with an inverted adaptor in our study does not entirely exclude the possibility that a shape-generic mechanism can account for the aftereffect observed with upright adaptors, it strongly implies the involvement of face-specific mechanisms.

Human scalp electrophysiology and functional imaging studies provide considerable evidence that schematic and real faces share common or overlapping neural representations. The most widely studied electrophysiological correlate of face perception is the N170 event-related potential, which is larger for faces than for other object categories (Bentin et al., 1996; Rossion et al., 2000) and it is sensitive to manipulations that affect the canonical configuration of the face, such as inversion (e.g., Rossion et al., 2000) or scrambling of the face parts (e.g., George et al., 1996; Macchi Cassia et al., 2006). Note however, that results are mixed as to whether N170 is modulated (e.g., Scott and Nelson, 2006; Kaufmann and Schweinberger, 2012) or not (Mercure et al., 2008) by more subtle changes concerning the second-order relations of a face. The N170 evoked by schematic faces that lack realistic facial features but preserve the basic configuration is similar in amplitude to the N170 evoked by real face images (Sagiv and Bentin, 2001; Latinus and Taylor, 2006). Furthermore, schematic faces reduce the amplitude of the N170 to subsequently presented real faces, while schematic houses do not adapt the component (Eimer et al., 2011), suggesting that the same neural mechanisms underlie the perception of both types of faces.

Several functional imaging studies have shown that the FFA is sensitive to inversion (e.g., Yovel and Kanwisher, 2005; Mazard et al., 2006) and the disruption of first-order relations in upright faces, even in the absence of real face parts (Liu et al., 2009). Although an initial study did not show any differential sensitivity to features versus spacing between features (Yovel and Kanwisher, 2004), additional studies showed that the FFA (Rotshtein et al., 2007; Goffaux et al., 2009; Rhodes et al., 2009b) or a region adjacent to the FFA (Maurer et al., 2007) is sensitive to second-order relations. Schematic faces activate the FFA stronger than non-face objects, albeit less than real faces do (Tong et al., 2000). On the basis of these results, it is conceivable that the schematic face-like adaptors of the present study activated higher-level processing sites that are sensitive to the basic configuration of the facial features (first-order relations) and the spatial distance among the elements (second-order relations). Assuming that the schematic adaptors and the real test faces activated an overlapping set of neurons, adaptation might have desensitized the neurons responding to the schematic faces, which resulted in a shift of the overall population response in the opposite direction, biasing the representation of the test face. Conceptually, face aftereffects are usually interpreted in the framework of a multidimensional face-space (Valentine, 1991), in which individual variations in facial attributes are coded in relation to an average face or norm and adaptation shifts the norm toward the adaptor along the dimension that corresponds to the adapted attribute (e.g., Leopold et al., 2001; Robbins et al., 2007; Rhodes and Leopold, 2011). In this regard, it is plausible that prolonged exposure to the schematic adaptor resulted in a shift of the norm that is used to code second-order properties, which in turn then biased the representation of the test face away from the adaptor.

The fact that the observed FDAE was insensitive to the reversal of adaptor contrast supports this idea. Nevertheless, sensitivity to contrast reversal would not be entirely incompatible with the assertion that the aftereffect originates from higher-level visual areas either. This manipulation has been shown to affect the response of single neurons in the macaque inferior-temporal cortex (Perrett et al., 1984; Ito et al., 1994; Ohayon et al., 2012; but see Rolls and Baylis, 1986) as well as the BOLD response of the human fusiform gyrus to face images (George et al., 1999). Further, it has long been known that photographic negation, which reverses the contrast polarity of the image, is detrimental to face recognition (Galper, 1970; Galper and Hochberg, 1971). Under normal lighting conditions regions of the face corresponding to the eyes and mouth appear darker than their surroundings and the contrast reversal of the image reverses this pattern, making these areas lighter than the surrounding areas. Hence we would expect an aftereffect when the face-like adaptor image contains dark spots in the eye and mouth regions. Contrary to this, we observed an aftereffect with white dots on a gray (Experiment 1) or black (Experiment 4) background and also with black dots on a white background (Experiment 4). In a series of experiments, Kemp et al. (1990) showed that negation reduces sensitivity not only to the displacement of eyes in real faces, but to similar changes in stimuli consisting of three black dots arranged in a face-like configuration in a real facial surround. A more recent study using continuous flash supression (CFS), a form of binocular rivalry, showed that the mechanisms governing adults' visual awareness are sensitive to inversion and negation of realistic face-stimuli as well as face-like patterns with three dark dots corresponding to the eyes and mouth, similar to our adaptor images (Stein et al., 2011). The authors conclude that even though CFS eliminates high-level face shape adaptation (Stein and Sterzer, 2011), a higher-level visual area such as the FFA could still play a role in these effects, based on the fact that activity in this area is informative of object category even if the stimulus itself is not consciously perceived (Sterzer et al., 2008). Whereas these studies point to the convergence of face-specific configural and contrast polarity cues, data from face adaptation studies show a somewhat different picture. The FDAE can be induced by both positive and negative polarity faces as well, and it is also selective to the polarity of the adaptor image (Yamashita et al., 2005). A more recent study has shown that the face identity aftereffect for famous faces is not affected by contrast reversal, as shown by the transfer of adaptation between positive and negative faces (Hills and Lewis, 2012). Our results, namely that schematic face-like images of opposite contrast polarity can be potent adaptors, is in line with these findings. This may be the result of dissociation between the coding of contrast polarity and configural properties at some levels of the visual system. The aftereffect in turn would depend on the adaptation of neurons tuned to the configural properties of the face, independently of contrast polarity. Another possibility, as suggested by Yamashita et al. (2005), is that positive and negative polarity faces adapt two separate mechanisms: face-specific and object-specific mechanisms respectively (see also Rhodes et al., 2004). However, in Experiment 3 we found that the adaptors consisting of white dots on a gray background, which approximate contrast negated faces, failed to induce an aftereffect when viewed upside-down. Since the effect of inversion is regarded as a hallmark of face-specific configural coding (Maurer et al., 2002; Rossion and Gauthier, 2002), this result seems to contradict the role of object-specific mechanism.

While it seems to be the case that the processing sites underlying these aftereffects are engaged in the coding of configural properties independently of contrast polarity, it does not necessarily follow that they are not sensitive to other lower-level image properties. In Experiment 5, we investigated adaptation to schematic face-like adaptors whose constituent elements had been replaced by visual noise. This manipulation disrupted the homogenous regions corresponding to the eyes and mouth. It also reduced the contrast between the blobs and their background, making them less salient compared to the white dots on a gray oval in Experiment 1. While the joint analysis of the two experiments did not show any difference, a separate analysis of data solely from Experiment 5 showed only a minor tendency for FDAE. This might be the result of the reduced contrast between the internal elements and their background. Higher-level areas of the human visual cortex show less sensitivity to contrast changes then lower level ones, and this is trend is more pronounced for faces than objects (Avidan et al., 2002). On the other hand, contrast strength has been shown to affect the FDAE, as high-contrast faces evoke stronger aftereffects than low-contrast ones (Yamashita et al., 2005). Therefore, our results may reflect certain contrast sensitivity of the adaptation sites underlying the FDAE, although the origin of this effect remains to be explored.

Finally, there are some important issues worth considering. First, we observed that participants tended to perceive test faces to be more expanded than contracted. As can be seen in **Figure 2** of Experiment 1, at 0% distortion, the percentage of contracted ratings remained below 50% even in the expanded adaptor condition. While the source of this effect is not clear, one factor that might have contributed to this effect is the asymmetrical sensitivity to different directions of distortion. Previous studies investigating the sensitivity to changes affecting facial configuration have shown that people are more sensitive to inwards than outwards shifts of the eyes (Haig, 1984; Kemp et al., 1990). This might have counteracted the aftereffect to the extent that the veridical face was more often reported as "expanded" than "contracted."

A further question to be addressed is whether the aftereffects in the present study are comparable in strength to the aftereffects obtained by real face adaptors. Although the present study only employed schematic face-like adaptors, the stimulus material partially (the Angelina Jolie face-line was used in both studies) overlapped with a previous study of our lab

(Zimmer and Kovács, 2011a). The comparison of results (see Figure 2 of Zimmer and Kovács, 2011a) shows that the aftereffects evoked by schematic adaptors are smaller in magnitude than the ones observed with real face adaptors (note however, that the methodological differences, such as the slightly shorter adaptation duration of the present study, limit the validity of this comparison). This difference suggests that besides configural processing, the adaptation of neural pools engaged in feature encoding also contributes to the FDAEs observed with real face adaptors.

In summary, we found that FDAE s can be evoked by adaptation to stimuli that only retain the basic configuration of a real face: three dots in the location of the eyes and the mouth, embedded in an oval. Aftereffects were also observed when the adaptor and test faces differed in size, suggesting that the perceptual bias depends at least in part on the adaptation of higher-level neural populations. However, with adaptors turned upside-down, we did not observe any aftereffects, which might be due to the disruption of face-specific configural coding. The aftereffects did not depend on the contrast polarity of the adaptor image either. On the other hand, replacing these elements with blobs consisting of visual noise reduced the aftereffects, which might be the consequence of the low-contrast of the elements. Thus, while the adaptation sites seem to be engaged in the coding of facial configuration independently of contrast polarity, they also appear to be sensitive to contrast manipulations affecting the saliency of the inner elements to a certain degree.

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Adaptation to antifaces and the perception of correct famous identity in an average face

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Previous experiments have examined exposure to anti-identities (faces that possess traits opposite to an identity through a population average), finding that exposure to antifaces enhances recognition of the plus-identity images. Here we examine adaptation to antifaces using famous female celebrities. We demonstrate: that exposure to a color and shape transformed antiface of a celebrity increases the likelihood of perceiving the identity from which the antiface was manufactured in a composite face and that the effect shows size invariance (experiment 1), equivalent effects are seen in internet and laboratory-based studies (experiment 2), adaptation to shape-only antifaces has stronger effects on identity recognition than adaptation to color-only antifaces (experiment 3), and exposure to male versions of the antifaces does not influence the perception of female faces (experiment 4). Across these studies we found an effect of order where aftereffects were more pronounced in early than later trials. Overall, our studies delineate several aspects of identity aftereffects and support the proposal that identity is coded relative to other faces with special reference to a relatively sex-specific mean face representation.

Keywords: aftereffects, adaptation, recognition, experience, face processing, prototypes, categories

INTRODUCTION

For each class of stimuli that the human visual system encounters, it may develop an individual representation, or prototype, made up of an average of the characteristics of all the different stimuli of that type that have been seen (Valentine, 1991; Enquist and Arak, 1994; Johnstone, 1994; Giese and Leopold, 2005; Loffler et al., 2005). Computer modeling has revealed that algorithms trained to discriminate different stimuli produce the strongest responses to stimuli that represent the average of the training set, even though this average was not previously encountered (Enquist and Arak, 1994; Johnstone, 1994). These findings have been interpreted as evidence that prototype formation is a property of learning to recognize different stimuli as members of a class (Enquist and Arak, 1994; Johnstone, 1994). Learning studies have examined how categorical perception develops using abstract stimuli. In classic studies it has been shown that exposure to different dot patterns with particular configurations results in abstraction so that the average of each of the patterns, while never previously seen, is recognized as belonging to the set of patterns from which it was derived (Posner and Keele, 1968). These results were originally taken as evidence for prototype formation, but there is much debate about whether it does represent abstraction of a prototype or whether people store individual exemplars and use these to determine category (Nosofsky and Zaki, 2002; Smith and Minda, 2002; Ashby and Maddox, 2005).

Faces have been the focus of much research regarding recognition and possible prototype formation. The notion of a multidimensional "face space" has proved extremely useful in helping to understand how faces are mentally represented (Valentine, 1991). In face space, each individual face is a point in a space with a theoretical average of all faces at the center. Individual faces lie on trajectories or vectors and caricatures move them outwards, away from the center of the distribution, while anti-caricatures move the face toward the center. Caricatures move away from average and so make faces more distinctive and recognized more quickly than veridical original identities (Rhodes et al., 1987; Benson and Perrett, 1994). Such studies were interpreted as evidence that the average face played a special role representing face identity (e.g., Benson and Perrett, 1994), a "prototype" model of face coding. Many researchers have thought that a prototype face could function as a norm that anchors coding of identity (Valentine, 1991; Leopold et al., 2001). Of course, this idea has been debated, with some researchers rejecting the view that an average face plays a special role and supporting instead the view that faces may be coded more directly as veridical representations of individuals or exemplars, an "exemplar" model (Valentine, 1991).

Studies of face adaptation to identity have been taken as evidence for a prototype model. Exposure to faces (i.e., adaptation) biases subsequent perceptions of novel faces by causing faces similar to those initially viewed to appear more prototypical (i.e., normal) than they would otherwise be perceived, reflecting the recalibration of a prototype in light of recent visual experience (Leopold et al., 2001, 2005; Rhodes et al., 2001, 2003, 2004; Webster et al., 2004; see Webster and MacLeod, 2011 for review). We note that in these studies it is also plausible that a population of exemplars becomes updated. In adaptation studies, for example, adaptation (exposure) to faces with contracted features causes novel faces with contracted features to be perceived as more normal than prior to this exposure (Rhodes et al., 2003, 2004). Analogous visual aftereffects have been observed following exposure to faces varying in identity (Leopold et al., 2001; Rhodes et al., 2001), ethnicity (Webster et al., 2004), sex (Rhodes et al., 2004; Webster et al., 2004), expression (Webster et al., 2004), and sexual dimorphism (Little et al., 2005; Buckingham et al., 2006).

While these findings might be consistent with an exemplar view, an adaptation study by Leopold et al. (2001) has shown evidence more in favor of prototype views. The researchers made use of "antifaces" for particular identities. Antifaces lie on the same vector as the original identity but exist in the other side of the average face and therefore have the appearance of a face possessing the opposite traits of the original face. For example, an antiface for an identity with a bigger-than-average nose would be a face that had a smaller-than-average nose. To compare, a caricature would have a larger nose than the original and an anti-caricature would have a nose somewhere between the original and average. Leopold et al. (2001) found that identification of a particular identity (e.g., Jim) was made easier by adapting to the antiface (AntiJim), but not to other antifaces. This finding has been replicated in later studies using similar methods (Leopold et al., 2005) and using entirely computer generated images faces (Anderson and Wilson, 2005). As adaptation biases perception along an identity trajectory away from the adapting stimulus, the antiface effects in these studies strongly suggest the average face defines such a trajectory. Importantly for this interpretation, the aftereffect must be selective for computationally opposite identities and not be a generalized contrast effect. This is possible if the non-opposite adapting faces were more similar to the test or probe faces than were the opposite adapting faces and so adaptation to non-opposite faces could lead to a general facilitation in any direction of face space rather than along a particular direction due to differences in perceptual contrast (Rhodes and Jeffery, 2006). Rhodes and Jeffery (2006) measured the face identity aftereffect for computationally opposite and non-opposite adapt-test pairs that had been matched on perceived dissimilarity to control for this confound and found similar results to previous studies, supporting a special role for the average face. Interestingly, the authors also suggest a model of coding that allows individuating information to be coded as deviations from average or prototype without an explicitly mentally represented average (Rhodes and Jeffery, 2006).

Recent neuroimaging and single-cell recording studies have also supported a prototype-referenced model of face coding (Giese and Leopold, 2005; Loffler et al., 2005). For example, neuroimaging of humans during adaptation to facial identities has shown that specific neural populations respond to faces falling along specific identity axes away from an average (Loffler et al., 2005) and similar results are seen whereby neurons in the macaque brain represent deviations from average (Giese and Leopold, 2005). Further experimental evidence comes from a recent study by Ross et al. (2010), which shows a decreased sensitivity to changes along the axis between a face and the average (caricature/anti-caricature) compared with equivalent sized changes in a different direction (lateral caricatures). This suggests that there is something special about the position of the average face and the axis between it and a given face.

Previous studies have examined the time-course of identity adaptation to elucidate the phenomenon, such as the effect of adaptation duration (Leopold et al., 2005). Here we examine effects of the nature of the stimuli used. The current studies investigated whether adaptation to antifaces made from famous female celebrities resulted in accurate perception of identity in a neutral face (experiment 1A) and whether this effect held true across size transformations (experiment 1B). We additionally compared internet and laboratory-based experiments (experiment 2) and also tested for independent contributions of color and shape information to identity aftereffects (experiments 3A and 3B). It has been shown that adaptation to eye-spacing, face shape, and sexual dimorphism can influence the perception of male and female faces in different directions simultaneously for judgments of both normality and attractiveness (Little et al., 2005), suggesting that faces are coded relative to a sex-specific norm (see also Bestelmeyer et al., 2008; Jaquet and Rhodes, 2008). Other studies have shown that face identity aftereffects for newly learned faces, as measured by recognition after exposure to antifaces, were significantly larger for pairs using an opposite generated from a same-sex average than an opposite generated from an androgynous average, suggesting identity is coded relative to a sex-specific norm (Rhodes et al., 2011). Thus, we also examined whether adaptation to male versions of female antifaces can influence the perception of female faces (experiment 4). Across all of the experiments we examined the effects of trial order because pilot studies conducted by the first and second author suggested adaptation to antifaces had greatest influence on recognition in early trials.

Previous studies of identity adaptation have tested the threshold for recognition of a newly learned face by presenting a series of anti-caricatures of varying strengths. Using this technique, for example, Rhodes and Jeffery (2006) found a change in threshold (50% correct identification) from 55.4% of the distance from average to target face to 43.5%. Two key differences here are that we are using famous faces, for which most of our participants should have a well-established representation, and that we present only the average face for testing. This type of test therefore has no inherent cues to the identity of the target and is a stronger test of the ability of adaptation to produce identification. Previous studies addressing identity adaptation use newly learned faces, faces learned under the same experimental conditions as the adaptation tests are carried out. By using famous faces we bypass any potential effects of learning/test congruence and examine a more natural form of familiarity. Such demonstrations are clearly important if identity adaptation effects are to have real-world validity.

EXPERIMENTS 1A AND 1B

We examined the influence of adaptation to antifaces for female celebrity images and subsequent perception of identity in a neutral probe (experiment 1A/B). Previous studies address newly learned faces and here we examine faces with which participants are likely to have longer term familiarity. Following previous studies, we examined the influence of changing size in the probe stimuli (experiment 1B) to examine the extent such aftereffects reflect adaptation of higher-level neural mechanisms (Leopold et al., 2001). Adaptation was tested by presenting participants with an "antiface," the opposite shape and color of a particular identity for 6 s, followed by a neutral average face for 1 s. Participants were then presented with the names of two identities, one correct and one incorrect, and asked to indicate which name the second face they saw most resembled. Following previous studies, we predicted that exposure to antifaces would result in an aftereffect such that a neutral face would resemble the real identity, leading to correct identification.

PARTICIPANTS

Participants in experiment 1A were 15 women and 17 men (mean age = 23.0, SD = 4.5). Participants in experiment 1B were 30 women and 9 men (mean age = 33.8, SD = 13.2). Different participants took part in each experiment. All participants were volunteers and were selected for being between the ages of 16–65 and being UK or US nationals to help ensure familiarity with the celebrity faces. The study was run over the internet and participants were recruited via a link from a research based website (www.alittlelab.com).

STIMULI

All stimuli were constructed using established (Perrett et al., 1998; Little et al., 2001, 2005) techniques for averaging and manipulating the appearance of face images in an objective, systematic manner (for technical details including mathematical algorithms see Benson and Perrett, 1993; Rowland and Perrett, 1995; Tiddeman et al., 2001).

First we created 20 composite female celebrity images. Ten images each of 20 female celebrities were collected and a composite image created for each. Composites were made by manually marking 179 feature landmark points on all faces delineating the main features (e.g., points outline, eyes, nose, and mouth) and the outline of each face (e.g., jaw line, hair line). The average location of each point on the faces for each individual composite was then calculated. The features of the individual faces were then morphed to the relevant average shape before superimposing the images to produce a photographic quality result average in both shape and color. Examples of individual composites can be seen in **Figure 1**. We created an average female celebrity image to act as the center of our feature space and this was done by averaging all 20 individual composite faces into a single image as described above. All images were symmetrized and standardized for size on interpupillary distance prior to transformation.

Antiface images were created by transforming the average female composite relative to a pair of face images specific to each identity: the individual celebrity composite image and the average female composite (see **Figure 1**). For example, using the difference between the composite Jennifer Aniston and the average composite we can compute a face that lies on the mirror opposite – an anti-100% face (see **Figure 2**: right hand panel). This procedure for manipulating faces through the mean is methodologically similar to that used in previous studies (Leopold et al., 2001).

Antifaces were used as adapting stimuli in the trials and the same average celebrity face was used as the probe in the trials. All images were resized to 360 × 496 pixels and an additional probe face was created at 70% of this size for use in experiment 1B.

PROCEDURE

Participants first filled in a short questionnaire addressing their age, sex, and nationality. They were then presented with the

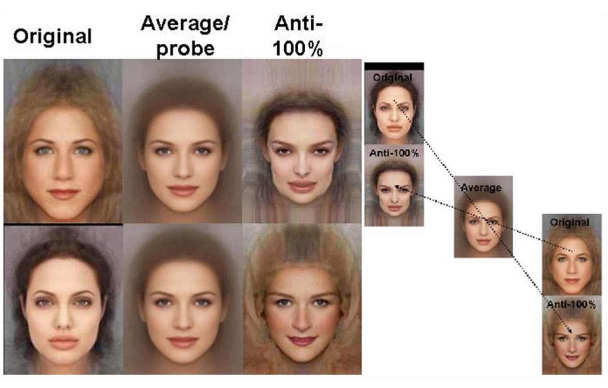

FIGURE 1 | Left: Examples of composite celebrity images (Jennifer Aniston and Angelina Jolie), anti-100% faces used as adapting stimuli, and the average female celebrity composite used as a probe face. Antifaces are created by transforming the original face through the average face in both shape and color. Right: Schematic example of face space showing antifaces "on the other side of the mean." Arrows designate direction of transform.

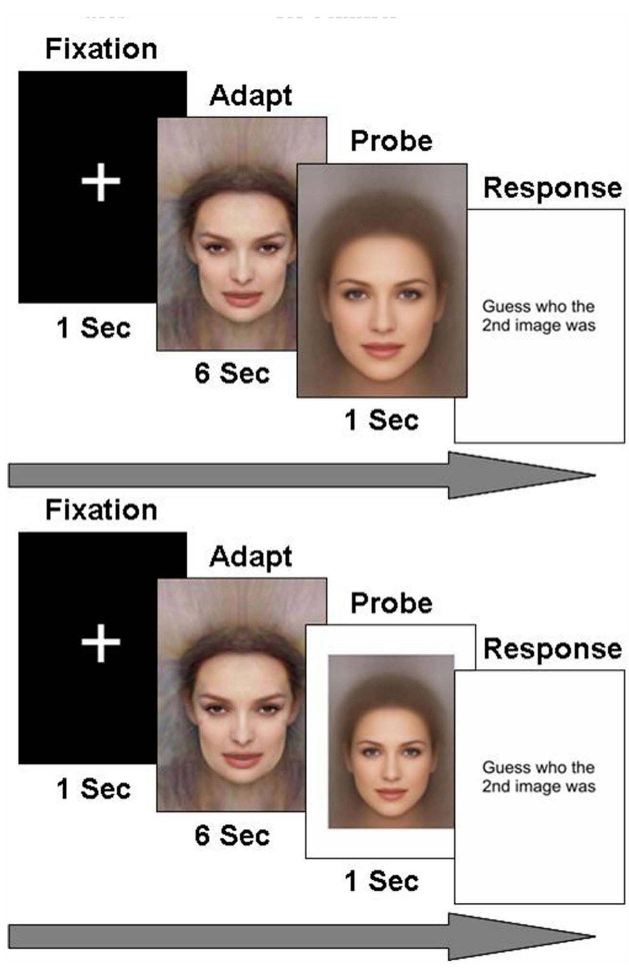

FIGURE 2 | Trial structure for full-size images (top) and 70% size images (bottom) as probe faces. The antiface for Jennifer Aniston is used here.

following instruction: "In this study you will see faces and be asked to guess which celebrity is hidden within the images. You will be presented with a fixation image (a white cross on a black background) followed by a face. Please stare at this face. After a few seconds it will disappear and a new face will appear briefly. You will then be asked to name which celebrity the second face looks like. The second face will look very similar each time and you may feel like you do not know who it looks like. Please guess anyway. Guessing will move you onto the next trial."

Each trial consisted of a fixation image presented for 1 s, an adapting antiface image for 6 s, the probe trial composite female image for 1 s, and finally the response image which asked participants to guess the celebrity (see **Figure 2**). Underneath the response image two celebrity names were presented as buttons. One name corresponded to the correct celebrity antiface and the other a random other name from the set. Names were paired such that, for example, names A and B when used as a pair were preceded once by antiface A and once by antiface B. Button order was randomized by side. Participants selected the name from the two alternatives which started the next trial. Trial order was randomized for each participant.

After the adaptation trials, participants were presented with the 20 original celebrity averages, for a recognition test. The recognition test composed of the unmanipulated composite of each celebrity and their name for which participants were asked "do you recognize this face?" with boxes presented alongside marked "yes" and "no." This test was presented on a single page and the faces presented in alphabetical order of surname.

RESULTS

We calculated percent of correct answers counting correct answers for only those trials for which the participant subsequently stated they recognized both of the celebrities for the appropriate trial. We also used scores that included all the answers given irrespective of stated recognition. We used these latter measures to calculate the correlation for each participant between order of trial and correct answers and average accuracy for the first 10 trials vs. the last 10 trials as measures of relative accuracy between the start and end of the test.

Recognition rates across experiments 1A and 1B in the post-test were very high with an average of 94% (SD = 14.9) of faces used in the test being recognized in their unaltered form. All tests are presented two-tailed.

Identity was recognized at rates greater than chance in both experiments. One-sample t-tests against chance (50%) revealed that participants showed correct recognition of identity in experiment 1A [$t(31) = 2.75$, $p = 0.010$] and experiment 1B [$t(38) = 2.37$, $p = 0.023$]. An independent samples t-test revealed no significant difference in accuracy between experiments 1A and 1B [$t(67) = 0.82$, $p = 0.415$]. Means can be seen in **Figure 3**.

Additional tests demonstrated that there was a weak effect of order such that accuracy was higher for earlier than later trials. One-sample t-tests against chance (0 = no correlation) revealed significant negative correlations between trial order and correct responses for both full size [mean $r = -0.12$, SD = 0.28, $t(31) = 2.46$, $p = 0.019$] and 70% [mean $r = -0.08$, SD = 0.23, $t(38) = 2.31$, $p = 0.027$] images. Paired samples t-tests revealed

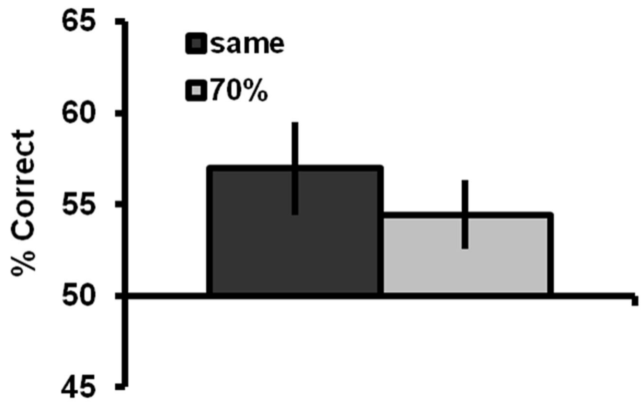

FIGURE 3 | Correct responses (as %, ±1 SEM) for experiments 1A (same-sized probe) and 1B (70% sized probe).

that participants were more accurate for the first 10 trials than the second 10 trials for both the full-size images [first 10: mean = 61.3%, SD = 19.8; second 10: mean = 49.1%, SD = 17.1; $t(31) = 2.63$, $p = 0.013$] and the 70% size images [first 10: mean = 57.7%, SD = 16.3; second 10: mean = 51.0%, SD = 16.6; $t(38) = 1.86$, $p = 0.071$], though for the latter comparison the p-value was only approaching significance.

DISCUSSION

Experiment 1A replicates identity aftereffects using famous faces rather than identities learned for the study. Experiment 1B also replicates scaling invariance of identity aftereffects using famous faces. As noted by others, it is possible that perception of correct identity after exposure to antifaces could be explained by several low-level aftereffects for orientation, spatial frequency, and color (Leopold et al., 2001). Following Leopold et al. (2001), we also note that such low-level adaptation appears unlikely, as individuals were free to scan the adapting images, which continually varies the retinal locations of the various facial features and such effects were not significantly influenced by a decrease in the size of the probe image. Robustness to changes in size is most consistent with identity aftereffects being related to higher-level adaptation, as noted by several previous authors (e.g., Leopold et al., 2001).

We also found consistent effects of order of trial such that aftereffects resulted in accurate perceptions of identity for early trials and less so for later trials. This finding is considered further in the general discussion.

EXPERIMENT 2

Experiments 1A and 1B were conducted over the internet. To address the validity of web-based tests of adaptation we replicated experiment 1A under laboratory conditions.

PARTICIPANTS

Participants in experiment 2 were 13 women and 11 men (mean age = 27.5, SD = 10.9). All participants were volunteers and were selected for being between the ages of 16–65 and being UK or US nationals to help ensure familiarity with the celebrity faces. The study was run under laboratory conditions.

STIMULI

Stimuli were identical to those used in experiment 1A.

PROCEDURE

The procedure was identical to experiment 1A except that the experiment was taken under laboratory conditions. The laboratory testing took place on one of two identical computers in the same laboratory. Images were presented on a 32-bit color 21″ (1280 × 1024 pixels) LCD monitor. Stimuli subtended approximately 9° × 12.4° of visual angle when viewed by participants approximately 80 cm from the computer screen.

RESULTS

Recognition rates for experiment 2 in the post-test were high with an average of 98% (SD = 5.5) of faces used in the test being recognized in their unaltered form.

Identity was recognized at rates greater than chance in experiment 2 and no difference in effect was found between experiments 1A and 2. A one-sample t-test against chance (50%) revealed that participants showed correct recognition of identity in experiment 2 [$t(23) = 2.50$, $p = 0.020$]. An independent samples t-test revealed no significant difference in accuracy between experiments 2 and 1A [$t(54) = 0.19$, $p = 0.954$]. Means can be seen in **Figure 4**.

An additional independent samples t-test revealed a significant difference in recognition rates between experiments 2 and 1A [$t(54) = 2.08$, $p = 0.042$]. Individuals recognized more of the celebrities under laboratory conditions, though this cannot influence accuracy as only trials in which participants recognized both celebrities were used to calculate accuracy.

Additional tests demonstrated that there was a weak effect of order such that accuracy was higher for earlier than later trials. A one-sample t-test against chance (0 = no correlation) revealed a close to significant negative correlation between trial order and correct responses [mean $r = -0.10$, SD = 0.25, $t(23) = 1.94$, $p = 0.065$]. A paired samples t-test revealed that participants were more accurate for the first 10 trials than the second 10 trials [first 10: mean = 63.3%, SD = 19.5; second 10: mean = 52.1%, SD = 18.9; $t(23) = 2.30$, $p = 0.031$].

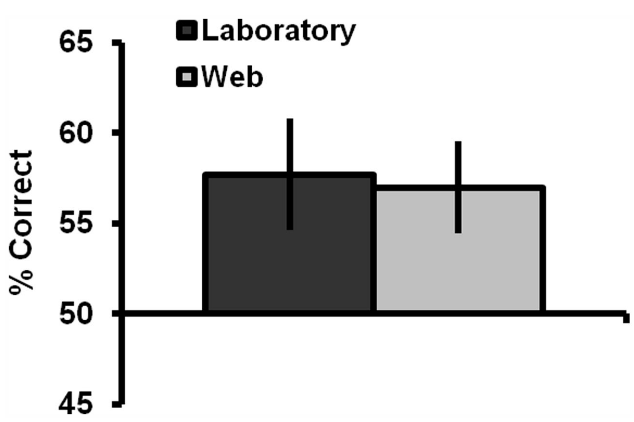

FIGURE 4 | Correct responses (as %, ±1 SEM) for trials where the test was conducted in the laboratory (experiment 2) or over the web (experiment 1A).

DISCUSSION

Experiment 2 replicated the findings of experiment 1A under laboratory conditions. While there was evidence that participants recognized more celebrities in the laboratory (90 vs. 98%) the size of the effect of adaptation on accuracy (correct recognition) was almost identical. Likewise, order effects were of almost equivalent magnitude in experiment 2 as in experiment 1A. Experiment 2 then demonstrates equivalency in results based on web-based and laboratory-based adaptation studies of this kind. We note that while individuals may intuitively feel that data collected in the absence of an experimenter may produce more variable results, there is growing evidence that adaptation effects seen under laboratory conditions are also seen in web-based studies (Jones et al., 2008, 2010). Our experiment here demonstrates that the same effect is seen in experiments 1 and 2 despite difference in recruitment, presence of experimenter, and variation in equipment.

EXPERIMENTS 3A AND 3B

Previous studies of identity aftereffects have simultaneously manipulated both shape and color information in face images when manufacturing adapting stimuli. By contrast, here we examined the independent contributions of shape and color in identity aftereffects.

PARTICIPANTS

Participants in experiment 3A (shape only) were 15 women and 7 men (mean age = 27.5, SD = 13.1). Participants in experiment 3B (color only) were 24 women and 8 men (mean age = 29.4, SD = 9.2). Different participants took part in each experiment. Participants were selected as for experiments 1A and 1B. The study was run over the internet and participants were recruited via a link from a research based website (www.alittlelab.com).

STIMULI

Stimuli were made in the same way as in experiments 1A and 1B, but here transformations were anti-100% in shape only or anti-100% in color only. Example images can be seen in **Figure 5**.

PROCEDURE

The procedure was identical to that used in experiment 1A. Participants were randomly allocated to a condition where they saw shape-only or color-only antifaces.

RESULTS

We calculated percent of correct answers as in experiments 1A and 1B. Recognition rates across 3A and 3B in the post-test were again very high with an average of 93.0% (SD = 12.6) of faces recognized.

Identity was recognized at rates greater than chance for shape adaptation in experiment 3A but not for color adaptation in experiment 3B. One-sample t-tests against chance (50%) revealed that participants showed significant recognition of identity for experiment 3A [shape only, $t(21) = 2.81$, $p = 0.010$] but not for experiment 3B [color only, $t(31) = -1.22$, $p = 0.230$]. An independent samples t-test revealed a significant difference in accuracy between experiments 2A and 2B [$t(52) = 2.99$, $p = 0.004$]. Means can be seen in **Figure 6**.

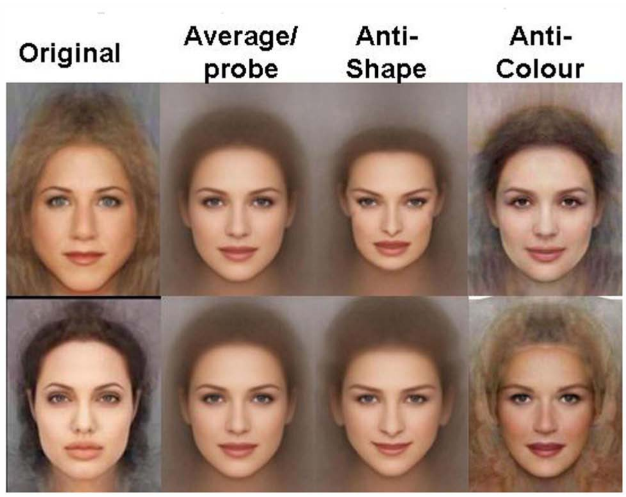

FIGURE 5 | Examples of composite celebrity images (Jennifer Aniston and Angelina Jolie), anti-100% faces used as adapting stimuli, and the average female celebrity composite used as a probe face. Antifaces are created by transforming the original face through the average face in either shape or color.

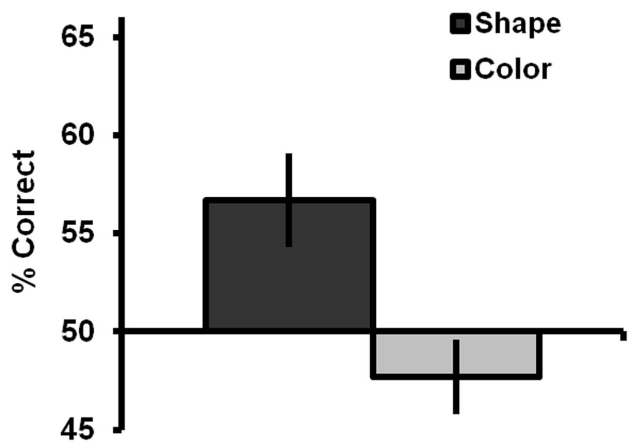

FIGURE 6 | Correct responses (as %, ±1 SEM) for trials where the adapting image was transformed in shape only (experiment 2A) or the adapting image was transformed in color only (experiment 2B).

Additional tests demonstrated that there was a weak effect of order such that accuracy was higher for earlier than later trials, though this effect was weaker in the color-only condition. One-sample t-tests against chance (0 = no correlation) revealed negative correlations between trial order and correct responses for both shape-only [mean $r = -0.10$, SD = 0.20, $t(21) = 2.30$, $p = 0.032$] and color-only [mean $r = -0.08$, SD = 0.24, $t(31) = 1.79$, $p = 0.084$] adapting images, though this was significant for the first and only tending toward significance for the second. Paired samples t-test revealed that participants were more accurate for the first 10 trials than the second 10 trials for the shape-only images [first 10: mean = 61.8%, SD = 15.9; second 10: mean = 51.4%, SD = 13.9; $t(21) = 2.47$, $p = 0.022$] but not for the color-only images [first 10: mean = 51.3%, SD = 17.0; second 10: mean = 44.4%, SD = 16.1; $t(31) = 1.60$, $p = 0.119$].

DISCUSSION

Experiments 3A and 3B demonstrated that shape rather than color is mainly responsible for accurate identification after exposure to antifaces. This finding supports previous studies suggesting that objects may be encoded primarily in terms of their luminance-defined bounding edge structure (see Biederman, 1987) and research on faces demonstrating that observers are able to recognize familiar faces that have been hue-reversed at levels equivalent to normal-hued faces (Kemp et al., 1996). Faces generally have similar spectral properties and observed face color can change dramatically under different lighting conditions. As color may be unreliable across time, it is logical for the visual system not to rely on color as a diagnostic cue of identity. Some studies have found a role for color in identity recognition. Lee and Perrett (1997) found recognition accuracy for famous faces was greater when viewing color caricatured stimuli over veridical images and that the removal of color information also decreased accuracy of recognition. Color here then facilitates recognition when the face is already a recognizable identity and perhaps that is key to finding the color effect. In Lee and Perrett's study the faces already possess the correct celebrity shape and so the face is in the correct area of face space. Potentially only when the face has some other cues to identity may color aid recognition in ambiguous tasks. Another study has shown that the contribution of color cues becomes evident when shape cues are degraded and that the contribution of color may lie not in providing cues to identity but in aiding low-level processes (Yip and Sinha, 2002). Other studies, however, have highlighted the use of color in face recognition (Russell and Sinha, 2007). As face adaptation effects are proposed to reflect high-level processes then again it makes sense that color cues play a smaller role. That said, as the color images demonstrate the same order effect as the shape images then some similarities in the processes may be evident, though we note such effects are weak for color. We also note that color may be less important than shape cues if our faces are relatively homogeneous in their color cues but are more variable in shape.

EXPERIMENT 4

Here we examined the effects of using male versions of adapting stimuli. Previous studies have shown that face aftereffects can be simultaneously produced in opposite directions in male and female faces (Little et al., 2005), suggesting that faces are coded relative to a same-sex norm, rather than a sex-neutral norm. Sex-specific effects of adaptation are also seen for identity for newly learned faces (Rhodes et al., 2011). Here we predicted that if adaptation to male faces has a limited influence on female face perception then adapting to anti-male faces that share the same properties of their anti-female face counterparts will not induce accurate perceptions of identity in the same way as the anti-female faces.

PARTICIPANTS

Participants in experiment 4 (male adapting face) were 31 women and 17 men (mean age = 30.4, SD = 10.2). Participants were selected as for experiments 1A and 1B. The study was run over the internet and participants were recruited via a link from a research based website (www.alittlelab.com).

STIMULI

Stimuli were made in the same way as in experiments 1A and 1B but here transformations were made against a composite androgynous celebrity image instead of the female composite and applied to the androgynous composite. This androgynous image was made by combining the female composite with a male equivalent made in the same way as the female image, from 20 individual composites of male celebrities each made from 10 different images. As before, this image was aligned and made symmetric prior to transform. Transforms were anti-100% in shape and color and each antiface contains the shape information apparent in the antifaces made through the female average. Moving through an androgynous shape means the antifaces also exhibit a level of apparent maleness akin and opposite to the femaleness of the individual celebrity. Example images can be seen in **Figure 7**.

PROCEDURE

The procedure was identical to that used in experiment 1A.

RESULTS

Recognition rates in experiment 4 in the post-test were again very high with an average of 94.4% (SD = 14.3) of faces recognized.

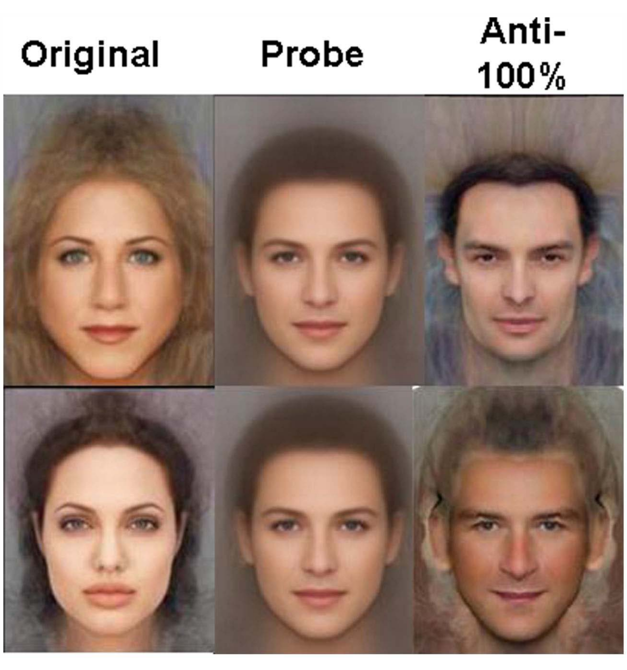

FIGURE 7 | Examples of composite celebrity images (Jennifer Aniston and Angelina Jolie), the androgynous celebrity composite used for transforming and as a probe face, and male versions of the antifaces used as adapting stimuli. Antifaces here are created by transforming the original face through the androgynous average face – 100%.

Identity was not recognized at rates greater than chance when adaptaing across sex of face and the effect was significantly different from that seen for same-sex faces in experiment 1A. A one-sample t-test against chance (50%) revealed that participants did not show correct recognition of identity in experiment 4 [$t(47) = -0.70$, $p = 0.489$]. We compared the accuracy scores with those from experiment 1A and an independent samples t-test revealed that sex of adapting face (female vs. male) significantly influenced accuracy [$t(78) = 2.64$, $p = 0.010$]. Means can be seen in **Figure 8**.

Additional tests demonstrated that there was no effect of order on accuracy when male faces were used as adapting stimuli. A one-sample t-test against chance (0 = no correlation) revealed no significant negative correlations between trial order and correct responses for male adapting antifaces [mean $r = -0.04$, SD = 0.25, $t(47) = 1.12$, $p = 0.269$]. A paired samples t-test revealed that participants were not more accurate for the first 10 trials than the second 10 trials for both the full-size images [first 10: mean = 50.8%, SD = 18.8; second 10: mean = 47.1%, SD = 15.3; $t(47) = 1.03$, $p = 0.310$].

DISCUSSION

Experiment 4 demonstrated that transformations through an androgynous prototype, creating a male adapting face with the opposite shape and color characteristics, resulted in no accurate aftereffects for identity. Accuracy when using a male adapting face result was significantly worse than when using a female despite the fact that, bar the masculine appearance, shape and color information was the same between the two types of adapting antiface. Theoretically, like the female antifaces, adaptation should have resulted in perception of the correct identity following the correct trajectory through the average. Unlike the previous experiments, order had no influence on accuracy for male adapting images suggesting that identity aftereffects are specific to congruent-sex faces.

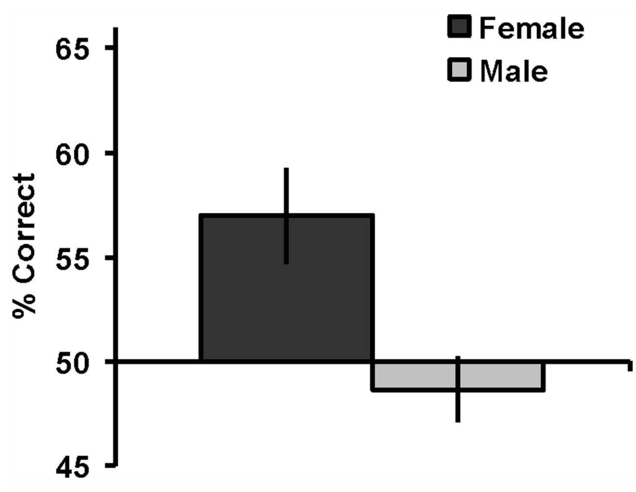

FIGURE 8 | Correct responses (as %, ±1 SEM) where adapting image was female and the probe the average female (data from experiment 1A) and where the adapting image was male and the probe image was androgynous (data from experiment 4).

Sex congruency in facial aftereffects is consistent with previous studies that have demonstrated that adaptation effects can be separable by sex of face such that the perception of males and females can be pushed in opposite directions (Little et al., 2005; Bestelmeyer et al., 2008) and other studies showing identity aftereffects are greater for newly learned faces when same-sex faces are used in the pairs (Rhodes et al., 2011). Such sex-specific effects are consistent with the idea that, rather than comparing faces with a single prototypic face, observers have separable representations of male and female faces, which would allow such separable manipulation. Our findings here also support this notion as adaptation to antifaces does not result in accurate perception when using a non-congruently sexed face.

GENERAL DISCUSSION

Our data add to a burgeoning literature showing that exposure to faces biases subsequent perceptions of novel faces (Leopold et al., 2001, 2005; Rhodes et al., 2001, 2003, 2004; Webster et al., 2004; Little et al., 2005, 2008; Buckingham et al., 2006; Bestelmeyer et al., 2008). The main finding across our studies was that adaptation to an antiface could make the same neutral average face appear to possess new identities specific to the identity of the antiface along a particular trajectory in face space (experiments 1–3). Such data strongly implies that the average face plays a special role in recognition of identity, supporting prototype referencing models of face recognition (see also Leopold et al., 2001, 2005; Rhodes and Jeffery, 2006). As noted earlier, this does not necessarily imply the prototype is explicitly mentally represented – the encoding of faces could involve contrastive neural mechanisms that reference the central tendency of the stimulus category (Rhodes and Jeffery, 2006). Such data also supports computer modeling studies suggesting prototype abstraction is a consequence of discrimination learning (Enquist and Arak, 1994; Johnstone, 1994). While the majority of the experiments presented here were web-based, our experiment 2 demonstrates the equivalency of results from web- and laboratory-based testing for this type adaptation experiment.

We found that shape information was of greater importance than color in coding face identity (experiments 3A and 3B). This is consistent with previous studies suggesting color is not crucial in recognizing objects (Biederman, 1987) or faces (Kemp et al., 1996) and that face color can change quickly. Of course, while adaptation here appears reliant on shape (possibly because the color cues alone do not allow the face to be disambiguated from other similarly colored identities which share the same color properties), color may help identify faces when presented alongside shape cues to identity (Lee and Perrett, 1997). Indeed some studies do find that color plays an important role in face recognition (Russell and Sinha, 2007).

Previous studies have shown category contingent aftereffects whereby exposure can influence different categories in different ways simultaneously suggesting separable representation (Little et al., 2005, 2008; Bestelmeyer et al., 2008). The results of experiment 4 support the notion that humans have distinct representations for male and female faces as we were unable to influence the perception of female faces in the correct direction with adaptation to a male face with the same antishape as an equivalent female antiface and are consistent with similar effects seen for newly learned faces (Rhodes et al., 2011). One study has demonstrated that adaptation to some aspects of visual appearance can cross from male to female faces (Jaquet and Rhodes, 2008). Though our data provide no support for the notion that aftereffects have any influence on perception across the category of sex, if adaptation can cross the category of sex, our results suggest across-sex effects are much weaker than for sex-contingent adaptation. It is commonly conceived that we recognize faces based on deviations from a single average representation within a single population of all faces encountered (Valentine, 1991), while our data and the studies cited above generally support the notion that perhaps we compare or relatively code faces against a specific prototype for each category.

One issue that was apparent across all of our experiments (bar experiment 4, which showed a null effect for adaptation to men's faces) was the effect of order: adaptation to antifaces resulted in accurate perception of identity most strongly for those faces seen early in the trials and less so for faces seen in later trials. One trivial explanation is simple trial fatigue such that individuals paid less attention to later trials. This is an unsatisfactory explanation given the trials were short, as was the overall test, and involved only the choice out of two alternatives. The task itself was also a relatively interesting one. Another explanation, while speculative, is that the order effect might reflect that the malleability we see in face perception after exposure is a finite resource so that repeated exposure to new faces results in weaker influences of later faces. It is possible, for example, that adapting to particular face shapes prevents later adaptation to new faces as the initial adaptation effects persist beyond the probe trials and this carry-over adaptation interferes with later adaptation. Further research is needed to investigate this potentially important issue for our understanding of flexible face processing.

Studies of adaptation also have potential implications for the neural representation of faces. Neural responses to identity are sensitive to differences across identity rather than physically equivalent within-identity changes (Rotshtein et al., 2005) and so the average face may then play an important role in helping categorize identity in terms of defining whether a face is more or less similar to another by defining a trajectory in face space. Indeed, neuroimaging and single-cell recording studies have also supported the notion of a prototype-referenced model of face coding (Giese and Leopold, 2005; Loffler et al., 2005). In future experiments measurement of the neural responses to adaptation to shape and color independently, and the effects of repeated adaptation to different faces will prove enlightening in further understanding the representation of faces. We note that although the results point to the locus of adaptation being mechanisms for coding high-level aspects of faces, further work is also needed to fully rule out lower level explanations/loci. While our data demonstrate the effects of adaptation on identity recognition, adaptation effects are seen for many aspects of face perception including sex and emotion classification as well as overall perceptions of normality. Alongside such effects, adaptation is also clearly relevant to low-level visual properties, such as blur, and there are commonalities in the properties of low and proposed higher-level adaptation effects

(Webster and MacLeod, 2011). Adaptation effects may then be a general feature of face processing applicable at several different levels of mental representation. An additional issue for prototypic mental representations of faces is how such representations are constructed from different views and image sizes. The distinction between low- and high-level adaptation effects and how the human visual system deals with variation in face stimuli in forming mental representations remain interesting avenues for future research.

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Face distortion aftereffects in personally familiar, famous, and unfamiliar faces

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The internal face prototype is thought to be a construction of the average of every previously viewed face (Schwaninger et al., 2003). However, the influence of the most frequently encountered faces (i.e., personally familiar faces) has been generally understated. The current research explored the face distortion aftereffect in unfamiliar, famous, and personally familiar (each subject's parent) faces. Forty-eight adult participants reported whether faces were distorted or not (distorted by shifting the eyes in the vertical axis) of a series of images that included unfamiliar, famous, and personally familiar faces. The number of faces perceived to be "odd" was measured pre- and post-adaptation to the most extreme distortion. Participants were adapted to either an unfamiliar, famous, or personally familiar face. The results indicate that adaptation transferred from unfamiliar faces to personally familiar faces more so than the converse and aftereffects did not transfer from famous faces to unfamiliar faces. These results are indicative of representation differences between unfamiliar, famous, and personally familiar faces, whereby personally familiar faces share representations of both unfamiliar and famous faces.

Keywords: adaptation effects, face distortion aftereffects, face perception, personally familiar versus unfamiliar faces

FACE DISTORTION AFTEREFFECTS IN PERSONALLY FAMILIAR AND UNFAMILIAR FACES

Face aftereffects have been looked at extensively over the past decade since Webster and MacLin's (1999) pioneering study. To date these aftereffects have only been tested using unfamiliar or famous faces (e.g., Zhao and Chubb, 2001; Carbon and Leder, 2005, 2006; Hills et al., 2010b). It has been found that some properties of the face aftereffects change as a function of familiarity (see Jiang et al., 2007). The present research aimed to explore the face distortion aftereffect (FDAE) using stimuli even more familiar to participants than famous people; personally familiar faces. We compared the FDAE in faces of participants' parents with unfamiliar and famous faces to establish whether these highly familiar visual representations were affected in a similar way. A brief overview will be presented highlighting (1) the processes involved during face recognition, (2) the FDAE in unfamiliar and familiar faces, and finally (3) why personally familiar faces are especially important in the study of adaptation effects.

FACE PERCEPTION AND RECOGNITION

Neural substrates found in a wide variety of brain areas are involved in face processing (Taylor et al., 2009) and enable humans an unrivaled expert ability to tell apart the small differences between countless unfamiliar faces even though as a visual pattern they are very similar. For recognition to occur, however, the visual percept needs to be matched to a stored representation in memory (Bruce and Young, 1986). Faces are coded and stored in terms of both their configural and featural information (Cabeza and Kato, 2000; Mondloch et al., 2002; Leder and Carbon, 2006) along with a number of other attributes including name (Bauer, 1984), personality traits (Fiske, 1995), voice (Kriegstein et al., 2005), and emotional responses experienced while perceiving an individual (Leibenluft et al., 2004). How personally familiar one is with a particular face determines how many attributes are stored and how robust the representation is (Burton et al., 1999a). As more attributes are stored with a face, the more brain regions become involved in coding that face (Eger et al., 2005).

In order to recognize a face from different angles (Zhao et al., 2003), different distances (Wallis and Rolls, 1997), and at different times in the day (Chen et al., 2006) it follows that the stored representation must be invariant to these differences (Bruce, 1994). Faces are constantly changing due to factors such as hairstyle, age, facial expression, and weight but regardless of this they are still recognizable even years later (Bahrick et al., 1975). Familiar faces can be recognized from minimal information and even from low quality video images (Burton et al., 1999b). Unfamiliar faces, on the other hand are difficult to recognize even under optimal conditions (Kemp et al., 1997). Invariance to image changes when recognizing familiar faces suggest that their representation involves a more robust and potentially three-dimensional one than the more pictorial representation of unfamiliar faces (Ryu and Chaudhuri, 2006).

Valentine (1991) argued that face recognition is achieved by comparing all faces to a prototype that has formed as an average of all faces perceived over a lifetime (Schwaninger et al., 2003). All faces (both familiar and unfamiliar) are thought to be coded in terms of how far they deviate from this prototype or norm. Norm-based encoding has gained much empirical support over the past decade (Leopold et al., 2001). It is thought that this prototype needs to have both flexibility and stability to cope with the demands that facial recognition requires. It needs to be flexible enough to be able to recognize a face that has not been seen for a while and therefore undergone some changes such as a change in hair style, as well as stable enough to still be able to distinguish one familiar face from another.

THE FACE DISTORTION AFTEREFFECT

Frisby (1979) has argued that adaptation is the psychophysicists' microelectrode as it made it possible to probe neural response properties without the need for direct brain recording. The process has been attributed to sensory neurons becoming excited, with their responses decreasing as they become habituated. If another stimulus is subsequently perceived, perceptual distortions occur, normally causing a contrastive aftereffect. Substantial research into the aftereffects of low-level stimuli, for example orientation perception (Gibson and Radner, 1937), color and contrast perception (Blakemore and Campbell, 1969), and spatial frequency perception (Blakemore and Sutton, 1969), have been well documented. More recently, adaptation has been shown to be helpful in understanding the coding mechanisms for higher-level stimuli such as geometric shapes (Suzuki and Cavanagh, 1998), body shape (Troje et al., 2006), and faces (e.g., Leopold et al., 2001).

Webster and MacLin (1999) conducted a seminal study using faces as adapting and test stimuli. They asked participants to rate unfamiliar faces, both before and after being adapted to a distorted facial image. They found that following adaptation to a distorted face (for example, compressed), the participants perceived undistorted faces to be distorted in the opposite direction (for example, expanded). This is the crux of the FDAE. These aftereffects transferred to other unfamiliar faces and appeared to transfer to inverted faces as well. Given that the aftereffects transferred across stimuli so readily, these authors suggested the aftereffect represented the way in which faces were coded.

Since Webster and MacLin's (1999) study, further evidence for the non-retinotopic and high-level locus for this FDAE has been found. Zhao and Chubb (2001) found that, although FDAEs were stronger when the adaptor and test images were the same size, a significant aftereffect was observed even when one image was four times larger than the other image. This highlights the size-invariance of the FDAE, suggesting that it is a higher-level phenomenon. Yamashita et al. (2005) have shown that the FDAE is resistant to a number of transformations (such as color changes and photographic negation).

Face distortion aftereffects, in unfamiliar and familiar faces, have a number of similarities and differences. Firstly even though recognition of unfamiliar faces is known to be viewpoint dependant while familiar face recognition is viewpoint-invariant (Bruce and Young, 1986) there is a debate on whether FDAEs transfer across viewpoints. Benton et al. (2006) found using unfamiliar faces the FDAE is viewpoint dependant, however (Hills et al., 2008, 2010a) argue that their results show something on the contrary. They found that 44% of the FDAE found by Benton et al. (2006) is actually viewpoint-invariant. In support of a viewpoint-invariant argument, Welling et al. (2009) found adapting to one view of an unfamiliar face with a raised mouth position caused a different view of the same face to be perceived as having a mouth looking lower than it was. After prolonged adaptation, the FDAE is partially viewpoint-independent in unfamiliar faces (Fang et al., 2007). In familiar faces, however, the FDAE is much more viewpoint-independent (Carbon et al., 2007).

Jiang et al. (2007) specifically tested the degree of familiarity that participants' have with a face and the magnitude of the face identity aftereffect (FIAE, that Hills and Lewis, 2012 argue is an analog of the FDAE). Jiang et al. also tested aftereffects following within- and between-viewpoint adaptation. They trained 90 participants on a set of 16 faces to varying degrees of familiarity. Familiarity was manipulated by presenting the images a different number of times and in different viewpoints. Jiang et al. found that the magnitude of adaptation was greater for within-viewpoint adaptation. However, there was still significant adaptation for between-viewpoint adaptation. Moreover, the largest aftereffects were observed for the most familiar faces. Indeed, the difference between the FIAE to same- and different-viewpoint adaptation was smallest for the extremely familiar condition. Similarly, researchers have found that these aftereffects are very short-lived when testing unfamiliar faces, but can last over 24 h in familiar faces (Carbon and Leder, 2005, 2006). Differences in the transfer of aftereffects across viewpoints in familiar and unfamiliar faces have been attributed to differential representations (c.f., Megreya and Burton, 2006; Ryu and Chaudhuri, 2006): the representation of familiar faces is based on viewpoint-invariant coding (potentially three-dimensional), whereas the representation of unfamiliar face is based on pictorial coding (two-dimensional).

The aftereffects transfer across different images of one unfamiliar face to another (Webster and MacLin, 1999) and of one familiar face to another (Carbon et al., 2007). However, these authors have not assessed whether the aftereffects transfer from a familiar face to an unfamiliar face. If the aftereffect does transfer across faces of different levels of familiarity, then this would provide strong evidence for the norm-based coding theories (Leopold et al., 2001) of face memory. This would provide evidence for rapid updating of the face prototype (Carbon and Leder, 2005). However, familiar faces are seen to have a more robust representation and thus should be somewhat impervious to aftereffects caused by adaptation in unfamiliar faces.

PERSONAL FAMILIARITY

Herzmann et al. (2004) studied reaction time, priming, and skin conductance response when participants were presented with personally familiar faces compared to famous and unfamiliar faces. Reaction time responses were faster to personally familiar and famous faces than unfamiliar faces and the skin conductance response was greater for the familiar faces than unfamiliar faces. Additionally, personally familiar faces produced similar cognitive effects to famous faces. The similar results between personally familiar and famous faces could be due to how familiar the personally familiar faces were. The stimuli they used were university lecturers which could be argued do not represent the personally familiar category as well as perhaps parents or siblings would. It is unclear, whether personally familiar faces would produce different aftereffects to familiar faces.

There is some evidence from brain imaging to suggest that personally familiar faces are represented differently to other classes of familiar faces. Taylor et al. (2009) has found that the neurological response to personally familiar, famous, and unfamiliar faces is indeed different. The presentation of personally familiar faces activated more regions of the brain than unfamiliar faces. Presenting images of the participants' parents caused a bilateralized activation of the cingulate gyrus, generally thought to be a multimodal processor (Turak et al., 2002). It is presumed to play a role in the integration of incoming sensory information perceived from the face (Devue and Brédart, 2007). While fewer brain regions were recruited for the processing of unfamiliar and famous faces than personally familiar faces, there were also some clear distinctions in the recruitment of the Fusiform Face Area (FFA; an area of the brain thought to be involved primarily with face perception). Taylor et al. found that personally familiar faces recruited the FFA bilaterally, whereas famous faces only activated the right-FFA. The processing of unfamiliar faces, on the other hand, appeared to recruit primarily the left hemisphere. Eger et al. (2005) have found similar results: greater response in the right-FFA when comparing famous faces with unfamiliar faces. In addition, famous faces cause greater adaptation in the FFA than unfamiliar faces. These results indicate that the FFA may be the locus for the FDAE and is likely to produce larger aftereffects for familiar faces than unfamiliar faces. In addition, these results suggest that there may be some differences in the transference of aftereffects from familiar to unfamiliar faces: specifically, since famous faces are predominantly processed in the right hemisphere and unfamiliar faces are predominantly processed in the left hemisphere, it should not be possible to cause adaptation that transfers across these types of faces. However, since personally familiar faces are processed bilaterally, aftereffects should transfer from these to both famous and unfamiliar faces and the converse should also be true.

THE PRESENT RESEARCH

The present study aimed to determine whether there are differences in the FDAE for unfamiliar, famous, and personally familiar faces in terms of the magnitude of the aftereffects. Furthermore, we aim to assess whether the aftereffects can transfer across faces of differing levels of familiarity. Thus, participants were adapted to a distortion in either an unfamiliar, famous, or personally familiar face and the magnitude of the aftereffect was assessed in unfamiliar, famous, and personally familiar test images. All participants viewed the same test images which had all been distorted by moving the eyes either further or closer to the mouth. We assessed whether the more distorted faces appeared undistorted following the adaptation in a method similar to McKone et al. (2005). This technique allows us to see how adaptation affects participants' subjective ratings of distortion and is analogous to participants perceiving a previously undistorted face as distorted following adaptation but allows for more trials.

METHOD

PARTICIPANTS

An opportunity sample of 48 (18 male) White British participants volunteered for this experiment as part of a course requirement. None of the participants knew each other (or each others' parents). They had a mean age of 23.6 years (ranging from 18 to 33 years) and self-reported they had normal or corrected to normal vision. All participants were psychology undergraduates, studying at Anglia Ruskin University.

MATERIALS

One unfamiliar, one famous, and one personally familiar face (per participant) were used. These were matched for age, gender, image size, quality, and pose as best as possible. All poses were frontal and expressionless. Unfamiliar and personally familiar faces were provided by the participants who were instructed to obtain a picture of their parent which was expressionless, full frontal headshot, in front of a plain, light background, wearing a white shirt, using the best quality camera available. Each participant was tested on their own parent's face and one of the other participants' parent's faces (thus, the stimuli were approximately matched across age) in addition to a famous face (this was also matched for approximate age). When submitting a photograph of a parent, participants were asked if they were familiar with a number of famous faces in order to ensure that an adequate level of superficial familiarity with the famous faces was maintained.

All pictures were then adjusted in Adobe Photoshop 7.0 so that the distance from the camera appeared the same. In addition, all backgrounds were masked out and matched. Each picture had a resolution of 96 dpi and the dimensions were constrained to 550×640 pixels (subtending visual angle 13.68° x 16.01°). Root mean contrast was kept constant across all stimuli by adjusting the brightness and contrast functions in Adobe Photoshop 7.0. They were then distorted by shifting the eyes up or down (see Hills et al., 2010b for a description of this procedure). Ten images shifted the eyes closer to the mouth by one pixel increments, producing images −1 through to −10, 10 images shifted the eyes further from the mouth, producing images +1 through to +10, and two extreme images were created (−25 and +25) in order to act as the adaptor stimuli. See **Figure 1** for an example of the stimuli used in this experiment. This shifting technique has been used in a number of studies that also use a configural manipulation of the facial stimuli (McKone et al., 2005). All images could still be identified as belonging to the individual from which the distorted images were created. The images were displayed on a high resolution 17″ (1280×1024) LCD color monitor using MatLab in a quiet dimly lit research laboratory.

DESIGN

Using a 3×3 mixed design, the number of images perceived to be distorted was measured for three different test-image types (unfamiliar, famous, and personally familiar; within-subjects) for the different adaptors (unfamiliar, famous, and personally familiar; between-subjects). Even though participants were assigned to either a positive or negative adaptor-type this had no bearing on the results and so direction of the distortion is not considered a variable. Participants were randomly placed in groups, with the condition that there were an equal number of participants in each group. The order of image presentation was randomized.

PROCEDURE

The experiment was conducted in two stages: pre- and post-adaptation. Participants were assigned to view either positively or negatively distorted adaptors. If a negative adaptor had been

FIGURE 1 | Running from left to right, a complete set of images for a negatively distorted parent including test images ranging from −1 through to −10 as well as the adaptor image of −25.

assigned, all the stimuli throughout their entire experiment were negatively distorted. Similarly, if participants had been assigned to a positive condition all the stimuli were positively distorted.

Stage 1: baseline

Participants were presented with the 10 distorted images from each of the types of faces (unfamiliar, famous, and personally familiar faces) that were distorted in the direction the participant had been assigned to. Each distorted face was shown 10 times each producing 300 trials. Participants were instructed to look at each image and judge whether it was "odd" or not (similar to McKone et al., 2005; Hills et al., 2010b). They were told some of the pictures were distorted and some were not. If they thought an image was normal they were asked to press the "M" key whereas if they thought the image was "odd-looking" they were asked to press the "Z" key. The face was on screen until participants responded. Preceding each face, a fixation cross appeared for 300 ms in the center of the screen.

Stage 2: adaptation task

Participants were then told they would first see an adaptor face for 1 min. This appeared in the center of the screen. Following this, there was a repeat of the baseline phase, except that preceding each test face, the adaptor face was presented for 4 s but at twice the size and shifted 50 pixels into one of the four quadrants of the screen. This was done to control for lower-level visual based adaptation that is observed in the FDAE – data from Hills et al. (2010a) that indicate face aftereffects are approximately 50% low-level, image-based and 50% that is potentially higher-level (see, e.g., Rooney et al., 2012). The position of the adaptor face was randomized across trials.

RESULTS

The number of faces rated as distorted post-adaptation was subtracted from the pre-adaptation baseline test phase. Perceiving

Table 1 | Mean number of test faces perceived to be distorted post-adaptation subtracted from the mean number of faces perceived to be distorted at baseline, for each image-type for every adaptor type.

		Test stimuli		
		Unfamiliar	**Famous**	**Personally familiar**
Adaptor type	Unfamiliar	21.63** (10.88)	6.25* (6.23)	14.63** (17.24)
	Famous	7.75* (6.44)	24.88** (10.97)	8.38* (4.87)
	Personally familiar	6.00* (6.61)	5.38* (2.42)	13.00** (16.00)

*All aftereffects were significantly greater than zero, as revealed by nine Bonferroni corrected one-sample t-tests (*p < 0.05 and **p < 0.001). Standard deviation is presented in parentheses.*

relatively less distortion during test means that the adaptor nullified the perceived distortion present in the test image, resulting in a greater aftereffect magnitude score. Perceiving relatively more distortion during test means that the adaptor did not affect the perceived distortion present in the test image as much, resulting in a smaller aftereffect magnitude score. The means are presented in **Table 1** and **Figure 2**. These results indicate that aftereffects were observed in all conditions. However, when the test stimuli matched the adaptor the aftereffect was of a larger magnitude than when it was not. Similarly, the aftereffects were larger when the adaptor was unfamiliar than when the adaptor was personally familiar or famous.

These data were subjected to a 3 × 3 mixed-subjects ANOVA. This revealed a significant interaction, $F(4, 90) = 12.38$, $MSE = 117.90$, $p < 0.001$, $\eta_p^2 = 0.36$. Bonferroni corrected simple effects showed that when the adaptor was unfamiliar, larger

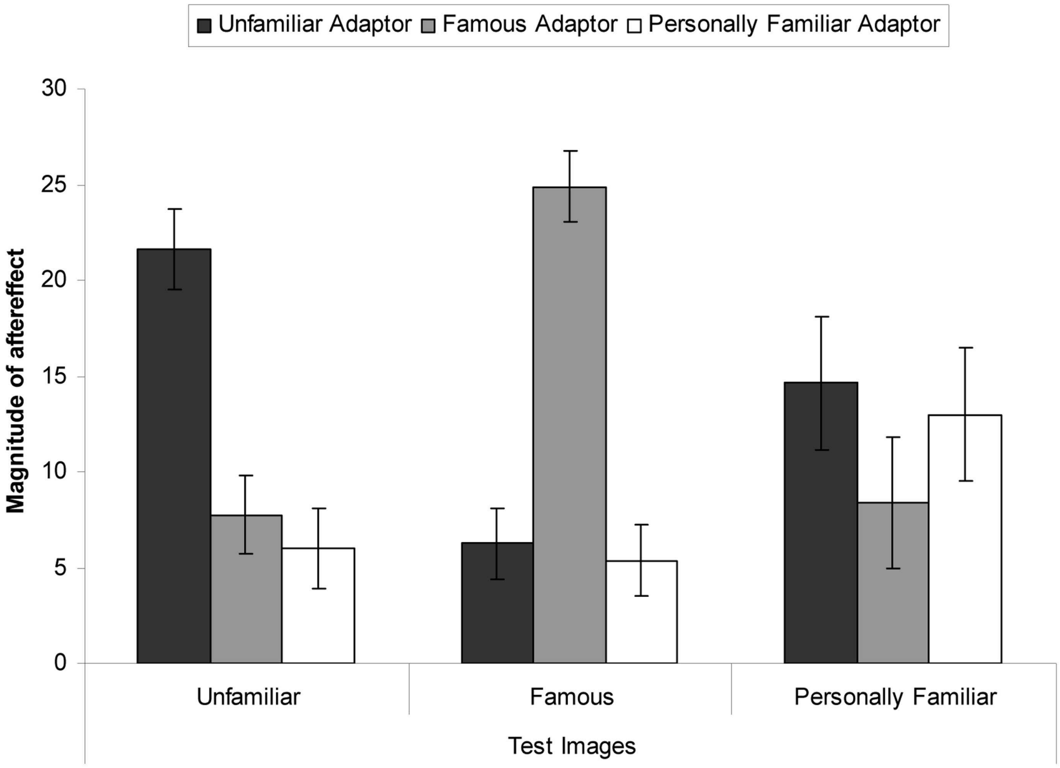

FIGURE 2 | Magnitude of aftereffect (mean number of test faces perceived to be distorted post-adaptation subtracted from the mean number of faces perceived to be distorted at baseline), for each image-type for every adaptor type. Error bars show standard error.

aftereffects were observed in the unfamiliar test images than the famous test images (mean difference = 15.38, $p < 0.001$) but not when the test images were personally familiar (mean difference = 7.00, $p = 0.262$). When the adaptor was famous, larger aftereffects were observed when the test images were famous than when they were unfamiliar (mean difference = 17.13, $p < 0.001$) or when they were personally familiar (mean difference = 16.50, $p < 0.001$). When the adaptor was personally familiar, marginally larger aftereffects were observed for personally familiar test images than famous test images (mean difference = 7.00, $p = 0.046$) and unfamiliar test images (mean difference = 7.63, $p = 0.062$).

There was also a significant main effect of adaptor type, $F(2, 45) = 5.75$, MSE = 31.28, $p = 0.006$, $\eta_p^2 = 0.20$. Dunnett *post hoc* tests were conducted, with the unfamiliar faces as the reference category. These revealed that when the adaptor was unfamiliar greater aftereffects were observed than when the adaptor was personally familiar (mean difference = 6.04, $p = 0.007$) but not when the adaptor was famous (mean difference = 0.50, $p = 0.954$). The main effect of test-image type was not significant, $F(2, 90) = 0.02$, MSE = 117.90, $p = 0.985$, $\eta_p^2 = 0.01$.

The mean number of faces perceived to be distorted at baseline ranged between 46.13 and 50.13 and there were no significant differences across any of the conditions (all $ps > 0.80$).

DISCUSSION

These results show an interesting and somewhat unexpected pattern of results. Firstly, the magnitude of the FDAE was typically greatest when the test images matched the adaptor type (except when the test images were personally familiar in which case there was no difference in the magnitude of adaptation for personally familiar and unfamiliar adaptors). Secondly, the aftereffect transferred from all adaptor types to all test stimuli. Thirdly, the aftereffect was weakest following adaptation to personally familiar faces, however this may be a result of there being lower matched-image adaptation than in the other conditions. Fourthly, the aftereffects in the personally familiar test images did not differ across adaptor type as much as the other conditions: the aftereffects in personally familiar faces was actually greater in the non-familiarity-match conditions than in the non-familiarity-match conditions for the other test faces. Finally, excluding the preceding effects, the aftereffects transferred least across unfamiliar adaptors to famous test images and famous adaptors to unfamiliar test images. We shall attempt to interpret each of these findings in turn.

The first two results summarized (FDAE greatest when adaptor and test images matched and that there was always some transference of the aftereffect) actually indicates some form of low-level aftereffect. Arguably, this aspect is likely to be based on similar mechanisms to shape aftereffects (Suzuki and Cavanagh, 1998) rather than any face norm-based coding. We make this supposition because all faces have a similar shape, and while they were positioned in different areas of the screen (thus the aftereffects are non-retinotopic), they were of a similar magnitude. Similarly, the fact that the transfer of aftereffect was typically lower when the image changed than when it was the same suggests some low-level image-based adaptation. In addition, it seems likely that there would be no reason to engage higher-level cognitive processing when lower-level more general processes would suffice. We would expect to see the neural locus of these aftereffects to be somewhere in the occipital lobe, before the FFA (see below for further elucidation of this point).

The third finding, that the aftereffects following adaptation to personally familiar faces was smaller than following adaptation to other types of faces and that they were surprisingly small when the test images were personally familiar face suggests that the representations of personally familiar faces is more robust and stable than those of unfamiliar and famous faces. This could come as a surprise, since we have already stated that humans are experts at recognizing personally faces that they have not seen in some time and those faces are likely to change in that time. Indeed, every morning, your partner will look slightly different to the night before. This could lead us to hypothesize that the representation of personally familiar faces should update more easily than unfamiliar people and thus be more adaptable. However, perhaps the robustness of the representation means that personally familiar faces are less adaptable because we know that we see them in many different conditions and thus consider any variant of the face acceptable to the identity. Alternatively, extreme familiarity may cause participants to know that those faces can never be distorted in that way. In other words, because we have so much experience of a personally familiar face, we know the entire variability of their face therefore adaptation cannot cause us to see a distortion in the personally familiar face, that is not physically possible, because of the restrictions placed on the representation of that face.

The preceding argument is similar to one made by Hills et al. (2010b) in terms of how face-space might develop. They found that children could be adapted to facial distortions that adults could not be: specifically, if each eye was shifted in different directions adults did not show aftereffects whereas children did. Both adults and children showed similar aftereffects to possible distortions (both eyes shifted together). Hills et al. theorized that as children become more familiar with faces, the neural responses to facial distortions becomes restricted such that only possible distortions can be processed as a face. Thus, the neurons that processed an impossible configuration are pruned since they are no longer useful (e.g., O'Leary and Koester, 1993). This is only conjecture, but fits the pattern of data here to: as personally familiar faces are encountered so frequently, we know the entire range with which they can be distorted, and anything beyond that is not coded as a face. Therefore, it is harder to be adapted to distortions in personally familiar faces.

We also found that aftereffects in personally familiar test faces were of similar magnitude whether the adaptor was unfamiliar or personally familiar. This effect is highly interesting for it suggests that there is significant correlation in the representation of personally familiar and unfamiliar faces and this is somewhat greater than the correlation in the representation of personally familiar and famous faces. This could be related to the fact that aftereffects seem easier to produce in personally familiar test faces than unfamiliar faces and famous faces overall (if you exclude the familiarity-matched conditions). Thus, something about the representation of personally familiar faces is linked to both unfamiliar and famous faces.

The final two findings are related to the possible neural architecture of these aftereffects. If the main locus of the FDAE is the FFA, and we accept that familiarity affects the hemisphere of processing (Taylor et al., 2009), then these results seem quite clear. Given that famous faces are primarily processed in the right-FFA and unfamiliar faces are primarily processed in the left-FFA (Taylor et al., 2009), it would be difficult for the aftereffects to transfer across these types of faces. In other words, we would expect that the viewpoint-dependent aftereffects to be located in the left-FFA, but viewpoint-independent aftereffects to be located in the right-FFA. There would be little communication between the left- and right-FFAs during the processing of faces, so the aftereffects are unlikely to transfer across.

This then links on to the idea that personally familiar faces are represented bilaterally (Taylor et al., 2009). If this is the case, then the FDAE should transfer from unfamiliar and famous faces to personally familiar faces and vice versa. However, this transfer should be of a smaller magnitude than within hemisphere (within class of face) transference, because only part of the processing has been adapted. If an aftereffect is caused by adaptation in an unfamiliar face, then neurons in the left-FFA will become adapted, thus responses to a familiar face will be smaller than without this adaptation. However, because there has not been any adaptation to the right-FFA, this aftereffect will be smaller than if the representation had been bilateral. To explain some transference of the aftereffect in all conditions, we would suggest that there is some low-level adaptation occurring prior to the FFA. This low-level aftereffect is unlikely to be lateralized and is likely to occur in early visual processing areas.

The previous explanation seems to fit with all the data except the fact that aftereffects were greater in personally familiar faces following adaptation to distortions in unfamiliar faces. This may be linked to our theorizing for the third finding. If adaptation is harder to produce in personally familiar faces but aftereffects can transfer to personally familiar from both unfamiliar and familiar faces because of shared neural architecture then we have at least a partial explanation.

These results also inform us how the representation of familiar and unfamiliar faces may differ. Given the face-space (Valentine, 1991) model for face memory, it is assumed that all faces are stored within this multidimensional space. Evidence for norm-based coding comes from aftereffects changing the locus of the prototype (c.f., Leopold et al., 2001). We have suggested that it is, firstly, harder to change the prototype when adapting to a personally familiar face and, secondly, changing the prototype by adapting to a famous face does not affect the prototype for unfamiliar faces. To interpret these results within face-space, we outline four possibilities that could be suggested are cause for the above results.

(1) It may be that personally familiar faces are not stored in the face-space. They are so familiar that they are stored as a unique entity. (2) There may also be a face-space that is used for the coding of familiar faces (located in the right hemisphere) and one used for the coding of unfamiliar faces (located in the left hemisphere).

These would be based on different prototypes. This would suggest that adapting to a particular personally familiar face would not cause any discernable change in the perception of an unfamiliar face in a typical face identity aftereffect paradigm. This hypothesis seems unlikely, given that the explanation for the face identity aftereffect is a simple shift in the perceptual space (c.f., Hulbert, 2001). (3) A more plausible explanation is that different dimensions of the face-space are represented in different hemispheres. The dimensions that are used to recognize famous faces are located in the right hemisphere (those representing internal features, Ellis et al., 1979) and the dimensions that are used to recognize unfamiliar faces are located in the left hemisphere (those representing external features). There may be direct communication between all the dimensions of the face-space, but when presented with a face only those dimensions that are relevant are actually used. (4) A final explanation is that unfamiliar faces are not actually faces at all (Megreya and Burton, 2006). Unfamiliar faces may actually be represented as objects and all aftereffects observed in unfamiliar faces are the result of shape aftereffects and have nothing to do with face-specific mechanisms.

It is clearly necessary that further research be conducted in order to answer the question of which of these models explains the present data (no face-space for personally familiar faces; two separate face-spaces; different dimensions for familiar and unfamiliar faces; or unfamiliar faces are not faces). It may be possible, for example, to create one type of aftereffect (say expansion) in famous faces and another type of aftereffect (say compression) in unfamiliar faces. If this result were possible, then it would indicate that there were two separate face-spaces for familiar and unfamiliar faces (c.f., Rhodes et al., 2004). To assess whether unfamiliar faces are not really processed as faces, it may be possible to explore aftereffects transferring from shapes and objects to faces (c.f., studies by Fang and He, 2005, on viewpoint aftereffects showing that this does not occur). If unfamiliar faces are not faces, then this transference should occur, but it should not occur for famous faces.

In conclusion, this study has provided further evidence for the distinct representations of unfamiliar, famous, and personally familiar faces. We have presented evidence for some image-based aftereffects and also some aftereffects that suggest different neural coding for unfamiliar, famous, and personally familiar faces. We have interpreted these findings within a neural architecture suggesting that these aftereffects are hemisphere specific.

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Shared or separate mechanisms for self-face and other-face processing? Evidence from adaptation

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Evidence that self-face recognition is dissociable from general face recognition has important implications both for models of social cognition and for our understanding of face recognition. In two studies, we examine how adaptation affects the perception of personally familiar faces, and we use a visual adaptation paradigm to investigate whether the neural mechanisms underlying the recognition of one's own and other faces are shared or separate. In Study 1 we show that the representation of personally familiar faces is rapidly updated by visual experience with unfamiliar faces, so that the perception of one's own face and a friend's face is altered by a brief period of adaptation to distorted unfamiliar faces. In Study 2, participants adapted to images of their own and a friend's face distorted in opposite directions; the contingent aftereffects we observe are indicative of separate neural populations, but we suggest that these reflect coding of facial identity rather than of the categories "self" and "other."

Keywords: self-face, familiar face, adaptation, personal familiarity

INTRODUCTION

Adaptation is a general feature of perceptual processing which describes an adjustment of neural sensitivity to sensory input. During adaptation, exposure to a stimulus causes a change in the distribution of neural responses to that stimulus with consequent changes in perception. The measurement of the perceptual changes or aftereffects produced by adaptation provides insight into the neural mechanisms which underlie different aspects of perception. Aftereffects have been extensively used to investigate the neural coding of basic visual properties such as color, motion, size, and orientation (Barlow, 1990) and of more complex visual properties such as face shape and identity (see Webster and MacLeod, 2011 for a review). Central to functional accounts of adaptation is the idea that neural sensitivity is adjusted to the average input, so that differences or deviations from this mean are signaled (Barlow, 1990; Webster et al., 2005).

In a seminal study of aftereffects in high-level vision, Webster and MacLin (1999) demonstrated that adapting to faces which were distorted in some way (compressed, expanded) led to subsequently viewed normal faces being perceived as distorted in the opposite direction (expanded, compressed). A number of subsequent studies have demonstrated robust adaptation aftereffects for faces, with manipulations of face shape using different forms of distortion (Rhodes et al., 2003; Carbon and Leder, 2005; Carbon et al., 2007; Jeffery et al., 2007; Carbon and Ditye, 2011; Laurence and Hole, 2011) or through the creation of anti-faces which manipulate aspects of facial shape that are crucial to identification (Leopold et al., 2001; Anderson and Wilson, 2005; Fang et al., 2007). These studies suggest that faces are coded with respect to a prototypical or "average face" and show that sensitivity changes with adaptation, so that perceptual judgments are made with respect to a shifted norm.

That these effects are present at a high-level of representation rather than solely the image-based level is reflected in the fact that the face distortion aftereffect transfers across faces of different sizes (Leopold et al., 2001; Zhao and Chubb, 2001; Anderson and Wilson, 2005), across different viewpoints (Jiang et al., 2006, 2007), across different facial expressions (Fox et al., 2008), and across different aspect ratios (Hole, 2011). Further evidence comes from studies demonstrating that naming famous faces (Hills et al., 2008) and imagining recently learned (Ryu et al., 2008) or famous faces (Hills et al., 2010) is sufficient to produce identity aftereffects in the subsequent visual perception of faces (see also Ghuman et al., 2010; Lai et al., 2012 for evidence of body-to-face and hand-to-face adaptation, respectively).

The study of contingent aftereffects offers a particularly useful tool for studying the neural coding of complex stimuli. If stimuli are coded separately, contingent aftereffects will occur, whereby adaptation to stimuli from different categories leads to aftereffects that are contingent on the category of the test stimulus. For example, adapting to green horizontal and red vertical lines leads to color aftereffects that are contingent on the orientation of the test stimulus (red horizontal and green vertical lines) because neurons are differentially tuned to the processing of horizontal and vertical lines (McCollough effect; McCollough, 1965; these effects are usually short-lived in face perception, e.g., Leopold et al., 2001; Rhodes et al., 2007; though see Webster et al., 2004; Carbon and Ditye, 2011). Contingent aftereffects provide evidence that distinct neural populations are involved in coding different categories of stimulus. By comparison, a cancellation of aftereffects across stimuli would suggest that they were coded by the same population of neurons (Rhodes et al., 2004). Interestingly, contingent aftereffects in face processing can tell us about the neural coding of social categories.

Little et al. (2005) report sex-contingent aftereffects for unfamiliar faces. That is, when participants adapted to a female face distorted in one direction, and a male face distorted in the opposite direction, contingent aftereffects occurred such that subsequently perceived female and male faces were perceived as distorted in opposite directions. The authors interpret this finding as suggesting separate neural populations for the coding of female and male faces. Others report aftereffects contingent on the sex (Jaquet and Rhodes, 2008), race (Jaquet et al., 2007; Little et al., 2008), and age (Little et al., 2008) of faces, suggesting that these attributes are coded by specific neural networks. These effects likely reflect separate coding along the lines of social category information; Bestelmeyer et al. (2008) report sex-contingent aftereffects for male and female faces (differ in sex category and structurally), but not for female and hyper-female faces (differ structurally), and Jaquet et al. (2007) report race-contingent adaptation, with larger opposite aftereffects for morphed faces which lie on different sides of a race category boundary than for faces which lie on the same side but differ physically from each other. These findings suggest that neurons representing faces may be tuned to high-level social category information. Adaptation to categories of faces may help us to identify them (Rhodes et al., 2010), and to enhance discrimination of faces from those categories (Yang et al., 2011), which may be useful for distinguishing the self-face (or kin-face; DeBruine, 2005; DeBruine et al., 2008; Platek et al., 2009) from other categories of face.

Familiarity affects how a face is recognized (e.g., Bruce and Young, 1986), and unfamiliar face recognition may be weaker and less stable than familiar face processing (Bruce et al., 1999; Hancock et al., 2000; Rossion et al., 2001; Liu et al., 2003). As such, testing for adaptation effects using familiar faces should increase our understanding of coding mechanisms specifically involved in the representation of familiar faces. Indeed, increasing familiarity with a recently learned face increases the magnitude of the face identity aftereffect (Jiang et al., 2007). While the majority of studies of face aftereffects have utilized unfamiliar face stimuli, some studies have begun to test the effects of familiarity. Several recent studies have demonstrated distortion aftereffects for famous faces (Carbon and Leder, 2005; Carbon et al., 2007; Carbon and Ditye, 2011), and Hole (2011) demonstrates identity-specific adaptation effects for famous faces, which are robust against changes in viewpoint, inversion and stretching. These are the first studies to demonstrate rapid visual adaptation for familiar faces. That is, although we demonstrate extremely high accuracy rates for remembering famous faces (Ge et al., 2003), these representations can still be rapidly updated by new visual experience.

Growing evidence suggests that our representation of personally familiar faces is different from our representation of recently learned faces and familiar famous faces that are not personally known to us. Tong and Nakayama (1999) introduced the idea of robust representation to explain difference in performance in visual search for one's own face and more recently learned faces. Despite hundreds of trials of exposure to a new target face, participants could find their own face faster and more efficiently. Tong and Nakayama (1999) suggest that robust representations are laid down over long periods of time and require less attention to process. Indeed, Carbon (2008) has shown that recognition of personally familiar others is robust to both minor and major changes in the appearance of the face, whereas recognition of famous and celebrity faces decreases dramatically with changes to the familiar, "iconic" appearance of these faces. This is because we have experience in viewing personally familiar faces over a variety of conditions (e.g., lighting, angle), and thus our representations of those faces should be more robust to change (see also Herzmann et al., 2004 for evidence from EEG). These findings suggest that studies of familiar face processing may benefit particularly from the use of personally familiar faces.

To date, few studies have investigated the effects of personal familiarity on adaptation effects. Although Webster and MacLin (1999) focus largely on unfamiliar face processing, they show that adaptation to distortion of one's own face is possible, and Rooney et al. (2007) report that people's perception of their own faces and of their friends' faces is rapidly changed by adaptation to distorted stranger faces. More recently, Laurence and Hole (2011) demonstrate that figural aftereffects are smaller when participants adapted to and were tested with their own face, compared with famous faces and unfamiliar faces. While Laurence and Hole demonstrate differences in self-/other face adaptation, their research did not compare adaptation effects for self-faces with effects for other personally familiar faces; in the investigation of self-/other face adaptation, level of personal familiarity with the "other" face may be an important consideration.

The conditions under which adaptation effects will transfer across faces is much debated. While several studies report that face adaptation aftereffects transfer across different adapting and test stimuli for unfamiliar faces (Webster and MacLin, 1999; Benton et al., 2007; Fang et al., 2007) and for famous faces (Carbon and Ditye, 2011), others report only identity-specific effects (unfamiliar faces: Leopold et al., 2001; Anderson and Wilson, 2005; famous faces: Carbon et al., 2007). Of interest is whether adaptation effects will transfer across images of different personally familiar faces (Study 2 of the current paper), and whether personally familiar face representations will be updated by adaptation to unfamiliar faces (Study 1 of the current paper), considering that personally familiar faces may have stronger representations relative to unfamiliar (e.g., Tong and Nakayama, 1999) and famous (e.g., Carbon, 2008) faces.

There is much debate as to the neural specialization of self-face processing, with interest focusing on how self and other are distinguished. Gillihan and Farah (2005) argue that one way that self-face representation might be considered "special" is if it engages neural systems that are physically or functionally distinct from those involved in representing others. Both neuroimaging and neuropsychological studies point to separate anatomical substrates for self-face processing, but the way in which these different regions contribute to recognition is not well understood. Evidence that self-face processing is special comes in part from studies of hemispheric specialization. Studies of split-brain patients, whereby the corpus callosum is severed and communication between the two hemispheres of the brain is inhibited, have produced evidence of the dissociation of self-face and other face processing (Sperry et al., 1979; Turk et al., 2002; Uddin et al., 2005b), as have several behavioral studies investigating the laterality of self-face specific processing (Keenan et al., 1999, 2000; Brady et al., 2004, 2005; Keyes and Brady, 2010), but these studies disagree as to the neural substrates underlying the dissociation. Brain-imaging studies also support the idea that self is somehow "special," and point to the involvement of large-scale, distributed neural networks in self-face recognition (Sugiura et al., 2000; Kircher et al., 2001; Platek et al., 2006; for EEG evidence see Keyes et al., 2010). In the current study we use visual adaptation to explore whether the neural mechanisms involved in representing one's own and other faces are shared or separate (Study 2).

THE PRESENT PAPER

The current paper has two aims. First, we test whether exposure to highly distorted unfamiliar faces changes the perception of attractiveness and normality of participants' own faces and their friends' faces by comparing ratings before and after adaptation (Study 1). It is not known whether aftereffects will transfer from unfamiliar faces, with which we have very limited visual experience, to personally familiar faces (self, friend), for which we have developed robust representations. If there is a common coding mechanism for all faces, we predict that aftereffects will transfer from unfamiliar to personally familiar faces. However, if distorted representations of unfamiliar faces are not substantial enough to update established representations of personally familiar faces, then we predict minimal transfer of adaptation effects from the unfamiliar adapting stimuli to the personally familiar test stimuli.

Our second aim is to test for the presence of distinct neural populations for the coding of self- and other faces using a contingent aftereffects paradigm. In Study 2, participants adapt to images of their own and a friend's face which have been distorted in opposite directions (either compressed or expanded) and we measure aftereffects in the perception of both the faces used as adapting stimuli (Self, Friend 1) and of a second friend's face (Friend 2). If separate categories exist for self and other at the neural level, we expect dissociated coding for self- and other personally familiar faces, as evidenced by self/other-contingent adaptation effects. Specifically, adapting to Self in one direction and Friend 1 in the opposite direction should lead to subsequently viewed images of Self being distorted toward the adapting Self stimulus and images of Friend 1 being distorted toward the adapting Friend 1 stimulus. Importantly, if "self" and "other" are coded as distinct social categories, test images of Friend 2 should be perceived as being distorted toward the Friend 1 adapting stimulus, as it belongs to the "other" category. Alternatively, if self and other do not represent dissociated neural populations, but rather are represented by a shared mechanism, we expect a cancellation of aftereffects.

STUDY 1

METHODS

Participants

Twenty-four students (11 males, $M = 21.8$ years, SD = 1.83 years) from University College Dublin volunteered to participate. The sample comprised 12 pairs of friends matched for gender and race, where each member of a pair was very familiar with the other's face. The study was approved by the UCD Research Ethics Committee, and informed consent was gained from all participants.

Stimuli

Each participant was photographed in identical conditions under overhead, symmetrical lighting while holding a neutral expression. Eleven images were created from each digitized photograph as follows: an oval region encompassing the inner facial features was selected in Adobe Photoshop®and distorted using the software's "spherize" function set to 11 different levels (−50, −40, −30, −20, −10, 0, +10, +20, +30, +40, +50). The resulting set included the original undistorted photograph, and two sets of five images in which the facial features were either compressed or expanded to different degrees (**Figure 1**). This process was repeated for each of the 24 participants' photographs. A set of test stimuli was created for each participant, comprising 11 "self" images and 11 "friend" images. Sets of test stimuli were paired such that the "self" and "friend" stimuli for one participant would serve as the "friend" and "self" images, respectively, for another participant. For each participant, the "self" image was mirror-reversed, as participants prefer and are more familiar with a mirror image of their own face over a true image (Mita et al., 1977; Brédart, 2003). A further 10 unfamiliar faces, unknown to any of the participants were photographed in identical conditions to the participants. These 10 images were distorted at the two most extreme levels (−50 and +50) to create two sets of 10 "adapting" faces for the "compressed" and "expanded" conditions respectively. For all images, an oval vignette (measuring 277 × 400 to 304 × 400 pixels) was used to select the face with inner hairline but excluding the outer hairline. The vignettes were presented on a fixed size gray background and the images saved as grayscale with pixel depth of 8 bits.

Procedure

The experiment was run using Presentation® on a Dell Precision 360 personal computer. The display was run at 75 Hz and a resolution of 1024 × 768 pixels. The images subtended a visual angle of ∼ 8° in width and 18° in height at a viewing distance of approximately 50 cm.

Testing comprised participants rating a face for either attractiveness or normality on a scale of 1–9 (1 = unattractive/unusual,

FIGURE 1 | An original, undistorted face is shown in the center with increased expansion and compression toward the right and left sides, respectively.

9 = attractive/normal) both before and after a period of adaptation. Prior to testing, each participant ran a practice session, whereby they rated an unfamiliar face at 11 levels of distortion; these practice images were not used again. In the first block of testing, 110 images were presented in a randomized order [22 images (11 self and 11 friend) × 5 repetitions each]. Images were displayed for 1.5 s and then replaced with a rating scale, shown on a gray background. Participants rated the face on a scale of 1–9 by pressing the numbers across the top of a keyboard. This initial rating phase was followed by the adaptation phase, where participants were asked to pay close attention to a sequence of faces, which were either expanded (+50; viewed by participants in the "expanded" condition) or compressed (−50; viewed by participants in the "compressed" condition) distortions of unfamiliar faces. The adaptation phase lasted for 5 min with each image – chosen at random with replacement from the set of 10 – displayed for 4 s with a gray background ISI of 200 ms.

After adaptation, the participants rated the 110 test faces [22 images (11 self and 11 friend) × 5 repetitions] a second time, under the same conditions as the first block of testing. To maintain the effects of adaptation an adapting face was presented for 8 s (followed by a gray screen for 500 ms) before each test face. To distinguish adapting from test faces, the word "RATE" was printed above each test face.

Design and analyses

Twelve participants rated the faces for normality and 12 for attractiveness. Six of each group adapted to compressed faces and six adapted to expanded faces. The data were analyzed using mixed model ANOVA with a between-subjects factor of "type of adaptation" (compressed/expanded) and within-subjects factors of "time of rating" (pre- and post-adaptation) and "test stimulus" (self/friend). The dependent variables were the distortion level of the face that was rated most normal/attractive, which was calculated pre and post-adaptation as explained below.

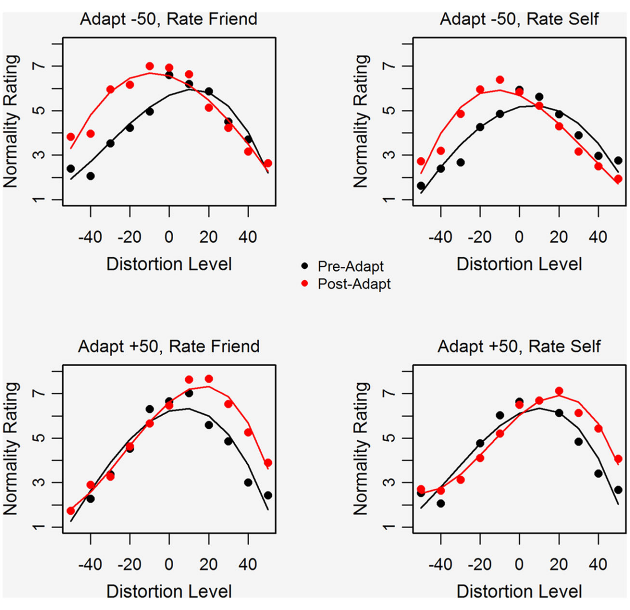

FIGURE 2 | Average normality ratings plotted as a function of face distortion level using black symbols for pre-adaptation ratings and red symbols for post-adaptation ratings. The right and left panels show ratings for Self and Friend respectively, for conditions in which participants adapted to compressed faces (top panel) or to expanded faces (bottom panel).

RESULTS

Figure 2 plots average normality ratings against distortion level for ratings made prior to and after adaptation. Separate plots are shown for ratings of Self and Friend (right and left panels) and for conditions in which participants adapted to extremely compressed or expanded faces (top and bottom panels). The solid curves (third-order polynomials fitted to the data generated by the six participants in each condition) are shown for both ratings made prior to (black) and after adaptation (red). Note that prior to adaptation participants rated faces that were slightly expanded as most normal, i.e., the maximum point of the black curve falls slightly to the right of the original, undistorted face. This preference for a slightly expanded face is also evident in the attractiveness data (not shown) and in the data of Rhodes et al. (2003) and may occur because the expansion of facial features leads to bigger, more widely spaced eyes which look more attractive. Following adaptation the distortion level rated as most normal shifts in the direction of the adapting stimulus, so that the maximum of the solid red line shifts further rightward in the case of adapting to expanded faces and leftward in the case of adapting to compressed faces.

Adaptation effects are clearly evident in **Figure 3** which plots the mean distortion level corresponding to the maximum rating for normality and for attractiveness. After adaptation, the rating of the most normal and most attractive face shifts in the direction of the adapting stimulus. Notably, the data for Self and Fiend exhibit very similar patterns. The same trends were seen in the attractiveness and normality data, reinforcing the idea that

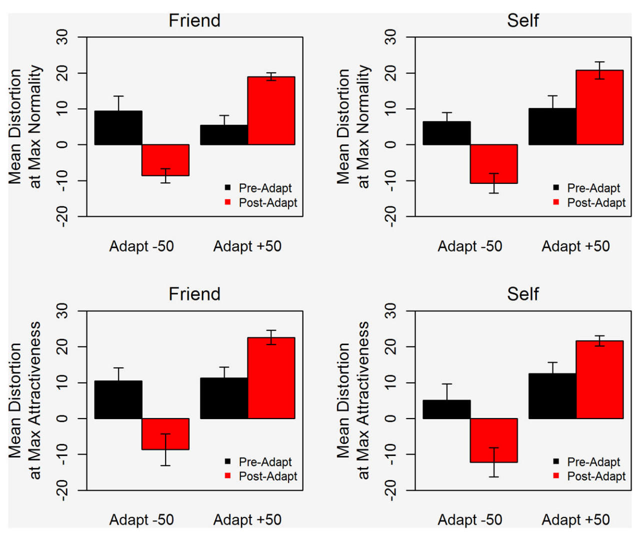

FIGURE 3 | Mean distortion level corresponding to the maximum rating of normality (top) and attractiveness (bottom) for images of Self (right) and Friend (left). Error bars show ±1 standard error of the mean.

ratings of normality and attractiveness are both based on perceived "averageness" (Rhodes et al., 2003).

Statistical analyses confirm these trends. Third-order polynomials were fitted to each participant's ratings of normality or attractiveness using R (R Development Core Team, 2010) and the maximum of the curve was estimated to calculate the distortion level corresponding to the maximum rating both pre- and post-adaptation in all conditions. This served as the dependent variable.

For the normality data, ANOVA showed a significant interaction between "type of adaptation" (compressed or expanded) and "time of rating" (pre- or post-adaptation), $F(1,10) = 133.03$, $p < 0.001$. Planned comparisons showed that after adapting to compressed faces, participants chose a maximum normality rating at a distortion level that was significantly shifted toward the "compressed" end of the continuum, $t(11) = -8.44$, $p < 0.001$ [mean difference, −17.62; 95% CI (−22.22, −13.02)]. Similarly, after adapting to expanded faces, the distortion level at maximum normality was significantly shifted toward the "expanded" end of the continuum, $t(11) = 7.22$, $p < 0.001$ [mean difference, −12.12; 95% CI (8.42, 15.81)].There was no main effect of "test stimulus" (Self or Friend), $F(1,10) = 0.025$, $p = 0.88$, and "test stimulus" did not interact with any other variables.

For the attractiveness data, there was also a significant interaction between "type of adaptation" and "time of rating," $F(1,10) = 135.66$, $p < 0.001$. Planned comparisons showed the shift in the distortion level at maximum attractiveness was significant for both compression, $t(11) = -8.12$, $p < 0.001$ [mean difference, −18.22; 95% CI (−23.17, −13.29)] and for expansion, $t(11) = 6.25$, $p < 0.001$ [mean difference, 10.28; 95% CI (6.67, 13.90)]. Again, there was no main effect of "test stimulus," $F(1,10) = 0.35$, $p = 0.56$, and "test stimulus" did not interact with any other variables.

DISCUSSION

Study 1 shows that the representation of highly familiar faces, including our own face, is rapidly updated by visual experience. This is consistent with recent reports of shifts in perceived identity following exposure to distorted celebrity faces (Carbon and Leder, 2005; Carbon et al., 2007). Here we show that comparable aftereffects – shifts in perceived attractiveness and normality – are rapidly obtained for personally familiar faces and that these effects can be achieved by exposure to unfamiliar faces. The fact that adaptation generalizes from unfamiliar to highly familiar faces, and that the aftereffects are of comparable magnitude for self-faces and friend faces, indicates a shared representation for all classes of face.

Our second study further explores whether aspects of the perceptual coding of self- and other faces are separate, but investigates for the presence of "opposite" or "contingent aftereffects," in contrast to the "simple aftereffects" induced in Study 1. A number of recent studies have shown that it is possibly to induce aftereffects that are contingent upon characteristics of the adapting faces, such as their sex (Little et al., 2005; Jaquet and Rhodes, 2008), race (Jaquet et al., 2007; Little et al., 2008), and age (Little et al., 2008). This methodology allows us explore the extent to which separate neural populations are involved in coding different categories of face.

STUDY 2

In Study 2 participants adapted simultaneously to their own face and to another highly familiar face ("Friend 1") distorted in opposite directions. If self and other faces are coded by common mechanisms we expect a cancellation of aftereffects, whereas contingent aftereffects would suggest separate coding of self and other faces. To address the possibility that any contingent aftereffects observed may reflect identity-specific coding, rather than separate neural representation of "self" and "other," a third type of test face was introduced: Friend 2. If "self" and "other" faces are represented as discrete social categories and are represented by separate neural populations, then aftereffects for Friend 2 should follow the pattern of contingent aftereffects observed for Friend 1. If, however, identity-specific coding is in play, then contingent aftereffects observed for Self and Friend 1 faces should "cancel" for Friend 2 faces.

METHODS

The general methods are the same as in Study 1.

Participants

Thirty students (12 males, $M = 21.8$ years, $SD = 2.82$ years) participated in Study 2. The sample comprised 10 groups of three friends matched for gender and race, where each member of a group was very familiar with the others' faces.

Stimuli

Four photographs were taken of each participant, one while smiling, one while biting the bottom lip, and two, taken on separate occasions, with a neutral expression. These served as different examples of the participant's face and comprised each participant's adapting and test Self images. For each participant, four further images of a close friend of the same sex were taken (one smiling, one biting lip, and two neutral), and these comprised the Friend 1 adapting and test images. Finally, for each participant, three images of a different close friend of the same sex were taken (one smiling, two neutral), and these comprised the Friend 2 test images. Different images – smiling, lip biting, neutral – were used to ensure that any adaptation effects would not be solely based on low-level properties of the stimulus.

The biting lip image and one of the neutral expression images were used as adapting stimuli (Self, Friend 1) and the smiling image and the two neutral expression images were used as the test stimuli (Self, Friend 1, Friend 2). The adapting and test stimuli were created in Photoshop® by selecting a circular region encompassing the eyes and nose region only, and distorting using the "Spherize" function. As the different face examples included different expressions, the mouth region was not included in the distortion so as to make a more uniform set of distorted images. For the adapting stimuli the distortion was set to either −50 or +50 for a highly compressed or expanded face. In total, there were 4 adapting stimuli: 2 (Self, Friend 1) × 2 (biting lip, neutral). There were 45 test images: 3 (Self, Friend 1, Friend 2) × 3 (1 smiling and 2 neutral) × 5 distortion levels (−26, −12, 0, +12, +26). Self images were always mirror-reversed while Friend images were shown in the original photographed orientation.

Procedure

The procedure was similar to that used in Study 1. Testing comprised participants rating a face for distortedness on a scale of 1–7 (1 = least distorted, 7 = most distorted) both before and after a period of adaptation. Prior to testing, each participant ran a practice session, whereby they rated an unfamiliar face at five levels of distortion. In the first block of testing, 135 images were presented in a randomized order [3 face identities (Self, Friend 1, Friend 2) × 3 examples (1 smiling, 2 neutral) × 5 levels of distortion × 3 repetitions each). Images were displayed for 1.5 s and then replaced with a rating scale, shown on a gray background. Participants rated the face on a scale of 1–7 by pressing the numbers across the top of a keyboard.

During the adaptation phase, participants attended to a sequence of adapting images which lasted for a total of 3 min. The sequence included equal numbers of their own face (from two examples compressed to −50) and their friend's face (Friend 1, from two examples expanded to +50) which were presented in random order. Each adapting image was displayed for 4 s with a gray background ISI of 200 ms.

In the post-adaptation testing phase, participants again rated the 135 test images for perceived distortedness. In order to maintain the effects of adaptation, an adapting face was presented for 6 s (followed by a gray screen for 500 ms) before each test face. This "top-up" adaptation contained equal numbers of highly compressed Self and highly expanded Friend 1 images which were presented in random order. Test faces were distinguished by the word "RATE" printed above each test face.

Design and analysis

The data were analyzed using within-subjects ANOVA with dependent variable of distortedness rating and factors of "time of rating" (pre- and post-adaptation), "level of distortion" (−26, −12, 0, +12, +26), and "test stimulus" (Self, Friend 1, Friend 2).

RESULTS

Figure 4 shows the mean distortedness ratings for the five test images before and after adaptation for Self, Friend 1, and Friend 2. The pattern of results is of primary interest here and suggests contingent aftereffects. Simultaneous adaptation to self and friend images distorted in opposite directions does not lead to a cancellation of aftereffects but rather to a shift in perceived distortedness that is biased in different directions for Self and Friend 1 images. For Self stimuli, the shift in perceived distortedness is greater for the compressed than for the expanded test images of Self (left plot). For Friend 1, however, the shift in perceived distortedness is greater for the expanded than for the compressed test images (right plot). Interestingly, the effects of adaptation on the perceived distortedness of the Friend 2 test images (center plot) are more evenly distributed across the distortion levels, as shown by the parallel downward shift of the ratings curve. The data are polynomial fitted to help illustrate these effects.

These observations are confirmed by statistical analyses. A three-way within-subjects ANOVA showed a three-way interaction between "time of rating," "test stimulus," and "level of distortion" to be significant, $F(8,232) = 13.54$, $p < 0.001$. This was further analyzed by conducting three 2-way ANOVAs separately on the Self, Friend 1, and Friend 2 data. Family-wise error was controlled using Bonferroni adjustment (0.05/3 = 0.017). ANOVA for the Self images shows a significant interaction between time of rating and distortion level on distortion ratings, $F(4,116) = 20.26$, $p < 0.001$, and planned comparisons of the pre- and post-adaptation mean ratings showed significant differences for levels 0, −12, and −26 only, with the estimated mean difference increasing as the images became more compressed [95% CI at "0" (0.58, 1.31); 95% CI at "−12" (1.06, 2.03); and 95% CI at "−26" (1.59, 2.50)].

Similarly, ANOVA for the Friend 1 images showed a significant time of rating by distortion level interaction, $F(4,116) = 5.91$, $p < 0.001$; here, planned comparisons of the pre- and post-adaptation mean ratings showed significant differences for all levels of distortion with the estimated differences increasing as the images became more expanded [95% CI at "−26" (0.62, 1.44); 95% CI at "−12" (0.70, 1.47); 95% CI at "0" (0.72, 1.31); 95% CI at "+12" (0.97, 1.70); 95% CI at +26" (1.38, 1.82)].

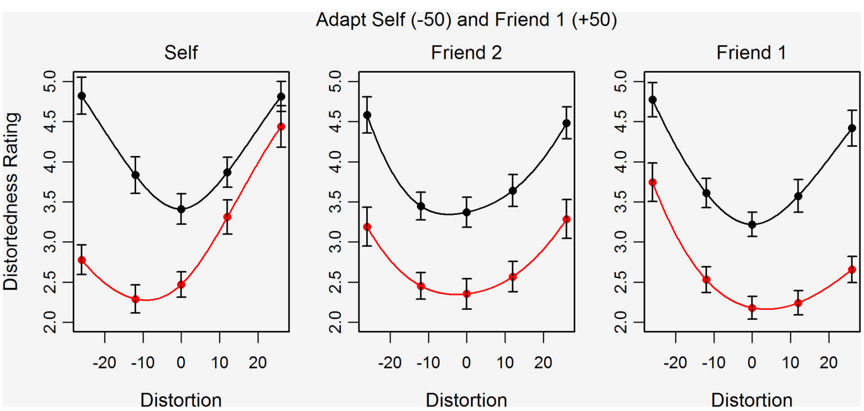

FIGURE 4 | Mean distortedness ratings for five versions of the test images both before (black) and after adaptation (red) to highly compressed Self and highly expanded Friend 1 faces in Study 2. Error bars show ±standard error of the mean. Separate plots are shown for Self (left), Friend 1 (right), and Friend 2 (center).

In contrast, ANOVA for Friend 2 images did not show a significant interaction between time of rating and distortion level, $F(4,116) = 1.88$, $p = 0.12$, suggesting that any perceptual change following adaptation is evenly distributed across distortion levels. Here, main effects of time of testing, $F(1,29) = 63.56$, $p < 0.001$, and distortion level, $F(4,116) = 23.65$, $p < 0.001$, were significant. Participants rated faces as less distorted following adaptation (pre = 3.91, SE = 0.10; post = 2.77, SE = 0.10), and rated faces overall as more distorted at higher levels of distortion ("−26" = 3.89, SE = 0.19; "−12" = 2.95, SE = 0.13; "0" = 2.86, SE = 0.15; "+12" = 3.10, SE = 0.15; " + 26" = 3.89, SE = 0.17). All planned comparisons reported are significant after Bonferroni correction to 0.05/5 = 0.01.

DISCUSSION

In line with other studies that have shown aftereffects contingent on characteristics of the adapting faces, these results show aftereffects that are contingent upon the identity of the adapting stimulus. Specifically, adaptation leads to a shift in participants' perception of distortion that is biased in the direction of the adapting stimuli: here the shift is greatest for compressed relative to expanded Self faces and for expanded relative to compressed Friend 1 faces. However, the perceptual change is evenly distributed across the spectrum of distortion for Friend 2 faces, suggesting that coding is at the level of individual facial identity and not in terms of "self" and "other."

These results also suggest shared or common coding of all faces. In the case of Friend 2, simultaneous adaptation to two other familiar faces adapted in different directions leads to a significant main effect of adaptation, i.e., faces at all levels of distortion are judged to be less distorted, suggesting that, on average and across all participants tested, Friend 2 faces share structural properties with both Friend 1 and Self faces. Similarly, in the case of Self and Friend 1, simultaneous adaptation to highly distorted versions of these images (in different directions) leads to an overall downward shift of the rating curves, albeit with significant bias in the direction of the adapting stimulus. This is in marked contrast to Study 1 where participants adapted to faces that were either compressed or expanded and the pre- and post-adaptation curves typically cross each other (see **Figure 2**). This suggests that, on average, Self faces share structural similarity to Friend 1 faces, so that we see a mixture of simple and contingent aftereffects. This is similar to what has been recently observed in studies of sex-contingent aftereffects (Jaquet and Rhodes, 2008). That these aftereffects are due to adaptation to the distorted faces, rather than simply to viewing faces, is supported by Webster and MacLin (1999), who show that viewing undistorted faces does not lead to aftereffects.

GENERAL DISCUSSION

In two studies we show that the visual representation of personally familiar faces, including one's own face, is subject to rapid adaptation. Aftereffects, characterized by shifts in the perception of attractiveness and normality (Study 1) and the perception of distortedness (Study 2), were demonstrated after exposure to distorted unfamiliar faces (Study 1), and after exposure to distorted self and friend faces (Study 2).

The fact that perceptions of one's own and a close friend's face are rapidly changed by exposure to distorted unfamiliar faces in Study 1 demonstrates that there exists a common representation for all classes of faces. Although adaptation effects have been shown previously for recently learned faces (Leopold et al., 2001) and for celebrity faces (Carbon and Leder, 2005; Carbon et al., 2007), this is among the first studies to date to demonstrate that personally familiar faces are subject to the same rapid effects of adaptation, and that adaptation effects can transfer from unfamiliar faces to more robustly represented personally familiar faces. Indeed, while Laurence and Hole (2011) demonstrated figural aftereffects for personally familiar faces (the self-face), their research focused on within-identity adaptation. In the current paper, we demonstrate cross-identity adaptation from unfamiliar to personally familiar, robustly represented faces. A more "robust" representation for personally familiar faces may involve a more detailed representation of facial configuration (e.g., Balas et al., 2007), and the observation here of aftereffects following exposure to faces with distorted configuration suggests that this configural representation can be tapped into and rapidly updated (see Allen et al., 2009, for evidence of a similarly robust configural representation for self-faces and other personally familiar faces).

Although our representation of and memory for highly familiar faces is more stable than that for recently encountered faces (e.g., Bruce et al., 1999; Hancock et al., 2000), a representation that is updated to incorporate both short- and long-term changes to facial shape and expression is useful for the recognition of familiar and more recently learned faces (Carbon and Leder, 2005; Carbon et al., 2007; Carbon and Ditye, 2011). This proposal is consistent with functional accounts of adaptation. Just as in "low-level" light adaptation where average luminance is discounted so that variations about the average are signaled, so "high-level" face adaptation may involve discounting some perceptual characteristics of a face (e.g., those associated with race) so as to better signal changes in identity or expression (Webster et al., 2005). Insofar as we have a particularly efficient representation for personally familiar faces, we conjecture that people may be particularly sensitive to subtle changes in expression in the faces of close friends and loved ones.

It is important to note that a large proportion of facial aftereffects can be attributed to low-level or retinotopic image-based properties (e.g., Xu et al., 2008; Afraz and Cavanagh, 2009; see Hills et al., 2010 for an estimation of the size of this contribution). In the two studies presented here, we avoided an over-reliance on image-based cues in several ways. First, the identities of the adapting (unfamiliar) and test (self, friend) faces were different (Study 1), and aftereffects were observed to transfer across identities. Second, where the identities of the adapting and test faces were the same (Study 2), we elicited aftereffects using adapting faces which were holding different facial poses than the test faces. Along with Carbon and Ditye (2011), we interpret the transfer of aftereffects across identities and across different images of the same person as evidence of perceptual adjustment at the representational level, rather than merely image-based artifacts. Further study is warranted to test the robustness of these aftereffects to image manipulation (size, viewpoint) and retinotopic displacement. Considering Afraz and Cavanagh's (2009) finding that such alterations reduce but do not remove face identity aftereffects, we expect any future investigation to confirm our interpretation that the results presented here represent aftereffects which are present at the representational level.

Study 2 demonstrates aftereffects that are contingent on facial identity in that concurrent adaptation to compressed Self faces and expanded Friend 1 faces leads to aftereffects that are more pronounced for compressed Self faces but for expanded Friend 1 faces. The data, in fact, show a mixture of simple and contingent aftereffects with an overall downward shift in the distortedness rating curves after adaptation. This is what we would expect if Self and Friend 1 faces are structurally similar, and parallels Jaquet and Rhodes (2008), who show dissociable but not distinct coding of male and female faces. While the aftereffects for Self and Friend 1 faces do transfer to Friend 2 faces, here faces at all levels of distortion tested were judged as "less distorted" after adaptation. We conclude that adaptation is operating at the level of facial identity and not at the level of a categorical distinction between self and other. Across the sample of participants tested, which comprised ten groups of three friends, Friend 2 faces will be structurally similar to both Self and Friend 1 faces.

We conclude that shared neural processes underlie the visual recognition of self- and other-faces. Our results do reveal separate or dissociable coding of individual faces but not a more general dissociation between self and other. The current evidence for a separation in self and other face recognition remains of great interest to the study of social cognition and we conclude that these differences must operate at a level beyond the representation of face shape and identity studied here. Indeed, while the self-face may be represented as "special" in the brain, this does not appear to be due to separate neural representation for the categories of self- and other face. Rather, any special status self-face representation may claim to hold might be dependent on a qualitatively different way of processing and representing the self-face relative to other faces (e.g., Keyes and Brady, 2010), with the literature to date revealing a promisingly consistent emphasis on differences in lateralization of self- and other-face recognition (e.g., Turk et al., 2002; Uddin et al., 2005a; Keyes et al., 2010).

In summary, we conclude that the representation of personally familiar faces can be rapidly updated by visual experience, and that while dissociable coding for individual faces seems likely, there is no evidence for separate neural processes underlying self- and other-face recognition.

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FIAEs in famous faces are mediated by type of processing

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An important question regarding face aftereffects is whether it is based on face-specific or lower-level mechanisms. One method for addressing this is to explore how adaptation in upright or inverted, photographic positive or negative faces transfers to test stimuli that are either upright or inverted and normal or negated. A series of studies are reported in which this is tested using a typical face identity aftereffect paradigm in unfamiliar and famous faces. Results showed that aftereffects were strongest when the adaptor matched the test stimuli. In addition, aftereffects did not transfer from upright adaptors to inverted test images, but did transfer from inverted adaptors to upright test images in famous faces. However, in unfamiliar faces, a different pattern was observed. The results are interpreted in terms of how identity adaptation interacts with low-level adaptation and highlight differences in the representation of famous and unfamiliar faces.

Keywords: adaptation, aftereffects, face processing, familiar faces, unfamiliar faces

INTRODUCTION

Face distortion aftereffects (FDAEs) have been reported whereby adaptation to a face distorted in one direction (e.g., compressed) will cause post-adaptation faces to appear distorted in the opposite direction (e.g., expanded; Webster and MacLin, 1999; Yamashita et al., 2005; Carbon et al., 2007; Little et al., 2008). One critical question is whether aftereffects in face recognition reflect expert face-specific mechanisms or lower-level generalized mechanisms (Hole, 2011). Adaptation is typically said to be due to some sort of fatigue of cells that respond to a particular characteristic (e.g., Ferster and Miller, 2000). Low-level adaptation is tied closely to the physical properties of the stimuli: the adaptor must match the test stimuli. For higher-level adaptation mechanisms, the adaptor and the test do not have to match so well and aftereffects can transfer across viewpoints and images. There is sufficient evidence to suggest that both lower- and higher-level adaptation mechanisms are involved in face aftereffects, but the relative involvement of each is not well understood.

In their seminal study, Webster and MacLin (1999) created a series of stimuli of faces that were distorted from the norm in a Gaussian fashion in vector format. The resulting set of faces was presented to participants using a nulling-match procedure, whereby participants had to adjust a distorted face to appear normal. After inspecting an adaptation face for 5 min and for 8 s between each test image, participants had to adjust the distorted face such that it would appear normal. The adjustments the participants made were distorted in the opposite direction to the adaptation stimuli the participants had seen. The results were replicated in a normal rating procedure.

Webster and MacLin also noted that adaptation to an undistorted face was not possible: in other words, staring at a normal face did not affect the perception of distorted faces. Moreover, aftereffects transferred across faces and even to the perceivers' own faces. The aftereffects occurred for upright faces and for inverted faces, but only if the orientation of the adaptor face was matched with the orientation of the test faces. The FDAE is partially size-tolerant since it transfers from an adaptor of one size to test stimuli of a different size, even the size difference is a factor of 4 (Zhao and Chubb, 2001). The magnitude of such aftereffects is significantly smaller when the test face and the adaptor do not match. FDAEs also transfer across parts of the retina (Hurlbert, 2001; Anderson and Wilson, 2005) and partially across viewpoints (Jiang et al., 2006). These results indicate that these aftereffects involve at least some higher-level mechanisms.

Yamashita et al. (2005) found that the magnitude of face aftereffects are dependent on the visual similarities between the adaptor and the test stimuli. Nevertheless, changes that affect the recognizability of faces affect the magnitude of aftereffects more than changes that do not affect the recognizability. Size and color differences between the adaptor and the test stimuli reduce the magnitude of adaptation significantly less than spatial frequency and contrast differences between the adaptation and test stimuli.

Often considered similar to FDAEs are face identity aftereffects (FIAEs), whereby the perceived identity of a face is altered after adaptation to a particular identity. Leopold et al. (2001) conducted an elaborate study into FIAEs. In their study, 200 faces were morphed together to produce a prototype face. This was assumed to be the center of the face-space (see Valentine, 1991). Due to the morphing process, each face identity could be measured in terms of Euclidean distances from the prototype face. Thus, a series of faces were created ranging from the prototype face to the face identity, each differing in identity "strength." Identification thresholds (the required identity strength to perceive the face identity) were taken before and after adaptation to an anti-face identity (opposite from the face identity in terms of Euclidean geometry). Post-adaptation to the anti-face, the identification threshold was lowered by 12.5% suggesting it was easier to perceive the identity following adaptation since the prototypical face is shifted. The magnitude of the aftereffects were similar for upright and inverted faces, provided that the adaptation and test faces were in the same orientation.

Another facet of the FIAE is that it transfers across viewpoints at least in some participants (Jiang et al., 2007, 2009). Their participants were adapted to a face image in one pose and tested on images in the same or different poses. Their results indicated that although significant adaptation occurred when the faces are in a different pose, the magnitude is significantly less than when the images are in the same pose. This study certainly indicates that this adaptation is not solely based on the visual similarity between adaptation and test (and thus higher-level). Similar results were obtained by Benton et al. (2006) in that some of their participants showed adaptation transferring across viewpoints while others did not. Hills et al. (2008) found an individual difference variable that moderated the magnitude of face aftereffects: the ability to visualize whereby participants who were better able to mentally visualize a scene showed larger aftereffects than participants less able to visualize. Suggesting that there is some higher-level mechanism behind these aftereffects leads on to the question of whether this mechanism is face-specific or if is based on shape-aftereffects (e.g., Suzuki, 2001, 2003).

Face recognition is characterized by an expert processing mechanism that relies on the configuration of two eyes above a nose above a mouth rather than processing features independently (typically referred to as configural coding as opposed to featural coding (e.g., Maurer et al., 2002). This configuration is disrupted in an inverted face (Yin, 1969), making it harder to recognize (e.g., Diamond and Carey, 1986). Photographic negation (reversed contrast polarity) of a facial image causes it to be recognized less accurately, but does not alter the type of processing engaged (e.g., Galper, 1970). Photographic negatives are generally associated with more error in encoding rather than a change in processing (e.g., Valentine, 1991; George et al., 1999; Russell et al., 2006).

Few studies have looked at the effect type of processing (expert and potentially face-specific configural coding versus inexpert and object-based featural coding) has on the magnitude of the FIAE. In the FDAE, Watson and Clifford (2003, 2006) have shown that aftereffects do not transfer as readily across orientations. However, aftereffects are observed in inverted faces even when the adaptor is upright, suggesting that adaptation does transfer from expert face-processing mechanisms to inexpert mechanisms. Hole (2011) has shown that adaptation to upright, inverted, or stretched famous faces caused significant aftereffects in upright test faces. This suggests that the FIAE does transfer from inexpertly coded faces to expertly coded ones.[1]

There is one caveat with much of the research presented thus far. It has been conducted on unfamiliar faces. Unfamiliar face perception is based on different mechanisms and neural systems than familiar (personally familiar, experimentally manipulated familiar, famous, or own faces) face perception (Ellis et al., 1979; Tong and Nakayama, 1999; Megreya and Burton, 2006; Gobbini and Haxby, 2007). The representation of familiar faces must be invariant to changes in viewpoint, expression, and other visual changes. This allows them to be recognized from minimal visual information and even from low quality video images (Burton et al., 1999). Unfamiliar faces are difficult to recognize even under optimal conditions (Kemp et al., 1997) because they are represented in a more pictorial and two-dimensional manner (e.g., Ryu and Chaudhuri, 2006). The representations of faces of different levels or types of familiarity is likely to be based on different mechanisms again (e.g., Taylor et al., 2009). Given that the representations of faces depends on levels of familiarity it is important to explore how face aftereffects represent themselves faces that are not unfamiliar. There have been limited studies conducted on adaptation in famous faces specifically.

Jiang et al. (2007) manipulated the level of familiarity participants had with computer-generated faces. In the highest level of familiarity, in which participants were presented with the same face in multiple views for 32 5-s exposures, the aftereffects transferred across viewpoint more so than in the lowest level of familiarity, in which participants were presented with the face in one view only. Furthermore, in the highest level of familiarity, the aftereffects transferred to faces under novel illumination conditions (Jiang et al., 2009). However, the aftereffects demonstrated by Jiang et al. are still in originally unfamiliar faces. Familiar faces have been viewed much more extensively in a variety of contexts and illumination conditions.

Carbon and Leder (2005, 2006) have shown that both the FDAE and the FIAE are longer lasting in famous faces than unfamiliar faces, but do not transfer to other faces in the same way that aftereffects in unfamiliar faces do (Carbon et al., 2007). Hills et al. (2010) have shown that non-visual adaptors can cause aftereffects in famous faces. Prolonged imagination, exposure to the name or to the voice cause aftereffects in faces to a similar degree as adaptation to a different image of the face.

This background summarizes three key areas of face aftereffects that require further elaboration: firstly, whether there is reliance on specific face-processing mechanisms in the FIAE. This can be tested by exploring how the aftereffects transfer from upright to inverted stimuli and vice versa. Secondly, how much (relatively) of the FIAE is low-level and how much is high-level. Part of this can be explored by assessing how aftereffects transfer across different image manipulations and most importantly to different images. A third question is whether the aftereffects are different across famous and unfamiliar faces.

EXPERIMENT 1A

An experiment was conducted that aimed to examine how the FIAE is affected by configural processing. Eight different adaptation stimuli were used comparing the effects of same and different adaptor image from that used at test, whilst also comparing the effects of orientation and negation of the magnitude of adaptation. Two hypotheses can be made regarding this study. Image-based adaptation may occur, whereby adaptation will be greater when the adaptor and test stimuli are matched, regardless of what the adaptor is. However, if the FIAE is based on some form of face-specific coding mechanism, then it is likely to be observed for

[1] 1It must be noted that some authors have found that inverted faces are processed both featurally and configurally but to different degrees (see, e.g., Miellet et al., 2011) given that there is a linear and not a step change in the how rotation affects face perception (Edmonds and Lewis, 2007; van der Linde and Watson, 2010). This suggests that inverted faces are processed *more* featurally than upright faces and *less* configurally. In other words, inverted faces are processed in a much less expert and face-specific manner than upright faces.

upright rather than inverted faces.[2] The difference between Experiments 1a and 1b is that the faces in Experiment 1a were famous, whereas the faces in Experiment 1b were unfamiliar.

METHOD

PARTICIPANTS

Thirty-two (9 male, mean age 21 years) Cardiff University students undertook this experiment as partial fulfillment of a course requirement. All participants had normal or corrected-to-normal vision. All were White British nationals who were familiar with the famous faces.

MATERIALS

Two different images of George Bush and Tony Blair were collected. They were matched for dimensions (100 mm × 160 mm) and resolution (72 dpi). Image one of George Bush was matched for pose and lighting with image one of Tony Blair. A series of morphs were created using Smartmorph™Software with 200 anchor points. Fifty morphs were created that ranged from 100% George Bush to 100% Tony Blair in increments of 2% (thus 50 images). Image two of George Bush was in a different pose and under different lighting conditions from image one of George Bush and matched to image two of Tony Blair. The "image two" pair were morphed together in the same way as the image one pair. The 100% images for each identity and each pair were also used as the adaptor.

These two sets of morphs were inverted into two addition sets. Two negated sets were also created using Adobe Photoshop™image manipulation software. These negated sets were subsequently inverted to create two additional sets of stimuli. The 50% image of each type of stimulus is presented in **Figure 1**. All stimuli were presented using SuperlabPro 2™Research Software on an RM PC.

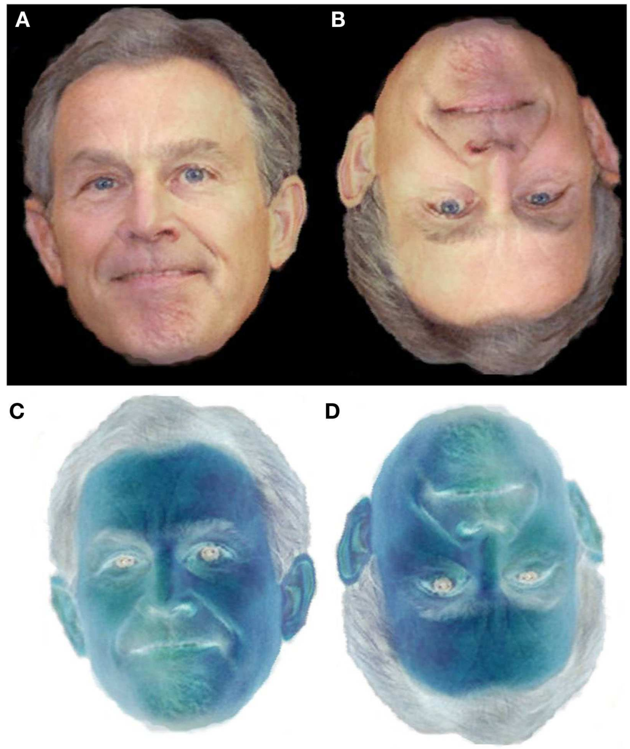

FIGURE 1 | Examples of the stimuli used in this Experiment. (A) The unaltered 50% midpoint. **(B)** The inverted 50% midpoint. **(C)** The negated 50% midpoint. **(D)** The inverted and negated 50% midpoint.

DESIGN

The adaptor was manipulated between subjects with four levels (same image, different image, negated image, or inverted image). A within-subjects manipulation was also implemented, whereby participants saw eight types of test faces: 2 (same or different image) × 2 (inverted or upright) × 2 (negated or control). The magnitude of adaptation was measured as the change in the PSE pre- to post-adaptation. Participants were randomly allocated to one of the between subjects conditions with the proviso that there was an equal number of participants in each condition ($N = 12$).

PROCEDURE

Participants were introduced to pictures of George Bush and Tony Blair that they would see in the experiment. The Experiment had three consecutive phases: baseline, adaptation, and test. The baseline phase involved the participants seeing all the morphs 10 times in a random order. They had to make a decision based on whether they thought the image looked more like George Bush (by pressing the G key) or Tony Blair (by pressing T key) based on the methodologies in Levitt (1971). Each morph was on screen until the participant responded. Between each morph a 100-ms Gaussian noise mask was on screen. The purpose of this baseline phase was to discover each individual participant's "natural" PSE.

Once the baseline had finished, the participants were instructed to rest for 2 min and then given a 3-min irrelevant distractor task. This distractor task involved a participants filling out a questionnaire about their experiences at University. Following this, participants were presented with the adaptor image for 60 s. They were told to examine the image that was presented on screen, which was either George Bush or Tony Blair.

Immediately following the adaptor, a repeat of the baseline procedure took place. However, preceding each test face, participants were presented with the adaptor for another 5 s (e.g., Hills et al., 2010). Once the test phase had been completed, participants were thanked and debriefed fully. The total experimentation time for each participant was approximately 75 min. A schematic representation of the procedure is presented in **Figure 2**.

RESULTS

The magnitude of adaptation was calculated by subtracting the PSE pre-adaptation from the PSE post-adaptation. There was no effect of image identity or pair, as such the data were collapsed across these variables. **Figure 3** shows the mean percentage increase in PSE in the George Busy–Tony Blair continuum for each of the test stimuli for each of the adaptor type. A positive

[2]While a non-face class of stimuli could be employed to ensure that we are really testing face-specific mechanisms, it is generally accepted that inverted faces are a useful control since they match upright faces on all low-level visual characteristics, but do not recruit "face-specific" brain regions (Gauthier et al., 1999), nor have the same "face-specific" ERP (e.g., Eimer, 2000).

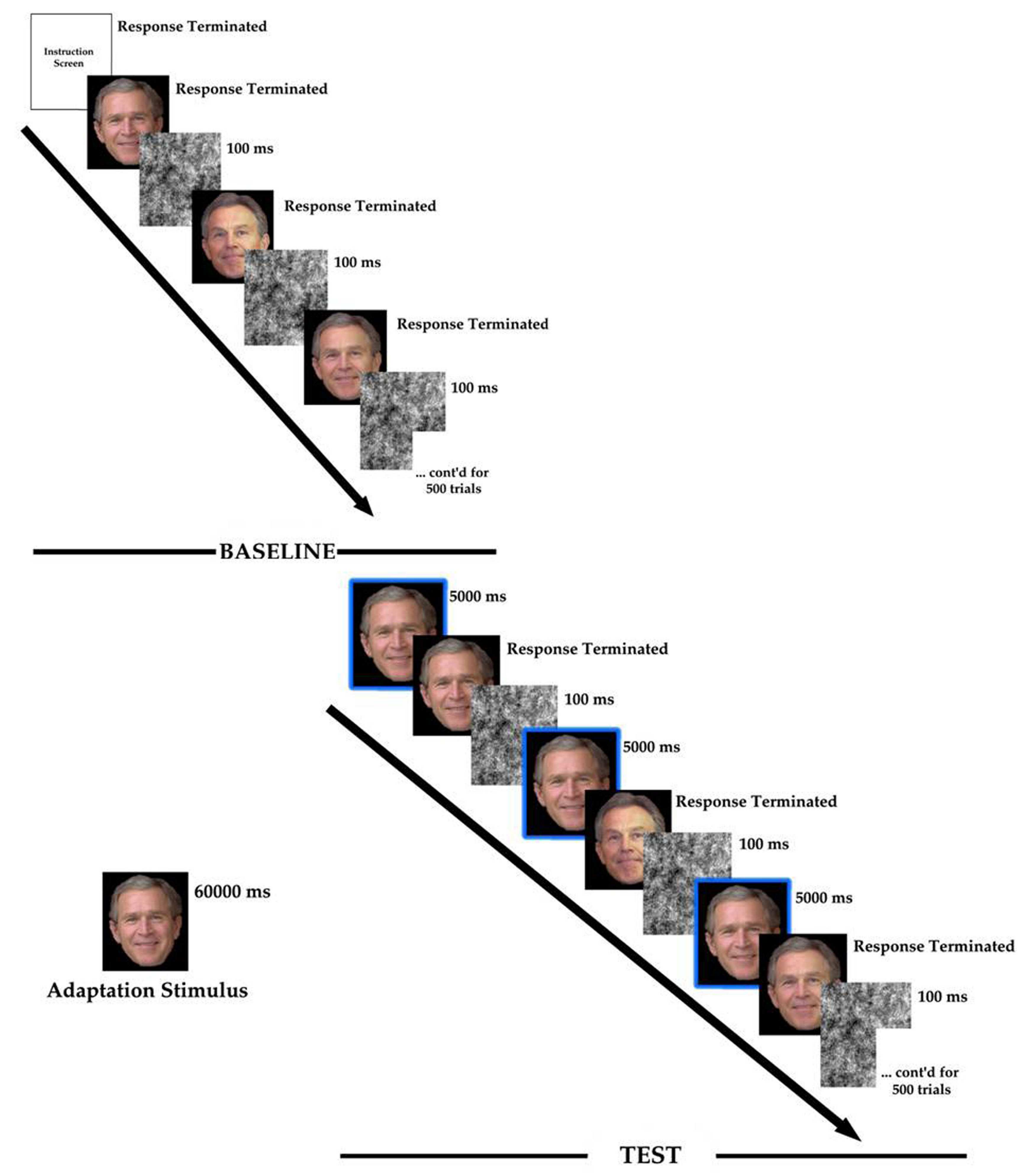

FIGURE 2 | The procedure for the experimentation. Those surrounded by the box are the adaptor repeated during the test phase.

number indicates more identity is needed to perceive the identity of the adaptor, i.e., reduced identity strength. The first analysis was a 4 (adaptor type) × 2 (orientation of test stimuli) × 2 (photographic positive/negative test stimuli) × 2 (same or different image). This revealed a significant four-way interaction, $F(3, 28) = 16.51$, MSE = 3.07, $p < 0.05$, $\eta_p^2 = 0.64$. The four-way

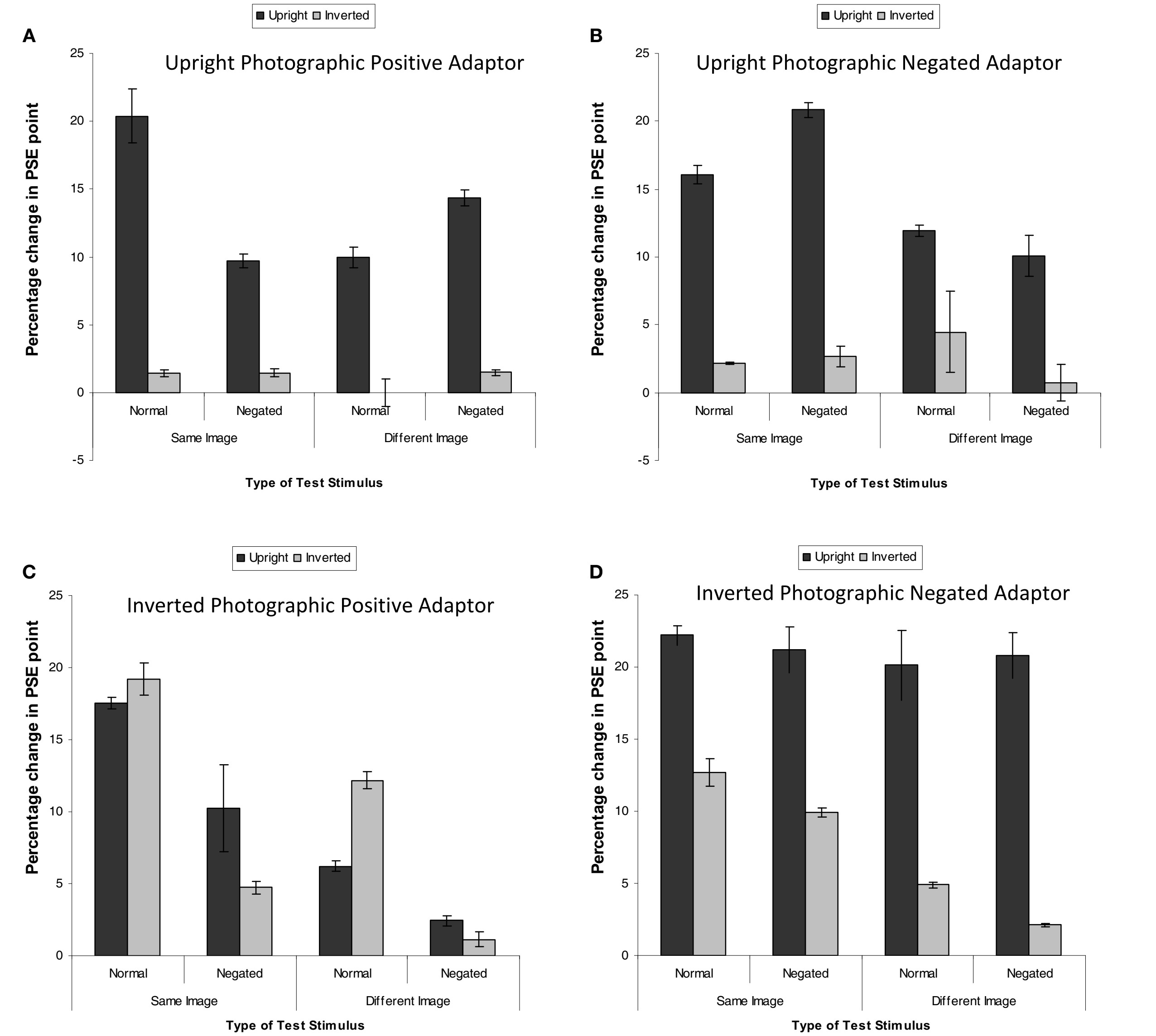

FIGURE 3 | Mean PSE (in identity strength needed to perceive the adapted identity) shift pre- to post-adaptation (as a measure of the magnitude of the aftereffect) for famous faces, when the adaptor is (A) upright and photographically positive, (B) upright and negated, (C) inverted and positive, and (D) inverted and negated. Darker bars represent upright test stimuli, lighter bars represent inverted test stimuli. Error bars represent standard error.

interaction is interpreted as the three-way interaction (between orientation, photographic negation, and image-change) is different depending on the adaptor type. This indicates that different adaptor types affect different mechanisms. To explore this, each three-way interaction for each adaptor type was analyzed. In addition, there was also a main effect of adaptor type, $F(3, 28) = 62.00$, $\text{MSE} = 9.47$, $p < 0.05$, $\eta_p^2 = 0.87$, in which aftereffects were larger following adaptation to the negated and inverted stimuli than all other stimuli (all $p\text{s} < 0.05$).

UPRIGHT PHOTOGRAPHIC POSITIVE ADAPTOR

Figure 3A indicates that greater adaptation occurred when the test stimuli were upright. The data were subjected to a $2 \times 2 \times 2$ within-subjects ANOVA. This revealed that greater adaptation occurred when the same image was used for both adaptation and test, $F(1, 7) = 66.44$, $\text{MSE} = 0.77$, $p < 0.05$, $\eta_p^2 = 0.91$. Greater adaptation was observed for upright test stimuli than inverted test stimuli, $F(1, 7) = 1664.92$, $\text{MSE} = 1.51$, $p < 0.05$, $\eta_p^2 = 0.97$. There were no significant differences in the magnitude of adaptation for negated test stimuli, $F(1, 7) = 3.44$, $\text{MSE} = 6.46$, $p > 0.10$, $\eta_p^2 = 0.33$. There was a significant interaction between image and negation, $F(1, 7) = 1027.69$, $\text{MSE} = 0.27$, $p < 0.05$, $\eta_p^2 = 0.99$, revealing that greater adaptation was found for same image unaltered test stimuli than same image negated stimuli (mean difference = 5.31, $p < 0.05$) and different negated test stimuli than different unaltered stimuli (mean difference = 2.96, $p > 0.05$). There was also an interaction between negation and orientation, $F(1, 7) = 68.50$, MSE = 0.89, $p < 0.05$, $\eta_p^2 = 0.91$. Simple effects showed that the effect of orientation was larger for unaltered stimuli (mean difference = 14.490, $p < 0.05$) than for negated stimuli (mean difference = 10.577, $p < 0.05$). Finally, there was a three-way interaction, $F(1, 7) = 167.24$, MSE = 1.12, $p < 0.05$, $\eta_p^2 = 0.96$.

UPRIGHT PHOTOGRAPHIC NEGATED ADAPTOR

A parallel analysis was run for when the adaptor was a negated image (**Figure 3B**). This revealed a significant effect of image, whereby greater adaptation was observed when the same image was used at adaptation and test than when a different image was used, $F(1, 7) = 288.52$, MSE = 14.95, $p < 0.05$, $\eta_p^2 = 0.98$. There was also a significant effect of orientation, whereby greater adaptation was observed when the test stimuli were upright than when they were inverted, $F(1, 7) = 350.06$, MSE = 6.84, $p < 0.05$, $\eta_p^2 = 0.98$. There was a significant interaction between image and orientation, $F(1, 7) = 123.82$, MSE = 1.88, $p < 0.05$, $\eta_p^2 = 0.95$. Simple main effects showed that the magnitude of adaptation was stronger for negated images than unadjusted images when the same image was used as the adaptor as those that made up the test morph continua (mean difference = 2.63, $p < 0.05$), whereas the magnitude of adaptation was stronger for unadjusted images than negated images when a different image was used as the adaptor to that at test (mean difference = 2.79, $p < 0.05$). There was also an interaction between negation and orientation, $F(1, 7) = 28.12$, MSE = 1.35, $p < 0.05$, $\eta_p^2 = 0.80$, which revealed itself in a greater magnitude of adaptation for negated upright stimuli than inverted stimuli (mean difference = 13.46, $p < 0.05$) which was greater than when the stimuli were unadjusted (mean difference = 10.69, $p < 0.05$).

INVERTED PHOTOGRAPHIC POSITIVE ADAPTOR

A further parallel analysis was run on the data when the adaptor was inverted (**Figure 3C**). This revealed a significant effect of image, whereby the same image produced greater adaptation than a different image, $F(1, 7) = 115.93$, MSE = 7.64, $p < 0.05$, $\eta_p^2 = 0.94$. There was also a main effect of negation, whereby there was less adaptation for negated images than control images, $F(1, 7) = 733.48$, MSE = 1.83, $p < 0.05$, $\eta_p^2 = 0.99$. Finally, there was a significant interaction between image and orientation, $F(1, 7) = 18.82$, MSE = 10.99, $p < 0.05$, $\eta_p^2 = 0.73$, revealing itself through greater magnitude of adaptation for same upright images than same inverted images (mean difference = 1.95, $p < 0.05$) and different inverted images than different upright images (mean difference = 2.33, $p < 0.05$). No other effects were significant.

INVERTED PHOTOGRAPHIC NEGATED ADAPTOR

A fourth analysis was run on the data for when the adaptor was both inverted and negated (**Figure 3D**). This revealed a significant effect of image, whereby greater adaptation was observed when the adaptation and test stimuli matched than when they were different, $F(1, 7) = 373.41$, MSE = 0.87, $p < 0.05$, $\eta_p^2 = 0.98$. There was a significant effect of negation, whereby greater adaptation was observed when the test stimuli were not negated than when they were, $F(1, 7) = 65.24$, MSE = 0.54, $p < 0.05$, $\eta_p^2 = 0.90$. There was also a main effect of orientation, $F(1, 7) = 261.97$, MSE = 11.42, $p < 0.05$, $\eta_p^2 = 0.97$, whereby inverted test stimuli were less adapted to than upright test stimuli. There was an interaction between image and orientation, $F(1, 7) = 24.68$, MSE = 3.49, $p < 0.05$, revealing itself through a larger main effect of orientation when the test stimuli were different from the adaptor (mean difference = 16.96, $p < 0.05$) than when the test stimuli were the same as the adaptor (mean difference = 10.39, $p < 0.05$). Finally, there was an interaction between negation and orientation, $F(1, 7) = 39.47$, MSE = 0.69, $p < 0.05$, $\eta_p^2 = 0.85$. Simple effects revealed that the main effect of orientation was greater for negated test stimuli (mean difference = 14.98, $p < 0.05$) than for unaltered test stimuli (mean difference = 12.38, $p < 0.05$).

EXPERIMENT 1B – UNFAMILIAR FACES

All aspects of the method were identical to Experiment 1a, except that a different set of 32 participants were recruited and were tested on unfamiliar faces. The unfamiliar faces were matched for image quality to the famous faces, but were from the NimStim Face Stimulus Set (Tottenham et al., 2002) and had been previously rated as a similar level of attractiveness and distinctiveness as the famous faces in a pretest. They were matched and morphed in the same way as in Experiment 1a. The procedure contained an extra phase when the participants were introduced to the faces (prior to the baseline). Participants were shown each face identity (with either the letter T or G underneath) for 5 s five times. Then they were presented the faces 10 times without the letter and asked to identify the face (by pressing either T or G). Participants were given feedback. After these trials, the participants were given a further 10 trials without feedback. Accuracy was above 95% for all participants at this point. Following this, the procedure was identical to Experiment 1a.

RESULTS

The analysis protocol was identical for Experiments 1a and 1b, and the mean PSE shift is presented in **Figure 4**. This revealed a significant four-way interaction, $F(3, 28) = 27.59$, MSE = 0.45, $p < 0.05$, $\eta_p^2 = 0.75$, similar to Experiment 1a. There main effect of adaptor type was not significant, $F(3, 28) = 1.44$, MSE = 18.10, $p > 0.25$, $\eta_p^2 = 0.13$.

UPRIGHT PHOTOGRAPHIC POSITIVE ADAPTOR

Figure 4 indicates that greater adaptation occurred when the test stimuli were upright (**Figure 4A**). The data were subjected to a 2 × 2 × 2 within-subjects ANOVA. This revealed that greater adaptation occurred when the same image was used for both adaptation and test, $F(1, 7) = 112.04$, MSE = 2.54, $p < 0.05$, $\eta_p^2 = 0.94$. Greater adaptation was observed for upright test stimuli than inverted test stimuli, $F(1, 7) = 101.65$, MSE = 2.06, $p < 0.05$, $\eta_p^2 = 0.94$. Greater adaptation was observed for photographic positive stimuli than photographic negative stimuli, $F(1, 7) = 77.14$, MSE = 2.36, $p < 0.05$, $\eta_p^2 = 0.92$. There was a significant interaction between image and negation, $F(1, 7) = 114.88$, MSE = 0.17, $p < 0.05$, $\eta_p^2 = 0.85$, revealing that greater adaptation was found for same image unaltered test stimuli than same image negated stimuli (mean difference = 5.32, $p < 0.05$) and different negated test stimuli than different unaltered stimuli (mean difference = 3.11, $p < 0.05$). There was also an interaction between

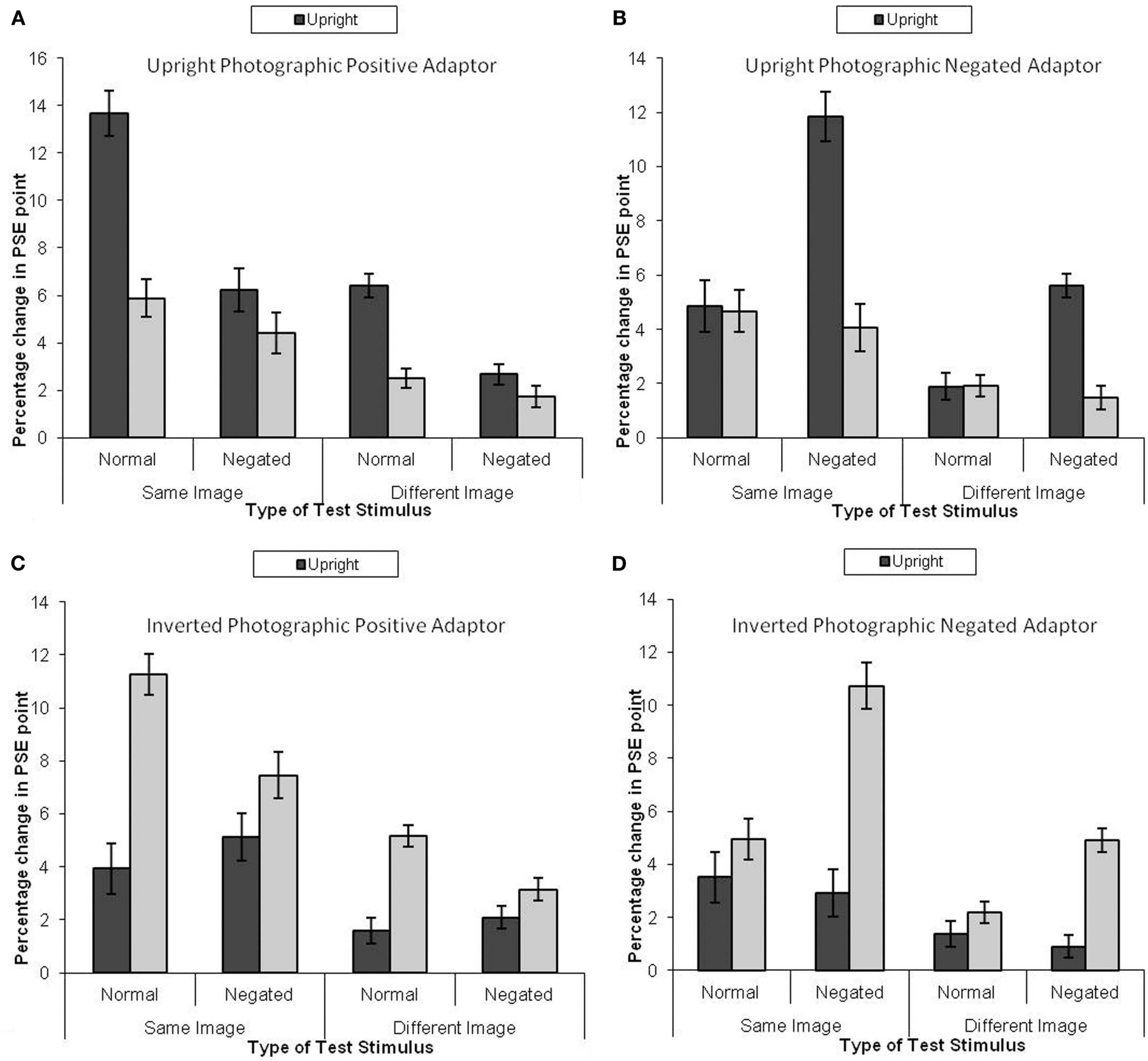

FIGURE 4 | Mean PSE (in identity strength needed to perceive the adapted identity) shift pre- to post-adaptation (as a measure of the magnitude of the aftereffect) for unfamiliar faces, when the adaptor is (A) upright and photographically positive, (B) upright and negated, (C) inverted and positive, and (D) inverted and negated. Darker bars represent upright test stimuli, lighter bars represent inverted test stimuli. Error bars represent standard error.

negation and orientation, $F(1, 7) = 39.90$, MSE = 2.01, $p < 0.05$. Simple effects showed that the effect of orientation was larger for unaltered stimuli (mean difference = 5.85, $p < 0.05$) than for negated stimuli (mean difference = 1.38, $p < 0.05$). Finally, there was a three-way interaction, $F(1, 7) = 40.16$, MSE = 0.23, $p < 0.05$, $\eta_p^2 = 0.85$.

UPRIGHT PHOTOGRAPHIC NEGATE ADAPTOR

A parallel analysis was run for when the adaptor was a negated image (see **Figure 4B**). This revealed a significant effect of image, whereby greater adaptation was observed when the same image was used at adaptation and test than when a different image was used, $F(1, 7) = 76.62$, MSE = 2.78, $p < 0.05$, $\eta_p^2 = 0.92$. There was also a significant effect of orientation, whereby greater adaptation was observed when the test stimuli were upright, $F(1, 7) = 57.58$, MSE = 2.52, $p < 0.05$, $\eta_p^2 = 0.89$. There were larger aftereffects in photographic positive images than negated images, $F(1, 7) = 27.34$, MSE = 3.41, $p < 0.05$, $\eta_p^2 = 0.80$. There was a significant interaction between image and photographic negation, $F(1, 7) = 14.02$, MSE = 0.67, $p < 0.05$, $\eta_p^2 = 0.68$. Simple effects showed that the magnitude of adaptation was stronger for negated images than unadjusted images when the same image was used as the adaptor as those that made up the test morph continua (mean difference = 3.18, $p < 0.05$), and when a different image was used as the adaptor to that at test (mean difference = 1.65, $p < 0.05$). There was also an interaction between negation and orientation, $F(1, 7) = 63.71$, MSE = 2.15, $p < 0.05$, $\eta_p^2 = 0.90$, which revealed itself in a greater magnitude of adaptation for negated upright stimuli than inverted stimuli (mean difference = 5.94, $p < 0.05$) and no difference when the test stimuli were unadjusted (mean difference = 0.88, p = ns).

INVERTED PHOTOGRAPHIC POSITIVE ADAPTOR

A further parallel analysis was run on the data when the adaptor was inverted (**Figure 4C**). This revealed a significant effect of image, whereby the same image produced greater adaptation than a different image, $F(1, 7) = 148.63$, MSE = 1.68, $p < 0.05$, $\eta_p^2 = 0.96$. There was also a main effect of negation, whereby there was less adaptation for negated images than control images, $F(1, 7) = 6.19$, MSE = 2.68, $p < 0.05$, $\eta_p^2 = 0.47$. The main effect of orientation was significant, whereby there was more adaptation for inverted images than upright images, $F(1, 7) = 83.80$, MSE = 2.42, $p < 0.05$, $\eta_p^2 = 0.92$. There was a significant interaction between photographic negation and orientation, $F(1, 7) = 16.65$, MSE = 3.38, $p < 0.05$, $\eta_p^2 = 0.70$, in which the aftereffects were greater when the test images were inverted than upright when they were photographic positive (mean difference = 5.45, $p < 0.05$) but not when the test images were negated (mean difference = 1.69, ns). Finally, there was an interaction between orientation and image type, $F(1, 7) = 117.64$, MSE = 0.22, $p < 0.05$, $\eta_p^2 = 0.94$, revealing itself through greater magnitude of adaptation for same inverted images than same upright images (mean difference = 4.83, $p < 0.05$) and different inverted images than different upright images (mean difference = 2.31, $p < 0.05$). No other effects were significant.

INVERTED PHOTOGRAPHIC NEGATE ADAPTOR

A fourth analysis was run on the data for when the adaptor was both inverted and negated (**Figure 4D**). This revealed a significant effect of image, whereby greater adaptation was observed when the adaptation and test stimuli matched than when they were different, $F(1, 7) = 97.87$, MSE = 1.66, $p < 0.05$, $\eta_p^2 = 0.93$. There was a significant effect of negation, whereby greater adaptation was observed when the test stimuli were negated than when they were not, $F(1, 7) = 15.11$, MSE = 3.67, $p < 0.05$, $\eta_p^2 = 0.68$. There was also a main effect of orientation, $F(1, 7) = 33.71$, MSE = 5.85, $p < 0.05$, $\eta_p^2 = 0.83$, whereby inverted test stimuli were more adapted to than upright test stimuli. There was an interaction between image and orientation, $F(1, 7) = 29.60$, MSE = 0.67, $p < 0.05$, $\eta_p^2 = 0.81$, revealing itself through a larger main effect of orientation when the test stimuli were the same as the adaptor (mean difference = 4.62, $p < 0.05$) than when the test stimuli were the different to the adaptor (mean difference = 2.40, $p < 0.05$). There was an interaction between negation and orientation, $F(1, 7) = 14.78$, MSE = 6.23, $p < 0.05$, $\eta_p^2 = 0.68$. Simple effects revealed that the main effect of orientation was greater for negated test stimuli (mean difference = 5.91, $p < 0.05$) than for unaltered test stimuli (mean difference = 1.11, ns). Finally, there was an interaction between photographic negation and image, $F(1, 7) = 26.39$, MSE = 0.33, $p < 0.05$, $\eta_p^2 = 0.79$, whereby negated images had a larger aftereffect than positive images when the test images were the same as the adaptor (mean difference = 2.60, $p < 0.05$) than when the test images were different to the adaptor (mean difference = 1.12, ns).

SUMMARY

These results indicate that the interaction between type of processing, image degradation, and face-specific mechanisms (as indicated by the factors: orientation, photographic negation, and image-change) depends on what the adaptor is. This will be further discussed in the Section "General Discussion." To address whether there are differences across familiarity, a five-way ANOVA combining Experiments 1a and 1b, thus containing the factors: familiarity (famous or unfamiliar faces); adaptor type; orientation (upright and inverted); negation (negated and normal); and image (same and different). Crucially, the five-way interaction was significant, $F(3, 56) = 7.77$, MSE = 1.76, $p < 0.05$, $\eta_p^2 = 0.29$. Additionally, the main effect of familiarity was significant, $F(1, 56) = 30.24$, MSE = 13.78, $p < 0.05$, $\eta_p^2 = 0.81$, in which aftereffects were significantly stronger for famous faces than unfamiliar faces (mean difference = 5.13). This suggests that the mechanisms behind adaptation in famous and unfamiliar faces are different. Further discussion of this is provided in the Section "General Discussion."

EXPERIMENT 2

A second experiment was conducted that aimed to examine how the FIAE is affected by other lower-level visual processing. Three different adaptors and three different test image manipulations were used. These compared the effects of high- and low-pass visual filtering on the FIAE in famous faces. Face identification is typically carried by spatial frequencies with a peak sensitivity between 8 and 13 cycles per degree (Näsänen, 1999), though higher spatial frequencies may be involved in early face identification (Halit et al., 2006). Based on this, identity aftereffects ought to be stronger for unaltered faces and low-pass faces. In addition to this, two further hypotheses (similar to Experiment 1) can be made regarding this study. Image-based adaptation may occur, whereby the greatest adaptation will be greater when the adaptor and test stimuli are matched, regardless of what the adaptor is. Alternatively, identity adaptation could occur, whereby aftereffects transfer across the image manipulations. Given that for identity recognition, a mismatch in spatial frequency of a single bandwidth from learning to test causes a recognition detriment of approximately 20% (Liu et al., 2000), we would expect that aftereffects should not transfer so readily across adaptors of one spatial frequency distribution to test stimuli of a different spatial frequency distribution.

METHOD

PARTICIPANTS AND MATERIALS

Sixty Cardiff University students undertook this experiment as partial fulfillment of a course requirement. All participants had normal or corrected vision. All were White British nationals who were famous with the famous faces.

The unaltered image pair 1 and associated morphs from Experiment 1 was used here. Two additional sets were created that were either high- or low-pass filtered. This filtering was completed using MATLAB software. The original faces were put through a bandpass filter by multiplying together a low-pass and high-pass Butterworth filter using the equations presented in Collin et al. (2004). Subsequently, the images were inversely transformed into the spatial domain. The filtered faces had center frequencies of 7.08 (for the low-pass filtered faces) and 14.15 (for the high-pass filtered faces) cycles per face, with a bandwidth of 0.5 octaves. These center frequencies were chosen given that they are just outside the peak sensitivity bandwidth used in face identification (Näsänen, 1999).

DESIGN AND PROCEDURE

A 3 × 3 mixed design was employed in which the type of adaptor was manipulated between subjects and the type of test stimuli was manipulated within-subjects. These were either unaltered, high- or low-pass filtered images. The experimental procedure was undertaken in the same way as Experiment 1.

RESULTS

The data, summarized in **Figure 5**, were subjected to a 3 × 3 mixed-subjects ANOVA. This revealed there was an effect of the test stimuli, $F(2, 114) = 4.50$, MSE = 49.47, $p < 0.05$, $\eta_p^2 = 0.07$, in which aftereffects were smaller in unaltered test stimuli than low-pass filtered test stimuli (mean difference = 3.85, $p < 0.05$). There was also a main effect of adaptor type, $F(2, 57) = 8.97$, MSE = 46.35, $p < 0.05$, $\eta_p^2 = 0.24$, in which, there was greater aftereffects following adaptation to the unaltered and high-pass filtered adaptors than the low-pass filtered faces (mean difference = 5.06, $p < 0.05$ and mean difference = 3.79, $p < 0.05$, respectively).

EXPERIMENT 2B

Experiment 2b was conducted in the same way as Experiment 2a, except that the faces were unfamiliar (the same as those used in Experiment 1b. A different set of 60 participants were recruited.

RESULTS

The data, summarized in **Figure 6**, were subjected to a 3 × 3 mixed-subjects ANOVA. This revealed there was a marginal effect of the test stimuli, $F(2, 114) = 2.78$, MSE = 39.23, $p = 0.07$, $\eta_p^2 = 0.05$, in which aftereffects were smaller in unaltered test stimuli than low-pass filtered test stimuli (mean difference = 2.69, $p < 0.05$). There was also a main effect of adaptor type, $F(2, 57) = 3.27$, MSE = 103.05, $p < 0.05$, $\eta_p^2 = 0.10$, in which, there was greater aftereffects following adaptation to the unaltered than the high-pass and low-pass filtered faces, though not significantly (mean difference = 4.35, $p = 0.07$ and mean difference = 3.81, $p = 13$, respectively).

SUMMARY

Similar to Experiment 1, a comparison across famous and unfamiliar faces was conducted by inputting the data into a 2 × 3 × 3 mixed-subjects ANOVA with the factors: familiarity of the face, adaptor type, and type of test stimuli. This time, the three-way interaction was not significant, $F(4, 228) = 1.17$, MSE = 44.35, $p = 0.32$, $\eta_p^2 = 0.02$. The main effect of familiarity was significant, $F(1, 114) = 33.10$, MSE = 74.70, $p < 0.05$, $\eta_p^2 = 0.23$, in which aftereffects were greater following adaptation to famous faces (mean difference = 5.24). Taken together, these results indicate that image degradation affects the FIAE famous and unfamiliar faces in a similar manner. However, aftereffects are greater in famous faces than unfamiliar faces.

GENERAL DISCUSSION

Across all conditions, the magnitude of the aftereffect was largest when the adaptor and the test stimuli matched. In fact, when the adaptor and test stimuli matched, the aftereffect was twice that of when they did not match. This indicates that the FIAE is based, at least partially, on low-level mechanisms. Specifically, approximately half of the observed aftereffect is low-level. This type of aftereffect is the same across famous and unfamiliar faces as revealed by the lack of significance of the three-way interaction in Experiment 2. In addition, there were differences across the nature

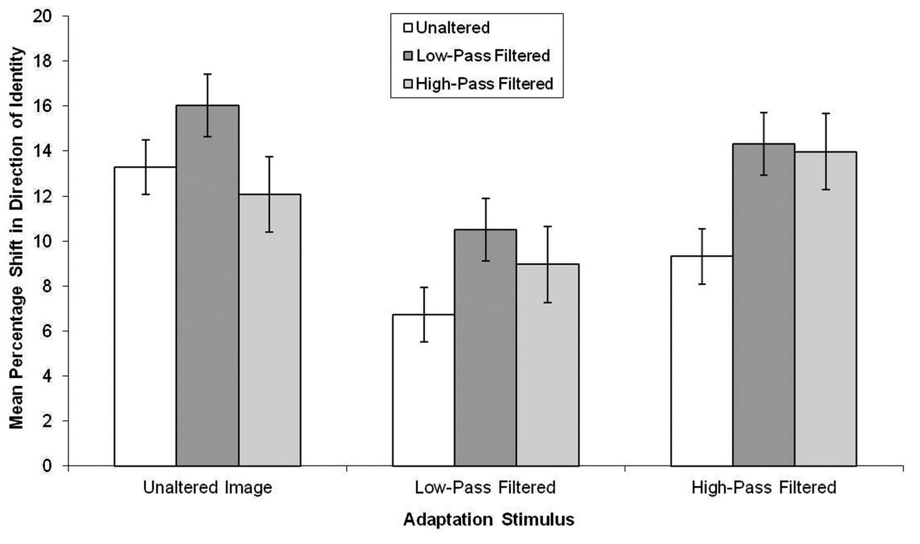

FIGURE 5 | Mean PSE (in identity strength needed to perceive the adapted identity) shift pre- to post-adaptation (as a measure of the magnitude of the aftereffect), for unaltered, low-pass, and high-pass filtered adaptation stimuli split by unaltered, low-pass, and high-pass filtered test stimuli for famous faces. Error bars represent standard error.

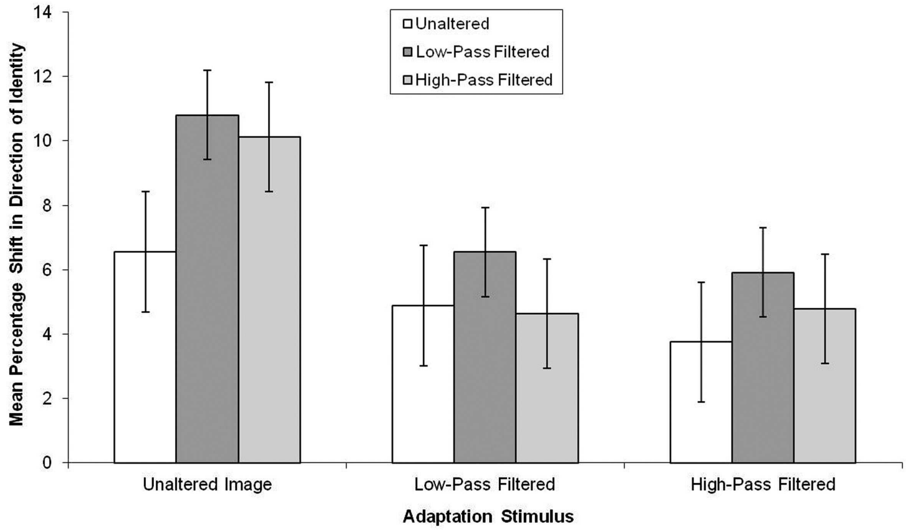

FIGURE 6 | Mean PSE (in identity strength needed to perceive the adapted identity) shift pre- to post-adaptation (as a measure of the magnitude of the aftereffect), for unaltered, low-pass, and high-pass filtered adaptation stimuli split by unaltered, low-pass, and high-pass filtered test stimuli for unfamiliar faces. Error bars represent standard error.

of the FIAEs for famous and unfamiliar faces as revealed by the five-way interaction in Experiment 1. The results for the unfamiliar faces directly replicate those found by Yamashita et al. (2005) when testing the FDAE. However, the results for famous faces are not consistent with these results (Experiment 1b).

Adaptation transfers across photographic negation and to a different image of the same face to a similar degree. Thus, photographic negation does not affect the FIAE in famous faces, possibly because it does not affect face-specific processing mechanisms. Identity can still be extracted quickly from a negated face, so the added error during encoding does not influence adaptation (see **Figures 3C,D**). Similarly, Experiment 2 demonstrated that low-level visual alterations to faces had similar effects on famous and unfamiliar faces, except that the aftereffects were typically larger in famous faces than unfamiliar faces. This is likely to be caused by more robust representations of famous faces (Ryu and Chaudhuri, 2006) and stronger aftereffects in famous faces than in unfamiliar faces (Carbon and Leder, 2005; Carbon and Ditye, 2012).

More interestingly, adaptation to an upright stimulus does not transfer to inverted test stimuli. This suggests that during the test phase, extracting identity from the inverted faces is unaffected by adaptation. This may be because it takes longer to recognize an inverted face (Valentine, 1988) and the response to the face is made before recognition is fully made (cf., the difference between a remember and a know response in the remember/know procedure).

The results are more intriguing when the adaptor is inverted. Here, the adaptation does transfer to upright stimuli (**Figures 3B,D** and **4B,D**). However, the magnitude of adaptation depends on how different the test stimuli are from the adaptor. The magnitude of adaptation is smaller when there are more differences between the adaptor and the test stimuli. When the adaptor is inverted and negated (**Figures 3D** and **4D**), the magnitude of adaptation does not depend on degree of difference between the adaptation stimuli and the test stimulus, since greater adaptation was noted for upright test stimuli.

These data are broadly consistent with those of Yamashita et al. (2005), in that the present study observed a transfer of adaptation from unaltered stimuli to negated images that was half that when the images matched. Yamashita et al. reported that this kind of transfer is small but still present. Here, we found that the effect was larger in famous faces than Yamashita et al. found and in unfamiliar faces. Perhaps, aftereffects in famous faces are more robust than in unfamiliar faces (Carbon and Leder, 2005, 2006) and more resistant to image manipulations.

These results are also somewhat different to those presented by Watson and Clifford (2006) in terms of the asymmetry of the adaptation effects transferring across upright and inverted faces. Specifically, here, we found that adaptation transfers more when the adaptor is inverted and the test stimuli are upright than vice versa. Watson and Clifford (2003, 2006) found the opposite asymmetry using unfamiliar faces. This highlights another difference in adaptation to famous and unfamiliar faces. Watson and Clifford (2003, 2006) explored aftereffects using different distortions to ours (gender-judgment and stretched faces). Thus, the differences in our results to Watson and Clifford may simply reflect different mechanisms in the FDAE compared to the FIAE. While this is possible, many authors suggest that the mechanisms for FDAE and FIAE are based on the shifting of a face prototype which suggests that the results ought to be comparable. Indeed, our results are consistent with those presented by Hole (2011) suggesting that familiarity is the critical variable here rather than methodological differences.

To explain why adaptation does not transfer from upright adaptation stimuli to inverted test stimuli could be based on the notion of expert face processing for upright faces. Since negation does not alter the manner of expert processing, this is plausible to explain the results when the adaptation stimuli are upright.

However, this explanation fails to account for the successful transfer of adaptation from inverted adaptation stimuli to upright test stimuli. Evidence has been presented to suggest that aftereffects in inverted faces are based on low-level visual processing rather than face-specific mechanisms (Susilo et al., 2010) so the transfer may not be expected. However, Susilo et al. tested the FDAE in unfamiliar faces. Thus, the nature of identity adaptation is more complicated than based on visual or expert face-processing skills.

One plausible explanation for the transfer from inverted adaptation stimuli to upright test stimuli may be based upon how participants process an inverted face. Extracting identity from an inverted face takes longer than in an inverted face, however, it is still completed within 5 s (Valentine, 1988) which is the length of time the adaptor was on screen for in the present study. Thus, even an inverted face can cause identity adaptation. However, an inverted test stimulus will not be affected by adaptation possibly because the presentation is too brief to activate the expert face recognition system.

Another possibility is that with briefer presentation, an inverted face does not give as much semantic information as an upright face. Whereas, prolonged exposure of an inverted face provides enough time to access semantic information about that face and its identity. In this way, an inverted face as the adaptation stimulus may allow participants to actively think about the identity of the person, whereas the brief presentation during the test phase may not. Nevertheless, these results need to be confirmed using a larger stimulus set (see, e.g., Carbon and Ditye, 2012).

Experiment 2 demonstrated that aftereffects were observed more strongly in low-pass filtered faces. This is likely to be the result of the fact that identity is carried in higher spatial frequencies (Schyns et al., 2002) and during early face processing (Halit et al., 2006). Based on this, during the test phase, participants are making quick responses and this response may rely on early face coding. This would make aftereffects appear larger in low-pass filtered faces. Rather surprisingly, aftereffects were greater following adaptation to unaltered and high-pass filtered stimuli than to the low-pass filtered stimuli. A mismatch in spatial frequency for learning to test in a recognition paradigm typically causes recognition deficits of approximately 20% (Liu et al., 2000) but there was no consistent reduction in the aftereffect when spatial frequencies did not match in this aftereffect paradigm. Potentially, this may relate to how the faces are processed. Early face processing relies on higher spatial frequencies, but later processing is more dependent on lower spatial frequencies (Halit et al., 2006). The adaptor is on screen for 5 s and which means that the early face processing could be inhibited in favor of later face processing using spatial frequencies in the lower bands. Thus, if the faces are stored more with low spatial frequencies than high spatial frequencies, then aftereffects are likely to be larger. This explanation can only be made hesitantly and requires further testing to see if during the adaptation phase, whether high or low spatial frequencies are employed.

This study highlights differences in the representation between famous and unfamiliar faces as revealed by aftereffects. Aftereffects in unfamiliar faces are more likely to be based on non-face-specific visual mechanisms (cf., Ryu and Chaudhuri, 2006). The FIAE in unfamiliar faces may actually be a variant of the FDAE since they are tested in similar paradigms and in unfamiliar faces identity is not the same as it is in unfamiliar faces. Thus, aftereffects in unfamiliar faces are likely to be low-level and more viewpoint-dependent. The neuroanatomical locus for this is likely to be in the striate cortex and the fusiform gyrus (cf., Hole, 2011; Hurlbert, 2001). However, identity is represented elsewhere in the brain (Rotshtein et al., 2005; Gobbini and Haxby, 2007; Kriegeskorte et al., 2007) and aftereffects in famous faces are likely to involve these areas (Hills et al., 2010). Indeed, viewpoint-invariant aftereffects have been found to be located in more posterior regions such as the posterior cingulate cortex, and the anterior temporal lobes (e.g., Eger et al., 2005; Furl et al., 2007). Face detection is said to involve the fusiform gyrus, whereas identity extraction involves the anterior inferotemporal cortex (Kriegeskorte et al., 2007). This is consistent with the suggestion that famous faces recruit additional brain regions that are more anterior than the fusiform gyrus. Thus, adaptation in famous faces is likely to involve more brain regions than adaptation in unfamiliar faces and lead to more robust aftereffects. This description is of course speculative and further research is required to confirm these suggestions.

One caveat with the explanations provided thus far and with the study in general is that there are substantial representational differences in faces of different levels of familiarity including the recruitment of different brain regions (Taylor et al., 2009). The results presented here only show how the adaptation is different in famous and unfamiliar faces which is not necessarily a novel finding. Nevertheless, this study has developed methods for investigating how faces of different levels of familiarity are stored: this method could be used to further elucidate different processing streams for familiar and unfamiliar faces (cf., sex-contingent aftereffects, Little et al., 2005) which is often ignored in the aftereffects literature. Similarly, given that there is behavioral evidence from recognition paradigms that other-race faces are not processed using the expert face-processing system (Tanaka et al., 2004), this method could be used to establish how different the processing of other-race faces is: if there is transfer of aftereffects from own- to other-race faces, then this suggests they are processed using similar mechanisms. If there is no transfer then the mechanisms used to process faces is likely to be different. This paradigm, thus, has scope for exploring the representation of different classes of faces.

In conclusion, these data seem to suggest two important facets of the FIAE. Firstly, there is some image-based adaptation that is occurring. This is lower-level and may exist to allow for differences between stimuli to be better detected. This is based on the fact that stimuli that are matched at adaptation and at test produce stronger FIAEs than unmatched stimuli. Secondly, part of the FIAE is based on face-specific mechanisms, since the FIAE is based in part on expert processing. As such FIAEs represent a unique class of high-level shape aftereffect due to expert processing involved in face processing, possibly based on configural coding.

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Face adaptation effects show strong and long-lasting transfer from lab to more ecological contexts

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A review on recent experiments on figural face aftereffects reveals that adaptation effects in famous faces can last for hours up to days. Such adaptations seem to be highly reliable regarding test–retest designs as well as regarding the generalizability of adaptation across different adaptation routines and adaptations toward different kinds of facial properties. However, in the studies conducted so far, adaptation and the subsequent test phase were carried out in typical laboratory environments. Under these circumstances, it cannot be ruled out that the observed effects are, in fact, episodic learn–test compatibility effects. To test for ecological validity in adaptation effects we used an adaptation paradigm including environmental and social properties that differed between adaptation and test phase. With matched samples ($n1 = n2 = 54$) we found no main effects of experimental setting compatibility resulting from varying where the tests where conducted (environmental condition) nor any interaction with effects of stimulus compatibility resulting from varying stimulus similarity between adaptation and test phase using the same picture, different pictures of the same person, or different persons (transfer). This indicates that these adaptation effects are not artificial or merely lab-biased effects. Adaptation to face stimuli may document representational adaptations and tuning mechanisms that integrate new visual input in a very fast, reliable, and sustainable way.

Keywords: face adaptation, ecological testing, external validity, face representation, figural aftereffects, face veridicality aftereffect, familiar faces, plasticity

INTRODUCTION

Adaptation is a continuous process that enables us to tune our cognitive apparatus to new, changing, and dynamic aspects of our external world. It takes effect across sense modalities in lower as well as higher areas of sensory processing by changing the firing patterns in neural populations that are sensitive to a given adaptive stimulus. In visual perception, for instance, exposure to color or motion direction shapes the perception of these features in subsequent neutral (i.e., achromatic or stationary, respectively) stimuli in a way that corresponds to a shift in baseline induced by adaptation.

Experimental research in recent years tells us that adaptation effects in the domain of faces are reliable (Rhodes et al., 2003), show robustness against many experimental variables such as size, orientation, and affine distortions (for an overview see Webster and Macleod, 2011) and are also sustainable (Carbon and Ditye, 2011). Carbon and colleagues have shown that adaptation toward distorted familiar faces can last up to 80 min (Carbon and Leder, 2006), several days (Carbon et al., 2007), or even 1 week (Carbon and Ditye, 2011), indicating instant and robust changes of the cognitive representation toward newly incoming visual information. In these studies, participants adapted to configurally distorted faces and were later asked to pick the veridical versions of these faces from of a sequence of different versions with varying distortions. After adaptation, the perceived veridical version was shifted toward the adapting distortion.

These long-term adaptation paradigms included an adaptation block, during which a number of manipulated faces were shown for multiple trials, followed by a delay period of hours or even days, and a subsequent test session. In contrast, in most studies looking at immediate (i.e., short-term) adaptation effects, the adaptation face was immediately followed by a test face, thus measuring aftereffects on a trial-by-trial basis rather than block-by-block. The question has been raised if long-term adaptation effects are the result of neural mechanisms that are similar to those of short-term adaptation as some of the reported effects could be also explained by generic effects of episodic memory adjustments. Perception might be temporarily biased as a specific test situation – the laboratory – provides reliable cues for episodic memory. Tulving defined episodic memory as a memory system that "receives and stores information about temporally dated episodes or events, and temporal–spatial relations among these events…[which] is always stored in terms of its autobiographical reference…" (Tulving, 1972, p. 385). On the basis of this original definition we could assume that the typical setting of face adaptation studies conducted under strict experimental conditions in laboratories (see **Table 1** for a list of example laboratory based face adaptation studies) with reliable environmental, situational, and social settings induce strong episodic memory traces during the adaptation phase that might be reactivated when the participants are tested for supposed adaptation effects.

If adaptation effects are primarily based on such episodic effects, then adaptation effects should decrease or be absent when environmental, situational, and social factors vary or change between adaptation and test phase.

THE PRESENT STUDY

In the present study, we tested the ecological validity of sustained face adaptation effects. Therefore, the environmental, situational, and social factors were set very differently in the adaptation phase and the test phase (*environmental condition*). The phases were separated by an extensive delay of at least 7 days. Test included the same pictures that were used for adaptation (*picture*) plus different pictures of the same persons (*identity*), and pictures of completely new faces (*novel*). The test for such transfer effects can add relevant information about the hierarchal locus of adaptation effects in face perception. While transfer of distortion effects across identities have been shown before (Webster and Maclin, 1999; Carbon et al., 2007; Carbon and Ditye, 2011), face identity aftereffects have shown to be highly dependent on viewpoint (Benton et al., 2006).

Table 1 | Lab-based studies on face adaptation.

Study	Transfer	Delay
Webster and Maclin (1999)	None	n/a
Leopold et al. (2001)	Anti-faces, position, size	150, 300, 600, 1200, 2400 ms
Rhodes et al. (2003)	Orientation	500 ms
Webster et al. (2004)	Gender, ethnicity, expression	250 ms
Carbon and Leder (2005)	None	4 s, 5 min
Kovacs et al. (2005)	Retinal position	500 ms
Little et al. (2005)	Different faces; gender	n/a
Leopold et al. (2005)	Anti-faces	n/a
Carbon and Leder (2006)	None	80 min
Carbon et al. (2007)	Different pictures/ different persons	5 min, 24 h
Fang et al. (2007)	Different faces; inverted faces	1 s
Rhodes et al. (2007)	Anti-faces, size	1000 ms
Kloth and Schweinberger (2008)	Size	7 min
Barrett and O'Toole (2009)	Age-groups	100 ms
Hills et al. (2010)	Imagery/perception	5 s
Carbon and Ditye (2011)	Different pictures/ different persons	24 h, 7 days
Hole (2011)	Upside-down; stretched	$\leq$2 min

Overview of a selection of lab-based empirical studies on face adaptation in chronological order systematizing the transfer conditions between adaptation and test ("transfer") and the documented duration of the adaptation effects.

MATERIALS AND METHODS

PARTICIPANTS

One hundred and eight undergraduate students (92 female; mean age: 22.6 years, range: 18–43) took part on a volunteer basis. Participants were naïve to the purpose of the experiment and had normal or corrected-to-normal vision, as assessed by the Snellen-Eye chart vision test. Participants were assigned to one of two levels of the *environmental condition* factor: half of the participants (43 female; mean age: 22.6 years, range: 18–43) to the *formal experimental laboratory* setting (same), the other half (49 female; mean age: 22.6 years, range: 18–37) to the *informal leisure room* setting (different). Groups were matched according to participants' age.

APPARATUS AND STIMULI

We used two different high-quality photo-portraits (images A and B) of 27 celebrities (frontal view; 220 × 240 pixels) who were well known to the participants (pop stars, politicians, super models, sportsmen: Pamela Anderson, Franz Beckenbauer, Boris Becker, Pierce Brosnan, George W. Bush, Nicholas Cage, Bill Clinton, George Clooney, Cindy Crawford, Tom Cruise, Princess Diana, Cameron Diaz, Verona Feldbusch, Thomas Gottschalk, Oliver Kahn, Nicole Kidman, Helmut Kohl, Madonna, Angela Merkel, Jack Nicholson, Brad Pitt, Julia Roberts, Claudia Schiffer, Gerhard Schröder, Michael Schumacher, Arnold Schwarzenegger, Rudi Völler). For the adaptation phase we attempted to create effective adaptors to achieve a strong adaptation effect. Following the advice of Carbon et al. (2007), we decided to create different versions of the original portraits by generating strong configural distortions: We gradually compressed or extended the distances between the eyes and the mouth for each picture by an amount of approximately 20 pixels (**Figure 1**). Each celebrity was randomly allocated to one of three stimulus sets (consisting of nine celebrities) that corresponded to the three levels of the factor *transfer*: *picture*, *identity*, and *novel*. The experiment was controlled by the experimental software PsyScope X B.46 (Cohen et al., 1993). In the test phase the original images and variants of these were used with eyes–mouth distances compressed or extended by 4 pixels (versions −1 and +1).

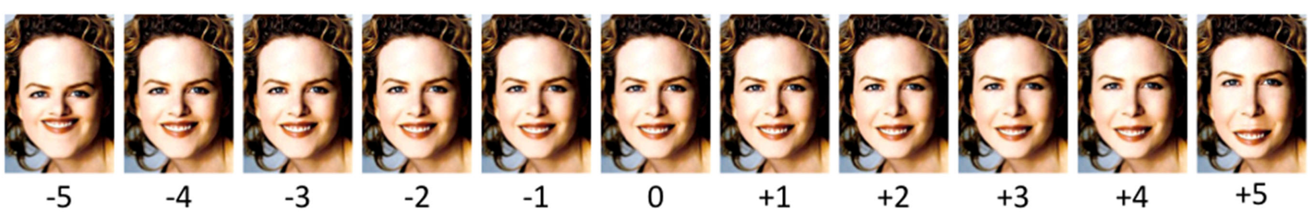

FIGURE 1 | Illustration of the stimulus continuum with the original face in the center (0), the adapting stimuli at the far ends (−5 and +5), and the test stimuli in between (−2 and +2).

For all participants the adaptation phase was carried out in the *formal experimental laboratory* setting. In this condition the program was run on a 17″ eMac desktop computer with completely white coating equipped with a white mouse and a white keyboard. The room was a laboratory explicitly signed as an "experimental lab" equipped with four testing cubicles, in which up to four individuals were tested in parallel. The walls, the cubicles, and the tables were also of white color; the windowless room was illuminated by artificial light of neon lamps. The experimenter gave instructions in an emphasized clear tone asking for strict obedience and an absolutely silent atmosphere. Making all these arrangements, we attempted to induce a strong laboratory atmosphere.

For the test phase, participants in the *informal leisure room* setting were invited to a leisure room of the department, situated in a different wing from the previously described lab, with a sofa placed at the window and a palm tree beside. The participants were invited to the room more like a guest than a participant. They were tested individually while personnel of the department were communicating with each other about different topics of social life not linked with the experiment. The test equipment consisted of a silver PowerBook 17″ laptop which the participants had to place on their lap in a very informal way. A very kind person in charge, different from the experimenter in the adaptation phase, provided pieces of instructions not explicitly asking for silence, obedience, or strict conduction of the experiment.

Participants in the control group under the *formal experimental laboratory* setting, in contrast, found the same environmental, situational, and social properties as in the adaptation phase.

As the adaptation phase was always conducted in the *formal experimental laboratory* setting, but the test phase took place either in the laboratory or the leisure setting, we will term the main experimental variable *episodic compatibility* with the two levels *laboratory* (fixed settings) and *ecological* (variable settings).

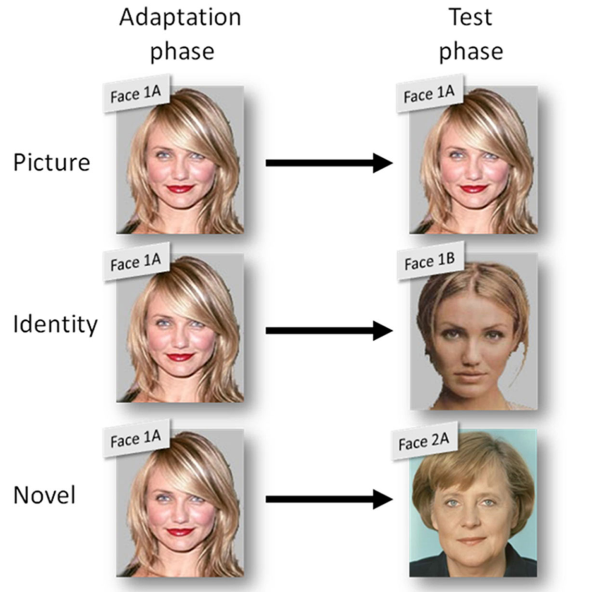

FIGURE 2 | Illustration of the three stimulus compatibility conditions (between adaptation and test phase): *picture* with same pictures of the same person (e.g., face picture 1A and 1A), *identity* with different pictures of the same person (e.g., 1A and 1B), and *novel* with pictures of different persons (e.g., 1A and 2A).

PROCEDURE

The experiment consisted of three phases: *adaptation*, *delay*, and *test*.

Adaptation phase

During the adaptation phase, participants were tested in the *formal experimental laboratory* setting. One third of them were exposed to the strongly compressed versions (−5), the original versions (0), or the strongly extended versions (+5) of celebrity faces, respectively. Faces assigned to the different compression sets were counterbalanced across participants. Further, participants were exposed either to image A or image B of a particular individual (see **Figure 2**).

The pictures assigned to the third stimulus set were not shown during adaptation. Each picture was presented 15 times during the adaptation phase fully randomized in order in five different screen positions for three different presentation durations: 2, 3, or 4 s. The unpredictability of presentation positions and durations aimed to exclude specific retinal effects and to ensure cognitive challenging characteristics of the task. Stimulus presentation was preceded by a sequence starting with a fixation cross (500 ms) in the center of the target position, followed by a rectangular frame (200 ms) used to guide participants' attention. After each stimulus presentation, participants were requested to do a gender-decision cover task that demanded to decide what gender the stimulus belonged to as quickly as possible after it had disappeared.

Delay phase

Adaptation and test phase were separated by an interval that was at least 7 days long (mean delay: 7.1 days, range: 7–10 days). During this time, participants did not return to the lab and no specific instructions were given.

Test phase

After the delay phase, the participants had to select the veridical face out of two versions of each face (two AFC task; original vs. −2, and original vs. +2). As in Carbon et al. (2007), we explicitly instructed the participants to base their decisions on their world knowledge (images known from TV/media/movies), and not on any images they had seen in the experimental context before. We also did not refer to any point of the previous adaptation phase conducted in the *formal experimental laboratory* setting. The participants had to reply to the question "Which is the veridical version of the face?" In each trial, either the slightly compressed version (−2) or the slightly extended version (+2) was presented side by side with the original one (0). Each celebrity was shown four times with the various versions appearing in different, randomized locations (*original left/compressed right; original right/compressed left; original left/extended right; original right/extended left*).

In order to test the generalization of possible adaptation effects, the within-subject factor *stimulus compatibility* was manipulated on three levels: In the case of the celebrities included in the first stimulus set, participants were tested with exactly the same picture that had been used for adaptation (*picture*). For the celebrities in the second stimulus set, the alternative image of the same individual was used for testing (*identity*). Additionally, the test phase included one image (A or B) of each celebrity out of the third stimulus set that had not been shown during adaptation (*novel*).

Importantly, participants in the *laboratory* group were tested in the same environmental, situational, and social context as in the adaptation phase, whereas participants in the *ecological* group were invited in a very informal way to the *informal leisure room* test setting where the context was massively changed between adaptation and test phase.

RESULTS

The analyzed dependent variable was *chosen target*, a variable with a definition range between −1 and +1, corresponding to constantly selecting the relatively compressed (i.e., versions −2 or 0) or relatively extended (i.e., versions +2 or 0) versions, respectively, while the value 0 means that on average participants have chosen the original face configuration. *Chosen target* was determined by the mean selections of each participant. Selections were scored according to their picture version: a score of −2 was used for −2 versions, 0 for 0, and +2 for +2).

A three-way mixed-design analysis of variance (ANOVA) was calculated with the two between-subjects factors *episodic compatibility* (*ecological:* change of the episodic activation between adaptation and test phase from lab setting to leisure context; *laboratory*: no change of the episodic activation, both phases conducted in lab setting) and *adaptation* (−5 = *strongly compressed*, 0 = *original*, +5 = *strongly extended adaptors*) and the within-subject factor *stimulus compatibility* (levels *picture*, *identity*, *novel*).

The only significant main effect we found was for *adaptation*, $F(2{,}102) = 23.6$, $p < 0.0001$, $\eta_p^2 = 0.316$, with $M_{-5} = -0.143$, $M_{\text{original}} = 0.003$, and $M_{+5} = 0.151$ (Bonferroni-corrected *post hoc* comparisons revealed significant differences between all possible pairs, *ps* < 0.0001). This demonstrates reliable and specific adaptation effects that were still observable after 7 days. The only further significant effect was the interaction between *adaptation* and *stimulus compatibility*, $F(4{,}204) = 7.2$, $p < 0.0001$, $\eta_p^2 = 0.124$, indicating differential amounts of adaptation for the different degrees of stimulus compatibility. Although adaptation was strongest for stimulus compatibility *picture*, $F(2{,}102) = 25.6$, $p < 0.0001$, $\eta_p^2 = 0.334$, followed by stimulus compatibility *identity*, $F(2{,}102) = 19.8$, $p < 0.0001$, $\eta_p^2 = 0.279$, the simple main effect of adaptation for condition *novel* was still significant, $F(2{,}102) = 6.3$, $p = 0.0028$, $\eta_p^2 = 0.109$. Most importantly, we didn't find any effect of *environmental condition* (see **Figure 3**) – neither a main effect nor an interaction, *ps* > 0.298 (see **Figures 3** and **4**).

Participants, who adapted to the original versions of the faces, did not show any perceptual biases in either direction.

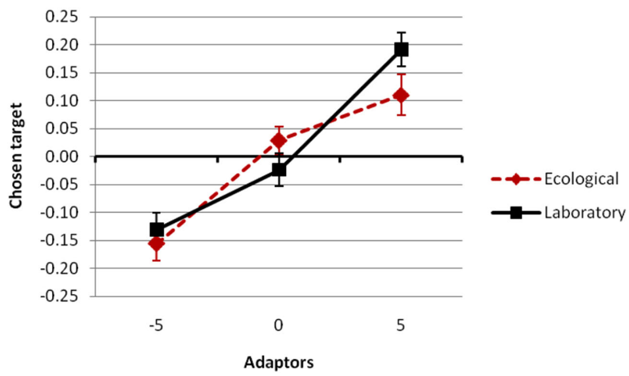

FIGURE 3 | Overall adaptation effect for the two *episodic compatibility* conditions *ecological* (leisure condition in the test phase; red dotted line) and *laboratory* (laboratory condition in the test phase; black solid line). Three kinds of adaptors were used varied across groups: −5 (participants adapted to strongly compressed versions of the faces), 0 (participants adapted to the original faces), and 5 (participants adapted to strongly extended versions). The average distortion value of the selected faces during test served as the dependent variable (Chosen target; *y*-axis). See Section "Results" for details.

DISCUSSION

As documented previously, incidental perception of geometrically distorted depictions of famous faces presented during a gender-decision task lead to sustained adaptation effects (Webster and Macleod, 2011). Adaptation was strongest when participants had to evaluate the veridicality of celebrities' depictions that they had already seen in the adaptation phase (stimulus compatibility *picture*), followed by different depictions of the same celebrities (*identity*), and depictions of celebrities that had not yet appeared within the experimental context (*novel*). Thus, even the veridicality decision on faces that had not been perceived in distorted versions during the adaptation phase of the experiment was systematically biased indicating adaptation effects being in action in at least three ways: (1) picture-specific effects, demonstrated by stronger effects for condition *picture* compared to *identity*, (2) identity-specific effects, demonstrated by stronger effects for conditions *picture* and *identity* compared to *novel*, and (3) general adaptation effects, demonstrated by significant effects for condition *novel*. This finding is compatible with the results of Carbon et al. (2007) who used a different test paradigm with a 1-out-of-11 face-selection task.

The overall adaptation effects still being active after seven or more days might be an indication of effects caused by permanent shifts and tuning of the cognitive representations of faces (cf. Carbon and Ditye, 2011). Integrating new visual information in already existing representations is a core mechanism in order to recognize and discriminate effectively between face exemplars. We suggest a continuous normalization process that is in place to tune face-selective neural systems and thus maximize their sensitivity range. A similar mechanism has been shown in the domain of color-adaptation (Vul et al., 2008). Two aspects of our results are compatible with the assumption that a general tuning mechanism modifies the whole facial representation system toward recently encountered, and highly distinctive, visual information (Rhodes et al., 2003): First, adaptation effects were still existent after 1 week, and, second, we have found general adaptation effects documented by the stimulus compatibility condition

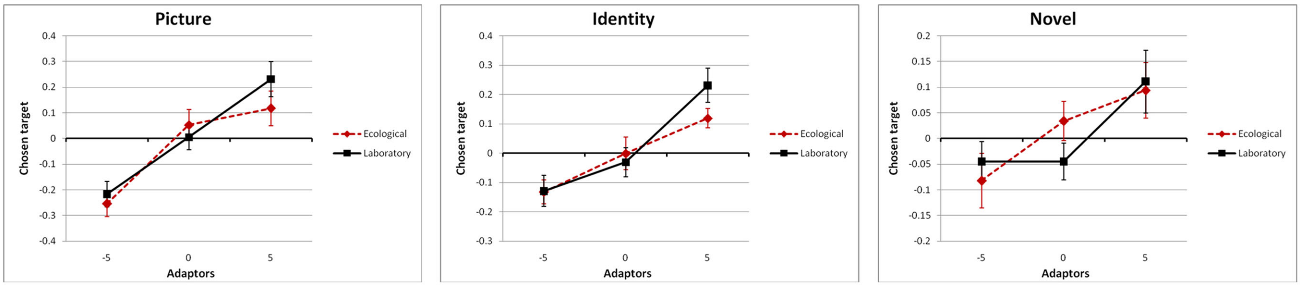

FIGURE 4 | Adaptation effects for the *stimulus compatibility* conditions *picture* (same depiction of the same persons in the adaptation and test phase), *identity* (different depictions of the same persons), and *novel* (depictions of different persons), split by the *episodic compatibility* conditions *ecological* (red dotted line) and *laboratory* (black solid line).

novel. This interpretation is also compatible with recent findings concerning adaptation effects of aesthetic appreciation found in the domains of artworks (Carbon, 2011) and of product design, for instance for cars (Carbon, 2010) and chairs (Faerber et al., 2010).

Most importantly with respect to the aim of this paper, even 1 week after adaptation, the directed effects on face veridicality decisions were not limited to typical, highly artificial laboratory environments. They also transferred to a test setting that was very different from the adaptation setting. Our findings also support the results of a recent study showing that the size of face adaptation effects is a function of adaptation duration (Strobach et al., 2011). On these grounds we suggest to exclude simple episodic learning effects *sensu* Tulving's (1972) definition as the major explanation for these adaptations. Instead, we favor the idea of adaptation effects being based on the systematic tuning and deflection of the whole face space (Valentine, 2001). According to these models, every face in the face space is coded by its deviation from one or more general face norms, which are abstracted from all faces ever encountered. This view is also in line with studies on facial attractiveness (Valentine et al., 2004) and the explanation of systematic changes of aesthetic appreciation given by Faerber and Carbon (2010).

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Selectivity of face distortion aftereffects for differences in expression or gender

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The perceived configuration of a face can be strongly biased by prior adaptation to a face with a distorted configuration. These aftereffects have been found to be weaker when the adapt and test faces differ along a number of dimensions. We asked whether the adaptation shows more transfer between faces that share a common identity, by comparing the strength of aftereffects when the adapt and test faces differed either in expression (a configural change in the same face identity) or gender (a configural change between identities). Observers adapted to expanded or contracted images of either male or female faces with either happy or fearful expressions, and then judged the perceived configuration in either the same faces or faces with a different gender and/or expression. The adaptation included exposure to a single face (e.g., expanded happy) or to alternated faces where the distortion was contingent on the attribute (e.g., expanded happy versus contracted fearful). In all cases the aftereffects showed strong transfer and thus only weak selectivity. However, selectivity was equal or stronger for the change in expression than gender. Our results thus suggest that the distortion aftereffects between faces can be weakly modulated by both variant and invariant attributes of the face.

Keywords: adaptation, aftereffects, face perception, facial expressions

INTRODUCTION

The appearance of a face can be strongly biased by adaptation to faces an observer has been exposed to previously. For example, after viewing a face that has been configurally distorted so that it appears too expanded, an undistorted test face appears too contracted (Webster and MacLin, 1999). Numerous studies have now characterized the properties of these aftereffects and their implications for the perception and neural representation of faces (Webster and MacLeod, 2011). In particular, aftereffects have been demonstrated for many of the characteristic dimensions along which faces naturally vary, including their individual identity (Leopold et al., 2001) and attributes such as their gender ethnicity, expression (Hsu and Young, 2004; Webster et al., 2004), or age (Schweinberger et al., 2010; O'Neil and Webster, 2011). Thus the adaptation may play an important role in shaping how different aspects of the face are encoded and interpreted.

Several studies have explored whether separate face aftereffects could be induced for different types of faces, for example so that male faces appear too contracted while female faces look too expanded. Partial selectivity has been found for a number of dimensions including differences in identity, gender, ethnicity, age, and species (Little et al., 2005, 2008; Yamashita et al., 2005; Ng et al., 2006; Jaquet and Rhodes, 2008; Jaquet et al., 2008). This selectivity is in part of interest because it might reveal the response characteristics or tuning of the underlying adapted mechanisms, and has also been examined to explore the extent to which distinct adaptable processes underlie the encoding of different facial attributes, for instance so that different norms or prototypes could be established for different populations of faces. However, the basis for this selectivity, and the extent to which it reflects face-specific versus more generic levels of visual coding, remain poorly understood (Webster and MacLeod, 2011).

In this study we compared the relative selectivity of the adaptation for two different facial attributes – changes in expression or changes in gender. Dimensions like gender reflect stable or invariant aspects of identity and thus distinguish one face from another, while facial expressions instead represent an example of variant facial configurations that correspond to changes in the state or pose of the same identity (Bruce and Young, 1986). A number of lines of evidence suggest that the variant and invariant properties of the face are represented in processing streams that are at least partially separable (Haxby et al., 2000; Andrews and Ewbank, 2004; Calder and Young, 2005; Said et al., 2011). Both gender and expression changes can induce strong adaptation effects (Hsu and Young, 2004; Webster et al., 2004; Little et al., 2005; Ng et al., 2006; Jaquet and Rhodes, 2008; Barrett and O'Toole, 2009) that are consistent with sensitivity changes that at least in part reflect high and possibly face-specific levels of response change (Bestelmeyer et al., 2008; Davidenko et al., 2008; Afraz and Cavanagh, 2009; Ghuman et al., 2010). Thus after adapting to a male face an androgynous face appears more female, while adapting to an angry face causes a test face to appear less angry. Studies have also shown that the aftereffects are selective for the specific expression, so that an angry face has a larger effect on the appearance of angry faces than happy ones (Hsu and Young, 2004; Rutherford et al., 2008; Skinner and Benton, 2010; Cook et al., 2011; Pell and Richards, 2011). Moreover, for both expression and identity the aftereffects appear to reflect shifts in the norm for each facial dimension rather than shifts along arbitrary axes determined by the morphing sequence (Rhodes and Jeffery, 2006; Benton and Burgess, 2008).

However, there are intriguing asymmetries between expression and identity adaptation. Expression aftereffects are weaker when the adapt and test faces differ in identity (Fox and Barton, 2007; Ellamil et al., 2008) or gender (Bestelmeyer et al., 2009). Conversely, changes in expression did not affect the degree of identity adaptation (Fox et al., 2008). These differences could not be attributed to the degree of physical difference between the images (e.g., so that two expressions of the same identity are more similar than two identities with the same expression; Ellamil et al., 2008; Fox et al., 2008) or to response changes to the low-level features of the images (Butler et al., 2008; Fox et al., 2008). This suggests that the asymmetry might at least in part reflect differences in how expressions and facial identities are encoded, and specifically, that the processes coding invariant features like identity or gender might reflect a more abstracted representation that is independent of the variant "pose" of the face. Consistent with this, other studies have found analogous asymmetric effects of expression or identity changes on face recognition and discrimination tasks (Schweinberger and Soukup, 1998; Schweinberger et al., 1999; Atkinson et al., 2005). (Conversely, there are also examples where changeable aspects of the face such as mouth shape can show aftereffects that show little dependence on identity (Jones et al., 2010).

One possible account of these differences in selectivity for attributes like expression or gender is that adaptation shows greater transfer between an adapt and test face when the two faces appear to be share a common identity – i.e., when both images appear to be drawn from the same person. This idea was suggested by Yamashita et al. (2005) in a study comparing how selective the face adaptation was for a variety of different "low-level" changes in the images. Some differences, including a change in size, average contrast, or average color between the adapt and test faces, had weak or no effect on the magnitude of the adaptation. Yamashita et al. noted that these stimulus changes had in common that they did not alter the apparent identity of the face. Conversely, bandpass filtering the images into different spatial frequency ranges, or inverting the contrasts so that the adapt and test images had different polarities, resulted in substantially weakened aftereffects, and these were stimulus manipulations that also caused the adapt and test face to look like different individuals. Their hypothesis might account for why face aftereffects are relatively robust to changes in size or position, differences which are in fact frequently introduced to try to isolate high-level and possibly face specific levels of the adaptation (Leopold et al., 2001; Zhao and Chubb, 2001; Afraz and Cavanagh, 2008). Moreover, the aftereffects are also surprisingly robust across global transformations such as uniformly stretching the images (Hole, 2011). This stretching alters many of the configural relationships in the image (e.g., the relative distances between the eyes and nose), yet again has little effect on the recognizability of the face (Hole et al., 2002). Finally, the proposal might also explain why aftereffects are selective for differences in the actual identity of faces (and may become more selective as the similarity between two identities decreases; Yamashita et al., 2005), but is not selective for differences in the identity strength of a given face (e.g., between a face and its caricature; Loffler et al., 2005; Rotshtein et al., 2005; Bestelmeyer et al., 2008).

We sought to test this hypothesis in the context of invariant versus variant aspects of the face. In particular, by this account aftereffects might show less selectivity for changes in expression because these changes do not alter the perceived identity of the face. Alternatively, the aftereffects should show less transfer when the gender is altered. To test this, we compared the relative selectivity for changes in expression or gender on the same configural aftereffect. Surprisingly however, the results instead suggest that if anything the adaptation was more selective for the expression difference, thus arguing against perceived identity as the primary factor controlling how adaptation to the configural distortion transferred from one face to another.

MATERIALS AND METHODS

SUBJECTS

Observers included the authors (denoted as S1 and S2 in the figures), and four additional observers who were unaware of the aims of the study, with different observers participating in different subsets of the experiments. All observers had normal or corrected-to-normal vision acuity and participated with informed consent. Experiments followed protocols approved by the University's Institutional Review Board.

STIMULI

Faces for the study consisted of full-color frontal view images of Dutch female and male faces with happy or fearful posed expressions, acquired from the Radboud Face Database (Langner et al., 2010; http://www.socsci.ru.nl:8180/RaFD2/RaFD?p = main). Two models (female 32 and male 23) were used throughout as the test images, while the same models as well as additional faces were chosen as the adapting images. In order to maximize the identity cues to the face, the images were not cropped and thus included the full outline of the head and neckline. (Models were dressed uniformly in black shirts and with their hair pulled back.) The images were distorted by a local expansion or contraction of the face relative to a midpoint on the nose, using a procedure similar to the algorithms described Webster and MacLin (1999) and Yamashita et al. (2005). Equal expansions were applied to the vertical and horizontal axes of the image. The magnitude of the distortion was varied in finely graded steps in order to generate an array of 100 images, which ranged from fully contracted (0) to fully expanded (100), with the original face corresponding to a level of 50 (**Figure 1**).

The images were displayed on a SONY E540 monitor, centered on a 16 by 12° gray background with a similar mean luminance of 15 cd/m^2. The test images subtended 5 by 5.8° at the 140 cm viewing distance, while the adapt images were shown 1.5 times larger in order to reduce the potential for an influence of low-level aftereffects. Observers viewed the stimuli binocularly in an otherwise dark room, and used a handheld keypad to record their responses.

PROCEDURE

Observers first adapted to either a single distorted face image or to alternating pairs of distorted images for a period of 2–5 min. In the single face condition, the adapt face image remained static and corresponded to a happy male, happy female, fearful male, or fearful female, shown either fully contracted or expanded. The

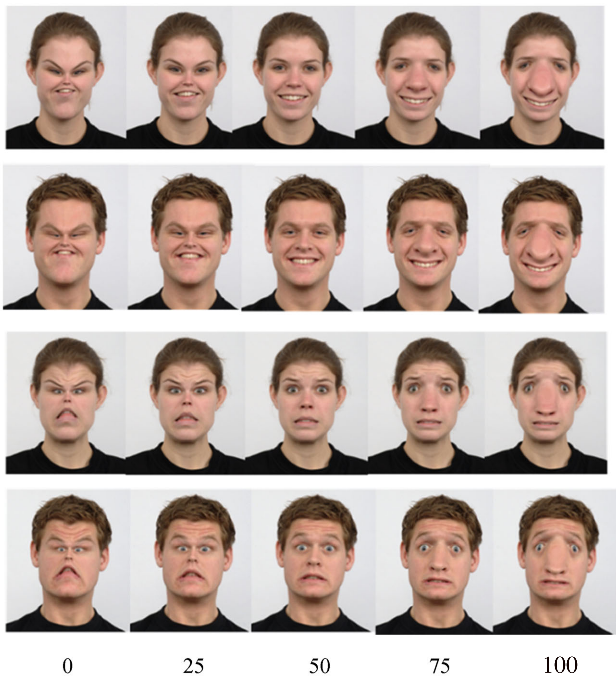

FIGURE 1 | Test faces corresponding to a happy female, happy male, fearful female, or fearful male. For each the face was distorted from maximally contracted (0) to maximally expanded (100). The original, undistorted face is shown in the middle column, corresponding to a level of 50.

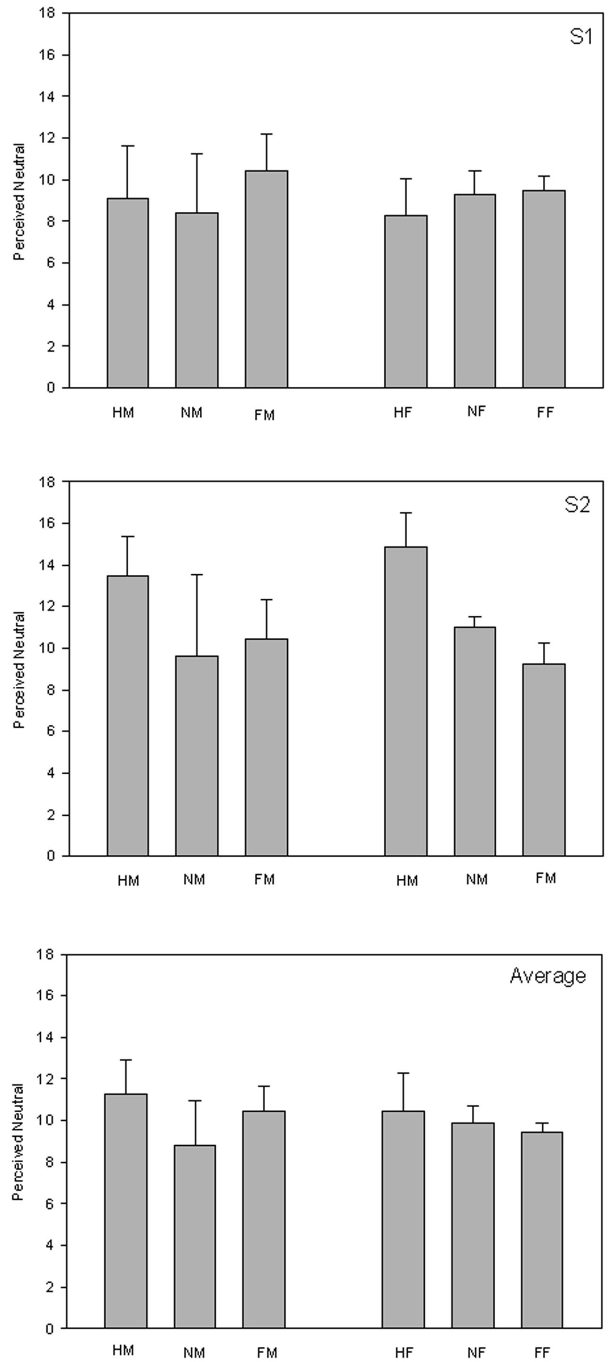

FIGURE 2 | Aftereffects for adapt and test faces with the same expression and gender. The aftereffects are plotted as the difference in the perceived neutral point for each test face after adapting to an expanded face versus a contracted face. The faces corresponded to the male and female models with a happy, fearful, or neutral expression. Panels plot the settings for the two individual observers and the average.

opposing face condition involved adapting to face images that differed either in expression and/or in gender which were paired with opposing distortions (e.g., to adapt to a contracted happy male and an expanded happy female). The faces were alternated at a rate of 1 image/s. After the initial adapt period, observers were presented test images shown for 1 s and interleaved with 4 s periods of readaptation, with a blank gray screen shown for 150 ms between each adapt and test period. Observers made a forced-choice response to indicate whether the test face appeared "too contracted" or "too expanded." The distortion level in subsequent tests was varied in a staircase with the level that appeared undistorted estimated from the mean of the final eight reversals. Either two or four test faces were shown in randomly interleaved order during the run, each adjusted by its own staircase. These consisted of test faces that were the same as the adapt, differed in expression, differed in gender, or differed in both expression and gender. In a single session each observer completed four repeated settings with the test images for a single adapting condition, with the order of adapt condition counterbalanced across sessions.

RESULTS

DISTORTION AFTEREFFECTS FOR NEUTRAL OR EXPRESSIVE FACES

The basic aftereffects we examined involved changes in the perceived configuration of faces with different expressions or genders after adapting to expanded or contracted faces. These distortions themselves can alter the perceived expression of the face (Zhao and Chubb, 2001; Neth and Martinez, 2009), and conversely the expression might alter the apparent distortion. Thus as a preliminary control experiment we examined whether adaptation to the distortions depended on the expression or gender. In pilot studies we in fact found that horizontal distortions in the images were difficult to judge because the neutral, undistorted level was unclear in the highly expressive faces. As noted in the methods, we therefore applied both vertical and horizontal distortions in the actual experiment. For these, observers could more reliably judge the undistorted face, and we found that simple aftereffects for these faces did not differ in magnitude from the aftereffects for the same configural distortions in images of faces with neutral expressions. These aftereffects are shown in **Figure 2**, which plots the difference between the physical distortion levels in the faces that appeared undistorted to the observer, after adapting to either the expanded or contracted face. A two-way ANOVA confirmed that there was not a significant effect of expression [$F(2,35) = 0.47$, $p = 0.63$] or gender [$F(1,35) = 0.05$, $p = 0.82$] on the strength of the aftereffects.

TRANSFER OF ADAPTATION ACROSS CHANGES IN EXPRESSION OR IDENTITY

To compare the selectivity of adaptation for different facial attributes, we first investigated the transfer from a single adapting face to either the same or a different face. The observers adapted for 2 min to the image of a happy male, a happy female, a fearful male, or a fearful female. For each they then judged the perceived configuration of images that were the same as the adapt, different in expression, different in gender, and different in expression and gender, with the displayed face chosen at random on each trial (**Figure 3**). Aftereffects were again assessed as the difference in the null settings after adapting to an expanded face versus a contracted face (**Figure 4**). These differences showed strong transfer of the adaptation across all four different test faces. That is, the aftereffects in the test faces were strong whether the adapt and test face were the same or different. The sizes of the aftereffects were compared with a Kruskal–Wallis one-way ANOVA on ranks, which showed a significant effect of the adapt–test combination [$H(3) = 16.29$, $p = 0.001$]. Pairwise comparisons revealed a significantly larger aftereffect when the test face was the same as the adapt versus when the test face differed in expression ($Q = 3.05$, $p < 0.05$) or both expression and gender ($Q = 3.80$, $p < 0.05$). However, the adaptation magnitude did not differ between when the test face was the same as the adapt or differed only in gender ($Q = 2.37$, NS). Finally, the aftereffects were also similar whether the test and adapt faces differed in gender or expression ($Q = 0.69$, NS). Thus overall the aftereffects tended to be modulated as much or more by the expression difference than by the gender difference between the faces.

CONTINGENT ADAPTATION

To better isolate the components of adaptation that are actually selective for the facial attributes, we next measured the aftereffects in a contingent adaptation task, in which the expanded and contracted distortions were paired with differences in the gender and/or expression of the face. This has the advantage that any non-selective adaptation is canceled out between the two opposing distortions, thus leaving a more sensitive probe of the selectivity (Yamashita et al., 2005). The observers were adapted for 2 min to a 1-s alternation between two opposing faces with opposite distortions that differed in either gender or expression, while the test faces consisted of two interleaved faces that were the same as the adapt faces (**Figure 5**).

Figure 6 plots the mean neutral settings after adapting to opposing distortions paired with the different expressions or genders. The selectivity of the adaptation was assessed by comparing the difference between the aftereffects for the same test face across the two adapting conditions. For the two test faces, these differences should be of opposite sign if the aftereffects were contingent on the facial attribute (since in one pair the difference corresponded to expanded adapt – contracted adapt, while for the other it was contracted adapt – expanded adapt). Alternatively, the difference should be similar for both faces if the distortion aftereffect did not depend on the value of the attribute. There were significant contingent aftereffects for the adapting face pairs whether they differed in expression [$t(31) = 6.67$, $p < 0.001$] or gender [$t(31) = 2.52$, $p = 0.017$]. However, the contingent aftereffects for expression differences were significantly stronger than for the gender differences [$t(31) = 2.27$, $p = 0.030$]. Thus again the results pointed to stronger selectivity for the expression differences.

TRANSFER OF ADAPTATION ACROSS GENDER AND EXPRESSION IN FACES WITH DIFFERENT IDENTITIES

In the preceding experiments, we utilized only two faces, which corresponded to two individual identities as well as two genders. Moreover, we had no way of controlling the magnitude of the identity difference relative to the expression difference. Thus a possible confound with the results was that "gender" and "expression" really do differ in the selectivity of the adaptation, but the identity differences may have been weak in the specific pair of faces

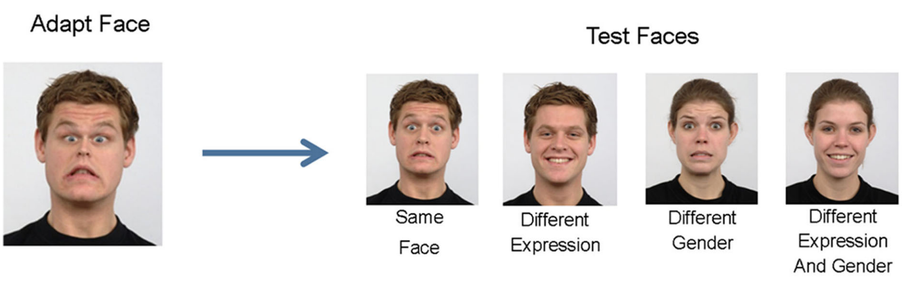

FIGURE 3 | Adaptation to a single image. After adapting to a single face image, the observers were presented with one of four test face images, which included the same adapt face, a face differing in expression, a face differing in gender, and a face differing in both expression and gender.

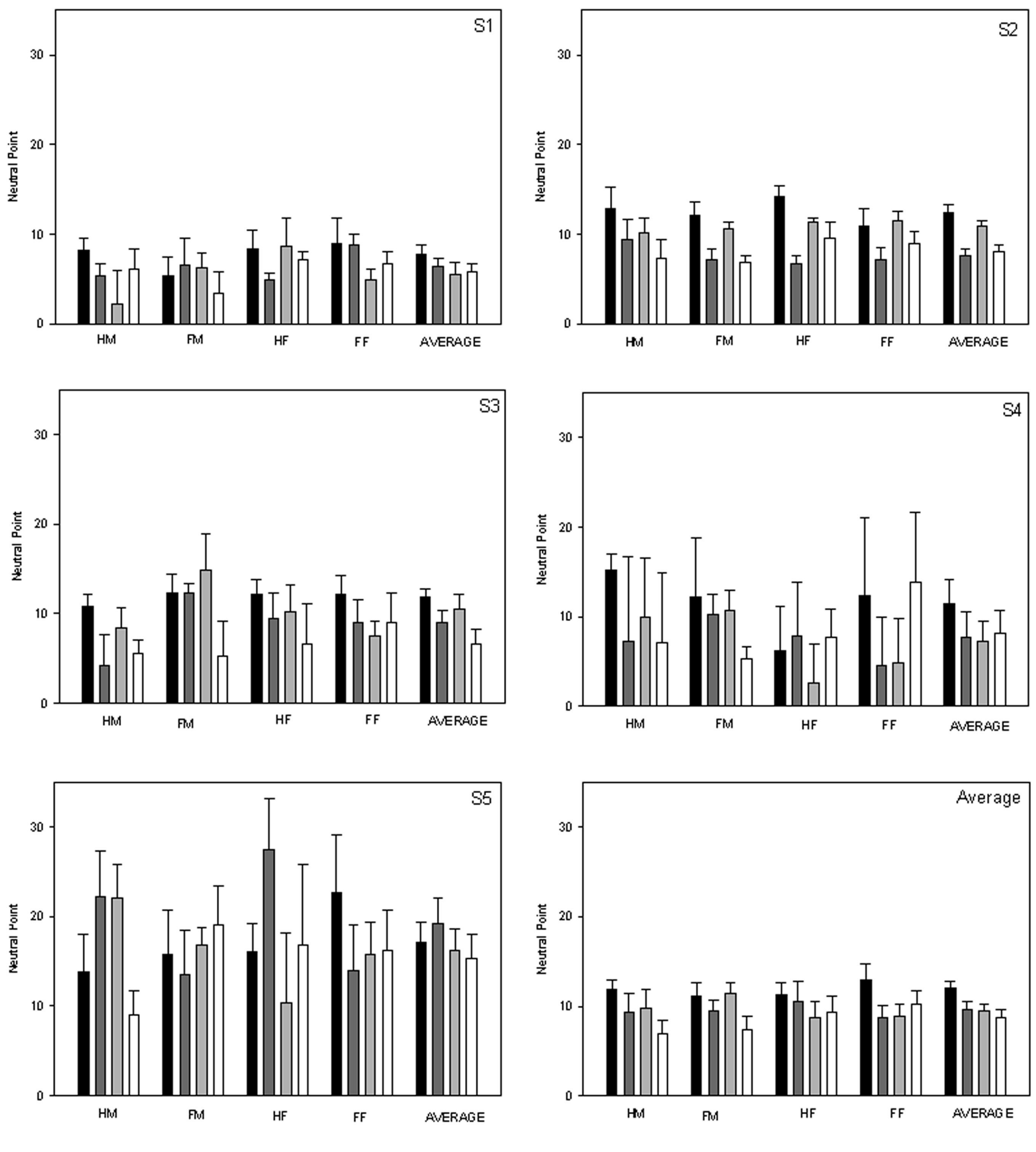

FIGURE 4 | Transfer of adaptation across individual faces. Aftereffects are plotted as the difference between the settings following adaptation to expanded or contracted faces. Sets of bars correspond to the four adapt faces (hm, happy male; fm, fearful male; hf, happy female; and ff, fearful female) or to the average for the four adapting faces. For each the bars show the settings when the test face was the same as the adapt (black), differed in expression (dark gray), gender (light gray), or both attributes (unfilled). Each panel plots the settings for the five individual observers or the average.

we tested. To control for this, in the final experiment, we tested the contingent adaptation aftereffects for sets of faces that might more directly capture the attributes of expression and gender. For this, we used 10 female and 10 male faces with the same happy and fearful expressions (**Figure 7**). The observer adapted to these 20 faces, which were interleaved with each other and alternated between

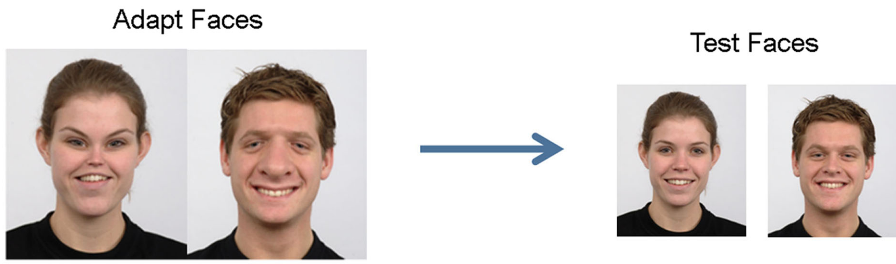

FIGURE 5 | Contingent adaptation. Observers adapted to an alternation between two faces with opposite distortions that differed in either gender or expression, and then judged the apparent distortion in each gender or expression.

the two distortions and in either gender or expression or both (**Figure 8**). They were then tested on the same two model faces used in the preceding experiments, but which were no longer part of the adapting set.

Aftereffects were now measured for four conditions. In the *expression difference*, the faces within each group were all happy or all fearful, but were drawn equally from males or females. In the *gender difference*, the two groups were all male or all female, with half showing a happy expression and half fearful. In the *correlated expression and gender difference*, each member of the adapting group had the same expression and gender (e.g., happy females versus fearful males or fearful females versus happy males). Finally, in the *conjunction of expression and gender differences*, observers were adapted to both expressions and genders within each group but combined in opposite ways. For example, they were exposed to expanded faces that were either happy females and fearful males, alternated with contracted faces that were either fearful females and happy males. Again, these conditions allowed us to compare adaptation to the attributes of expression or gender which were now less closely tied to a given individual identity. The latter two cases also allowed us to test what happens when the adapting images differ along more than one dimension, and whether this depends on whether these differences are covarying or reflect higher order combinations of the adapting attributes.

Mean settings at which the test faces appeared undistorted are shown in **Figure 9** for each of the four adapting contingencies. The results showed significant selective aftereffects for the expression difference [$t(14) = 4.55$, $p < 0.001$], and for a difference in both expression and gender [$t(30) = 5.03$, $p < 0.001$]. However, for the gender difference the selectivity did not reach significance [$t(15) = 1.34$, $p = 0.20$]. Moreover, a significant contingent aftereffect was not found when the observers were adapted to different conjunctions of gender and expression [$t(15) = -0.218$, $p = 0.76$]. Thus in this case the selectivity of the aftereffects across all of the conditions appeared to largely depend on the differences in expression.

DISCUSSION

As noted in the Introduction, our study was motivated by the possibility that face distortion aftereffects might be more robust to image changes that preserved the identity of the face than to changes that caused the adapt and test faces to appear to be drawn from different individuals (Yamashita et al., 2005). This difference is generally consistent with the selectivity of the aftereffects for low-level transformations in the images, as well as a number of higher-level aspects of the adaptation. We therefore asked whether this difference might be manifest when comparing the selectivity of aftereffects between natural variations within the same face versus between different faces. However, we did not find stronger transfer when the adapt and test images showed different expressions of the same face than when they differed in gender and thus identity. Instead, in our case the aftereffects tended to be more selective for the expression change. Moreover, selectivity for both the expression and gender differences were surprisingly weak. We consider the relative selectivity and the general lack of selectivity in turn.

An obvious problem in interpreting comparisons across the facial dimensions is that the differences in expression may have represented larger physical differences in the images. The differences in selectivity could then simply reflect the degree to which the adapt and test faces differed as images. Indeed, this factor has been suggested as a possible reason for differences in the susceptibility of identity versus expression adaptation to suppression from visual awareness (Moradi et al., 2005; Adams et al., 2010, 2011; Yang et al., 2010). However, by this account the previously reported asymmetries between expression and identity aftereffects should have been reversed, for again the identity aftereffects showed greater transfer across expression (implying that the expression differences were weaker; Fox and Barton, 2007; Fox et al., 2008). Fox and Barton also showed that this could not account for the asymmetries they observed by showing that there were not corresponding differences in discrimination thresholds for the faces (Fox et al., 2008). In our case, we did not evaluate an independent measure of facial similarity. Yet we did not observe stronger selectivity when the faces differed in both expression and gender, which might have been expected if overall similarity were the important factor in determining the degree of transfer. Moreover, even if the expression change introduced a larger physical difference in the image, the images corresponded to natural patterns of variation in the face, and thus coding and adaptation for the relative attributes might be expected to be matched to the relative range of variation along the two dimensions (Robbins et al., 2007; Webster and MacLeod, 2011). In any case, these differences would not alter our conclusion that natural variations in the same identity owing to a change in expression resulted in similar or more selective aftereffects than natural variations across identities owing to a change in

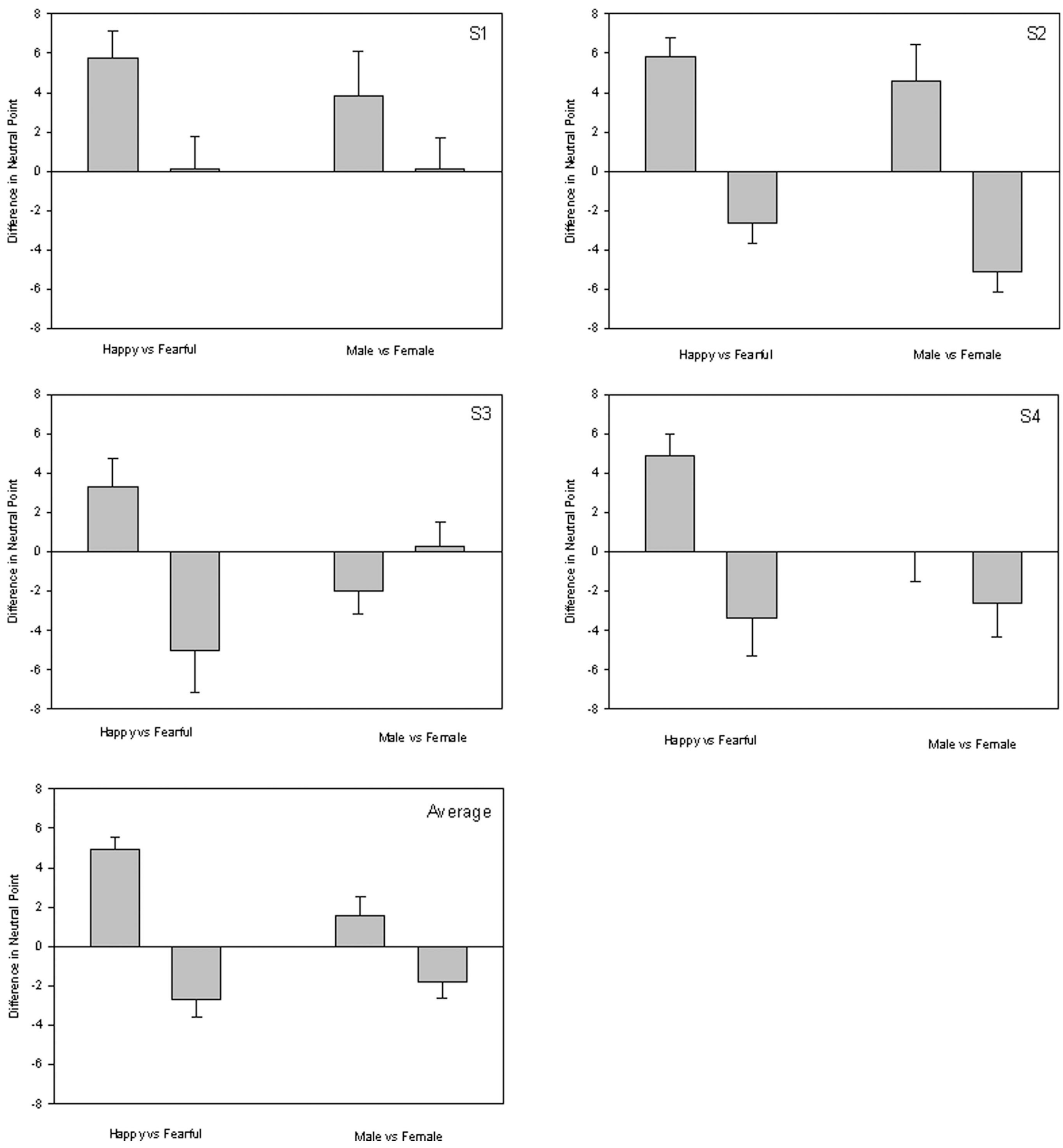

FIGURE 6 | Aftereffects for the contingent adaptation for expression or gender. Bars plot the difference between the settings for the happy or fearful face (left) or male or female face (right) after adapting to opposing distortions in the faces. Panels show the settings for the four observers or the mean.

gender. Thus our results would still be inconsistent with a strong form of the proposal that the aftereffects transfer more strongly across changes that preserve identity (though this assumes that the expression changes were not so strong that they in fact masked the model's identity).

Why might our conditions have led to a different pattern of selectivity for identity and expression than found previously (Fox and Barton, 2007; Fox et al., 2008)? An important difference between our studies is that these previous studies tested the effect of facial changes directly on identity and expression aftereffects.

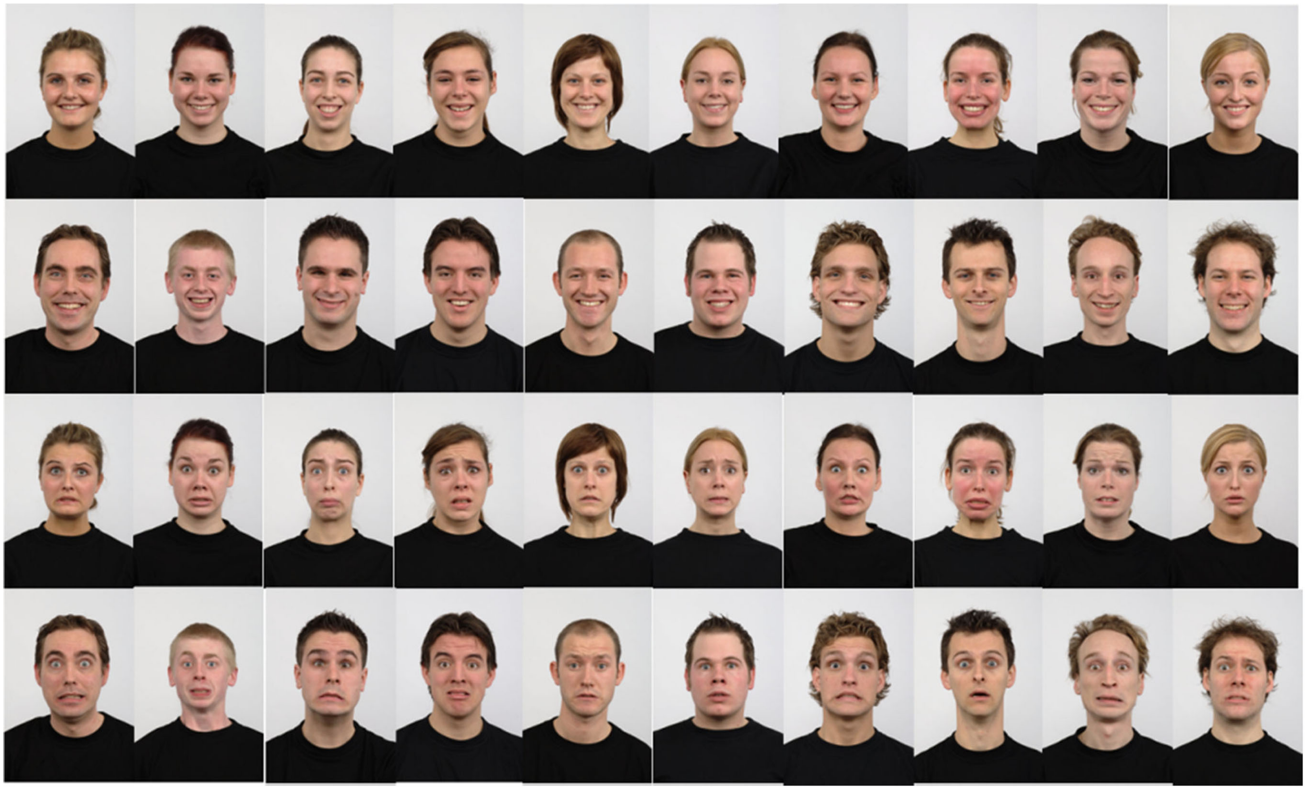

FIGURE 7 | Face sets shown for adaptation to populations of female or male, or happy or fearful faces.

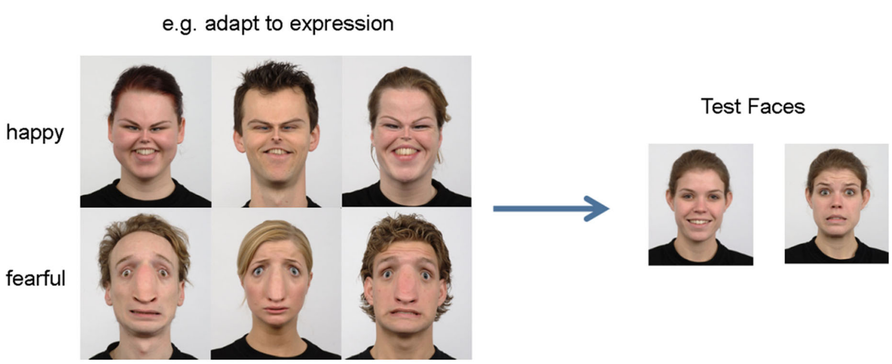

FIGURE 8 | Adaptation to different face sets with different attributes. Observers viewed an alternation between two faces with opposite distortions that were drawn at random from sets that differed in either gender and/or expression, and then judged the apparent distortion in each gender and/or expression.

That is, they tested how a change in identity affected the perceived expression of the face or vice versa. In contrast, our aftereffects instead measured how the same configural change (the perceived expansion or contraction of the face) was modulated by a difference in gender or expression. This had the advantage that the same aftereffects could be compared for different variations between the adapt and test images. However, it has the important drawback that the aftereffects are not directly tapping the perception of the specific dimensions of gender or expression. Thus our results are not inconsistent with asymmetries between expression and identity aftereffects, but instead suggest that the configural changes induced by adaptation to the distorted faces can be affected by differences in both expression and gender. Thus again they are inconsistent with the specific hypothesis we tested that the distortion aftereffects would be stronger between faces that shared a common identity.

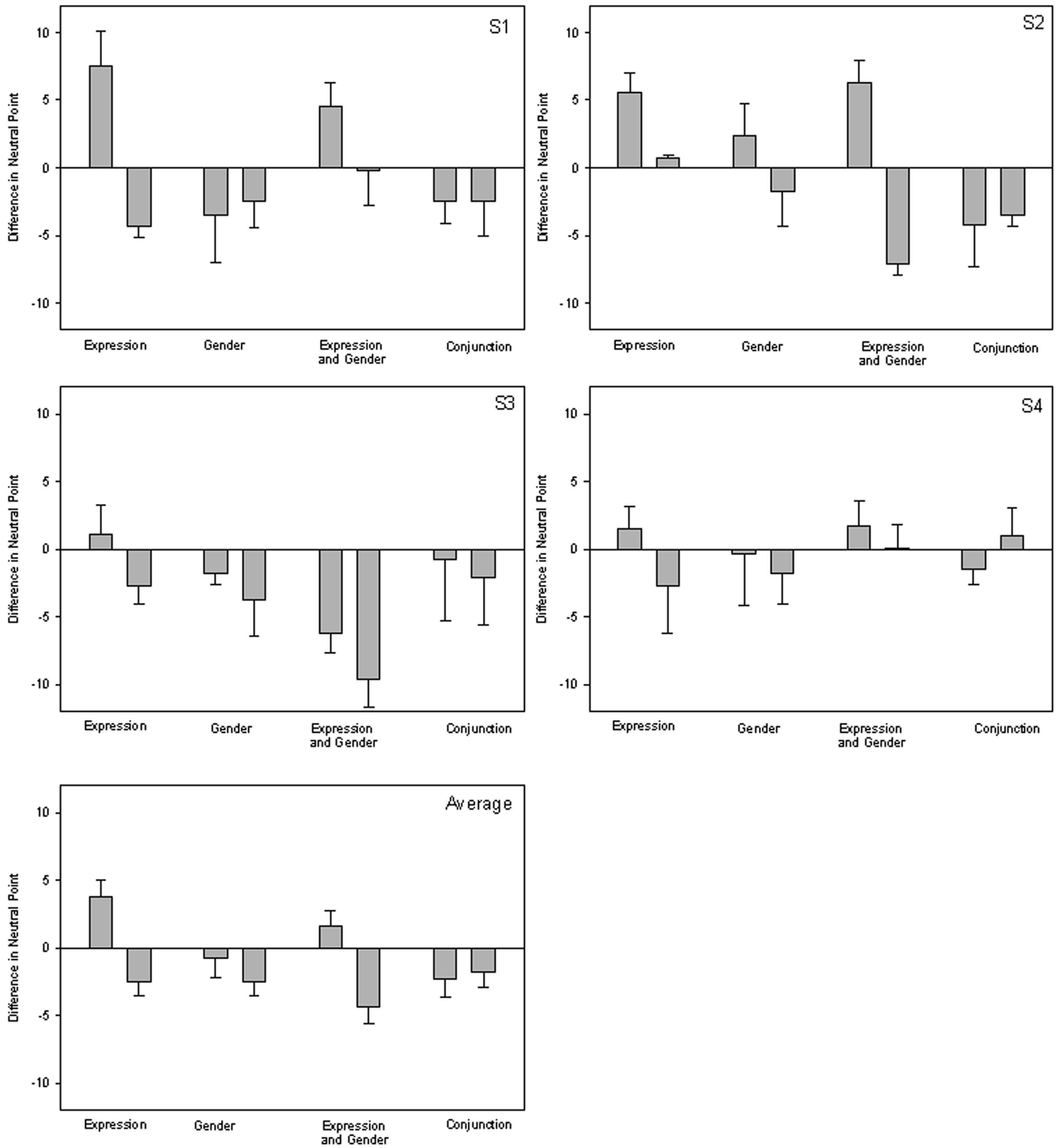

FIGURE 9 | Adaptation to opposing distortions in sets of faces. Bars plot the settings for the two opposing conditions when the sets of faces differed in expression, gender, both gender and expression, or conjunctions of gender and expression. Panels show the settings for four observers or the mean.

A conspicuous feature of our results was that the degree of selectivity we observed for both expression and gender was in fact very weak. The aftereffects were instead arguably notable for the high degree of transfer across fairly obvious changes in the appearance of the adapt and test faces. This is all the more compelling because the images were not cropped and thus provided unusually strong cues to the identity difference. The strong transfer is consistent with studies that have pointed out that changes in facial attributes lead to only partial selectivity in the distortion aftereffect (Jaquet and Rhodes, 2008), though it remains possible that the degree of selectivity varies with the specific form and magnitude of the configural change.

The basis for selectivity in face aftereffects is uncertain. One account assumes that different types of faces might be encoded relative to distinct norms (Little et al., 2005, 2008; Jaquet and Rhodes, 2008; Jaquet et al., 2008). In this case adaptation to distortions in a male or female face might therefore each induce a mean shift in the appearance of the subpopulation. Selectivity in such models assumes that the channels are very broadly tuned along one coding dimension (since this broad tuning is require to account for the normalization observed in face adaptation), while more narrowly tuned along other dimensions (so that stronger distortion aftereffects occur when the adapt and test have shared attributes). By this model, for the specific conditions we examined the channels coding the configural distortions are fairly broadly tuned for both gender and expression, and in particular, are not more selective for the identity attribute of gender than they are to the variant attribute of expression.

Webster and MacLeod (2011) noted that the contingent adaptation for different facial attributes could also reflect a form of tilt-aftereffect in the multidimensional space, so that adaptation to a specific identity trajectory (or "angle" in the space) biases the appearance of other face trajectories away from the adapting axis. For example, after adapting to an axis defined by a variation from expanded males to contracted females, male and female faces might appear "tilted" toward opposite distortions, while androgynous contracted or expanded faces would be shifted toward opposite genders. This pattern is similar to the changes in perceived hue following adaptation to different color directions (Webster and Mollon, 1994), and has the advantage that the aftereffects still reflect shifts relative to a single common norm. However, selective response changes in this model reflect a form of "contrast adaptation" that adjusts to the variance of the faces, and is distinct from the "mean adaptation" that characterizes most face aftereffects (Webster and MacLeod, 2011). Adaptation induced changes in the perceived variance of faces has been difficult to demonstrate (MacLin and Webster, 2001), suggesting that this form of adaptation may generally be weak. Under this model then, the weak selectivity we found for changes in expression or gender is consistent with the possibility that adaptation to the facial distortions primarily induces a mean bias in the face norm rather than a bias in perceived contrast or gamut of faces relative to the norm.

Finally, it remains possible that the configural aftereffects we tested show weak tuning for the subtle image variations that define different faces, because the aftereffects depend at least in part on response changes at more generic levels of visual coding. Adaptation can potentially arise at many if not all levels of the visual pathway (Webster, 2011; Webster and MacLeod, 2011). While the size difference between the adapt and test images provided a commonly used control for simple retinotopic afterimages (Zhao and Chubb, 2001), the distortions we probed have nevertheless been found to include both shape-generic as well as shape-specific and possibly face-specific components. For example, Dickinson et al. (2010) have noted that the aftereffects for configural distortions could in part arise from changes in the distribution of local orientations in the images, a pattern which could be preserved even when the adapt and test images differ in size. On the other hand, aftereffects for the distortions survive the size change even when the faces are altered to remove all internal structure except the eyes and mouth, so that the aftereffect in this case cannot be driven by the local texture (Yamashita et al., 2005). Moreover, aftereffects for distortions along one axis (e.g., horizontally stretching the face) transfer across changes in head orientation, and thus must again include a response change that is specific to the object (Watson and Clifford, 2003). Susilo et al. (2010) further examined the extent to which the configural aftereffects might be face-specific. They found that distorting faces by varying eye-height induced aftereffects which showed complete transfer from faces to "T" shapes when the images were inverted, but only partial transfer when the images were upright. This suggested that aftereffects for the distorted faces were driven by non-selective shape aftereffects for the inverted images, while reflecting both shape and face-selective response changes in upright faces. Again, in the present experiments we used configural distortions in order to have a common metric for comparing the expression and gender aftereffects. The fact that these aftereffects were contingent on the facial attributes indicates that the adaptation was not dependent on the distortion alone. Yet as the preceding studies suggest, it is also unlikely that they reflected response changes in mechanisms that were responsive only to faces. Different configural manipulations may vary in the extent to which they isolate face-specific levels of processing (Susilo et al., 2010), and these might reveal different patterns of selectivity from those we observed. Whatever the response changes and coding sites underlying the current configural aftereffects, our results suggest that they can adjust to the attribute of the configural change to a large extent independently of the specific face carrying the change, and in particular do not show more selectivity for an invariant attribute like gender than for a variant attribute like expression.

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Selectivity of face aftereffects for expressions and anti-expressions

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Adapting to a facial expression can alter the perceived expression of subsequently viewed faces. However, it remains unclear whether this adaptation affects each expression independently or transfers from one expression to another, and whether this transfer impedes or enhances responses to a different expression. To test for these interactions, we probed the basic expressions of anger, fear, happiness, sadness, surprise, and disgust, adapting to one expression and then testing on all six. Each expression was varied in strength by morphing it with a common neutral facial expression. Observers determined the threshold level required to correctly identify each expression, before or after adapting to a face with a neutral or intense expression. The adaptation was strongly selective for the adapting category; responses to the adapting expression were reduced, while other categories showed little consistent evidence of either suppression or facilitation. In a second experiment we instead compared adaptation to each expression and its anti-expression. The latter are defined by the physically complementary facial configuration, yet appear much more ambiguous as expressions. In this case, for most expressions the opposing faces produced aftereffects of opposite sign in the perceived expression. These biases suggest that the adaptation acts in part by shifting the perceived neutral point for the facial configuration. This is consistent with the pattern of renormalization suggested for adaptation to other facial attributes, and thus may reflect a generic level of configural coding. However, for most categories aftereffects were stronger for expressions than anti-expressions, pointing to the possible influence of an additional component of the adaptation at sites that explicitly represent facial expressions. At either level our results are consistent with other recent work in suggesting that the six expressions are defined by dimensions that are largely independently normalized by adaptation, possibly because the facial configurations conveying different expressions vary in independent ways.

Keywords: adaptation, aftereffects, face perception, facial expressions

INTRODUCTION

Facial expressions are important stimuli for signaling our emotional states and thus are critically involved in many social functions. Most humans are consequently adept at recognizing them, and failures in recognition are symptomatic of serious cognitive and neurological impairments (Calder et al., 2001). The human face displays an enormous variety of expressions, including a set of six basic expressions of emotion that correspond to happiness, anger, sadness, fear, disgust, and surprise (Ekman, 1992). The facial configurations signaling these states reflect highly stereotyped action patterns (Ekman and Friesen, 1978) and are to a large extent (though not completely, e.g., Russell, 1994) common across cultures, suggesting that they are primarily innate and universal.

An actively investigated question is how information about expressions is encoded in the visual system, and whether different expressions are represented by common or distinct pathways. Functionally, expressions convey information about affect, and it remains unclear whether basic emotions are independent or represent complementary or related states. For example, circumplex models of affect hold that different emotions are polar opposites (Plutchik, 2001) or represent differences in a smaller number of underlying dimensions such as valence or arousal (Russell, 1980; Posner et al., 2005). The perception of expressions involves changeable aspects of the face and is thought to involve cortical areas which differ from the areas that are primarily responsible for invariant aspects of the face such as identity. Specifically, the Superior Temporal Sulcus has been implicated in expression recognition while identity recognition has instead pointed to the importance of a distinct network including the Fusiform Gyrus (Kanwisher et al., 1997; Haxby et al., 2000; Rossion et al., 2003). Many different neural structures appear dedicated to generating and processing the basic expressions of emotion (Adolphs et al., 1994, 1995, 1996; Morris et al., 1998; Sprengelmeyer et al., 1998; Kesler/West et al., 2001; Said et al., 2011), and thus the relationships between these different categories are complex and still unresolved. On the one hand, diverse evidence from studies of disease, lesions, and neuroimaging have revealed partially shared pathways for some expressions. Yet on the other hand, the same approaches have also provided widespread evidence for selective impairments and activation patterns for the perception of different expressions, arguing strongly against the possibility that all expressions are encoded as dimensions of a common single representation (Calder et al., 2001).

In this study we examined the visual coding of facial expressions by measuring how the perception of expressions changes with adaptation. Viewing a stimulus can lead to large aftereffects in the appearance of subsequent stimuli. These adaptation effects have been widely used as a tool for probing the visual coding of stimulus features like color, motion, or orientation (Webster, 2011), and recently a number of studies have used adaptation to examine the processing of facial configurations (Webster and MacLeod, 2011). The appearance of a face can be strongly biased by prior adaptation. For example Webster and MacLin (1999) showed that adapting to a distorted face (e.g., one in which the features are expanded) induces a negative aftereffect in the appearance of the original face (e.g., so that the face appears too contracted). Similar negative aftereffects have been found for many of the dimensions that characterize natural variations in faces, including individual identity (Leopold et al., 2001) and facial categories such as gender and ethnicity (Webster et al., 2004).

Several previous studies have demonstrated that perceived expression can be biased by prior exposure to a face with a different expression (Russell and Fehr, 1987; Hsu and Young, 2004; Webster et al., 2004; Fox and Barton, 2007; Furl et al., 2007a,b; Benton and Burgess, 2008; Ellamil et al., 2008; Rutherford et al., 2008; Skinner and Benton, 2010; Cook et al., 2011; Pell and Richards, 2011). These experiments have thus shown that – like other aspects of face perception – the perception of facial expressions is highly adaptable. Importantly, this work has also suggested that the adaptation depends in part on the high-level configural properties of the face, and not simply on low-level properties such as the local features, nor on conceptual properties such as the conveyed emotion (Fox and Barton, 2007; Butler et al., 2008; Rutherford et al., 2008). (However, low-level features can also contribute; Xu et al., 2008.) Thus the adaptation to facial expressions appears to tap into visual pathways that may at least partly mediate the visual recognition of expressions, and may therefore provide a method for exploring how information is organized within these pathways.

A number of these studies have previously explored the interaction between different expressions. For example, Hsu and Young (2004) found that adapting to fearful, happy, or sad expressions produced selective losses in sensitivity to the adapted emotion, but also showed some facilitation across the expressions. Rutherford et al. (2008) instead asked observers to label the expression of a face with a neutral expression after adapting to each basic expression. They also observed asymmetric interactions where negative expressions were similar in inducing more responses that the neutral face appeared happy, while adapting to the happy expression caused the neutral test to specifically be judged as more sad. Pell and Richards (2011) further found an asymmetric relationship between the aftereffects for anger, fear, and disgust and argued from these that these expressions were encoded in partially overlapping representations. In contrast, Skinner and Benton (2010) recently reported that adaptation to faces with anti-expressions (formed by morphing each basic facial expression through an average expression and thus toward a face image with the opposite facial configuration) produced highly selective changes in the ratings for each expression. For example, a face with the opposite expression of happy selectively increased the probability of judging the average face as happy. More recently Cook et al. (2011) instead explored adaptation effects along the principal axes of variation in natural expressive poses of a face (so that the axes were not tied to the canonical expressions). They showed that adaptation to positive or negative excursions along the first or second principal axis led to opposing aftereffects along that axis, but not to the (second or first) orthogonal axis.

The results of these studies thus differ in the extent to which adaptation to one expression might influence the perception of other expressions. In turn, this has implications for understanding the extent to which the visual encoding of different expressions might be separable (at least at the coding levels affected by the adaptation). In this study we sought to further explore this question by measuring how adaptation to each basic expression affected the sensitivity to different expressions. In particular, we assessed the changes in the recognition of each expression relative to a face with a neutral expression. The stimulus spaces explored by Skinner and Benton (2010) and Cook et al. (2011) – which have provided the strongest evidence for norm-based representation of expression – were instead anchored by the average expression in their samples. This has the advantage that the reference is defined by the stimulus distribution, but the disadvantage that this average could itself appear non-neutral and in particular could convey a possible expression. An average of two expressions can appear strongly biased after adapting. For example, viewing a happy or angry face biases the perceived expression of an intermediate morph between the two expressions toward the unadapted face (Webster et al., 2004). We took advantage of the fact that for expressions there is a "psychologically neutral" face pose defined by the neutral expression, and then asked how the canonical expressions defined as trajectories relative to this reference interacted in the adaptation. To address this question, we first conducted an experiment that examined how adaptation to one expression affected the recognition of the same or different expressions. In a second experiment, we instead asked how this recognition was affected when observers were adapted to one of the basic expressions or to the corresponding "anti-expression" representing the opposite configural change in the face.

MATERIALS AND METHODS

SUBJECTS

Observers included author IJ and 17 additional observers who participated either voluntarily or for partial course credit and who were naïve with respect to the aims of the study. A total of 12 subjects were tested in the first experiment and 7 in the second, with IJ tested in both. All had normal or corrected-to-normal vision. Participation was with informed consent and all experiments followed protocols approved by the university's Institutional Review Board.

STIMULI

We used two different sets of stimuli for the two experiments – one which allowed us to assess the adaptation effects for images of actual faces, and the second based on simulated faces that allowed us to generate both expressions and their anti-expressions.

Experiment 1

For the first experiment, the images of emotional facial expressions were generated from the California facial expressions (CAFE) dataset (Dailey et al., 2001). The facial expressions used in this set had been certified according to the facial action coding system (FACS). Expressions of the six basic emotions and a neutral expression were selected from a single male individual in the CAFE dataset (individual 27, facial codes 027_n5, 027_a2, 027_d1, 027_f2, 027_h2, 027_m2, and 027_s1). These facial expressions were used for the neutral expression and to define the maximum intensity for each expression. The same individual was used for the adapt and test in order to maximize the strength of the expression aftereffects, which are selective for identity (Fox and Barton, 2007). While our results are thus restricted to a single identity, the highly stereotyped action patterns characterizing different expressions suggest that the pattern we observed is general.

All pictures were converted from the CAFE database into gray-scale bitmaps and presented at a size of 253×400 pixels. For each emotional expression, 101 graded intensities of the expression were created by morphing between the neutral facial expression and each basic expression using the Gryphon Software Corporation program MORPH Version 1.5 (see **Figure 1**). Sets of facial expressions were produced for each of the six basic emotions (anger, disgust, fear, happy, sad, and surprised), ranging in emotional intensity from 0 (the neutral face) to 100 (maximum intensity, corresponding to the original image of the expression).

Experiment 2

To create pairs of expression and anti-expressions, images of the emotional facial expressions were generated using the Singular Inversions FaceGen Modeler program. This software is based on a 3D morphable model of faces, and details of the software and image set are described in O'Neil and Webster (2011). The program provides realistic portrayals of faces with varying identities and characteristics, including gender, ethnicity, age, and expression. Simulated faces from this program have been used in a number of other recent studies of face perception and adaptation (Shimojo et al., 2003; Russell et al., 2006; Schulte-Ruther et al., 2007; Oosterhof and Todorov, 2008; Potter and Corneille, 2008; O'Neil and Webster, 2011), and similar model faces have been found to convey information about expression that are reasonably comparable to images of actual faces (Dyck et al., 2008). One advantage of these modeled faces is that the strength of each of the basic expressions can be linearly titrated for a single fixed identity and pose, for which we chose a frontal view of an average Caucasian male face of 30 years as provided by FaceGen (**Figure 2**). A second advantage is that the strength can be varied in positive and negative directions to create both expressions and anti-expressions. That is, positive values produced the requested expression (e.g., anger) while negative values inverted the configural changes and thus yielded anti-expressions. For each pair, an array of 201 faces was created that ranged from the full ant-expression (intensity = -1) to the full original expression (intensity = $+1$).

PROCEDURE

For both experiments, stimuli were presented on a computer controlled CRT monitor. The face images subtended ~7° in height and were shown on a uniform background of ~ 28° by 37°. Subjects binocularly free-viewed the display from approximately 60 cm in an otherwise dark room, and responded using a hand-held keypad. They were asked to continuously view the adapting image but were not given specific instructions for viewing or fixation.

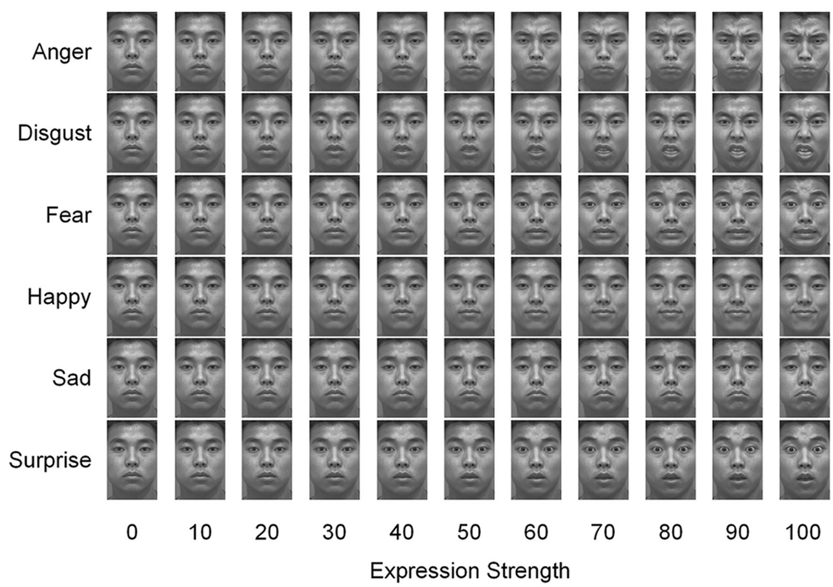

FIGURE 1 | A subset of the face image arrays used in Experiment 1. The face was varied from the neutral expression to one of the six basic expressions (corresponding to different rows). Successive images along each row correspond to an increment of 10 units in expression strength formed by morphing between the neutral face (0) and the original posed expression (100).

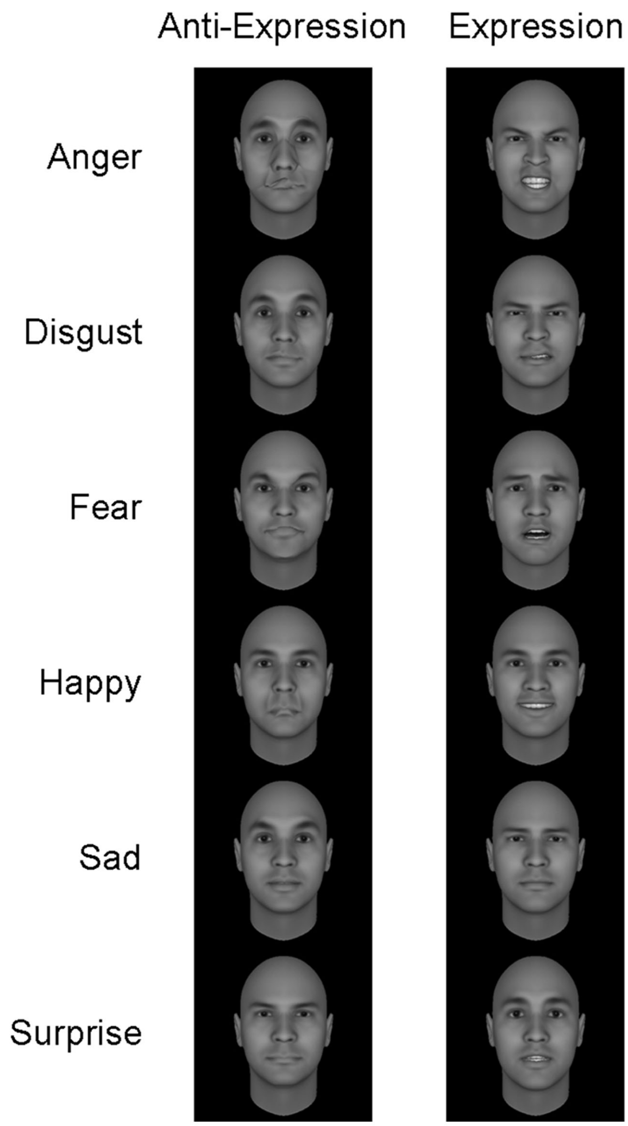

FIGURE 2 | Examples of the basic expressions and anti-expressions in the simulated face. Anti-expressions were set to produce the opposite spatial configurations of equivalent morph strength for each basic expression.

Experiment 1

The first experiment measured changes in the threshold intensity for recognizing different expressions after adapting to a given expression. In daily sessions lasting up to 1 h, observers were adapted to a single face image but were tested on all expressions, with the order of adapting expressions randomized across sessions. At the start of each run, the subject viewed the maximum intensity of one of the expressions or the neutral face for 5 min. Following this, a test face was presented for 1000 ms and then cycled with 3 s periods of readaptation, with the test and adapt images separated by 250 ms during which the screen was blank. The test face was drawn at random from one of the six expression categories, and the subject was thus required to make a six-alternative forced choice response to indicate the expression shown. The initial level along each category was chosen at random. Thresholds for identifying each expression were found by varying subsequent levels with a staircase procedure. Six staircases were run simultaneously within each session, one for each expression, and settings continued until the staircase for each image set completed 10 reversals. Thresholds were estimated from the mean of the last seven reversals. In order to keep the task consistent throughout the run, when a staircase for a particular emotion terminated, the staircase continued, but the subject's responses for that staircase were no longer recorded.

Experiment 2

The second experiment tested for interactions between adaptation to each expression and its anti-expression. In a daily session subjects adapted to and made settings for only one expression. The task involved making a forced choice response to decide whether the presented face did or did not have the target expression. We chose this over an alternative of asking which side of neutral the test face was on, since there were obvious asymmetries in the ability to classify positive or negative excursions. That is, while expressions were easy to identify, the anti-expressions were difficult to judge, precisely because they did not look like a basic expression (see **Figure 2**). Stimuli were varied in a staircase to estimate the category boundary based on the stimulus level at which the face was equally likely to be judged to have or not have the expression. Subjects made these settings after adapting to a neutral face or to the target expression or anti-expression shown at full strength, with the test face again varied by the staircase.

RESULTS

EXPRESSION RECOGNITION FOLLOWING ADAPTATION

Figure 3 plots for each expression the changes in recognition thresholds (i.e., the difference between the image levels required to correctly identify the presented expression after adapting to a given expression or to the neutral face). Positive values correspond to a higher threshold for the test expression and thus to loss in sensitivity to that expression, while negative values correspond to a reduced threshold and thus facilitation for the test expression. The results reveal that the aftereffects are strongly selective for the adapting expression. Specifically, the primary effect of the adaptation was to reduce recognition of the adapted expression, with little systematic effect on recognition for the unadapted expressions.

To evaluate these effects, the thresholds were compared with a two-way repeated measures ANOVA testing the variables of adapt category (seven levels including neutral) and test category (six levels). There was not a main effect of adapt expression [$F(6,66) = 1.23$, $p = 0.30$] but a significant effect for the test expression [$F(5,55) = 5.91$, $p < 0.001$]. Holm–Sidak comparisons revealed that this resulted because the absolute threshold for identifying fear in the face was higher than for disgust [$t(55) = 3.92$, $p = 0.0002$], happiness [$t(55) = 4.59$, $p < 0.0001$], or sadness [$t(55) = 4.53$, $p < 0.0001$]. (Note that these differences in absolute sensitivity to the expressions are not shown in **Figure 3**, which instead plots the *change* in the thresholds, i.e., the difference in thresholds after adapting to each expression vs. the neutral face). There were no other significant differences in absolute sensitivity to the different categories.

There was a significant interaction between the adapting and test categories [$F(30,330) = 10.05$, $p < 0.001$], and Holm–Sidak comparisons revealed strongly selective aftereffects for most expressions. Specifically, adaptation significantly altered the recognition thresholds only for the adapted expression for fear [$t(330) = 4.20$, $p < 0.001$], happiness [$t(330) = 3.86$, $p < 0.001$], sadness [$t(330) = 7.79$, $p < 0.001$], and surprise [$t(330) = 4.18$, $p < 0.001$]. Adapting to anger similarly increased the recognition threshold for anger [$t(330) = 5.52$, $p < 0.001$], though this also raised the threshold for sadness [$t(330) = 2.67$, $p = 0.008$]. The one exception to this pattern was thus for disgust, for which none of the aftereffects reached significance. Finally, all of the significant changes in the thresholds reflected a decrease in recognition after adaptation. That is, there was no case where adaptation to any expression enhanced the tendency to correctly identify an expression.

The results thus suggest that the aftereffects of adaptation to different facial expressions are highly selective for the adapting expression. In only one case was significant transfer observed (from adapting to anger on identifying sad). Moreover, the results failed to reveal any suggestion that adaptation to one expression facilitated the perception of a different expression; instead, almost all of the aftereffects are confined to a reduced response to the adapting axis. This suggests that – at least as probed by the present adaptation task – the representations of the different expressions are largely independent.

CHANGES IN PERCEIVED EXPRESSION FOLLOWING ADAPTATION TO EXPRESSIONS AND ANTI-EXPRESSIONS

As noted in the section "Materials and Methods," in the second experiment subjects determined the stimulus level at which the target expression became visible after adapting to the neutral face or to either the expression or anti-expression. **Figure 4** plots for each category the changes in the settings (i.e., the setting when adapted to either the expression or anti-expression minus the setting when adapted to the neutral face). Large aftereffects are evident for most of the expressions. In particular, there is a clear trend for adaptation to each expression to make the target expression less visible, while adapting to the anti-expression induced the opposite change and thus made the expression more visible.

To evaluate these effects, the category boundaries were compared with a two-way repeated measures ANOVA testing the variables of adapt expression (six levels) and expression strength (three levels). There was a main effect of adapt expression [$F(5,30) = 6.66$, $p < 0.001$]. Holm–Sidak *a posteriori* comparisons revealed this resulted from the threshold for detecting a sad face being much larger than for the happy [$t(30) = 5.64$, $p < 0.001$]

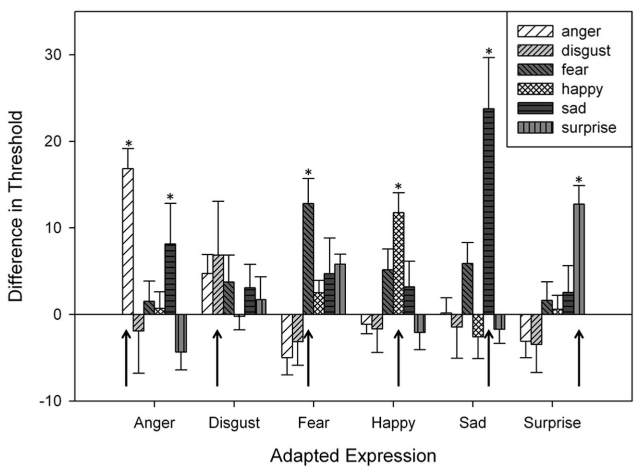

FIGURE 3 | Changes in recognition thresholds following adaptation (Experiment 1), averaged across 12 observers. Each bar plots the difference in the thresholds under adaptation to one of the basic expressions vs. for the neutral expression. Positive values correspond to a threshold increase. Each cluster of six bars corresponds to the six test expressions and a different adapting expression. Aftereffects when the adapt and test expression were the same are indicated by arrows. Asterisks indicate aftereffects that are significantly different from 0.

or angry expression [$t(30) = 3.60$, $p = 0.001$]. No other adapt expressions differed in their category boundaries.

There was also a main effect for expression strength [$F(2,12) = 71.71$, $p < 0.001$], with significant differences between all three conditions [all $t(12) > 3.36$, $p < 0.0057$]. There was no evidence of a significant adapt expression × expression strength interaction [$F(10,60) = 1.40$, $p = 0.20$]. However, Holm–Sidak *a posteriori* comparisons revealed that the settings for the target expression differed from neutral for all expressions [all $t(60) > 4.74$, $p < 0.001$] while the anti-expression differed for all expressions [all $t(60) > 1.86$, $p < 0.035$] except for anger [$t(60) = 1.28$, $p = 0.11$] and fear [$t(60) = 1.57$, $p = 0.062$].

Finally, we also compared the size of the aftereffects for the expression and anti-expression faces with a two-way repeated measures ANOVA testing the variables of adapt expression (six levels) and expression sign (two levels, excluding neutral). There was a main effect of expression sign [$F(1,6) = 22.31$, $p = 0.003$], due to the aftereffects for the anti-expression being smaller than for the target expression. There was no evidence of a significant adapt expression × expression strength interaction [$F(5,30) = 1.683$, $p = 0.169$]. However, Holm–Sidak *a posteriori* comparisons revealed that the aftereffects for the target expression were greater than the anti-expression for anger, disgust, fear, and surprise [all $t(30) > 2.409$, $p < 0.022$], while there was no observed difference in aftereffects for happy or sad [all $t(30) < 1.408$, $p > 0.169$].

Thus unlike the independence observed between adaptation to different actual expressions, each expression tended to show complementary aftereffects to the anti-expression. Thus the aftereffects for opposite facial configurations appeared yoked, in contrast to the different and at least conceptually complementary expressions of the basic emotions. However, for the conditions we tested the anti-expression aftereffects were weaker than for the actual adapting expressions.

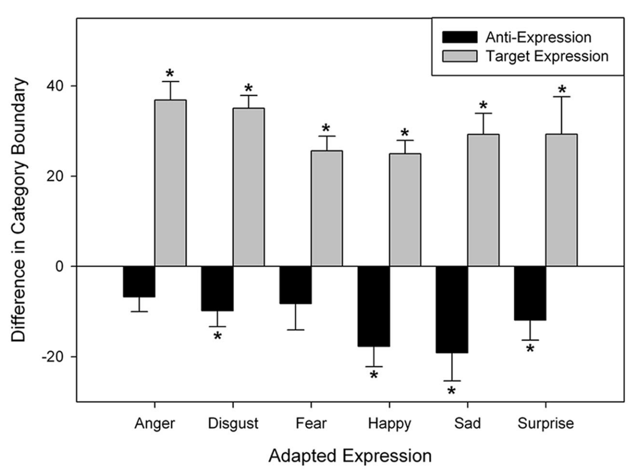

FIGURE 4 | Changes in the stimulus boundary for perceiving each basic expression after adapting to the expression or to the anti-expression (Experiment 2), based on the mean settings for seven observers. Each bar plots the difference between the stimulus level when adapted to the expressive vs. neutral face. Positive values indicate reduced sensitivity to the expression while negative values correspond to facilitation. Asterisks indicate aftereffects that are significantly different from 0.

DISCUSSION

In this study we used adaptation to explore the visual representation of facial expressions. Consistent with previous work, we found that the perceived expression of a face can be strongly biased by prior adaptation to a facial expression (Russell and Fehr, 1987; Hsu and Young, 2004; Webster et al., 2004; Fox and Barton, 2007; Furl et al., 2007a,b; Benton and Burgess, 2008; Ellamil et al., 2008; Rutherford et al., 2008; Skinner and Benton, 2010; Cook et al., 2011; Pell and Richards, 2011). In our case these aftereffects were strongly selective for individual expressions. Specifically, adapting to an expression such as anger or happiness reduced sensitivity to anger or happiness in the face, while producing little change in sensitivity to other categories. Moreover, the changes in the thresholds for the adapting category did not lead to consistent increases in sensitivity to other categories. Thus the different basic expressions could be adapted largely independently. These results are consistent with the selective expression aftereffects reported by Skinner and Benton (2010) and Cook et al. (2011), and shows that this selectivity also occurs when the expressions and adaptation are probed relative to a neutral facial expression defined independently of the expression set. Again, the aftereffects relative to this neutral point are important for characterizing the selectivity of the adaptation, for the neutral expression may have a special status similar to the neutral identity that has been found to be important for defining the properties of face identity aftereffects (Rhodes and Jeffery, 2006).

Studies of face adaptation have varied widely in the strategies used to control for low-level or image-based aftereffects, for example between the local contours in the image. These steps include varying the size, position, or identity of the adapt and test stimuli (Webster and MacLeod, 2011). A limitation of our study was that we kept these parameters the same in order to maximize the strength of the adaptation, and thus the opportunities for interactions between the different expressions. While this could potentially have allowed the intrusion of lower-level aftereffects, these are strongly sensitive to spatial position (Xu et al., 2008), and have been found to be less evident when the faces are freely viewed without constraining fixation (Butler et al., 2008), as in our study. The nominally high-level aftereffects are themselves selective for position and size (Afraz and Cavanagh, 2008, 2009), and thus should also have been strongest when the adapt and test image were equated. Our stimuli should therefore have included a potential response change at higher levels where the image was represented as a face or expression. Thus adaptation-dependent interactions between different expressions arising at such sites should still have occurred, but were not observed in our conditions. On the other hand, it remains possible that aftereffects arising at early levels might mask a high-level aftereffect. Thus we cannot exclude the possibility that a different pattern of expression aftereffects might arise when the adapt and test faces share fewer image features. One argument against this is that our results again confirm the independence of different expression aftereffects reported by Skinner and Benton (2010), who included a stationary fixation point but moving adapting image as a more explicit control for image-based adaptation.

While we observed little sign that adapting to one canonical expression facilitates an "opposite" expression, such interactions have been observed in previous studies. What could account for this difference? One case where interactions do clearly occur is when the stimuli are varied between two expressions, rather than in expression strength. For example, as noted in the Introduction, Webster et al. (2004) measured expression aftereffects in faces formed by morphing between two expressions such as happy and angry. Adapting to either expression caused the blended face to appear more like the unadapted expression. However, this composite face represented a mixture of two expressions rather than a neutral expression (which would only occur if two expressions were formed by opposite facial configurations). Thus their study probed the effects of adaptation on ambiguous expressions rather than neutral ones, and the fact that adaptation biased this ambiguity by selectively reducing sensitivity to one expression is consistent with the present findings. It is less certain how our results relate to the facilitation observed by Hsu and Young (2004), who measured sensitivity to expression in faces that varied between neutral and a given expression; or to Rutherford et al. (2008), who had subjects label the expressions perceived in a neutral face after adapting. In both cases prior adaptation to one expression made it more likely that the test faces would be labeled with a different expression. However, as we showed in Experiment 2, adaptation does in most cases alter the appearance of a neutral face – by inducing the opposite configural change in the face. This might cause a neutral face to appear more ambiguous, which could in turn increase the tendency to ascribe a different expression to it. Thus the facilitatory effects might not reflect a direct coupling between different categories. In any case, our results are similar to Hsu and Young (2004) in suggesting that any facilitation across expressions is substantially weaker than the reduction in sensitivity to the adapting expression, suggesting that any potential opponent-like couplings are correspondingly weaker.

A number of studies have examined the potential sites at which adaptation biases perceived expressions (Fox and Barton, 2007; Butler et al., 2008; Ellamil et al., 2008; Rutherford et al., 2008; Xu et al., 2008). As we noted in the Introduction, the aftereffects cannot be accounted for solely by low-level local features alone, such as the curvature of the mouth, or by high-level abstractions, such as emotional meaning. This suggests that the adaptation is acting partly at a site at which the expression is being represented in terms of its visual configuration. This "visual" locus may also explain why we observed little cross-talk between the different expression categories. The information for different expressions corresponds to combinations of changes in different facial features (Smith et al., 2005; Nusseck et al., 2008). Thus while different expressions might have conceptually opponent relationships (e.g., an individual is either happy or sad) the visual information conveying those states are not subject to the same constraints. Adaptation to the visual information in the face might therefore not reveal the functional relationships between the different emotional states conveyed by expression categories (Cook et al., 2011).

Our results are consistent with the possibility that this visual site of the adaptation may in part be prior to an explicit representation of the expression, and thus occurs at a more generic level of the configural coding of the face. That is, at least part of the expression adaptation may act at a site common to many other facial attributes that have been examined with adaptation, by altering the representation of the spatial configuration of the face. In line with this, changing the facial configuration by distorting the image imbues the face with different expressions; (Ganel et al., 2004) and these distortions are highly adaptable (Webster and MacLin, 1999). Moreover, principal components analyses of facial variations point to distinct overlapping sources of variation between different identities or expressions, suggesting that at the visual level, expression, and generic shape are somewhat confounded (Calder and Young, 2005). It is also consistent with the finding that expression adaptation is selective for individual identity, so that whatever is adapted includes the shape information about identity, again arguing against a site where the expression has been explicitly extracted (Fox and Barton, 2007; Ellamil et al., 2008). (Intriguingly, the opposite has not been found. That is, identity adaptation completely transfers across a change in expression, suggesting that in this case adaptation might tap into a level where identity is coded independently of expression, Fox et al., 2008; or alternatively, it might conceivably act at a common level but information from this level is then pooled in different and asymmetric ways to form distinct representations of identity and expression).

In our study the primary evidence implicating a generic configural effect of the adaptation is from the aftereffects we found for anti-expressions. For most expressions, adapting to these faces also biased the appearance of the near-neutral face, yet these stimuli appear much more ambiguous and in this sense have less ecological validity than the basic expressions. If the adaptation were acting directly on processes coding expression then we might expect little response change from the anti-expressions, simply because these correspond to configural variations that are not clearly used to signal or detect expressions. However, as a change in facial shape they have a more equal status to an expression change, implying again that the adaptation may act at the level of the basic configural representation. In this regard our results again confirm the findings of Skinner and Benton (2010) in suggesting that the aftereffects reflect average shifts or a renormalization in the perceived expression of the face, consistent with a norm-based code of the type that has been suggested for invariant attributes of the face (Rhodes et al., 2005; Webster and MacLeod, 2011).

Are there also signs of an expression-specific site of the adaptation? One hint of this in our study was that the aftereffects for the anti-expressions were substantially weaker than for most of the basic expressions. This asymmetry is atypical of other reported aftereffects including facial distortions (Webster and MacLin, 1999; Rhodes et al., 2003; Watson and Clifford, 2003) and facial categories such as gender or ethnicity (Webster et al., 2004; Little et al., 2005; Ng et al., 2006; Jaquet et al., 2007; Jaquet and Rhodes, 2008) where opposites of the dimension appear to exert more equal effects on the neutral point. If mechanisms are sensitive only to the strength of a given expression – and if these mechanisms can be directly adapted – then the strongest response changes should occur only for faces with the appropriate expression.

However, there are a number of alternative accounts for the asymmetries we observed. First, because we measured when an expression became apparent, the category boundary was always physically closer to the expression than the anti-expression. Thus the differences could in part reflect how far aftereffects to one level of the stimulus continuum spread to other levels – a local response shift would favor the locally closer expression. An argument against this is that the degree of asymmetry was not closely related to the threshold levels for detecting different expressions, and indeed was strongest for anger which had a relatively low threshold. Second, there were discrete qualitative changes on either side of the physically neutral face because most of the expressions include exposed teeth, while the complementary configurations did not. This could have provided a spatially local stimulus clue to the neutral point which might have been more impervious to adaptation, since it seems unlikely that a purely visual aftereffect to a closed mouth would affect the perception of the teeth. Given this difference it is surprising that strong aftereffects for anti-expressions were observed for some dimensions like happy faces which also included an open smile. Finally, the anti-expressions included changes in features such as eye brow thickness which could have introduced an apparent change in identity cues (though these changes corresponded to variations in the same identity with the brows raised or lowered). Moreover, for anger in particular, the full anti-expression included distortions which were outside the range of natural facial variations. We allowed this because these unnatural expressions nevertheless represented the equivalent opposing distortion in the linear model of the face, and because face aftereffects remain robust even when the adapting faces do not appear as plausible images of a real face (MacLin and Webster, 2001; Robbins et al., 2007; Seyama and Nagayama, 2009). Given these potential confounds, we cannot be certain of the basis for the asymmetries. Nevertheless, it is important to note that these stimulus asymmetries are inherent in the properties of actual facial expressions and not just in the stimuli we chose to probe them. That is – actual expressions often do include an open mouth that has no obvious facial counterpart in the anti-expression, and it is likely that there are not facial poses that are complementary and equal in intensity to the facial action patterns representing actual expressions. Thus the asymmetries are again at least consistent with sensitivity changes at expression-specific sites. And again, the facilitation found for most anti-expressions is inconsistent with changes only at these sites, and therefore also strongly implicates response changes at a more general level of configural coding.

We were motivated to explore the adaptation effects for facial expressions in part because there are only a small number of well-defined and salient dimensions to expressions. This differs from the perceptual attributes underlying facial identity, which remain very poorly defined in both number and form. This low-dimensional space offers the hope of quantifying the "tuning" properties for expression representations in the same way that adaptation has traditionally been used to characterize the channel selectivities of visual features such as color or form (Webster and MacLeod, 2011). What can our results say about these channels? On the one hand, in our case the different expressions do appear to be encoded largely independently. That is, to a first approximation the adapted level of the visual system appears to represent the basic expressions as independent sources of information, and this is again consistent with the fact that as stimuli the basic expressions vary in independent ways (Smith et al., 2005; Nusseck et al., 2008) and also that we derive independent meanings from them. Our results thus support other evidence that different expressions are not encoded in terms of a common underlying framework (Calder et al., 2001). Yet on the other hand, our findings are not conclusive on whether the adaptation is producing sensitivity changes within mechanisms that are specifically tuned to the configurations defining different expressions. This is because we cannot exclude the possibility that the response changes are along an undefined set of dimensions which are in turn combined to form a representation of the expression (Cook et al., 2011). The latter is again hinted at by the fact that clear aftereffects occur for most of the anti-expression faces. These stimuli in fact present somewhat of a conundrum for modeling the adaptation (Webster and MacLeod, 2011). Similar to the types of models that have been developed to describe other facial aftereffects (Rhodes et al., 2005), representations of an expression might involve a balance between two mechanisms – one tuned to the expression and the other to the anti-expression. Yet the problem in this case is that the anti-expressions correspond to a set of stimuli that we rarely see, making it questionable that a mechanism would be built to detect them. And if the neutral face depends on how these two pools are balanced by adaptation, then the frequency differences mean that in the native state sensitivity should be strongly biased against the expression. Alternatively, a potential way out of this dilemma is again if the adaptation is acting at a more generic site coding different facial configurations. Processes for detecting a given expression could then be cobbled together from whatever dimensions might underlie the configural coding, without the need to build an opposing process. This leaves however the puzzling result that these opposing configurations generally lead to substantially weaker aftereffects. In any case, the point is that even for the simpler case of expressions it is not clear whether adaptation can be used to dissect the underlying channel structure.

Regardless of the possible sites of the response changes, adaptation may play important functional role in calibrating face perception, influencing judgments of expression as well as other attributes. One putative role of adaptation is to calibrate visual coding so that we can judge stimuli relative to a norm, and this role seems particularly relevant to expression perception since this involves detecting how the face deviates from neutral. A second possible role is to heighten sensitivity to these deviations by positioning the response to be maximally sensitive around the neutral point. Given that we are each exposed to different subsets of facial configurations that can be confounded with expressions (Neth and Martinez, 2008), adaptation may be critical for defining and maintaining an appropriate model of the neutral face. And given the social importance of facial expressions, this adaptation would also be critical for our ability to derive meaning from the face.

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Residual fMRI sensitivity for identity changes in acquired prosopagnosia

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While a network of cortical regions contribute to face processing, the lesions in acquired prosopagnosia are highly variable, and likely result in different combinations of spared and affected regions of this network. To assess the residual functional sensitivities of spared regions in prosopagnosia, we designed a rapid event-related functional magnetic resonance imaging (fMRI) experiment that included pairs of faces with same or different identities and same or different expressions. By measuring the release from adaptation to these facial changes we determined the residual sensitivity of face-selective regions-of-interest. We tested three patients with acquired prosopagnosia, and all three of these patients demonstrated residual sensitivity for facial identity changes in surviving fusiform and occipital face areas of either the right or left hemisphere, but not in the right posterior superior temporal sulcus. The patients also showed some residual capabilities for facial discrimination with normal performance on the Benton Facial Recognition Test, but impaired performance on more complex tasks of facial discrimination. We conclude that fMRI can demonstrate residual processing of facial identity in acquired prosopagnosia, that this adaptation can occur in the same structures that show similar processing in healthy subjects, and further, that this adaptation may be related to behavioral indices of face perception.

Keywords: face perception, identity, expression, fMRI, adaptation, sensitivity, prosopagnosia

INTRODUCTION

Prosopagnosia is a neurological syndrome characterized by the failure to recognize familiar faces in the absence of more pervasive dysfunction of vision or memory (Barton, 2003). Patients with the acquired form can have a variety of lesions, most often damage to inferomedial occipitotemporal cortex, either bilaterally or in the right hemisphere only (Bodamer, 1947; Landis et al., 1986; Barton, 2003). Functional magnetic resonance imaging (fMRI) studies have shown a number of face-selective regions in the occipital and temporal lobes (Kanwisher et al., 1997; Haxby et al., 2000; Ishai et al., 2005), including the fusiform face area (FFA), the occipital face area (OFA), and the posterior superior temporal sulcus (pSTS) in both right and left hemispheres (Haxby et al., 2000). These regions are proposed by some as an anatomic "core" for face processing (Gobbini and Haxby, 2007). It seems probable that damage to these regions is involved in at least some if not most cases of acquired prosopagnosia, but the extent of damage to the various modules of this network in prosopagnosia is not yet known. Given the variety of lesions associated with prosopagnosia (Barton, 2008a,b), it is also likely that patients will differ in both modules affected and modules spared (de Gelder et al., 2003; Rossion et al., 2003a,b).

One question of interest is the residual function of spared regions of the face network in prosopagnosia. Identifying surviving face-selective regions in acquired prosopagnosia with a standard contrast between viewing faces and viewing objects (Rossion et al., 2003a,b) does not tell us the type of face information being processed by spared regions. Faces are a source of many types of information, including identity, expression, gaze direction, attractiveness, age and gender, among others. Cognitive models often segregate these different types of information into separate processing streams (Bruce and Young, 1986). Current anatomic models go even further and attempt to link specific functions to specific regions, for example, initial perception of facial structure in the OFA, perception of facial identity in the FFA, and perception of facial expression in the pSTS (Haxby et al., 2000). However, this segregation of function may not be as complete as the model suggests: a number of studies have shown some sensitivity to facial identity in the OFA (Rossion et al., 2003a,b; Avidan et al., 2005) and the pSTS (Winston et al., 2004; Fox et al., 2009a,b) on the one hand, and to facial expression in the FFA (Vuilleumier et al., 2004; Ganel et al., 2005; Fox et al., 2009a,b) on the other. In prosopagnosia, where patients have lost the ability to recognize facial identity, one can ask (1) which, if any, surviving face-selective modules still show sensitivity to identity, and (2) whether this correlates with residual ability to discriminate facial identity on behavioral tests.

One method used to assess the specific function of cortical regions is fMRI adaptation (Grill-Spector et al., 2006). This technique has shown that the fMRI BOLD signal declines with repeated presentations of identical stimuli. Furthermore, the technique can be exploited to determine what aspects of a stimulus are being processed in a region, by varying one stimulus property or dimension while keeping others constant. If the repeated stimuli vary only along a dimension that is irrelevant to the processing performed by a specific region, adaptation will still occur. However, if the varying dimension is being processed in this region, then repeated presentations will be treated as different stimuli, and no adaptation will be found (i.e., a "release from adaptation" will occur). In this way it is possible to determine what aspect of a stimulus is of interest to a cortical region. This method has been used in healthy subjects to demonstrate sensitivity to structural changes in a face within the OFA (Rotshtein et al., 2005), sensitivity to identity changes in the FFA (Winston et al., 2004; Rotshtein et al., 2005), and sensitivity to expression changes in the pSTS (Winston et al., 2004).

To date, there has been only one study of fMRI adaptation in an acquired prosopagnosic patient, patient PS. This study found residual sensitivity to facial identity changes, not in the spared right FFA, but in an object-selective region of the ventral lateral occipital cortex (Schiltz et al., 2006; Dricot et al., 2008). A similar fMRI adaptation study in four congenital prosopagnosic subjects found sensitivity to facial identity in both the undamaged OFA and FFA (Avidan et al., 2005). In contrast, a case of congenital "prosopamnesia" showed normal adaptation to familiar faces but not to unfamiliar faces in the right FFA (Williams et al., 2007).

Of note, the adaptation effects seen in the congenital prosopagnosia study were reported for the group, not for each subject (Avidan et al., 2005). While it may be valid to group congenital prosopagnosic subjects who have no apparent neurological lesion, the heterogeneity of damage in acquired prosopagnosia (Barton, 2003) makes group analyses difficult to interpret. Thus, it is important to design an fMRI adaptation method that can reveal significant sensitivity to identity or expression changes in an individual. The power of group analyses lies in the averaging of results across a number of subjects (Friston et al., 1999). In a similar fashion, averaging across multiple scans within a single subject can increase the power to detect a significant effect in that subject. By performing and averaging across multiple adaptation scans in each individual, we aimed to identify significant adaptation effects in single subjects.

Our goal was to use such a method to determine whether surviving face-selective regions of individuals with acquired prosopagnosia had any residual sensitivity to facial identity and/or expression. We assessed three patients on a wide array of behavioral tests to characterize their face processing deficits, and in particular their residual behavioral sensitivity to facial structure. All three patients then underwent fMRI testing, first with a face-localizer to determine which regions of the core face network (bilateral OFA, FFA, and pSTS) had or had not survived their lesion, and then with our adaptation paradigm to determine the residual sensitivity to identity and expression changes in these surviving regions. Given current models, we hypothesized that we would find residual sensitivity for identity changes in the right FFA, and for expression changes in the right pSTS. In addition, we hypothesized that residual sensitivity in the fMRI experiment may be indicative of a residual ability of prosopagnosic subjects to discriminate the structural properties of faces, as determined by our own experimental tests and standard neuropsychological instruments such as the Benton Face Recognition Test (Benton and van Allen, 1972).

METHODS

PATIENTS

Three brain-damaged patients with acquired prosopagnosia participated in this study. Informed consent was obtained and the protocol was approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital, in accordance with The Code of Ethics of the World Medical Association, Declaration of Helsinki (Rickham, 1964). The focus of this research was to demonstrate the presence of residual sensitivity within face-selective regions of cortex in prosopagnosic individuals using an adaptation paradigm. Our goal was not to compare this residual sensitivity to the general population but rather simply to determine whether or not we could definitively demonstrate the presence of such a phenomenon in these brain-damaged individuals. [For data from three healthy right handed control subjects (C01-28 year old male, C02-34 year old male, C03-27 year old female) with normal or corrected-to-normal vision and no history of neurological disorders please see **Supplemental Figure 1**].

All patients had detailed neuropsychological and neurological examinations, supplemented with Goldmann perimetry and Farnsworth-Munsell 100-hue tests. The tests used to characterize their face perceptual abilities are listed in **Table 1**. Face perception is commonly segmented into a number of different cognitive processes, ranging from the early processing of facial structure relevant to the perception of (1) facial identity or (2) facial expression, to latter stages of facial memory which can be accessed both (3) overtly and (4) covertly. First, identity perception was assessed with the Benton Facial Recognition Test (Benton and van Allen, 1972) and with a 3-alternative forced-choice oddity test (chance = 33%) for discriminating identity changes in morphed facial stimuli (Fox et al., 2011). Importantly, normal scores on the Benton Facial Recognition Test do not necessarily indicate normal identity perception (Farah, 1990; Duchaine and Weidenfeld, 2003), and therefore, more weight should be given to performance on the morphed-face discrimination test, which has been shown to be a more sensitive measure of impaired perceptual processing (Fox et al., 2011). Second, expression perception was assessed with the revised version of the Reading the Mind in the Eyes Test (Baron-Cohen et al., 2001), and with a forced-choice oddity test of the discrimination of morphed-expression changes, equivalent in difficulty to the oddity test for morphed-identity changes (Fox et al., 2011). Third, overt short-term facial memory was assessed with the Warrington Recognition Memory Test (Warrington, 1984), and long-term facial memory with a Famous Face Recognition Test that required subjects to indicate which of a series of 20 famous and 20 anonymous faces was familiar (Barton et al., 2001). This test included a similar series of 20 famous and 20 unfamiliar names with the patient selecting the famous name and then providing semantic information about the name to ensure that semantic memory stores were intact. A 37-item facial imagery test was also used to assess the adequacy of facial memory stores independent of the status of perceptual processes (Barton and Cherkasova, 2003). Fourth, covert facial memory

Table 1 | Results from the battery of face tests.

Modality	Test	Max	B-AT1	R-AT1	R-IOT1
Faces—Identity	Benton facial recognition	54	45	41	45
	Morph discrimination	100%	72*	56*	83*
Faces—Expression	Reading the mind in the eyes	36	24	19*	26
	Morph discrimination	100%	100	92	92
Faces—Memory	Words, WRMT	50	45	41	41
	Faces, WRMT	50	27*	17*	33*
	Famous face recognition (d′)	3.92	1.52*†	1.22*	1.96
	Face imagery (%)	100%	n/a	71*	82
Faces—Covert	Name-cued forced-choice	20	11*	8*	n/a
	Occupation sorting	41	21*	24*	n/a

Impairments are indicated in red.

(WRMT = Warrington Recognition Memory Test). For normative data on these previously published tests please consult the appropriate references included herein.

†Due to poor knowledge of celebrities, a version of this test using personally familiar faces was given to B-AT1.

was assessed with two tests using a direct strategy, a name-cued forced-choice test that showed subjects a famous face (that they claimed not to recognize) paired with an anonymous one and asked them to indicate which was the face named by the examiner, and an indirect strategy, an occupation-sorting test that required subjects to sort famous faces they did not recognize on the basis of whether they were politicians or actors (Barton et al., 2001).

The first patient, identified as B-AT1 (B = bilateral; AT = anterior temporal,) is a 24 year-old right-handed male who had herpes simplex encephalitis three years prior (**Figure 1**). Since recovery, he has noted extreme difficulty in recognizing and learning faces, though he can recognize some family members. General memory and mental functioning is unaffected, allowing him to attend college and hold full-time employment. He has mild topographagnosia, and mild anomia for low-frequency items (although semantic knowledge of these items is evident). He had acuity of 20/20 and normal visual fields. He performed normally on the Benton Facial Recognition Test, but was mildly impaired in discrimination of morphed-identity changes. Facial expression processing was unaffected. He was severely impaired on the Faces component of the Warrington Recognition Memory Test, but not the Words component. He did poorly on a modified familiar face recognition test that used pictures of his relatives rather than celebrities, due to limited knowledge of the latter (which also invalidated the test of facial imagery). He showed no evidence of

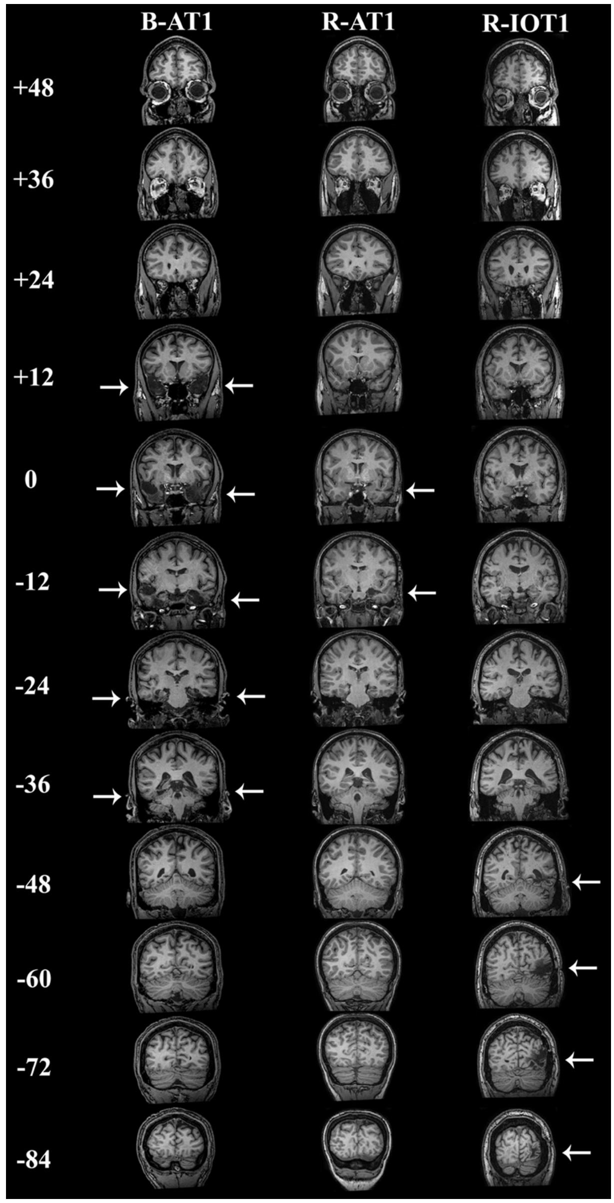

FIGURE 1 | Coronal T1-weighted MRI brain images of the three patients, standardized to Talairach space. Slices were taken every 12 mm, from $y = +48$ mm to $y = -84$ mm. B-AT1 has large bilateral lesions of the anterior temporal lobes following herpes encephalitis (+12 to −36 mm). R-AT1 has a small surgical lesion in the right anterior temporal lobe, additionally affecting the right hippocampus and amygdala (0–12 mm). R-IOT1 has a single right inferior occipitotemporal lesion from his prior hemorrhage (−48 to −84 m).

covert recognition on either the name-cued forced-choice or the occupation-sorting test.

The second patient, R-AT1 (R = right hemisphere; AT = anterior temporal), is a 24 year-old right-handed female. One year prior to testing she had a selective right amygdalohippocampectomy for epilepsy (**Figure 1**), following which she has had difficulty recognizing faces, needing to rely on voice or other means to recognize individuals. General mental functioning was intact:

she is currently attending university, although she has problems with visual memory and relies on verbal strategies to study. She had acuity of 20/20 and normal visual fields. She performed normally on the Benton Facial Recognition Test (**Table 1**), but was impaired on the more difficult discriminations of morphed-identity changes. The Reading the Mind in the Eyes Test suggested reduced recognition of expression, but the perception of morphed-expression changes was normal. She was impaired on the Faces but not the Words component of the Warrington Recognition Memory Test. Face recognition was reduced on the Famous Face Recognition Test and she had reduced facial imagery. There was no evidence for covert face recognition on either the name-cued forced-choice or the occupation-sorting tests.

The third patient, R-IOT1 (R = right hemisphere, IOT = inferior occipitotemporal), is a 49 year-old left-handed male who twelve years prior had suffered an occipital cerebral hemorrhage from rupture of an arteriovenous malformation (**Figure 1**). Immediately following this event he complained of trouble recognizing hospital workers and needed to rely on hairstyle, facial hair, or voice for person recognition, a problem that has not resolved. He also displayed letter-by-letter reading immediately after the hemorrhage but this had resolved quickly. On examination his acuity was 20/20 and he had a left superior quadrantanopia and mild topographagnosia. He performed normally on most face tests, including the Benton Face Recognition Test (**Table 1**), but was mildly impaired on the discrimination of morphed-identity changes. He did better on the Famous Face Recognition Test than any other prosopagnosic patient, but claimed that because we used well-known images, he was recognizing the pictures and not the people (because he recognized these images, he also could not do the covert tests, as they used similar images). In support of this, he was significantly impaired on a famous faces test using less typical images of celebrities [11/25; (Duchaine, 2000)] and on the Faces (but not the Word) component of the Warrington Recognition Memory Test, which tests short-term recognition with anonymous people. Facial expression processing was unaffected.

STIMULI

Face images were selected from the Karolinska Database of Emotional Faces (Lundqvist and Litton, 1998) and from our laboratory's collection. All images were cropped about the face and uniformly sized to 512 by 634 pixels. A standard gray oval was placed over each face to occlude the neck, hairline and picture background while leaving internal facial features and external face contour unaffected (**Figure 2**). Quartets of face images were selected such that for a given image, a second image showed the same identity with a different version of the same expression, a third image showed the same identity with a different expression, and a fourth image showed a different identity (of the same gender as the first image) displaying the same expression as the given image. Forty such quartets were created, 20 using female faces and 20 using male faces. Five facial expressions were included amongst the faces (anger, fear, happiness, sadness, disgust) with each expression appearing ten times (5 for each gender) as the base expression (displayed in 3 of the 4 images) and 10 times as the different expression (displayed in 1 of the 4 images).

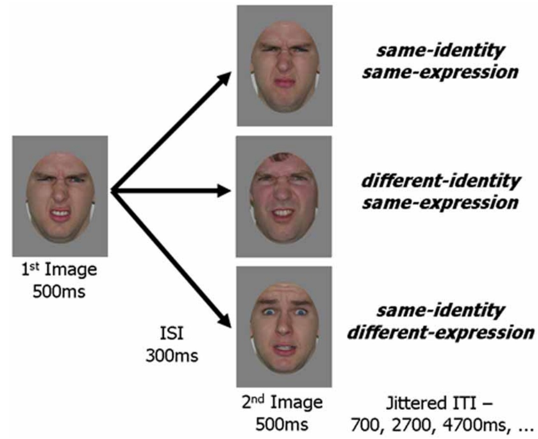

FIGURE 2 | Schematic representation of an experimental trial. In all three experimental conditions the first image was the same. The second image in the pair was either a new picture with the same identity and same expression as the first image, a picture of a different person with the same expression or a picture of the same person with a different expression. An image pair was presented within every *TR* (2 s) and fixation trials were randomly intermixed with experimental trials.

DESIGN

Images from each of the 40 face quartets were paired to create the three experimental conditions. The same image was always presented as the first in each pair with the second image varying between conditions: *same-identity/same-expression, different-identity/same-expression, same-identity/different-expression*. This resulted in 40 unique trials for each of the three experimental conditions.

Six other faces (3 males, 3 females), which were different from the faces used in the experimental conditions, displaying 3 different expressions (anger, fear, happiness) were selected and formatted in a gray oval as described above. Upright and inverted versions of these six faces were created. Two face pairs were formed from each of the six identities; upright-inverted and inverted-upright. These 12 pairs became target trials in the fMRI adaptation experiment.

PROCEDURE

An experimental trial consisted of a pair of faces presented within each repetition time ($TR = 2$ s). The first face was presented for 500 ms and followed by a 300 ms inter-stimulus-interval (ISI). This was followed by a 500 ms presentation of the second face and a 700 ms inter-trial-interval (ITI). In order to avoid retinal adaptation image location randomly varied from image to image within a region of 50 by 50 pixels.

For each experimental scan 32 of the 40 face quartets were randomly selected, and all 3 experimental trials (one from each condition: *same-identity/same-expression, different-identity/same-expression, same-identity/different-expression*) from these quartets were presented during the scan. This resulted in 32 experimental trials per condition (from the 32 randomly selected face quartets) and 96 trials total. In addition to these experimental trials 10 of the 12 target trials (i.e., inverted faces) were randomly selected and included. Participants were asked to respond to the inverted face in these target trials with a keypress, which acted as a means to ensure subjects attended to the faces. Finally, 48 fixation trials, in which the face images were replaced by a fixation cross, were randomly interspersed among the experimental and target trials, producing the jittering required for rapid event-related experimental designs (Grill-Spector et al., 2004; Serences, 2004). The same procedure of random selection and randomized trial order was used to create six different experimental scans. Each experimental scan began with 1 fixation trial and ended with 6 fixation trials. All six experimental scans were presented to each participant in random order.

fMRI

Structural and functional MRIs were performed on all participants. All scans were acquired in a 3.0 Tesla Philips scanner. Stimuli were presented using Presentation 9.81 software and were rear-projected onto a mirror mounted on the head coil. Whole brain anatomical scans were acquired using a T1-weighted echoplanar imaging (EPI) sequence, consisting of 170 axial slices of 1 mm thickness (1 mm gap) with an in-plane resolution of 1 mm × 1 mm (FOV = 256). T2-weighted functional scans ($TR = 2$ s; $TE = 30$ ms) were acquired using an interleaved ascending EPI sequence, consisting of 36 axial slices of 3 mm thickness (1 mm gap) with an in-plane resolution of 1.875 mm × 1.875 mm (FOV = 240).

We used a dynamic localizer that presented videos of moving faces and moving objects (Fox et al., 2009a,b) to identify regions of the core face network (i.e., right and left OFA, FFA, and pSTS) (Haxby et al., 2000). This localizer contrasts video-clips of faces changing in expression (i.e., from neutral to happy) with those of objects undergoing types of motion without large translations in position (i.e., basketball rotating). Video-clips of objects were gathered from the internet, and video-clips of faces were provided by Chris Benton, Department of Experimental Psychology, University of Bristol, UK (Benton et al., 2007), with all video-clips resized to a width of 400 pixels. Prior work in our laboratory demonstrated that this dynamic localizer is more sensitive in localizing regions of the core face network (98% success rate) than the standard technique which contrasts static images of faces and objects (Fox et al., 2009a,b). Importantly work from other laboratories also suggests that a dynamic signal can act to enhance facial identity recognition in prosopagnosic patients (Longmore and Tree, 2013) making dynamic stimuli a more appropriate choice to activate the core face network. Patients performed a “one-back task”: that is, they pressed a button if a video was identical to the previous one. Fixation blocks began and ended the session and were alternated with image blocks, with all blocks lasting 12 s. Eight blocks of each image category (object, face) were presented in a counterbalanced order. Each image block consisted of 6 video-clips (5 novel and 1 repeated) presented centrally for 2000 ms each. The dynamic localizer was followed by presentation of the six experimental scans.

The first volume of each functional scan was discarded to allow for scanner equilibration. All MRI data were analyzed using BrainVoyager QX Version 1.8 (www.brainvoyager.com). Anatomical scans were not preprocessed, but were standardized to Talairach space (Talairach and Tournoux, 1988). Preprocessing of functional scans consisted of corrections for slice scan time acquisition, head motion (trilinear interpolation), and temporal filtering with a high pass filter in order to remove frequencies less than 3 cycles/time course. Functional scans were individually co-registered to their respective anatomical scan, using the first retained functional volume to generate the co-registration matrix.

The dynamic localizer time course was analyzed with a single subject GLM, with objects (O) and faces (F) as predictors, and a F > O contrast was overlaid on the whole brain. Using a False-Discovery-Rate of $q < 0.05$ (corrected for multiple comparisons), we identified the core regions of face perception, bilaterally, within each participant (Haxby et al., 2000). Contiguous clusters of face-selective voxels located on the lateral temporal portion of the fusiform gyrus were designated as the FFA, while clusters located on the lateral surface of the inferior occipital gyrus were designated as the OFA. Face-selective clusters located on the posterior segment of the superior temporal sulcus were designated as the pSTS. Following a technique to maximize face-selectivity in each region-of-interest (ROI) (Fox et al., 2009a,b), we selected the 50 voxels, contiguous with the peak voxel, that displayed the highest t-value for the F > O contrast. These 50 voxel clusters were then subject to the experimental analyses.

Experimental MRI scans were analyzed using a deconvolution analysis that accounts for non-linear summation of the blood oxygen level dependent (BOLD) response in rapid event-related designs. The deconvolution analysis samples BOLD activity at trial onset (time = 0 s) and a further 9 times in 2 s intervals, resulting in an unbiased model of the hemodynamic response (HDR). The inverted target trials were included as a separate condition in the deconvolution analysis, to account for all non-fixation trials, but were not included in subsequent analyses.

Within each ROI, results from the six experimental scans were combined using a multi-study GLM function that used the three experimental conditions (*same-identity/same-expression, different-identity/same-expression,* and *same-identity/different-expression*) as functions within the GLM (BrainVoyager). While one cannot determine the significance of differences in a single scan in a single subject, averaging across multiple scans enables the assessment of statistical significance in the single subject. Significant adaptation of the HDR may take a number of forms including a reduced HDR-peak due to neural fatigue or a narrowing of the full-HDR due to a facilitated neural response (Grill-Spector et al., 2006). To examine both possibilities we first collapsed data across all three experimental conditions. Then, within each ROI, the full-HDR was defined as the sum of all consecutive time points that showed a significant increase from baseline ($p < 0.05$, 1-tailed). The HDR-peak was defined as the time point exhibiting a maximal increase in BOLD activity, or the average of this time point and adjacent time points that did not significantly differ ($p > 0.05$, 1-tailed). Using these definitions, the values of the full-HDR and HDR-peak were then determined for each of the three experimental conditions. Contrasts of the *different-identity/same-expression* > *same-identity/same-expression* and the *same-identity/different-expression* > *same-identity/same-expression* were performed, using the multi-study GLM, to assess identity and expression adaptation, respectively. Significant release from adaptation in the *different* conditions was set at $\alpha < 0.05$, and would indicate sensitivity of the ROI to changes in identity or expression. Only positive release from adaptation values indicate sensitivity to the varied stimulus; negative values would suggest priming of an ROI to the presented stimulus and are not discussed herein (in fact only one control demonstrated a negative release from adaptation in the L-FFA). The difference values resulting from these two contrasts are presented graphically. As all effects in the full-HDR condition were replicated in the HDR-peak condition, but were stronger in the latter, we only present the results of the HDR-peak analyses (**Figure 3**). Release from adaptation is therefore, defined as a difference in peak beta values from the modeled HDR, with the specific contrasted conditions outlined above.

RESULTS

B-AT1 has extensive bilateral damage to the anterior temporal lobes, which extends to the inferior surface of the middle temporal lobe (**Figure 1**). Functional MRI located all six regions of the core face-processing system (**Table 2**; **Figure 4**). Release from adaptation when identity changed was found in the right FFA (0.14 ± 0.07, $p < 0.05$; **Figure 5**) and in the right (0.27 ± 0.11, $p < 0.05$) and left (0.18 ± 0.06, $p < 0.005$) OFA (**Figure 6**). No sensitivity to expression changes was observed.

R-AT1 has a small lesion in the anterior right temporal lobe that affects the anterior hippocampus, amygdala, and overlying temporal cortex (**Figure 1**). All six ROIs of the core face processing system were identified (**Table 2**; **Figure 4**). Release from adaptation when identity changed was found in the right FFA (0.24 ± 0.10, $p < 0.05$; **Figure 5**) and the left OFA (0.33 ± 0.11, $p < 0.005$; **Figure 6**). No sensitivity to expression changes was observed.

R-IOT1 has a unilateral right lesion affecting both the occipital and posterior temporal cortex (**Figure 1**). The functional localizer failed to identify an OFA or FFA in the right hemisphere, though the right pSTS and all three regions in the left hemisphere were identified (**Table 2**; **Figure 4**). Release from adaptation when identity changed was observed in the left FFA (0.41 ± 0.13, $p < 0.005$; **Figure 5**), and the left OFA (0.43 ± 0.15, $p < 0.005$; **Figure 6**). No sensitivity to expression changes was observed.

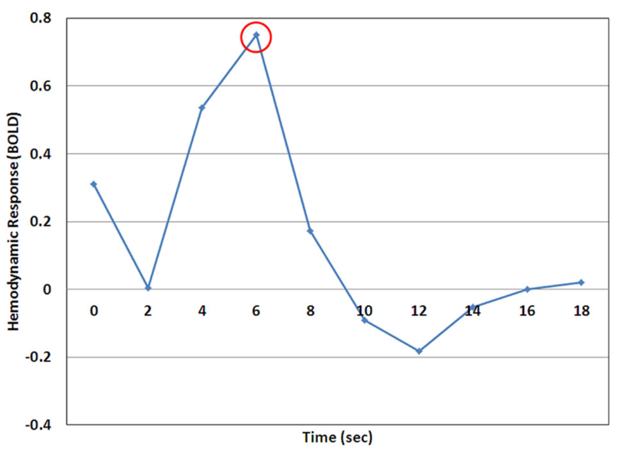

FIGURE 3 | A representative example of the hemodynamic response (HDR) as calculated by the deconvolution analysis. In this case the time point at 6 s (encircled) would be considered the HDR-peak and the value at this time point would be used for analysis.

DISCUSSION

RESIDUAL SENSITIVITY TO IDENTITY CHANGES IN THE FUSIFORM FACE AREA

A surviving right FFA was found in two prosopagnosic patients (B-AT1 and R-AT1; **Figure 4**).In both it showed residual sensitivity to facial identity, with larger responses to different than to repeated identities (**Figure 5**). This sensitivity to identity is consistent with the role of the right FFA in identity processing in current models of face perception (Haxby et al., 2000), and prior fMRI adaptation studies using group-based analyses (Andrews and Ewbank, 2004; Winston et al., 2004; Rotshtein et al., 2005; Fox et al., 2009a,b). However, this finding contrasts with the only previous study of identity adaptation in acquired prosopagnosia (patient PS), which did not find such sensitivity in the spared right FFA (Schiltz et al., 2006; Dricot et al., 2008). An important difference is that both of our patients had damage limited to the anterior temporal lobes, with sparing

Table 2 | Results of the dynamic functional localizer, with brains standardized to Talairach space.

Subject	Region	Maximum *t*-value	Minimum *t*-value	*X*	*Y*	*Z*
B-AT1	**ROFA**	**12.37**	**11.18**	**30**	**−88**	**−5**
	RFFA	**13.09**	**10.25**	**39**	**−52**	**−20**
	RpSTS	**9.67**	**7.62**	**45**	**−49**	**−2**
	LOFA	9.43	7.45	−30	−85	−8
	LFFA	5.96	5.04	−39	−55	−26
	LpSTS	5.9	4.95	−60	−46	4
R-AT1	**ROFA**	**14.88**	**11.27**	**27**	**−70**	**−20**
	RFFA	**11.29**	**6.46**	**36**	**−58**	**−11**
	RpSTS	**14.18**	**10.81**	**42**	**−40**	**4**
	LOFA	12.92	11.31	−42	−70	−8
	LFFA	11.90	9.99	−39	−43	−26
	LpSTS	11.66	8.81	−57	−46	13
R-IOT1	**ROFA**	**LESION**				
	RFFA	**LESION**				
	RpSTS	**5.52**	**3.67**	**57**	**−40**	**13**
	LOFA	6.50	4.85	−37	−82	−20
	LFFA	4.73	3.18	−33	−67	−23
	LpSTS	7.42	5.23	−42	−40	4

The peak 50 voxels were defined as the region-of-interest with maximum and minimum t-values reported. Right hemispheric regions of interest are bolded.

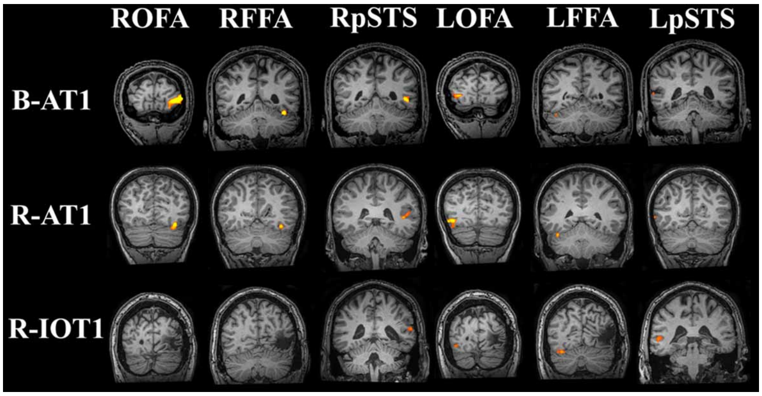

FIGURE 4 | Core system regions-of-interest identified with the functional localizers (all brains standardized to Talairach space). All six regions of the core system were identified in B-AT1 and R-AT1. Due to the location of the lesion, R-IOT1 does not display a right OFA or right FFA. However, a right posterior STS (pSTS) was identified along with all three core regions in the left hemisphere.

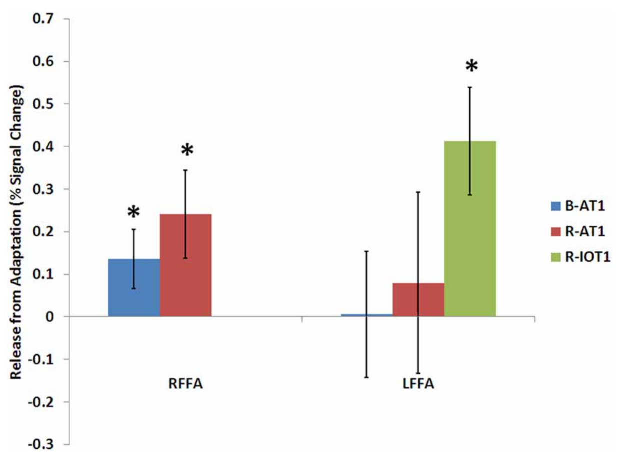

FIGURE 5 | Release from adaptation in response to identity changes as seen in the fusiform face areas of the three patients. Significant release from adaptation was observed in the right FFA of both B-AT1 and R-AT1. In contrast, R-IOT1 who did not have a right FFA due to damage, exhibited significant release from adaptation in the left FFA. $^*p < 0.05$.

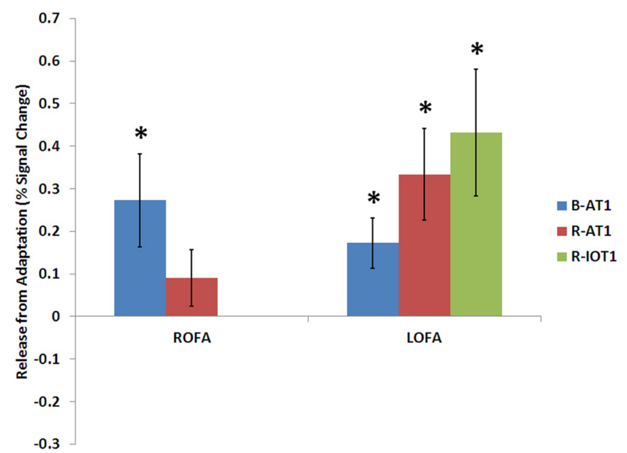

FIGURE 6 | Release from adaptation in response to identity changes as seen in the occipital face areas of the three patients. Significant release from adaptation was observed in the left FFA of all three patients and only in the right OFA of B-AT1 (R-IOT1 did not have a right OFA due to damage). $^*p < 0.05$.

of all six core regions of the face processing network, while PS had loss of the right OFA and left FFA (Rossion et al., 2003a,b). This suggests that residual sensitivity to face identity in the FFA may depend upon inputs from other surviving core face-processing regions, a hypothesis that should be tested in additional patients.

The left FFA did not show sensitivity to identity changes in either patient B-AT1 or R-AT1, but significant sensitivity was observed in the left FFA of R-IOT1, who differs from the others in that he is strongly left-handed (**Figure 5**). This raises the possibility of anomalous lateralization, as suggested in prior cases of prosopagnosia in left-handed individuals with unilateral left occipitotemporal lesions (Tzavaras et al., 1973; Mattson et al., 2000; Barton, 2008a,b). While all fMRI studies show smaller and less frequent face-selective activity in the left fusiform region than the right, it may be that the left FFA has a greater role than normal in face-processing in a left-handed subject like R-IOT1. If so, this could explain why adaptation effects for identity were found in the left FFA of R-IOT1 but not in the other patients.

RESIDUAL SENSITIVITY TO IDENTITY CHANGES IN THE OCCIPITAL FACE AREA

Beyond the FFA, we also found identity adaptation in the OFA of our three patients (**Figure 6**). The right OFA is spared in B-AT1, and R-AT1 (**Figure 4**) but identity adaptation was found in the right OFA only for B-AT1 (**Figure 6**). In contrast, we observed identity adaptation in the surviving left OFA of all three patients (**Figure 6**). The OFA is traditionally thought to be involved in the early perception of facial structure prior to the decoding of facial identity (Haxby et al., 2000; Rotshtein et al., 2005; Fox et al., 2009a,b). While this ability to detect structural changes ultimately leads to identity recognition, it may be that the release from adaptation we observe in the OFA reflects response to a structural change at an early perceptual level and is not necessarily linked to a perceived identity change. However, while it is sometimes claimed that the OFA may encode facial structure relevant to both identity and expression, we did not find a similar release from adaptation when expression changed. In fact, none of the face-selective regions in any patient showed release from adaptation when expression changed, not even the right pSTS, which has shown such adaptation sensitivity to expression in previous group studies (Winston et al., 2004; Fox et al., 2009a,b). Failure to demonstrate adaptation for expression may have many origins, including lack of power in the individual subject, or even a requirement for enhanced attention, given that more pronounced activity is found for expression-based signals during expression-based tasks than during an irrelevant experimental task (Narumoto et al., 2001; Fox et al., 2009a,b). However, the fact that sensitivity to expression was not observed anywhere in this study leaves open the possibility that the sensitivity we report in the OFA is in fact a response to the structural differences between two different faces rather than sensitivity to the identity change itself, as the structural change between two identities is often more readily apparent than the structural change between two expressions. Importantly, adaptation effects for identity have not previously been reported or examined in the left OFA, thus, another possibility is that the sensitivity to identity changes we observe in the left OFA of these three patients may actually reflect a compensatory change in the face network of these brain-damaged patients much like the report which demonstrated identity adaptation effects in the ventral lateral occipital complex, a region not normally implicated in face processing, in the prosopagnosic patient PS (Dricot et al., 2008).

NO RESIDUAL SENSITIVITY IN THE POSTERIOR SUPERIOR TEMPORAL SULCU

We did not find any identity adaptation in the right pSTS of any patient. Residual processing of identity in the STS has been suggested by some as a possible compensatory mechanism in prosopagnosia, particular by those who promote a dissociated dorsal route of face processing as an explanation for covert recognition (Tranel et al., 1995). While our behavioral tests did not show any covert face processing in any of these four patients, it should be stressed that the dissociable dorsal route has been advanced primarily by those studying autonomic indices of covert recognition (Bauer and Verfaellie, 1988; Tranel et al., 1995). Indeed, it may be that covert behavioral and covert autonomic measures index different phenomena, with the former emerging from residual function of the normal face-processing network, while residual electrodermal responsivity to faces may reflect activity in a separate pathway for mediating autonomic reactions to faces (Schweinberger and Burton, 2003). For these reasons, our data are limited in the conclusions that can be drawn regarding the anatomic correlates of covert face recognition. However, our data would at least suggest that following a variety of patterns of damage in prosopagnosia, residual sensitivity to face identity appears more likely in other components of the core face-processing network than in the pSTS.

Another possibility for the failure to identify adaptation to facial expression within the current design may be the restriction of our analysis to predefined ROIs. A recent study by Mur et al. (2010) demonstrated adaptation to repeated presentation of faces in areas outside the traditional face areas, including the parahippocampal place area and early visual cortex. They argue that this may represent an attentional affect rather than specific face-sensitivity within these regions. However, the possibility remains that the pSTS which we identified with our localizer did not in fact capture the collection of neurons that are most involved in expression recognition, and which would demonstrate a measurable release from adaptation with expression changes. Further experimentation with whole-brain analysis rather than predefined ROIs may identify just such a region.

RESIDUAL SENSITIVITY AND BEHAVIORAL PERFORMANCE

It is interesting to compare the patient's residual ability to discriminate faces of different identities and parallel these findings with the fMRI adaptation results for identity. B-AT1, R-AT1, and R-IOT1 all performed normally on the Benton Face Recognition Test and had mild to moderate deficits on the morph discrimination test for identity; on the fMRI experiment all showed identity adaptation effects in at least one face-selective region. In contrast, a prosopagnosic patient in another study, PS, was significantly impaired on the Benton Facial Recognition Test and showed no identity adaptation effects in the FFA (Rossion et al., 2003a,b). These results suggest that residual perceptual sensitivity to aspects of facial structure related to identity may have an anatomic correlate in the residual neural sensitivity of the FFA and OFA to these same structural properties.

In conclusion, we devised an fMRI adaptation protocol which can reveal significant adaptation to facial identity in the single subject. In three acquired prosopagnosics with a variety of lesions, we found residual sensitivity to identity in the spared right FFA of two right handed prosopagnosic patients with anterior temporal damage, and in the spared left FFA of one left-handed prosopagnosic patient who had loss of the right FFA and OFA. We also observed sensitivity to identity within the left OFA of these three patients, which may reflect either normal sensitivity to facial structure or a compensatory enhancement following damage to the face processing network. The presence of adaptation effects for identity paralleled residual ability to discriminate between different faces, as measured by the Benton Facial Recognition Test but not the more difficult morphed-face discrimination test. Further study in a larger cohort of subjects with either acquired or congenital prosopagnosia would be of interest.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2013.00756/abstract

Supplemental Figure 1 | (A) Control data for the *different-identity/same-expression* > *same-identity/same-expression* contrast. A significant release from adaptation (*) for identity changes was seen within the right FFA of C01 and C03, and within the left OFA of C03. A trend in the same direction (#) was observed in the right OFA of C03. **(B)** No significant release from adaptation was observed for changes in expression, following the *same-identity/different-expression* > *same-identity/same-expression* contrast. When compared to the data from the patient population we again see a release from adaptation to identity changes in the right FFA (2/3 controls) but there is no evidence of sensitivity to facial expression with this experimental design.

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On the hierarchical inheritance of aftereffects in the visual system

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The emotion perceived in a face can be influenced by prior exposure to a face expressing a different emotion. Here we show that displacement along a particular emotional axis, that encoding happiness and sadness, can be effected solely by a systematic change in the angle, at the center of the mouth, between the left and right halves of the mouth. We then demonstrate that adaptation to a face with the mouth distorted to change this angle, such that the face expresses an emotion on this axis, causes a face with a neutral expression to be perceived as having the opposite expression. By abstracting the mouths from the faces and examining the magnitude of the angle aftereffects in the mouths alone and in an unfamiliar orientation, we show that the magnitudes of the angle aftereffects are sufficient to account for the changes in perceived emotion in the faces. Further, by applying the distortion to the mouths asymmetrically so that the distortion is manifested by a change in orientation of the mouth stimulus rather than a change in angle, we show that the magnitude of the aftereffect can be predicted by the local tilt aftereffect. We argue, therefore, that the aftereffects of emotion are due to misperception of morphology of the face and that the misperception is due to the local change in perceived orientation due to the systematic application of the tilt aftereffect in a tilt aftereffect field. All adaptation experiments were performed using stimuli that were either high-pass or low-pass filtered for spatial frequency. Results showed that the spatial frequency specificity of the aftereffects was the same for the face, angled mouth, and oriented mouth stimuli, lending further support to the hypothesis that the aftereffects are instantiated in processes early in the visual cortex and that the aftereffects assumed to be higher level are, in fact, inherited.

Keywords: tilt aftereffect, shape aftereffect, face aftereffect, tilt aftereffect field, adaptation

INTRODUCTION

Concerning the study of the functionality of mechanisms of the brain a frequently cited aphorism is that aftereffects represent the psychologist's microelectrode (Frisby, 1979). The justification for this comparison is the similarity between the neurophysiologically derived functions describing the response of single neurons and the perceptual deficits introduced by adaptation. An example is the function describing the response of neurons of the primary visual cortex to a line as its orientation is varied, and orientation specific deficits in sensitivity to gratings revealed in psychophysical tasks after adaptation to gratings of a particular orientation. The aftereffect, a perceptual deficit in this instance, mirrors the decline in neuronal sensitivity [comprehensive recent reviews of potential neural mechanisms of adaptation are provided by Kohn (2007) and Clifford et al. (2007)]. The stimulus selectivity of the visual system revealed by this particular aftereffect is known as an orientation channel (Graham, 1989) and sensitivity to the whole range of orientations is afforded by a set of channels with differing preferred orientations. Such is the utility of adaptation in the demonstration of tuning of the visual system to particular stimuli that it has become the method of choice for inferring the algorithmic units of vision in the absence of neuro-physiological data. For example, adaptation to a sinusoidal grating of a particular orientation results in a notch in the graph describing contrast sensitivity to the same grating as a function of orientation (Gilinsky, 1968; Blakemore and Campbell, 1969) but not in that of a grating with a substantially different frequency (Blakemore and Campbell, 1969). This leads to the assumption that, on a local level, the visual system is tuned for gratings of a particular orientation and spatial frequency. Significantly, however, the effect of adaptation to a grating is observed even if the point of fixation is allowed to move freely around the adapting pattern, resulting in a homogeneous adaptation of a region of the visual field to the oriented grating [Arend Jr and Skavenski (1979) showed that observers preferentially fixate certain phases of gratings of particular spatial frequencies, but also that the fixation on the preferred phase was on average less than twice that of any other phase. Given the logarithmic nature of the time-course of adaptation, this inhomogeneity in the duration of adaptation would be only weakly reflected in the state of adaptation. Different observers exhibited different preferred phases]. This observation suggests that the sensitivity that is lost is sensitivity to lines or boundaries of a particular orientation and spatial scale. The receptive fields of neurons of the primary visual cortex are well described by oriented spatial weighting functions with regions of excitatory and inhibitory response to light (Hubel and Wiesel, 1977; Kulikowski et al., 1981; Field and Tolhurst, 1986). The notch in the contrast sensitivity function post adaptation can be understood as due to a reduction in sensitivity of those neurons whose receptive fields approximated the luminance profile of the adapting grating, for some period of the adapting interval, and were therefore stimulated by the grating.

At this point it is instructive to consider how the local orientation of extended features of a stimulus might be represented. The responses from the receptive fields of the simple cells in the primary visual cortex are not unique to particular stimuli and, therefore, it has long been recognized that they cannot represent specific feature detectors (Marr, 1976). For example, certain cells of the primary visual cortex have receptive fields with excitatory and inhibitory areas adjacent along a boundary and, thus, respond to a change in luminance at an edge. An inappropriately oriented but high contrast edge could, therefore, elicit the same response as a more appropriately aligned edge of lower contrast. The visual system resolves this ambiguity by sampling small regions of the visual field over the whole range of orientations. Because these samples are all subject to the same local contrast environment, the cell with the orientation that most closely matches the orientation of the edge would give the largest response. Judgment of orientation is, however, more precise than would be inferred from the orientation tuning of a single cell (Westheimer et al., 1976; Jastrow, 1892; Westheimer, 1990). It has, therefore, been proposed that the perceived local orientation is determined within a population of orientation selective cells (Westheimer, 1990), perhaps by the centroid of the response of a population of orientation selective cells that span the whole orientation spectrum. This form of explanation was first used to explain a repulsion in perceived auditory frequency from the frequency of an adapting tone by Georg von Bekesy (Bekesy, 1929). The population of cells that samples the orientations in the same local region is clustered within a volume of cortex known as a hypercolumn. A hypercolumn is subdivided into columns perpendicular to the cortical sheet with each column containing neurons with receptive fields of a particular orientation selectivity (Hubel et al., 1978). The preferred orientation changes systematically across the hypercolumn and, because the orientation tuning of a neuron is broad in comparison with the incremental change in orientation selectivity across columns, the response to an oriented feature extends across a number of adjacent columns. One can envisage this distribution of activation as a histogram of activity on the cortical sheet, but how might this distribution represent a particular orientation? A model proposed by Gilbert and Wiesel (1990) represented neuronal responses of the orientation selective cells as vectors in the Cartesian plane and the perceived orientation as the vector sum of these vectors. A horizontal line is, however, as different in orientation from a vertical line as is possible. Similarly a line at −45° to the vertical is as different as possible in orientation from a line at 45° to the vertical. If, therefore, we represent orientation in a Cartesian reference frame with vertical and horizontal on the positive and negative y axis, respectively and 45° and −45° on the positive and negative x axis, respectively then orientation is uniquely represented as a vector in this double angle space (Clifford, 2002). The preferred orientations of the orientation columns can be represented as vectors in this space and a line of a particular orientation can then be represented by the vector sum of the response of all orientation columns of a hypercolumn. This model assumes, of course, that the components of each vector can be encoded in some way to allow the vector summation. The model does not speculate on how this might be achieved neuronally but a natural consequence of this representation is that adaptation to a particular orientation, resulting in a reduction in sensitivity to that orientation, causes the resultant vector representing a test line to be repelled from the orientation of the adapting line. From a mechanistic point of view the aftereffect is due to a displacement in the centroid of the response of a bank of orientation selective channels due to modification of the relative sensitivities of the channels by prior adaptation to a specific orientation. A reduction in the sensitivity of the channels stimulated by the adaptor leads to a repulsion of the centroid from the adapting orientation. Such repulsion is indeed observed and is known as the tilt aftereffect (Gibson, 1937). Clifford et al. (2001) showed that this model can account for the tilt aftereffect observed for hard edged circular windowed gratings and Dickinson et al. (2012a) subsequently showed that it can predict the observed magnitude of the tilt aftereffect as a function of the orientation difference between the adapting and test orientations of groups of Gabor patches.

In the previous paragraph we have seen that if a particular mechanism for representation of orientation is accepted, then an explanation for the tilt aftereffect naturally follows. The aftereffect is a misrepresentation of orientation, a purely geometrical property, and the explanation we have provided for it is feed forward. This explanation links the tilt aftereffect to variations in neuronal sensitivity within a particular volume, a hypercolumn, of the primary visual cortex. A hypercolumn deals with a small region of the visual field with neighboring hypercolumns dealing with adjacent regions. Since the primary visual cortex is retinotopically arranged, that is mapped to the retina in a manner that preserves spatial order across the visual field, the tilt aftereffect experienced in any particular region of the visual field will be determined by the difference in orientation between adaptor and test in the corresponding region of the retina (Knapen et al., 2010). Recognition that orientation can be misperceived locally due to adaptation, however, begs the question of how extended objects might be misperceived. In an elegant adaptation experiment Blakemore and Over (1974) showed that if a curved adapting grating, concave to the right, was scanned repeatedly along the horizontal midline then a subsequently viewed straight vertical line was perceived as concave to the left; but if the adapting grating was scanned along the vertical midline then the line appeared undistorted. In the first instance the region of cortex in spatial correspondence with the top half of the test stimulus becomes adapted to an orientation anticlockwise of vertical and the bottom half clockwise of vertical. In the second the top and bottom halves are similarly adapted to orientations both clockwise and anticlockwise of vertical. Blakemore and Over concluded that this apparent adaptation to curvature was consistent with a systematic application of the tilt aftereffect, and indeed it is consistent with the mechanism proposed above to explain the tilt aftereffect. For the first adapting method the resultant vector representing the orientation of the vertical, linear test grating would be anti-clockwise of vertical for the top half of the stimulus and clockwise of vertical for the bottom. For the second adapting method the resultant vector would be vertical for all regions of the test stimulus because the adaptation is symmetrical about the vertical. The results of this experiment are, therefore consistent with a locally constrained adaptation combined with the accumulation of adaptation across eye movements.

Dickinson et al. (2010) proposed a general mechanism to account for shape aftereffects based on the tilt aftereffect. They postulated that shape aftereffects could be predicted by a systematic application of the tilt aftereffect across the stimulus, concomitant with a misrepresentation of the locus of extended features to preserve continuity of those features. This mechanism was shown to predict the selective misperception of a coincident circle and Cartesian grid after adaptation to a radial frequency (RF) pattern, a pattern deformed from circular by a sinusoidal modulation of radius, or a Cartesian grid deformed in the same manner. Dickinson et al. (2012b) went on to show that the adaptation was retinotopic and rapidly acquired as would be predicted by a retinotopically constrained (Afraz and Cavanagh, 2008; Knapen et al., 2010) and rapidly induced (Sekuler and Littlejohn, 1974) tilt aftereffect. The representation of the tilt aftereffect extended over space was referred to as a tilt aftereffect field. The tilt aftereffect field is a scalar field which represents the tilt aftereffect at any point in the visual field, determined locally by the orientation difference between the adapting stimulus and the test stimulus. It is easy to imagine how complexities in this representation might arise. The null adaptation result of Blakemore and Over, however, is readily accommodated by allowing the adaptation to be accumulated over time resulting in a null tilt aftereffect field when the orientation channels with preferred orientations clockwise and anticlockwise of the test orientation are symmetrically adapted. Another problem that was identified in Dickinson et al. (2010) was that when lines of different orientations intersect they are likely to be subject to different tilt aftereffects due to the same adaptation history. This problem was circumvented by treating the lines close to horizontal and vertical as being subject to separate tilt aftereffect fields [cells of V1 do not respond to orientations perpendicular to their preferred orientation (Ringach et al., 2002)]. Thus, the simplicity of the tilt aftereffect field representation of shape aftereffects is somewhat compromised for complex stimuli but the general principal, that shape aftereffects are due to the systematic application of the tilt aftereffect is in no way invalidated. Dickinson et al. (2010) therefore proposed that the tilt aftereffect field explanation for shape aftereffects would generalize across all extended visual stimuli and should be entertained as a possible explanation for all such aftereffects. Because the tilt aftereffect field is simply a representation of the tilt aftereffect over an extended area, the shape aftereffects due to application of this field require no recourse to the heuristic influences intrinsic to the visual system that are used to make sense of scenes. The aftereffects would be, therefore, purely a consequence of morphological differences between the adapting and test stimuli. Aftereffects due to adaptation to semantic information, however, can reasonably be expected to act at the level of internal representations of the world.

The face might be considered one of the most evocative visual stimuli, suffused with ecologically relevant information. A large proportion of such information is morphologically signaled, and arbitrary geometrical transformations of face shape are seen to act on identity (Blanz et al., 2000). The morphology of a specific face is different from that of a face with a morphology representing the mean of a population of faces. Faces, then, can be specified by the geometrical transformation required to transform the mean face to the specific face. If the opposite transformation is applied to the mean face an anti-face with a distinct identity results. When adapted to the anti-face, however, an observer is more inclined to identify the mean face as the original specific face, than when un-adapted (Leopold et al., 2001; Wilson et al., 2002; Rhodes and Jeffery, 2006). Within a particular identity, though, particular changes in the morphology of the face signify changes in emotional state and if these emotional states are to be useful within a population of individuals then the processing of such differences must generalize across identities. In a recent study Skinner and Benton (2010) created anti-expressions in faces using the process of applying a geometrical transformation opposite to that required to produce the expression from a face with a neutral expression. The expressions manipulated were happiness, sadness, fear, anger, disgust, and surprise. After adaptation to a face with an anti-expression, observers were required to report which of the six expressions was perceived in a neutral face. In the majority of trials, the observers reported the expression opposite to the anti-expression. For example, they reported fear in a neutral face after exposure to a face with an anti-fear expression. Both identity and expression aftereffects, therefore, are recognized to be consistent with geometrical transformations opposite in sign to the transformations applied to the test patterns to create the adaptors. The effects of adaptation are assumed by the authors of these studies to act at the levels of visual processing associated with the analysis of faces, and claims are made regarding the nature of such analyses on the basis of the selectivity of adaptation effects. It is, however, possible that the adaptation takes place earlier in the visual processing hierarchy and Dickinson et al. (2010) showed that adaptation to an arbitrarily transformed face produced the percept of the opposite transformation in an untransformed face. Naturally this result would also be expected to apply to transformations of faces that conferred meaning. Moreover, the relationship between the magnitude of the aftereffect and the size of the transformation of the adaptor revealed by Dickinson et al. (2010) was the same as that for the same transformation introduced into a circle, which was shown to be consistent with the application of a tilt aftereffect field. Although this result shows that the aftereffect might be consistent with the application of a tilt aftereffect field, a face is a much more complex stimulus than a circle and so it is more difficult to demonstrate this explicitly. It is, though, possible to test some further predictions of this interpretation.

If the adaptation is manifested at the higher levels of visual processing associated with analysis of faces, then the aftereffects should be dependent on the semantic information content of the face. If it is simply due to a tilt aftereffect field, however, then it should depend on the local feature properties of the stimulus. A system incorporating some redundancy might display both local morphological and semantic adaptation. Xu et al. (2008) showed that adaptation to a curve can influence the perception of high level facial expressions and Benton (2009) used the folded face illusion to show that introducing a vertical shear in a neutral face could cause the face to appear happy or sad. Dickinson et al. (2012b) showed that adaptation to a local orientation field that might be expected to introduce this shear, as a result of the misperception of the orientation of the features orientated close to the horizontal, can cause a subsequently viewed unmanipulated face to have the opposite demeanor. That is, the aftereffects of adaptation to the orientation fields cause the orientations of the face to undergo the same transformations as they do in the folded faces. As we shall show, simply introducing shear, effectively an angle, solely into the mouth of an adaptor face can produce the same emotion aftereffects. Restricting the manipulation to the mouth allows us to then abstract the mouth from the face to test whether adaptation to the angle introduced into the mouth can produce a perceived angular change in a linear mouth sufficient to account for the perceived change in demeanor of the face. For this manipulation the mouth is presented rotated through a right angle to require the judgments to be made at a mouth orientation that is experienced less frequently than in the horizontal. In a further manipulation of the abstracted mouth, we apply the opposite transformations to the two sides of the mouth (that is the transformation of the two sides of the mouth result in clockwise or anti-clockwise rotations of both sides of the mouth about the center of the mouth) to create adapting and test stimuli that are essentially linear but effectively rotated, to determine if adaptation to a rotated, or tilted, mouth can produce a perceived rotation in a mouth sufficient to account for the previous two manipulations (see **Figures 1**, **2**). The adapting and test mouths are again presented rotated anti-clockwise through 90 degrees so that the orientations of the test mouths span the vertical. By requiring the observers to report whether manipulated faces appear happy or sad in an unadapted condition we demonstrate that the demeanor of the faces can be reliably reported for both the high- and low-pass filtered stimuli which then allows us to examine cross adaptation between these two stimulus types. If adaptation due to the semantic content of the faces occurs then adaptation should be strongly evident for the face stimuli but somewhat reduced for the angled mouth and oriented mouth stimuli because the semantic information is present in the face stimuli but not in the angled mouth and oriented mouth stimuli. If, though, the adaptation occurs solely at the local level then adaptation should be similar across the three stimulus types (face, angled mouth, and oriented mouth). In addition to these spatial manipulations of mouth shape the face and mouth stimuli are high-pass and low-pass filtered for spatial frequency. It has been shown that the tilt aftereffect is selective for spatial frequency (Ware and Mitchell, 1974) and that interocular transfer of the aftereffect is correlated with stereo-acuity (Mitchell and Ware, 1974). The second of these studies demonstrated an absence of transfer in stereo-blind subjects. Collectively these two investigations suggest that the locus of the mechanism supporting the tilt aftereffect is earlier than the convergence of the information from the two eyes onto binocularly driven neurons. If, then, the face and angle aftereffects observed in the face and angled mouth stimuli are simply the effects of a tilt aftereffect field we can reasonably expect that the aftereffects would be larger for adapting and test stimuli matched in spatial frequency than for stimuli with differing spatial frequency, and also that the difference in the sizes of the effects would be the same for the oriented mouth, angled mouth and face stimuli. Differentially selective aftereffects for the different stimulus types might, however, be indicative of the presence of a higher level (semantic) aftereffect.

MATERIALS AND METHODS

Four experienced psychophysical observers ED, MT, RG, and TM, all with normal or corrected to normal visual acuity, participated in the experiment. The experiment complied with the requirements of the University of Western Australia research ethics committee and was therefore conducted in accordance with the Declaration of Helsinki. ED is an author and informed consent for participation in the experiment was obtained from MT, RG and TM.

Stimuli were presented on a Sony G520 monitor from the frame buffer of a Cambridge Research Systems Visage visual stimulus generator. The monitor was luminance calibrated using a CRS Optical and associated software at a refresh rate of 100 Hz. Adaptor and test stimuli were each presented for durations of 160 ms with a 500 ms inter-stimulus interval interposed. Screen luminance during the inter-stimulus interval, before the adapting interval and after the test interval was 9 cd/m^2. The screen was viewed from a distance of 135 cm, at which distance each screen pixel subtended 1 min of visual angle.

A member of the Human Vision Laboratory, VB, posed for a photograph whilst displaying a neutral expression, neither happy nor sad. The image of the face was composed of 1024 × 768 pixels with a mouth width of approximately 270 pixels, or 270 min of visual angle when presented in the experiment. In order to create the happy and sad faces from this image the horizontal midline of the mouth was displaced vertically upwards or downwards, respectively, by the tangent of a specified angle multiplied by the distance from the center of the mouth out to a distance of 157′. The vertical displacement beyond this distance was returned linearly to zero over the next 40′. Pixels above and below the midline were moved by the same amount scaled by a Gaussian profile in the vertical with a standard deviation of 50′ to allow a smooth transition into the undistorted region of the face (see **Figure 1**). The faces used for the adaptor stimuli had displacements equating to a rotation of the horizontal midline of the mouth about the center of the mouth by angles of 15 degrees above (positive) and below (negative) the horizontal applied to the neutral face to create faces that appeared very happy and very sad, respectively. This manipulation will be referred to as a displacement in angle with the convention for faces that a positive displacement in angle results in a smiling face. Nine faces were used to create test

FIGURE 1 | Example face stimuli. The left hand column shows, from top to bottom, faces with angles of +15, +8, 0, −8, and −15 degrees introduced to the mouth as described in the material and methods section. The third face from the top in the left hand column is cropped from the original photograph of VB taken by Matt Tang of the Human Vision Laboratory of the University of Western Australia. The middle and right hand columns are high-pass and low-pass filtered versions of the same faces, respectively. From top to bottom the faces change from appearing happy to sad. The faces with +15 and −15 degree deformations in angle introduced to the mouth were used as adapting stimuli. Those with +8 and −8 deformation in angle were the extreme ends of the spectrum of test stimuli used in the method to constant stimuli to determine the point of subjective equality, the face which observers would report as happy or sad with equal probability. The high pass filter stimuli in the middle column retain the same high spatial frequency energy as in the original images. Removing the low frequencies reduces the overall mean luminance in the face and therefore these images are best viewed by zooming in on the sub-images, although they are depicted as used in the experiment.

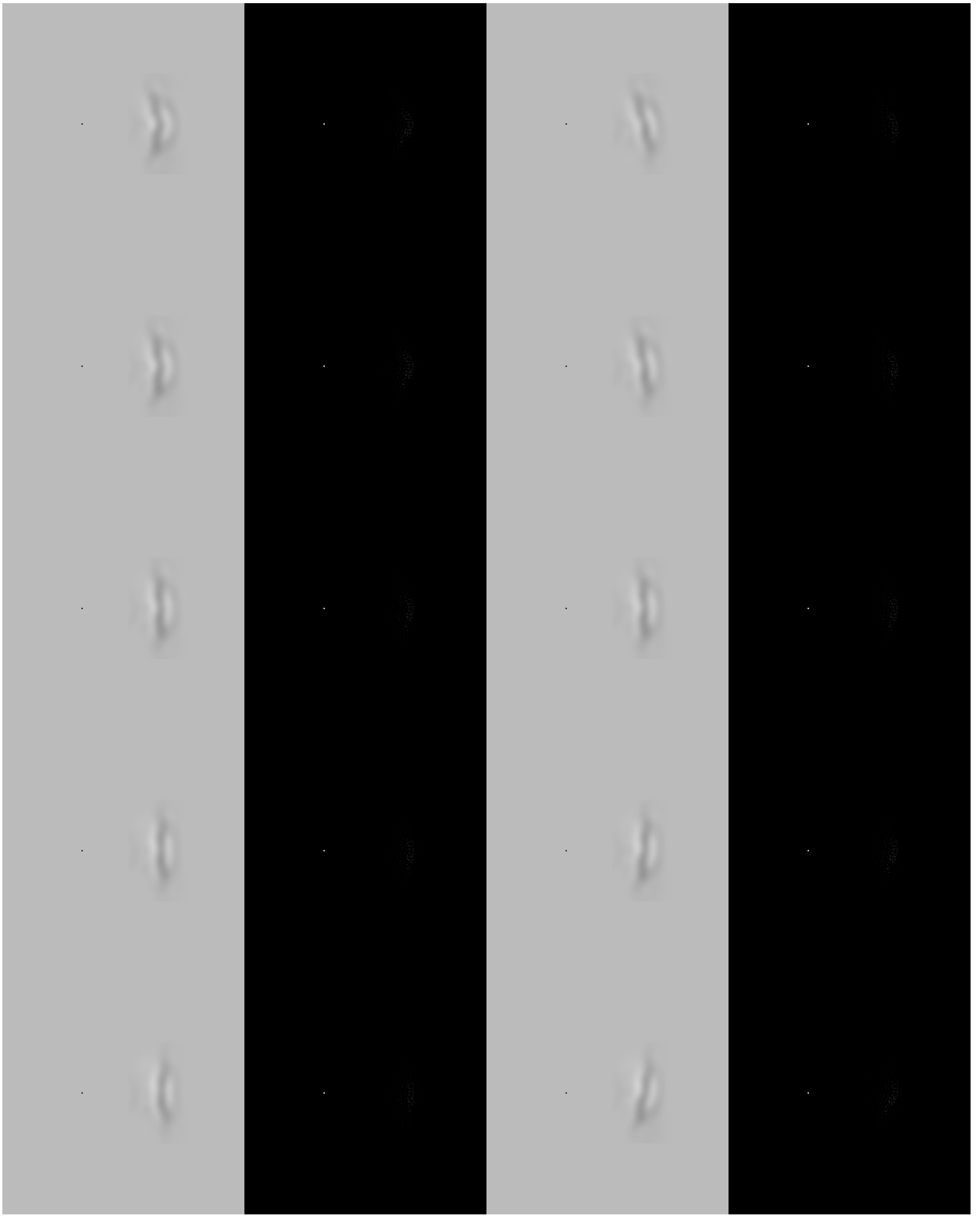

FIGURE 2 | Example angled and oriented mouth stimuli. The two columns on the left half of the figure show mouths abstracted from the faces and turned anticlockwise through 90°. The deformations in angle in these examples are +15, +8, 0, −8, and −15 degrees above the horizontal midline of the mouth. The columns in the right hand half of the figure show mouths with the opposite displacement applied to the right and left halves of the mouth to create mouths that appear oriented. The pairs of angles introduced to the right/left halves of the mouth, in these examples are +15/−15, +8/−8, 0/0, −8/+8, and −15/+15 degrees above the horizontal midline of the mouth (before the mouth was rotated). For these stimuli only the low-pass and high-pass spatial frequency versions of the stimuli are shown.

stimuli with displacements equating to angles of −8, −6, −4, −2, 0, +2, +4, +6, and +8 degrees. High- and low-pass filters were applied to all of these faces. The high-pass filters removed all spatial frequencies of less than 3.6 c/° and the low-pass filters removed frequencies of greater than 1.8 c/°. A band of spatial frequencies with a range of an octave was, therefore, completely removed from the stimuli and separates the frequency content of the high- and low-pass stimuli. In order to verify that the test faces were perceived to express happiness and sadness observers were asked, in an unadapted condition, to report whether they perceived the test faces as happy or sad. The test faces were reliably reported as happy if they had a positive displacement of the mouth and sad if they had a negative displacement (essentially 100% reliable at the two extremes of the range of stimuli used for the test faces).

To create the angled mouth stimuli a two dimensional Gaussian luminance contrast window was applied to the face stimuli centered on the middle of the mouth in order to smoothly match the luminance of the abstracted mouth to a flat background luminance. The background luminance of the low-pass stimuli was 63 cd/m^2 and the high-pass stimuli 0 cd/m^2. The standard deviation of the horizontal axis, of the window was 50′ and the vertical axis 25′. Following the application of this window a rectangular area of 320 × 190 pixels, centered on the midpoint of the mouth was abstracted and pasted into flat images with the appropriate background luminance. The mouth was rotated anti-clockwise through 90 degrees and presented four degrees of visual angle to the right of a fixation point at the center of the screen (see **Figure 2**). No fixation mark was used for the face stimuli but observers were instructed to fixate the bridge of the nose which was approximately four degrees of visual angle above the mouth. Across the stimulus types, therefore, the mouths were at an eccentricity of four degrees. The same convention of displacement in angle applies to the angled mouth stimuli but, as the mouths are rotated anti-clockwise through a right angle, positive displacements in angle result in mouths that are concave to the left.

The oriented mouth stimuli were created from the mouth stimuli by matching the top halves of the mouth stimuli (actually the right half of the mouth) with positive displacements to the bottom halves of the stimuli with negative displacements and vice versa. An oriented mouth stimulus with an anti-clockwise tilt of 8 degrees, for example, would have the top half of a mouth with a +8 degrees displacement and the bottom half of a mouth with −8 degrees displacement. The convention for the oriented mouth stimuli is that a positive displacement in angle is an anti-clockwise rotation. These stimuli were again presented 4 degrees of visual angle to the right of a centrally located fixation point. Example face stimuli are presented in **Figure 1** and example angled and oriented mouth stimuli in **Figure 2**.

Each of the three stimulus types (face, angled mouth, oriented mouth) were filtered to give low-pass (LP) and high-pass (HP) filtered versions of the stimuli. For each condition the method of constant stimuli (MOCS) was used to determine the point of subjective equality (PSE); a neutral expression for the faces (neither happy nor sad), a straight mouth for the angled mouth stimuli and a vertical mouth for the oriented mouth stimuli for the LP and HP versions of the three stimulus types. For each of the test stimuli (LP and HP filtered face, angled mouth and oriented mouth stimuli) the PSE was determined in the absence of an adaptor and under four conditions of adaptation to the same stimulus type, the four conditions being LP and HP stimuli with positive (+15 degrees) and negative (−15 degrees) displacements in angle, as previously defined. To summarize, there are six test stimuli, comprising LP and HP filtered versions of the face, angled mouth and oriented mouth stimuli. Adaptation was restricted to similar stimulus types (faces with faces for example) and the points of subjective equality determined for adapting stimuli with positive and negative deformation and with similar and dissimilar filter conditions. For each condition (adaptor—test pair), three blocks of 180 trials were performed. For all conditions the test stimuli used in the MOCS were divided equally across stimuli with −8, −6, −4, −2, 0, +2, +4, +6, and +8 degrees of displacements in angle. These stimuli ranged from sad to happy for the faces, concave to the right to concave to the left for the mouth stimuli and clockwise of the vertical to anti-clockwise of the vertical for the orientated mouth stimuli. On each trial the observer was required to report whether the face appeared happy or sad, whether the mouth stimulus appeared concave to the left or right or whether the oriented mouth stimulus appeared oriented anti-clockwise or clockwise of vertical using the left or right mouse button respectively. The test stimuli comprised HP or LP filtered stimuli of the three stimulus types and for each of these a no adaptor condition and HP and LP adaptor conditions (each with conditions with +15 and −15 displacements in angle) were performed using the same test stimulus type. The probabilities of reporting that the test stimuli were happy, concave to the left or anti-clockwise of vertical were calculated, as appropriate, for each level of displacement. A cumulative normal distribution was fitted to the probabilities with the mean yielding the displacement in angle for the stimuli required to give the PSE, that is; a neutral expression for the faces, a straight mouth for the angled mouth stimulus and a vertical oriented mouth stimulus, respectively. Afterwards aftereffect magnitudes were derived by taking difference between the PSEs for positive (+15) and negative (−15) displacements in angle for each adaptor condition (for example the difference between the points of subjective equality for a high-pass filtered test face after adaptation to low-pass filtered faces with positive and negative displacements in angle applied to the mouths). These aftereffect magnitudes were used for statistical testing.

RESULTS

The results in the form of psychometric functions are presented in **Figures 3–5** and **6** for observers ED, MT, RG, and TM, respectively.

The column of graphs on the left (right) of **Figures 3–5** and **6** shows data for the LP (HP) test pattern conditions as previously described. The top pair of graphs in the figures shows the results for the face stimuli for the observers. The ordinate represents the probability of responding that a face is happy and the abscissa the displacement in angle of the mouth of the test pattern (positive indicates deformation toward smiling and negative

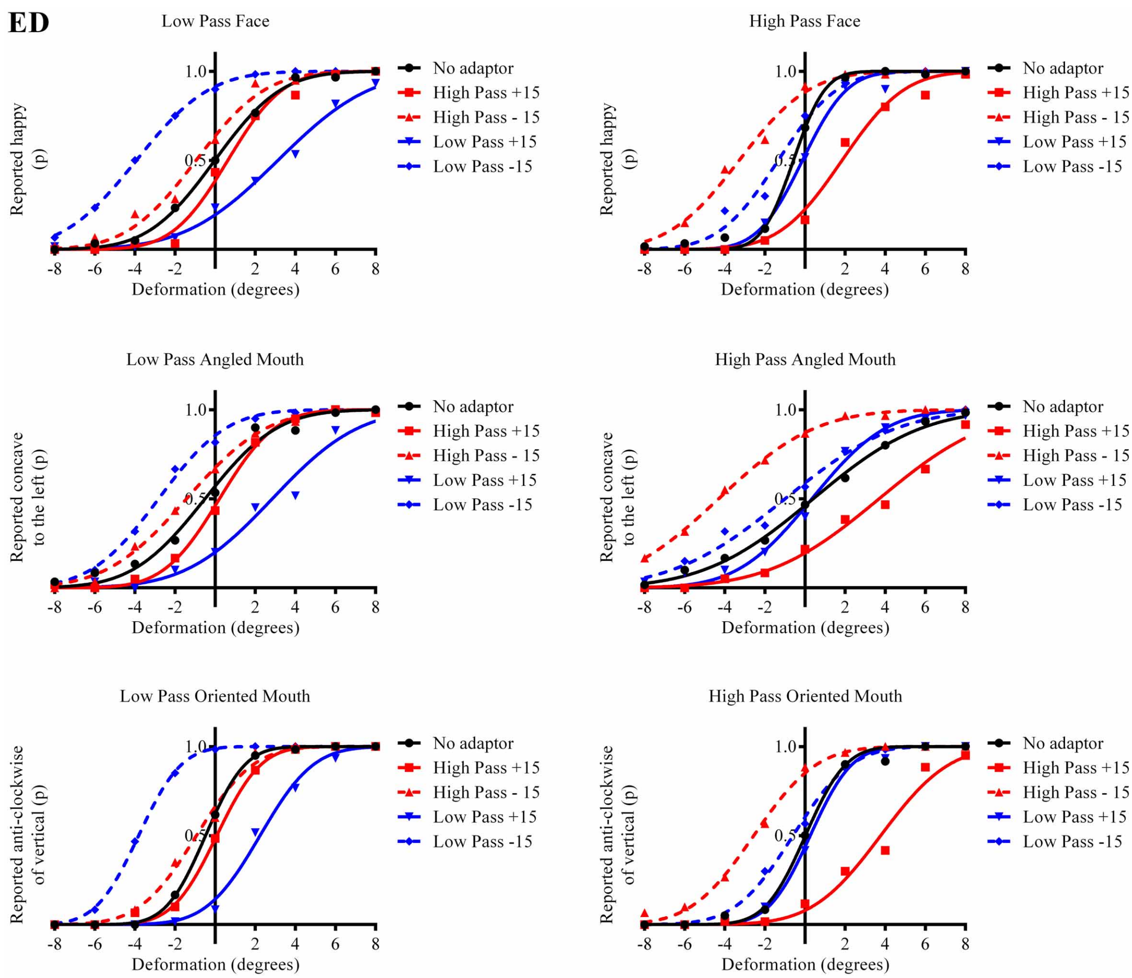

FIGURE 3 | Psychometric functions for Observer ED. The three rows of graphs present data for the three stimulus types; faces, angled mouths and oriented mouths from top to bottom. Adaptation was examined within but not across these stimulus types but the same sizes of deformation in angle were used in the mouths of the adapting stimuli in each case (equating to an introduction of either +15 or −15 degrees of rotation of the two halves of the mouth about the center of the mouth and with respect to the midline of the mouth). The left column of graphs displays the data for the low-pass (LP) spatial frequency test stimuli and the right column the high-pass (HP) test stimuli. Each graph, therefore, represents data for a single test stimulus (top left is the data for a LP test face, for example, and this information is used as the label for each graph). For each test stimulus four adapting conditions were examined; these being positively (+15 degrees of deformation in angle) and negatively (−15) deformed LP and HP versions of the same stimulus type. The red lines represent the fitted psychometric functions for the HP spatial frequency adaptors and blue lines LP. Solid lines represent the psychometric functions for positively deformed adaptors (+15) and dashed lines negatively deformed (−15). The solid black lines are the functions fitted to the data from the un-adapted conditions. As an example of the convention for the representation of data, the dashed blue line in the top left graph represents the probability of responding that the LP test face appears happy, after adaption to a LP adapting face with a deformation in angle of −15 degrees applied to the mouth, as a function of the deformation in angle applied to the test face. In this example it is clear that adapting to the negatively deformed adapting face (which appears sad) results in the observer reporting that the test face appears happy more frequently for all amplitudes of test face deformation. The point of subjective equality (PSE), the point at which the observer reports happy and sad with equal probability is displaced toward negative values for deformation in angle of the test face. That is, a test face must be deformed toward sad in order to appear neutral after adaptation to a sad face. In all cases it is evident that after adaptation the stimuli perceived as untransformed are in fact transformed in the direction of the adaptor. This transformation is required to null the aftereffects of the adaptation. For this observer the aftereffects of adaptation are much larger for the adaptor and test stimuli with similar spatial frequency content than for those that are dissimilar.

toward frowning). The legend indicates the adaptation condition. Data pertaining to LP and HP adaptors are plotted in blue and red, respectively. Adapting conditions that are labeled +15 are happy and −15 sad. The functions fitted to the data of the happy (sad) adaptor conditions are solid (dashed) lines. It is immediately evident that after adaptation to a happy (sad) face a neutral face is reported to appear sad (happy) in more than half of the trials. In order for a test face to be reported happy (sad) in an equal proportion of trials, the PSE, it must be transformed toward happy (sad). The aftereffect causes the test face to be perceived as more different to the adaptor face than it actually is. The same effect is observed for adaptor and test face

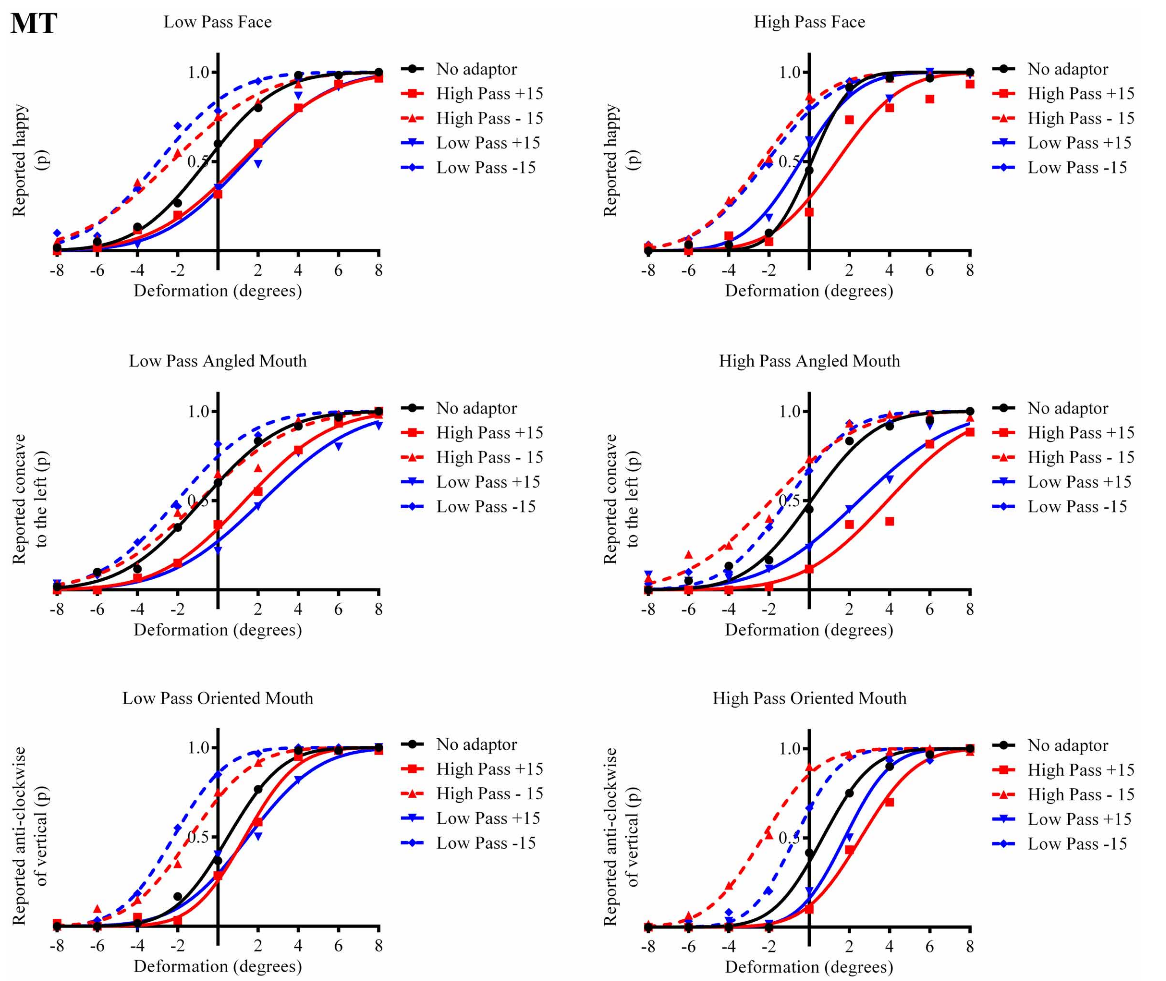

FIGURE 4 | Psychometric functions for Observer MT. The format of these graphs is the same as those for Observer ED in **Figure 3**. The one substantial difference from the data for Observer ED is that there is a smaller difference in the magnitude of the aftereffect between the conditions where the adaptor and test stimuli had the same and different spatial frequency content. The aftereffects of adaptation, though, are still largest for the stimuli with similar spatial frequency content.

pairs that are both HP, and both LP in spatial frequency. The middle and bottom pairs of graphs show the comparable results for the angled and oriented mouth stimuli, respectively. For the angled mouth stimuli positive (negative) deformations in angle produces stimuli that are concave to the left (right). Observers were required to report whether the test stimuli were concave to the left or right. It is clear from the data that adaptation to a stimulus that is concave to the left, for example, results in a decrease in the probability of reporting that the test stimuli are concave to the left. For the oriented mouth stimuli a positive deformation in angle results in the stimulus being oriented anti-clockwise of vertical. Observers were required to report whether the test stimuli were oriented anti-clockwise or clockwise of vertical. Adaptation to a stimulus with a positive deformation in angle resulted in a reduction in the probability of reporting that the test stimuli were oriented anti-clockwise of vertical. The common qualitative result across the three stimulus types is that adaptation results in repulsive aftereffects. In order to compare the aftereffects quantitatively the magnitudes of the effects, measured as the differences between the points of subjective equality for adaptors with different signs of deformation in angle (+15 and −15) were calculated, and are presented in **Figure 7**. The column of graphs on the left (right) show the magnitudes of the aftereffect for test stimulus pairs that were of similar, that is HP/HP or LP/LP (dissimilar, HP/LP or LP/HP) spatial frequency. The bottom row of graphs shows the averaged data of the four observers. **Figure 8** shows the results for a repeat of the experiment using a different face, AJ, transformed in the same manner as the image of VB.

The data summarized in the bottom row of graphs of **Figure 7** were tested statistically. A two-tailed, paired t-test of the data of the four observers showed that the aftereffect magnitudes for the conditions with similar spatial frequencies in the adaptor and test (the left hand column of graphs) did not differ across conditions where the adaptor and test patterns were both high (HP/HP) frequency, or both low (LP/LP) frequency ($p = 0.9294$, $t_{(11)} =$

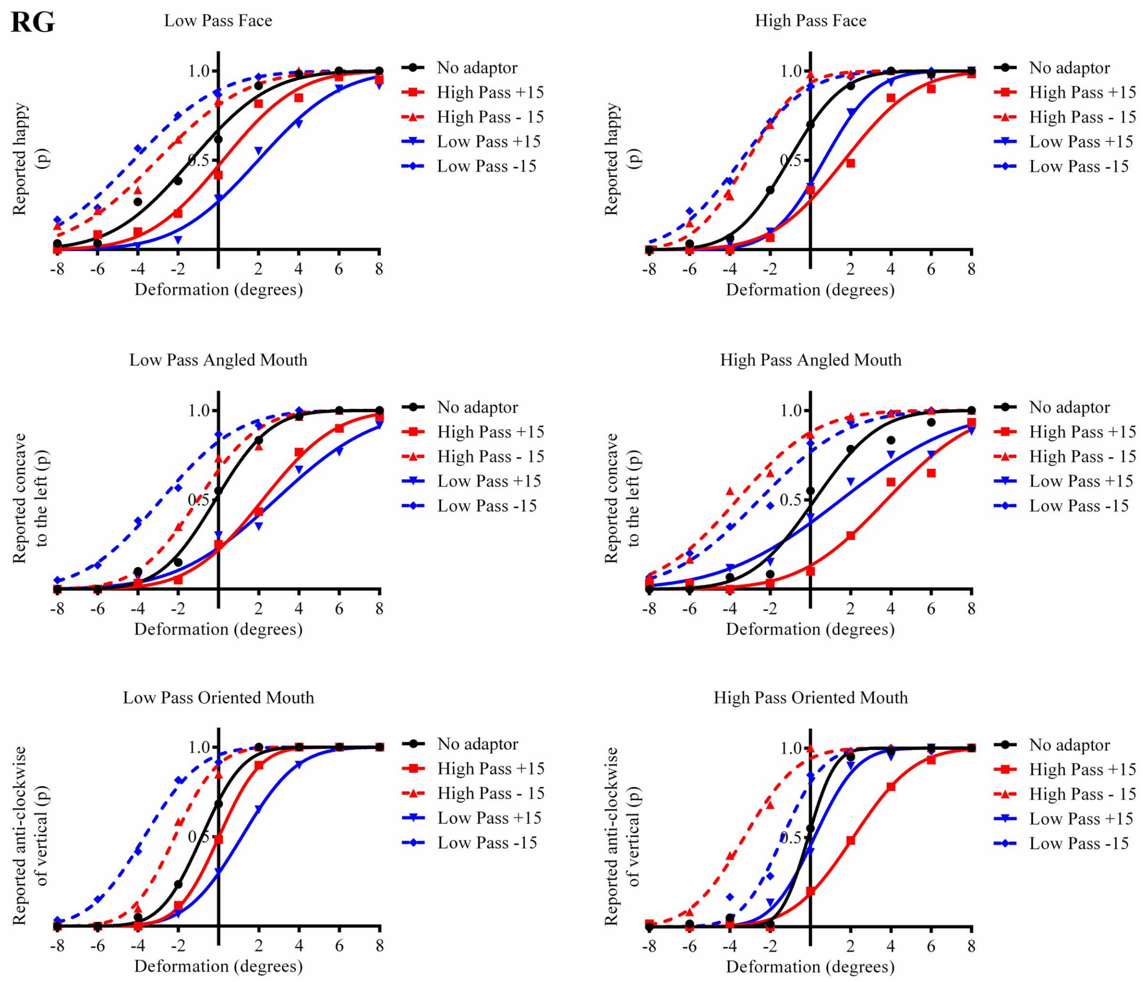

FIGURE 5 | Psychometric functions for Observer RG.

0.09066). The means of these populations were 5.568 ± 0.939 (95% CI) and 5.532 ± 0.549 degrees, respectively. These conditions were, therefore, combined within stimulus types into conditions of similar spatial frequency in test and adaptor for further analysis. Furthermore, a paired *t*-test of the aftereffect sizes for conditions with dissimilar spatial frequencies across adaptor and test (HP/LP or LP/HP; the right hand column of graphs) did not differ in the order of the frequencies used ($p = 0.9689$, $t_{(11)} = 0.03994$). The means for these populations were 2.430 ± 0.488 and 2.415 ± 0.824 degrees, respectively. These conditions were also combined within stimulus types into conditions of dissimilar spatial frequency. The aforementioned means show that the aftereffect magnitudes for conditions where the adaptor and test had spatial frequencies in the same range were greater than twice those where their spatial frequencies were in different ranges. The magnitudes for the conditions with dissimilar spatial frequencies were, however, also significantly greater than zero (a result that might be attributed to second-order tilt aftereffects or a bandwidth for the spatial frequency channels that was broader than the band separating the HP and LP spatial frequency ranges). Following these amalgamations of conditions we are left with six conditions to compare, these being face, angled mouth and oriented mouth stimulus types with similar or dissimilar spatial frequencies in the adaptor and test patterns. A One-Way ANOVA incorporating Tukey's multiple comparisons test was used to compare the magnitudes of the aftereffects within these populations. The results of the multiple comparisons test are reported in **Table 1**.

To summarize the results reported in **Table 1**, the magnitudes of the aftereffects were only significantly different when pairwise comparisons were made between a condition with similar spatial frequency content across adaptor and test stimulus and a condition with dissimilar spatial frequency content across adaptor and test. All three stimulus types; faces, angled mouths and oriented mouths, show the same dependency on the similarity between the spatial frequency content of adaptor and test.

DISCUSSION

The results of this study demonstrate that adaptation to a happy face causes a face with a neutral expression to look sad and vice

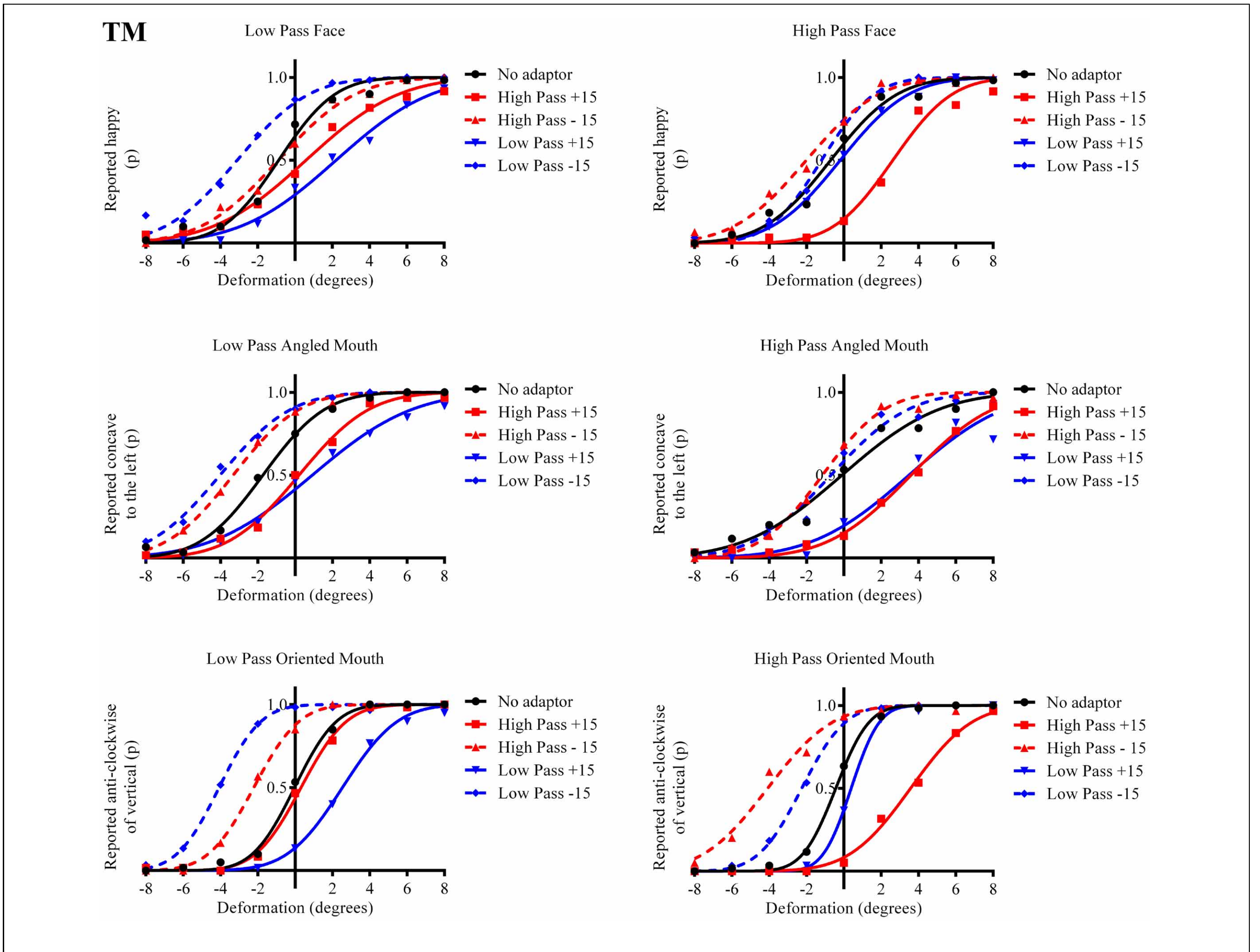

FIGURE 6 | Psychometric functions for Observer TM.

versa. This result has been demonstrated in the past (Xu et al., 2008). The expression of the face is in this instance, however, entirely dictated by the shape of the mouth and the magnitude and direction of the aftereffect can be predicted by an angle aftereffect introduced into a straight mouth, abstracted from the face, by adaptation to the manipulated angled mouth used in the face adaptor. In turn, the angle aftereffect can be predicted by the tilt aftereffect introduced into a vertically oriented mouth by an oriented mouth tilted from the vertical. Moreover, the spatial frequency specificity of these three effects is the same, pointing to the same, low level, adaptation effect being responsible for all three. We propose that the results can all be understood as due to a reduction in sensitivity in the orientation selective neurons of the primary visual cortex that were stimulated during adaptation. When adaptor and test orientations are different, the response of the population of neurons sensitive to the whole range of orientations is biased toward neurons that were not previously stimulated, that is those whose preferred orientations are more different from the adaptor than the test. The resultant vector sum of the activity in the population of neurons with the complete range of preferred orientation is therefore skewed giving rise to the tilt aftereffect (Bekesy, 1929; Gilbert and Wiesel, 1990; Clifford et al., 2001; Clifford, 2002; Dickinson et al., 2012a,b). The tilt aftereffect is a local and retinotopic phenomenon (Knapen et al., 2010) but it has been shown that its systematic application over space in a tilt aftereffect field can provide an explanation for complex shape aftereffects including, perhaps, face shape aftereffects (Dickinson et al., 2010). It is recognized that the aftereffects apparent at one level of visual coding might be inherited from adaptation at lower levels, but Dickinson et al. (2010) was the first explicit demonstration that complex shape aftereffects could be wholly accounted for by a spatially extended field representing the tilt aftereffect experienced locally. Dickinson et al. (2012a) showed that the same shape aftereffects could be predicted by a local population encoding of orientation within a tilt aftereffect field. Dickinson et al. (2010) proposed that a tilt aftereffect field could account for face aftereffects. The current study is totally consistent with this interpretation, showing that a change in morphology of the face due

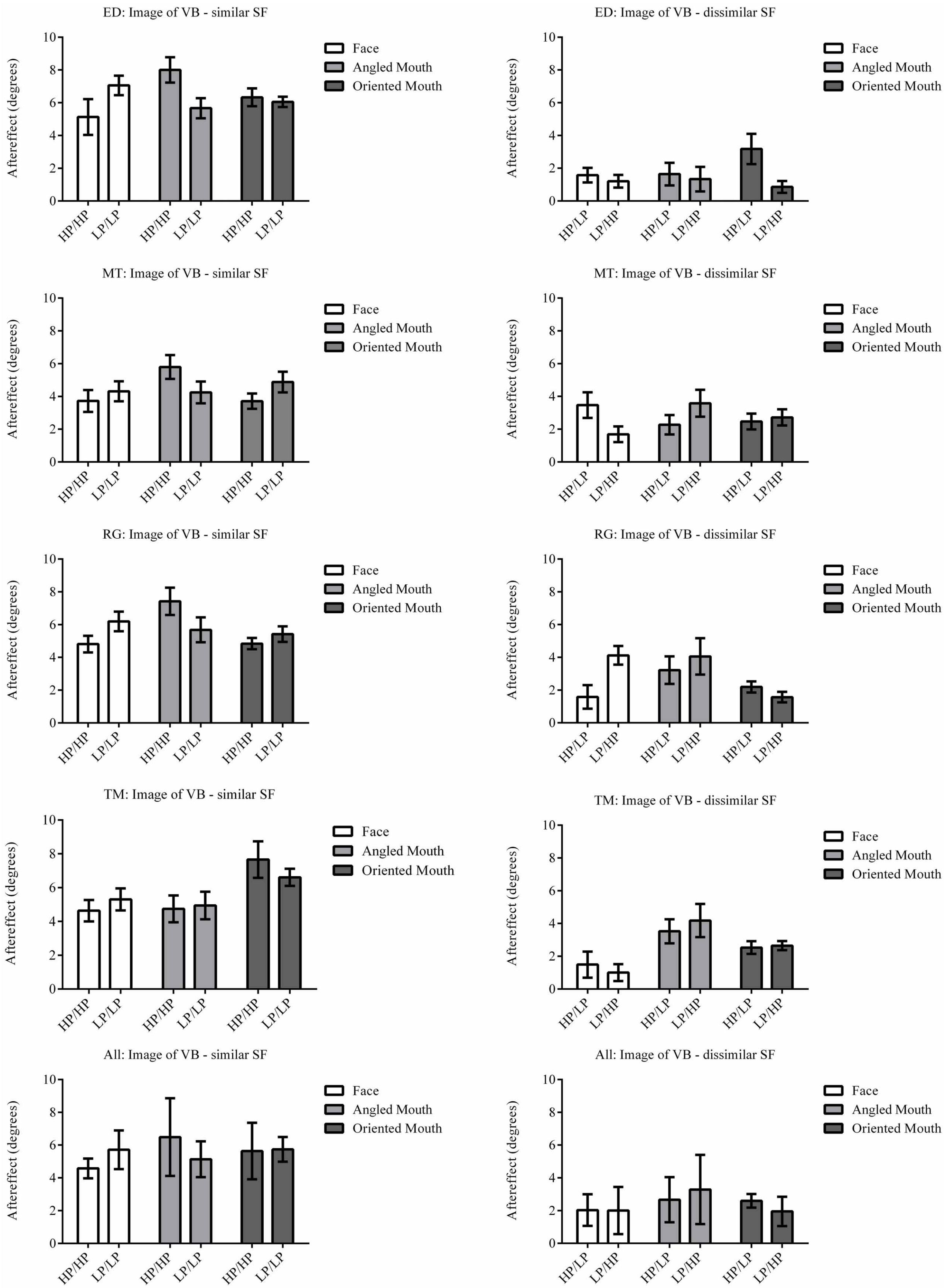

FIGURE 7 | Continued

FIGURE 7 | Aftereffect magnitudes for Observer ED. The aftereffect magnitudes displayed are the differences between the points of subjective equality for the same adaptor (in terms of stimulus type and spatial frequency) with positive and negative deformations in angle. For example the difference between the points of subjective equality for the low-pass filtered face after adaptation to high-pass filtered faces with deformations in angle of +15 and −15 degrees is represented by the column filled in white (labeled "Face" in the legend) and annotated HP/LP in the bottom graph. The magnitude of the aftereffect is similar across face, angled mouth and oriented linear mouth stimuli for conditions that have the same spatial frequency content in adaptor and test (left column of graphs), and also for conditions that have dissimilar spatial frequency content in adaptor and test (right column of graphs). Conditions with similar spatial frequency content in adaptor and test have larger aftereffects than those with dissimilar (comparing the left column of graphs with the right).

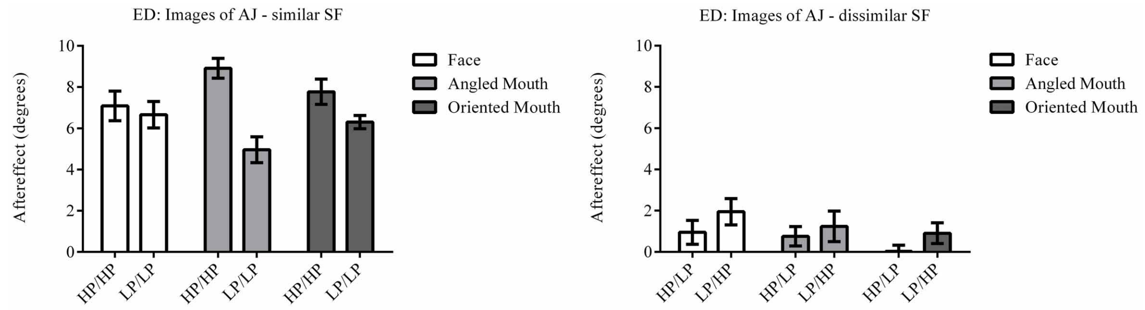

FIGURE 8 | Aftereffect magnitudes for Observer ED for stimuli derived from a different face: AJ. These data are from a repetition of the experiment using stimuli derived from a different face with the same transformations applied. The magnitudes of aftereffects are similar to those shown in **Figure 7**, demonstrating the patterns of results are not specific to a single face.

Table 1 | This table compares the magnitudes of the aftereffects across six conditions.

	Face: Similar SF	Angled mouth: Similar SF	Oriented mouth: Similar SF	Face: Dissimilar SF	Angled mouth: Dissimilar SF	Oriented mouth: Dissimilar SF
Face: Similar SF		$p = 0.8324$	$p = 0.9225$	$p < 0.0001$****	$p = 0.004$**	$p < 0.0001$****
Angled mouth: Similar SF	$q_{(42)} = 1.703$		$p > 0.9999$	$p < 0.0001$****	$p < 0.0001$****	$p < 0.0001$****
Oriented mouth: Similar SF	$q_{(42)} = 1.382$	$q_{(42)} = 0.3202$		$p < 0.0001$****	$p = 0.0002$***	$p < 0.0001$****
Face: Dissimilar SF	$q_{(42)} = 8.006$	$q_{(42)} = 9.708$	$q_{(42)} = 9.388$		0.5188	0.9973
Angled mouth: Dissimilar SF	$q_{(42)} = 5.555$	$q_{(42)} = 7.258$	$q_{(42)} = 6.938$	$q_{(42)} = 2.450$		0.7976
Oriented mouth: Dissimilar SF	$q_{(42)} = 7.356$	$q_{(42)} = 9.059$	$q_{(42)} = 8.738$	$q_{(42)} = 0.6497$	$q_{(42)} = 1.801$	

The conditions are face, angled mouth and linear orientated mouth stimuli with similar and dissimilar spatial frequency (SF) content in the adaptor and test pairs. For example the condition Face: Dissimilar SF represents data pertaining to adaptor-test face stimulus pairs with dissimilar spatial frequency content. That is, a high-pass (HP) adaptor face and low-pass (LP) test face (HP/LP) or a LP adaptor face and HP test face (LP/HP). The data for each condition are compared with the data for each of the other five conditions using an ANOVA with a tukey multiple comparisons test. The q-values for the tukey test are entered below the major diagonal and the corresponding p-values above. Four asterisks denote $p < 0.0001$, three $p < 0.001$, and two $p < 0.01$. The top right hand quadrant of data cells all show significant differences between the aftereffect magnitudes for these pairings of conditions. These pairings represent all of the comparisons between a condition with similar SF content in the adaptor and test and a condition with dissimilar SF content. All other comparisons (similar vs similar and dissimilar vs dissimilar SF content) are not significantly different whatever the pairing of stimulus type (face with oriented mouth for example).

to a local tilt aftereffect can account for the change necessary to allow reliable reporting of the demeanor of a face. This conjectured explanation for face aftereffects makes strong testable predictions. It also predicts some of the controversies currently unresolved in face processing literature. For example, currently under discussion is whether faces are identified by explicit neural templates or by reference to a norm. This dichotomy is prompted by the differing representations of orientation (or spatial scale) and color at a local level (Webster, 2012). Orientation, as we have discussed, is represented by a continuum of orientation channels, while saturation of a color increases monotonically from a neutral gray. The argument is made that similar principles might underlie representations at successive levels of visual processing and, therefore, that we might expect the effects of adaptation to reveal the representation used for a particular visual stimulus. Adaptation within a channel based system might be expected to produce aftereffects that produce repulsion of perceptual representation away from the adaptor whilst adaptation within a norm based system might produce a displacement of the norm. Dickinson et al. (2010), using an adapting face distorted by a sinusoidal modulation of radius, demonstrated that the magnitude of the face distortion aftereffect increases with the amplitude of distortion of the adaptor to a point, and then decreased beyond this amplitude. This might be interpreted as an indication that face morphology is encoded in a channel based fashion. The position of the rollover of the size of the aftereffect with respect to the maximum orientation difference introduced by the distortion of the face, however, was consistent with the maximum in the curve that describes the tilt aftereffect as a function of orientation difference. We suggest, therefore, that face aftereffects that depend upon differences in the morphology of adapting and test faces can often be predicted by a tilt aftereffect field. Certain manipulations of face stimuli have been developed, however, that might not yield to a tilt aftereffect field explanation, for example those manipulating eye height (Susilo et al., 2010). We suggest that other local field explanations such as local spatial scale or aspect ratio adaptation might account for these.

A tilt aftereffect field explanation for shape adaptation, of course, is agnostic to the representation of the higher level properties of the visual stimulus. This is not to say that adaptation does not occur in higher level but that morphological aftereffects are unlikely to be of any value in elucidating the mechanisms of representation of high level stimulus properties, unless aftereffects that are demonstrably not local can be identified. The inheritance of the effects of adaptation in lower levels, though, does offer a potential solution to the vexed question of what purpose the aftereffects serve. Because the mechanisms pertaining to the higher levels of shape analysis are invariant under the effects of adaptation at lower levels, the tilt aftereffect field provides a general mechanism for exaggerating the perceived difference in the higher level stimulus properties of successively presented stimuli. The state of adaptation is shown in this study to be rapidly acquired and large thereby rendering successively experienced facial expressions more perceptually different than they otherwise would be.

Having proposed this model it has to be conceded that this view and methodology is unconventional. Rather than attempting to demonstrate that lower-level aftereffects can account for the change in a higher-level percept following adaptation, conventional studies typically use presumed properties of low-level effects to devise experiments that mitigate these effects. It has been argued that some aftereffects, rather than being retinotopic, are spatiotopic or even position invariant. If the tilt aftereffect is considered to act locally in a retinotopic manner then any systematic aftereffects that were not retinotopic could be assumed to be high-level. Evidence, however, is equivocal. Melcher (2005), for example, claimed that face, form and tilt aftereffects were spatiotopic, while Knapen et al. (2010) reported that the tilt aftereffect was constrained to retinotopic coordinates. These results are, obviously, mutually exclusive. Dickinson et al. (2012b), however, showed that rapidly acquired shape and face aftereffects are retinotopic which may suggest a resolution to this conflict. If the effects of adaptation are accumulated at a point on the retina, as suggested by the results of Blakemore and Over (1974), then the aftereffect experienced at a point in space would be dependent on the history of retinotopic adaptation over eye movements. The experimental paradigm employed by Dickinson et al. (2012b), using an adaptation time of 160 ms, precluded eye movements during adaptation and, therefore, the retinotopic aftereffects revealed might be assumed to indicate that the presumed high-level aftereffects of other experiments, that purported to control for low-level aftereffects, could in fact arise from spatially distributed retinotopic low-level aftereffects accumulated over successive eye movements during adaptation. Other attempts to mitigate low-level effects, for example by introducing a mismatch in size of adaptor and test might be compromised by the same effect. Even in the absence of these accumulation effects the assumption that a spatial mismatch of adaptor and test entirely mitigates low-level effects is erroneous. Local differences in orientation would exist and those differences would be expected to produce tilt aftereffects. The effects would be different to those experienced for spatially matched conditions, and for certain transformations of adaptor and test might not be expected to systematically bias the judgment made (see Dickinson et al., 2010), but they would exist nonetheless. It is often assumed that the local aftereffects are totally eliminated by controls for low-level effects, and that the residual adaptation is, therefore, due to high-level adaptation, but perhaps it is more likely that the controls only reduce the low-level effects.

A novel recent paper exploited the phenomenon of crowding in an effort to dissociate aftereffects of orientation and facial expression (Xu et al., 2012). The stimuli consisted of curved lines, or cartoon faces incorporating the same curved line as a mouth. The curved line either made the cartoon face smile or frown. Adaptation effects were studied both within and across these stimulus types (with the curves retinotopically coincident). It was found that the crowding effect of curves flanking an adapting curve reduced the curvature aftereffect more than the facial expression aftereffect. Conversely, crowding of the adapting face with flanking faces reduced the facial expression aftereffect more than the curvature aftereffect. These effects are indeed consistent with the predicted specificity of crowding at the higher and lower levels of representation of the stimuli, but it is still possible to speculate that the different conditions of crowding might have a differential effect on involuntary eye movements. In conclusion, although there is some evidence to suggest that controls for low-level aftereffects leave some residual aftereffect that might be attributed to high-level adaptation the results of this study demonstrate that under certain circumstances high-level aftereffects can be wholly accounted for by inheritance of low-level aftereffects. We, therefore, advise caution in the presumption of knowledge of the locus of the psychologist's microelectrode when performing adaptation studies.

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Adaptation improves face trustworthiness discrimination

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Adaptation to facial characteristics, such as gender and viewpoint, has been shown to both bias our perception of faces and improve facial discrimination. In this study, we examined whether adapting to two levels of face trustworthiness improved sensitivity around the adapted level. Facial trustworthiness was manipulated by morphing between trustworthy and untrustworthy prototypes, each generated by morphing eight trustworthy and eight untrustworthy faces, respectively. In the first experiment, just-noticeable differences (JNDs) were calculated for an untrustworthy face after participants adapted to an untrustworthy face, a trustworthy face, or did not adapt. In the second experiment, the three conditions were identical, except that JNDs were calculated for a trustworthy face. In the third experiment we examined whether adapting to an untrustworthy male face improved discrimination to an untrustworthy female face. In all experiments, participants completed a two-interval forced-choice (2-IFC) adaptive staircase procedure, in which they judged which face was more untrustworthy. JNDs were derived from a psychometric function fitted to the data. Adaptation improved sensitivity to faces conveying the same level of trustworthiness when compared to no adaptation. When adapting to and discriminating around a different level of face trustworthiness there was no improvement in sensitivity and JNDs were equivalent to those in the no adaptation condition. The improvement in sensitivity was found to occur even when adapting to a face with different gender and identity. These results suggest that adaptation to facial trustworthiness can selectively enhance mechanisms underlying the coding of facial trustworthiness to improve perceptual sensitivity. These findings have implications for the role of our visual experience in the decisions we make about the trustworthiness of other individuals.

Keywords: face adaptation, face trustworthiness, face discrimination, adaptation, psychological, face perception, functional benefit

INTRODUCTION

Prolonged exposure to a visual stimulus can alter the tuning of neurons that encode that stimulus by a process known as adaptation (Barlow and Hill, 1963). A consequence of this process is that the perception of subsequently viewed visual stimuli is biased in the opposite direction to the adaptor. For example, after adapting to a leftward moving grating, subsequently viewed gratings can appear to move in a rightward direction. These perceptual biases, known as aftereffects, have been demonstrated following adaptation to stimuli as diverse as orientation (Gibson and Radner, 1937), speed (Goldstein, 1957), contrast (Ross et al., 1993), spatial frequency (Blakemore and Campbell, 1969), facial configuration (Webster and MacLin, 1999), biological motion (Jordan et al., 2006; Troje et al., 2006), actions (Barraclough et al., 2009), and complex natural scenes (Greene and Oliva, 2010).

Although such biases in perception appear to be maladaptive, adaptation can calibrate the system to the population of stimuli to which it is exposed, making efficient use of a limited neural bandwidth. For example, adapting to a stimulus of constant velocity distorts the speed at which the stimulus is perceived, but increases sensitivity to changes in velocity (Clifford and Langley, 1996). Thus, adaptation allows for increased differential sensitivity at the cost of absolute sensitivity. Being able to detect smaller differences around the adapted level (average input) is clearly advantageous and shows the functional benefit of adaptation. Furthermore, this differential sensitivity increases as a function of adaptation duration, allowing us to detect even smaller differences to stimuli to which we are commonly exposed (Clifford and Langley, 1996).

Improved discrimination following adaptation has been demonstrated for relatively simple stimuli, coded by lower-level visual processing mechanisms, such as motion (Phinney et al., 1997), speed (Clifford and Langley, 1996), and orientation (Clifford et al., 2001). Adaptation to more complex stimuli, like faces, is thought to result from adaptation acting on mechanisms at a high-level in the visual system where faces are represented. Face aftereffects, however, show many similar characteristics to lower-level aftereffects, including a logarithmic build up with exposure to the adapting stimulus and a logarithmic decay over time (Leopold et al., 2005; Rhodes et al., 2007a). Recently a number of studies have examined whether face adaptation can also enhance sensitivity for faces, however, results have been equivocal. Rhodes et al. (2007b) found no improvement in sensitivity to facial identity following adaption to an average face (but see Wilson et al., 2002). Similarly, studies into adaptation on facial gender and ethnicity also failed to find any improvement in sensitivity (Ng et al., 2008). More recently, adaptation to both facial gender (Yang et al., 2011) and face viewpoint (Chen et al., 2010) have been shown to improve sensitivity around the adapted level. In addition, Rhodes et al. (2010) have demonstrated that face adaptation can lower identification thresholds to an adapted race (Asian or Caucasian), a finding that offers insight into the own-race bias.

In this study we tested if adapting to facial trustworthiness can improve trustworthiness discrimination. Trustworthiness is a multi-dimensional judgment and correlates highly with the valence of the face, with happy faces being perceived as trustworthy and angry faces as untrustworthy (Todorov et al., 2008; Sutherland et al., 2013). Adapting to angry or happy faces results in neutral faces being judged as more trustworthy or untrustworthy, respectively (Engell et al., 2010), demonstrating a role of emotion adaptation on facial trustworthiness. Furthermore, adapting to facial trustworthiness has a direct influence on the subsequent perception of facial trustworthiness (Wincenciak et al., 2013). Wincenciak et al. showed that exposure to trustworthy and untrustworthy faces resulted in repulsive aftereffects in female observers, where subsequent test stimuli appeared less like the adapting stimuli. In contrast, trustworthiness adaptation appeared not to bias face perception in male observers. Although this shows the capacity for trustworthiness adaptation to bias perception in female observers, we wanted to examine the potential benefit of improved trustworthiness discrimination following adaptation in both female and male observers.

We examined whether adapting to different levels of facial trustworthiness increases sensitivity around the adapted level. Three experiments were performed. In the first experiment we measured trustworthiness discrimination thresholds for an untrustworthy female face after participants adapted to an untrustworthy female face, a trustworthy female face, or did not adapt. In the second experiment we measured trustworthiness discrimination thresholds to a trustworthy female face, using the same adaptation conditions as in experiment 1. In the third experiment we examined whether adapting to an untrustworthy male face would improve discrimination to an untrustworthy female face. The third experiment was conducted to examine if any improvement in sensitivity transfers across changes in gender and identity as would be expected if an identity-independent representation of trustworthiness is being adapted.

METHODS

PARTICIPANTS

Participants were University of York students and staff. All had normal or corrected to normal vision. Participants gave informed consent and were paid for their participation. Experiments were approved by the ethics committee of the Department of Psychology, University of York, and were performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

Twelve participants took part in experiment 1 (6 female, mean age = 27, $SD = 3.6$). Ten of the participants from experiment 1 took part in experiment 2 (5 female, mean age = 28, $SD = 3.24$). Fifteen participants took part in experiment 3 (6 female, mean age = 29, $SD = 7.9$), 7 of whom had taken part in experiment 1, and 6 of whom had taken part in experiment 2. All participants were naive to the aims of the study, except in experiments 1 and 2 where one of the authors was a participant (B. D. Keefe), and in experiment 3, where two of authors were participants (B. D. Keefe and N. E. Barraclough).

STIMULI

Face stimuli were obtained from The Perception Lab, University of St Andrews. The original set of stimuli included 99 faces (49 male) of Caucasian students, age range 17 to 25, displayed on a white background with a neutral expression, minimal makeup and no jewelry, and were horizontally aligned and scaled to the same interpupillary distance. Each face was rated for trustworthiness using a 7-point Likert scale by independent observers. Untrustworthy and trustworthy face prototypes generated by averaging (Rowland and Perrett, 1995) separately the 8 most untrustworthy and the 8 most trustworthy faces of each sex from the bank of 99 images. To generate female and male faces that varied on the level of trustworthiness that they conveyed, we morphed between each of the two same sex prototypes (Tiddeman et al., 2001). First, for both female and male faces we created caricatures of the untrustworthy face by generating new faces conveying 50% more untrustworthiness than the untrustworthy prototypes. Second, for each gender, we generated a continuum of 101 faces by morphing between the trustworthy prototype and the untrustworthy caricature. Each face stimulus on this continuum (see **Figure 1**) conveys a particular level of untrustworthiness, and this is expressed as the percentage level of the morph.

EXPERIMENTAL PROCEDURES

A PC running Matlab 2010a (The MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) was used to control the experiment, display the stimuli, and record participants responses. Participants sat in a dimly lit room ~57 cm away from a 24 in TFT monitor (Acer GD245HQ, 1920 × 1080 pixels, 100 Hz refresh rate) on which all visual stimuli were presented. We measured trustworthiness-discrimination thresholds (JNDs) using a 2-IFC procedure.

In experiment 1 JNDs were measured for an untrustworthy female face (80) under 3 conditions: after adapting to an untrustworthy female face (80), after adapting to a trustworthy female face (40), or without adaptation. The adaptation procedure is illustrated in **Figure 2**. An initial 40 s of pre-adaptation was followed by a 1 s blank interval. Following the interval two test faces (a standard and a comparison face) were presented for 1 s each, with a 400 ms inter-stimulus interval. The screen then went blank and participants indicated which of the two faces was more untrustworthy using a key press. On all following trials the test faces were preceded by 5 s of top-up adaptation, followed by a blank screen for 100 ms. For the no adaptation condition, participants completed the same 2-IFC procedure without any adaptation. A fixation cross was displayed at the center of the monitor during blank intervals, and participants were required to maintain fixation. The degree of untrustworthiness conveyed by the standard face was always 80 and the degree of untrustworthiness conveyed by the comparison face was varied using adaptive staircase procedures. Participants completed each condition with

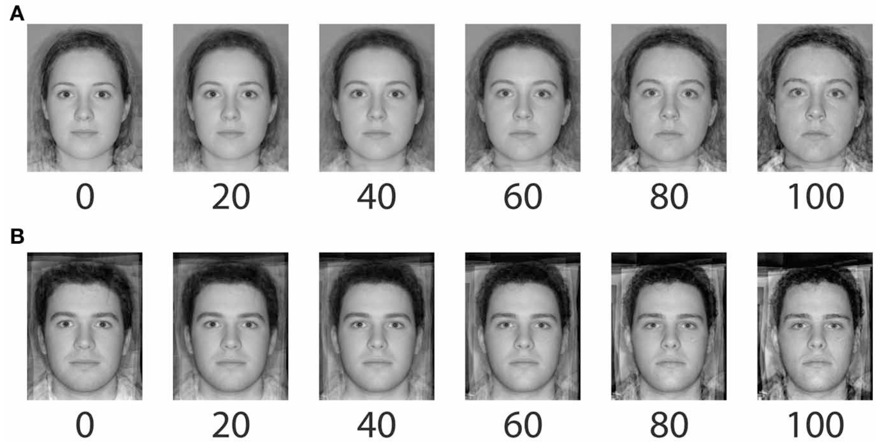

FIGURE 1 | The continua of (un)trustworthy face stimuli shown as a percentage of the morph level. Stimuli were generated by morphing between the trustworthy prototype (illustrated here as the 0 face) and the caricatured untrustworthy prototype (illustrated here as the 100 face). Female faces **(A)**, and male faces **(B)**.

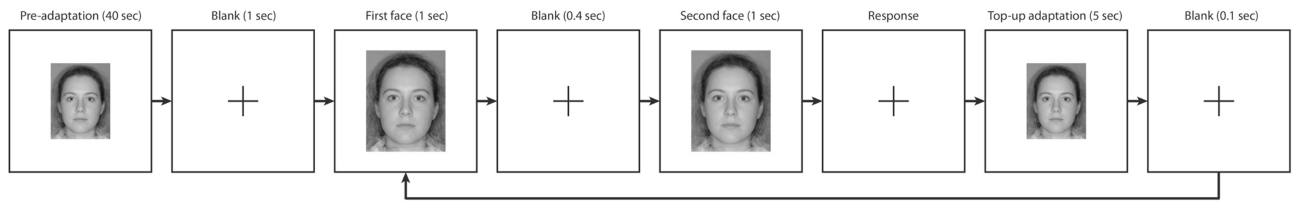

FIGURE 2 | Overview of the experimental procedure.

each of 2 interleaved staircase reversal rules (1-up, 2-down; 2-up, 1-down). We did not determined thresholds from the staircase endpoints; these procedures were used to distribute trials at informative points along the psychometric function, which was fitted using the data from all trials. The step size was initially 8%, and was halved on each of the first 3 reversals. The staircase quit after 14 reversals, typically resulting in ∼45 trials per staircase type (∼90 trials per psychometric function). The order of the standard and comparison within each trial was randomized. Participants adapted to each condition in separate testing blocks with at least 5 min between blocks. The order of testing block was counterbalanced across participants. To avoid local (feature) adaptation, the adapting stimulus was 75% the size of the test stimulus (adapting stimulus subtended $\sim 7.4 \times 9.4°$; test stimulus subtended $\sim 9.9 \times 12.6°$).

In experiment 2, we measured JNDs for a trustworthy female face (40) after participants adapted to a trustworthy female face (40), adapted to an untrustworthy female face (80), or without adaptation. We chose to use the trustworthy female face (40) rather than an even more trustworthy female face (e.g., 20) to ensure that participants were able to perform the discrimination task. People are better at discriminating untrustworthy faces (Oosterhof and Todorov, 2008) therefore by using the trustworthy female face (40) as the standard face, a greater range of comparison trustworthy female faces were available during the adaptive staircase. Otherwise, the experimental procedure was identical to that used in experiment 1.

In experiments 1 and 2 the adapting and test faces were similar on multiple dimensions other than trustworthiness (e.g., identity and gender). Conceivably identity adaptation (Leopold et al., 2001; Rhodes and Jeffery, 2006; Rhodes et al., 2010) could explain any effect of adaptation to our untrustworthy stimuli. In order to rule out this possibility we conducted a third control experiment (Experiment 3) where we examined whether adapting to an untrustworthy male face would improve discrimination of an untrustworthy female face (80).

To account for individual difference in the perception of trustworthiness conveyed by male and female faces, for each participant we matched perceived trustworthiness between the male adaptor face and the female standard test face. Each participant first completed a 2-IFC procedure to measure their point of subjective equality (PSE) between the untrustworthy female face (80) and male faces. A method of constant stimuli was used in which the standard was always an untrustworthy female face (80; see **Figure 1A**). The comparison was always a male face from the male trustworthiness continuum (see **Figure 1B**). Nine male comparison faces ranging from 60 to 100 in 5% steps were used. On each trial the two test faces were presented for 1 s each, separated by a 500 ms inter-stimulus interval. The screen then went blank and participants indicated which of the two

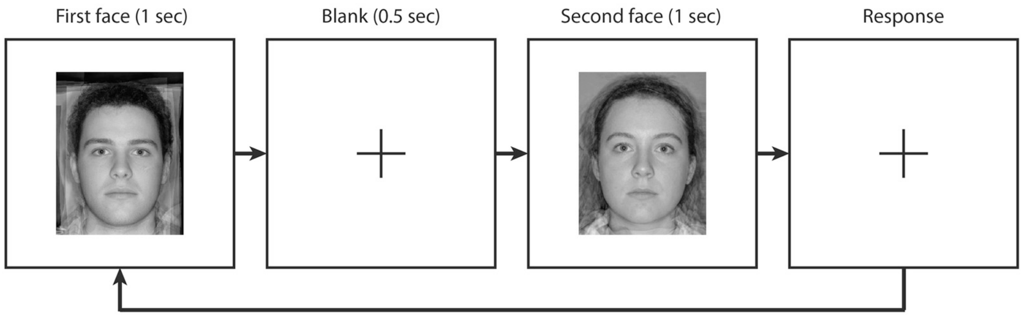

FIGURE 3 | Overview of the experimental procedure used to derive the PSE of the male face in experiment 3.

faces was more untrustworthy using a key press (**Figure 3**). The order of the standard and the comparison was randomized on each trial.

For each participant the psychometric function was fitted to data from 90 trials (10 for each level of the comparison). The PSE was defined as the 50% point of the psychometric function and represents the point at which the male face was perceived with the same level of trustworthiness as the standard female face (80). Each participant's PSE was subsequently used to determine the degree of untrustworthiness conveyed by the male adapting face for each participant.

During the adaptation experiment JNDs were measured under 2 conditions: for an untrustworthy female face (80) following adaptation to an untrustworthy male face (matched for untrustworthiness), and without adaptation. The experimental procedure was identical to that used in experiments one and two.

GENERAL ANALYSIS

For each participant and condition in each of the three adaptation experiments, JNDs were computed by first fitting cumulative Gaussians psychometric functions to the data. We divided the resulting standard deviations by $\sqrt{2}$ to give an estimate of the standard deviation on a single interval [because we used a two-interval experimental procedure; (Green and Swets, 1974)]. The resulting values are JNDs because they indicate the % change in untrustworthiness that can be discriminated at the ~76% level.

RESULTS

EXPERIMENT 1

Experiment 1 measured the effects of adaptation to untrustworthy (80) and trustworthy (40) female faces on discrimination thresholds around an untrustworthy female face (80). Average trustworthiness discrimination thresholds are shown in **Figure 4**. An ANOVA with adaptation condition as a within subjects factor and participant gender a between subjects factor showed a significant main effect of adaptation condition [$F_{(2, 20)} = 6.28, p < 0.01\ \eta_p^2 = 0.39$]. Planned pair-wise comparisons confirmed that JNDs were smaller when adapting to an untrustworthy face compared to either adapting to a trustworthy face ($p < 0.05$), or no adaptation ($p < 0.05$). The JNDs in the no adaptation and trustworthy adaptation conditions were equivalent ($p < 0.05$). A significant main effect of participant gender [$F_{(1, 10)} = 15.96$, $p < 0.01\ \eta_p^2 = 0.62$] was observed as female participants had lower discrimination thresholds (M = 3.1, SD = 1.1) than males (M = 5.3, SD = 2.0). There was no significant interaction between adaptation condition and participant gender [$F_{(2, 20)} = 2.52, p > 0.05, \eta_p^2 = 0.20$].

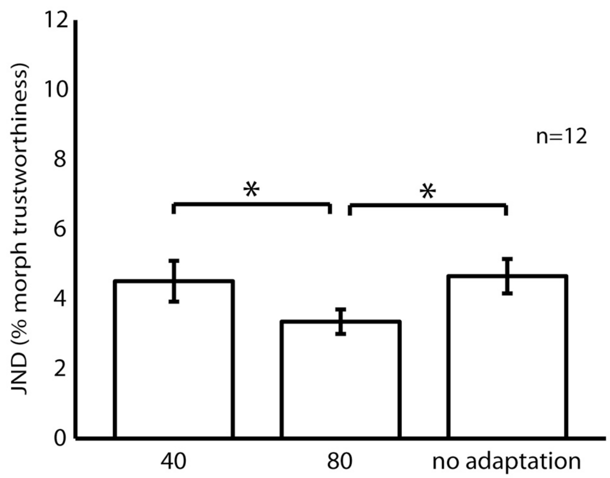

FIGURE 4 | Trustworthiness discrimination thresholds for an untrustworthy female face (80) following adaptation to a trustworthy female face (40), an untrustworthy female face (80), and no adaptation. Error bars denote ± SEM. Asterisk denote a significant difference between conditions (*$p < 0.05$).

EXPERIMENT 2

Experiment 2 measured the effects of adaptation to untrustworthy (80) and trustworthy (40) female faces on discrimination thresholds for a trustworthy female face (40). **Figure 5** shows the trustworthiness discrimination thresholds. As with experiment 1 we analysed discrimination thresholds with ANOVA, and found a significant main effect of adaptation condition [$F_{(2, 16)} = 11.80$, $p < 0.01\ \eta_p^2 = 0.60$]. Planned pair-wise comparisons confirmed that JNDs were smaller when adapting to a trustworthy face, compared to either adapting to an untrustworthy face ($p < 0.001$), or no adaptation ($p < 0.05$). JNDs did not differ significantly

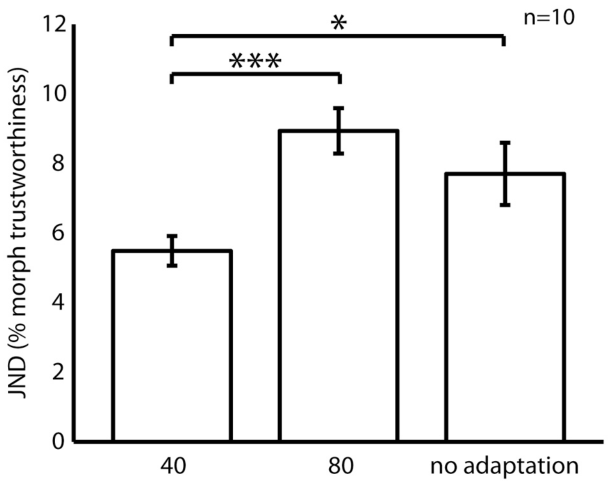

FIGURE 5 | Trustworthiness discrimination thresholds for a trustworthy female face (40) following adaptation to a trustworthy female face (40), an untrustworthy female face (80), and no adaptation. Error bars denote ± SEM. Asterisk denote a significant difference between conditions (*$p < 0.05$; ***$p < 0.001$).

between the untrustworthy and no adaptation conditions ($p > 0.05$). No effect of participant gender [female, $M = 6.98$, $SD = 2.0$; male, $M = 7.78$, $SD = 4.7$; $F_{(1,\ 8)} = 0.49$, $p > 0.05$ $\eta_p^2 = 0.06$], or interaction between participant gender and adaptation condition [$F_{(2,\ 16)} = 0.67$, $p > 0.05$ $\eta_p^2 = 0.08$] was observed.

EXPERIMENT 3

Experiment 3 examined the effects of adapting to an untrustworthy male face on discrimination thresholds for an untrustworthy female face (80). For each participant the male adaptor face was matched on untrustworthiness ($M = 80$, $SD = 5.7$) to the female standard face (80). Following adaptation to the untrustworthy male face discrimination thresholds for the female untrustworthy face were significantly lower ($M = 4.16$, $SD = 1.38$) compared to the no adaptation condition [$M = 4.93$, $SD = 1.81$; one-tailed t-test, $t_{(14)} = 1.88$, $p < 0.05$]. The reduction in face discrimination thresholds seen when the adapting stimulus gender and identity were different from the test faces (Experiment 3) was 65% of the size of the reduction in discrimination thresholds seen when the adapting stimulus gender and identity were the same as the test faces (Experiment 1). The improvement in face trustworthiness discrimination with adaptation was reduced, but still present when the adapting face was a different identity and gender.

DISCUSSION

Here we show that adaptation to an untrustworthy or a trustworthy face results in a selective improvement in discrimination thresholds for facial trustworthiness. Adaptation to an untrustworthy face, but not adaptation to a trustworthy face, improves discrimination of untrustworthy faces. Conversely, adaptation to a trustworthy face, but not adaptation to an untrustworthy face, improves the discrimination of trustworthy faces. This selective enhancement of face perception occurs even when the adapting face has a different gender and identity to the subsequent test faces.

Previous studies have indicated that visual adaptation to facial emotion (Engell et al., 2010) and facial trustworthiness (Wincenciak et al., 2013) can bias the perception of facial trustworthiness. We show here, as for low-level stimuli (cf. Clifford and Langley, 1996) that high-level adaptation to facial trustworthiness can have a functional benefit. Exposure to a specific degree of face trustworthiness benefits subsequent perception of similar faces. These improvements in the ability to discriminate the trustworthiness of faces are likely to result from a temporary, but selective, enhancement of the sensitivity of the system underlying the perception of these stimuli.

The improvements in face trustworthiness discrimination are small, but significant and comparable to those found for face gender (Yang et al., 2011) and face orientation adaptation (Chen et al., 2010). The small improvements in sensitivity that we see occurred over a relatively short period (~40 s). As increases in sensitivity are proportional to the length of adaptation, we would expect to see greater improvements in face trustworthiness discrimination over longer periods as might be expected under real world viewing conditions (Clifford and Langley, 1996). Indeed, it has been suggested that prolonged exposure to specific face types may contribute to the "own-race bias," the ability to better detect differences between individuals of our own race than those of another (Rhodes et al., 2010).

These other previously observed improvements in face discrimination (i.e., identity and gender adaptation) cannot fully explain the effects we observe in this study; although they may have contributed somewhat to the decrease in discrimination thresholds during experiments 1 and 2. However, during experiment 3 participants adapted to a face with a different identity and gender to the test stimuli. Still, we observed a beneficial effect of adaptation to an untrustworthy face on the discrimination of subsequent untrustworthy faces. It is likely, therefore, that a selective enhancement of specific mechanisms underlying the perception of facial untrustworthiness is responsible in part for the effects we observe. These mechanisms thus appear to be independent to both face gender and identity, complementing previous research indicating that (un)trustworthy aftereffects resulting from exposure to one identity face can bias perception of (un)trustworthiness in another identity face (Wincenciak et al., 2013).

It is not entirely clear what mechanism might underlie the greater improvement in (un)untrustworthy face discrimination observed when adapting and test faces have the same gender and identity (Experiments 1 and 2). One possibility is that the perception of face (un)trustworthiness relies on both identity-dependent and identity-independent mechanisms. The results we observed during experiments 1 and 2 might result from the enhanced effect of the simultaneous adaptation of both of these mechanisms. Similarly, Fox and Barton (2007) have shown, using an adaptation paradigm that face expression aftereffects transfer both within and across face identity, arguing for both an identity-dependent and an identity-independent representation of facial expression. Fox and Barton's expression aftereffects are larger when adapting and test face have the same identity, presumably resulting from the adaptation of both identity-dependent and identity-independent representations of facial expression.

An alternate explanation is that the greater improvement in (un)trustworthy face discrimination observed in experiments 1 and 2 results from a simultaneous beneficial influence of gender (Yang et al., 2011) and/or identity (Rhodes et al., 2010) face adaptation. The task of the participants was to explicitly discriminate the degree of untrustworthiness conveyed by the 2 test faces, but we cannot rule out the influence of other factors on this judgment. Facial trustworthiness judgments correlate highly with the emotional valence of faces and can be viewed as an overgeneralization of emotion. Happy people who are more likely to help us and can be approached are viewed as more trustworthy than angry people, who may want to harm us and should be avoided (Oosterhof and Todorov, 2008; Sutherland et al., 2013). Had participants judged which of the test faces was more happy, instead of which was more untrustworthy, we may have found similar results. We have not tested this possibility in the current study because such a finding would not change the interpretation of the results. Adaptation to the perceived valence of the face and other attributes, such as attractiveness that correlate with trustworthiness, are adaptation to trustworthiness, by virtue of the multi-dimensional judgment of this trait.

Female observers were better at discriminating untrustworthy faces, but not trustworthy faces, compared to male observers. This difference in ability might arise as females may pay more attention to these stimuli than males. Previous research has also indicated that there may be a difference in the way that female and male observers process facial (un)trustworthiness. Dzhelyova et al. (2012), during an event related potential (ERP) study of the perception of untrustworthy and trustworthy faces, showed that female observers were more accurate in the perception of facial trustworthiness than male observers. Furthermore, Wincenciak et al. (2013) found that only female observers showed typical repulsive aftereffects, where test stimuli looked *less* like the adapting stimuli, following adaptation to trustworthy and untrustworthy faces. We found no interaction between the gender of the participant and the adapting condition in either experiment 1 or 2. Therefore, the beneficial effect of facial (un)trustworthy adaptation was no different in female and male observers. Such a functional benefit in male observers is interesting given that other research has demonstrated the absence of typical repulsive aftereffects in males (Wincenciak et al., 2013), suggesting adaptation improves, but does not bias, perception of facial (un)trustworthiness in male observers. In future work it would be interesting to examine whether male and female observers show this functional benefit when adapting to and discriminating male facial (un)trustworthiness.

In conclusion, we have shown that adapting to facial (un)trustworthiness can calibrate our visual system, selectively increasing sensitivity, thereby allowing us to detect smaller changes in facial trustworthiness. This process appears to be relatively fast acting, occurring even after exposure to a face for ∼1 min. Longer term exposure to faces conveying specific levels of untrustworthiness that might occur with either a specific job (e.g., Police) or from living with particular individuals may confer more pronounced functional and social benefits. Improvements in face discrimination may enhance discrimination between who we should invest in and who we might best avoid (Oosterhof and Todorov, 2008; Sutherland et al., 2013).

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Bodies adapt orientation-independent face representations

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Faces and bodies share a great number of semantic attributes, such as gender, emotional expressiveness, and identity. Recent studies demonstrate that bodies can activate and modulate face perception. However, the nature of the face representation that is activated by bodies remains unknown. In particular, face and body representations have previously been shown to have a degree of orientation specificity. Here we use body-face adaptation aftereffects to test whether bodies activate face representations in an orientation-dependent manner. Specifically, we used a two-by-two design to examine the magnitude of the body-face aftereffect using upright and inverted body adaptors and upright and inverted face targets. All four conditions showed significant body-face adaptation. We found neither a main effect of body orientation nor an interaction between body and face orientation. There was a main effect of target face orientation, with inverted target faces showing larger aftereffects than upright target faces, consistent with traditional face-face adaptation. Taken together, these results suggest that bodies adapt and activate a relatively orientation-independent representation of faces.

Keywords: face perception, body perception, perceptual adaptation, face inversion effect, body-face interaction, face adaptation, aftereffects, body inversion

INTRODUCTION

Faces and bodies provide a wealth of salient information that helps us navigate our social worlds and we employ specialized mechanisms to recognize and process these stimuli. Faces and bodies share useful properties: they co-occur at a high frequency and convey similar information about age, gender, and identity. Thus, information derived from the face and body can provide significant context to aid social perception. Recent studies demonstrate that perceptual representations of faces can be activated and modulated by viewing bodies without visible faces (Peelen and Downing, 2007; Brandman and Yovel, 2010; Ghuman et al., 2010; Brandman and Yovel, 2012; Schmalzl et al., 2012). However, little is known regarding the nature of the face representation activated by bodies. Here we use a recently described body-face adaptation aftereffect (Ghuman et al., 2010) to examine whether bodies activate faces according to the orientation of the body or in an orientation-independent manner.

Perceptual adaptation has been called the "psychologists' microelectrode" for its utility in carefully probing the nature of how stimuli are represented in the brain (Frisby, 1979). Perceptual adaptation is the process through which extended viewing of a stimulus produces an opposing aftereffect, such that a feature is more likely to be perceived as the opposite of that seen in the adapting stimulus. For instance, after viewing a line tilted to the right for several seconds, a vertical line is more likely to be perceived as tilting to the left (Gibson and Radner, 1937). When a stimulus is viewed for an extended period of time, the prolonged activation of neurons tuned to the properties of that stimulus elicits an adjustment of their response properties. This recalibration of the neurons' tuning is thought to underlie the measured perceptual adaptation aftereffects (Leopold et al., 2001; Clifford et al., 2007; Webster and MacLeod, 2011).

Perceptual adaptation has been reliably demonstrated to occur for a variety of visual properties, from basic aspects such as form and motion to higher-level qualities such as face identity (Leopold et al., 2001), gender (Webster et al., 2004), and expression (Fox and Barton, 2007). For instance, adapting to a male face results in an opposing aftereffect whereby subsequently viewed gender-neutral faces appear more feminine (Webster et al., 2004). Such effects are interpreted to reflect changes in the norm-based representation of the visual features and spatial relationships of faces, known as the "face space" (Leopold et al., 2001; Webster and MacLeod, 2011), which is used to determine face gender, identity, and expression. We have previously investigated how the "face space" is modulated by viewing bodies, finding that adapting to bodies without visible heads induced aftereffects of subsequently viewed faces (Ghuman et al., 2010). This cross-category, body-face adaptation suggests a tight coupling of these representations, such that the bodies alone can activate the network underlying face perception.

Cross-category face adaptation has primarily been shown for face identity aftereffects. For instance, Hills et al. (2010) established that face identity aftereffects can be produced by voices and identity-specific semantic information. However, Ryu et al. (2008) suggest that perceived or imagined faces can elicit face identity aftereffects. This complicates the interpretation of other examples of cross-modal face identity adaptation, because it is difficult to rule out the possibility that explicit face imagery could be causing the adaptation. The cross-modal gender adaptation addresses this possibility by reducing specific identity representations that might prompt mental imagery. Other than the body-to-face aftereffect (Ghuman et al., 2010), generally studies of gender adaptation have failed to find cross-modal adaptation. In particular, gender-specific voices do not adapt face perception (Kloth et al., 2010), nor do male and female hands (Kovacs et al., 2006) or gender-specific objects (male and female shoes, lipstick, etc.; Ghuman et al., 2010). These results suggest that the tight, intrinsic conceptual relationship between bodies and faces is what allows for cross-modal perceptual adaptation.

The face inversion effect, wherein accuracy of recognition is reduced and reaction time is slowed when faces are viewed upside down as compared to upright (Yin, 1969; Haxby et al., 1999; Rossion and Gauthier, 2002), is a hallmark of face perception. The face inversion effect is disproportionate in comparison to the physical change in the configuration of the stimulus properties and in comparison to other objects commonly encountered only in the upright orientation (Rossion and Gauthier, 2002). Recent studies suggest that bodies also display a behavioral inversion effect (Reed et al., 2003) analogous to that observed for faces, and the body inversion effect may require the presence of a head and may be mediated by face-selective mechanisms (Brandman and Yovel, 2010). These findings suggest that specialized mechanisms exist in the brain to process upright faces and potentially upright bodies.

Face–face adaptation also shows a degree of orientation dependence. Specifically, gender face adaptation is greater when the orientation of the faces is aligned compared to when the faces are in opposing orientations [i.e., adaptation aftereffects of upright faces (↑F) to ↑F are greater than inverted faces (↓F) to ↑F and aftereffects of ↓F to ↓F are greater than ↑F to ↓F; Rhodes et al. (2004), Watson and Clifford (2006), the full pattern of results is ↓F to ↓F > ↑F to ↓F = ↑F to ↑F > ↓F to ↑F]. Face identity and viewpoint adaptation display a relatively similar pattern of adaptation with regards to inversion, with some quantitative distinctions (Fang et al., 2007; Rhodes et al., 2009; Hills and Lewis, 2012). However, face gender adaptation is reduced, not abolished, when the adaptor and target faces are of opposite orientation (Rhodes et al., 2004; Watson and Clifford, 2006). These results suggest that there are both orientation-dependent and orientation-independent face representations and that face aftereffects reflect adaptation of both.

In the present study, we use these findings as a basis for examining the orientation specificity of the face representations activated and adapted by bodies. Specifically, we compare the magnitude of the body-face adaptation aftereffect for upright bodies (↑B) to ↑F, ↑B to ↓F, inverted bodies (↓B) to ↑F and ↓B to ↓F. We use this paradigm to test between two potential hypotheses: (1) Bodies activate face representations according to the orientation of the body. If this alternative were true, then we would expect the aftereffects for ↑B to ↑F to be greater than ↓B to ↑F and for ↓B to ↓F to be greater than ↑B to ↓F, analogous to face–face adaptation as discussed above (Rhodes et al., 2004; Watson and Clifford, 2006). (2) Bodies activate orientation-independent face representations. If this alternative were true, then we would expect the aftereffects for ↑B to ↑F to be similar to ↓B to ↑F and for ↓B to ↓F to be similar to ↑B to ↓F.

To test between these hypotheses, we conducted two experiments. In Experiment 1 we examined the orientation dependence of each process by testing the transfer of body-face adaptation between upright and inverted stimuli. The bodies used in this experiment were shown from the neck down, with no visible heads (**Figure 1A**). Some evidence suggests that the body inversion effect is preserved for bodies with their faces obscured but abolished for bodies without heads (Yovel et al., 2010). Thus, orientation dependence or independence may require the presence of a faceless head. To further explore the role of the presence or absence of a head in body-face interactions, our second experiment replicated the first but involved bodies with obscured faces rather than bodies without heads (**Figure 1B**).

MATERIALS AND METHODS

SUBJECTS

A total of 52 individuals participated in this study. After exclusion due to an inability to distinguish the target faces (responding that the faces came from a single gender on more than 85% of all trials, making it unclear if these subjects were complying with the instructions), there were 25 subjects in Experiment 1 and 21 subjects in Experiment 2. Ages ranged from 18 to 49. All subjects were naïve to the goals of the study. The Institutional Review Board of the University of Pittsburgh approved all procedures and written informed consent was obtained for all subjects.

STIMULI

Target face stimuli for all experiments were constructed from photographs of 6 male and 6 female frontal-view faces with neutral expressions from the Karolinska Directed Emotional Faces (KDEF; Lundqvist et al., 1998) stimulus set. For each of the 6 male and female face pairs from the KDEF set, male-to-female face morphs were constructed (**Figure 1E**) using Morpheus Photo Morpher™. Each face image was cropped with a uniform oval that removed all non-facial features. The 10, 30, 40, 50, 60, 70, and 90% morphs were used in these experiments. Adapting body stimuli consisted of photographs of 20 male and 20 female bodies in each experiment. Face pictures in both experiments and body pictures in Experiment 1 were the same as in Ghuman et al. (2010); body pictures in Experiment 2 were collected from the Internet. Adobe Photoshop was used to convert all body and face images to grayscale and to resize the images to best fill a gray square subtending approximately 6.5° of visual angle. Stimuli were presented in the middle of the screen.

PROCEDURE

The adaptation paradigm was adjusted from Ghuman et al. (2010). For both experiments, each adaptation trial began with subjects viewing an adaptation image [a male or female body, upright or inverted, with (Experiment 1) or without (Experiment 2) a head] for 5 s. Following adaptation, a target face (upright or inverted) was presented for 200 ms followed by a 2000 ms fixation cross in the center of the screen (**Figure 1C**). Subjects made a two-alternative forced-choice response to classify the face gender as quickly and accurately as possible.

Experiment 1 used images of bodies cropped to remove the head (**Figure 1A**) as adapting stimuli and male-to-female face morphs as target stimuli. The experiment was divided into four blocks consisting of 78 trials each, with the face and body images' orientations held constant within each block, and faces were

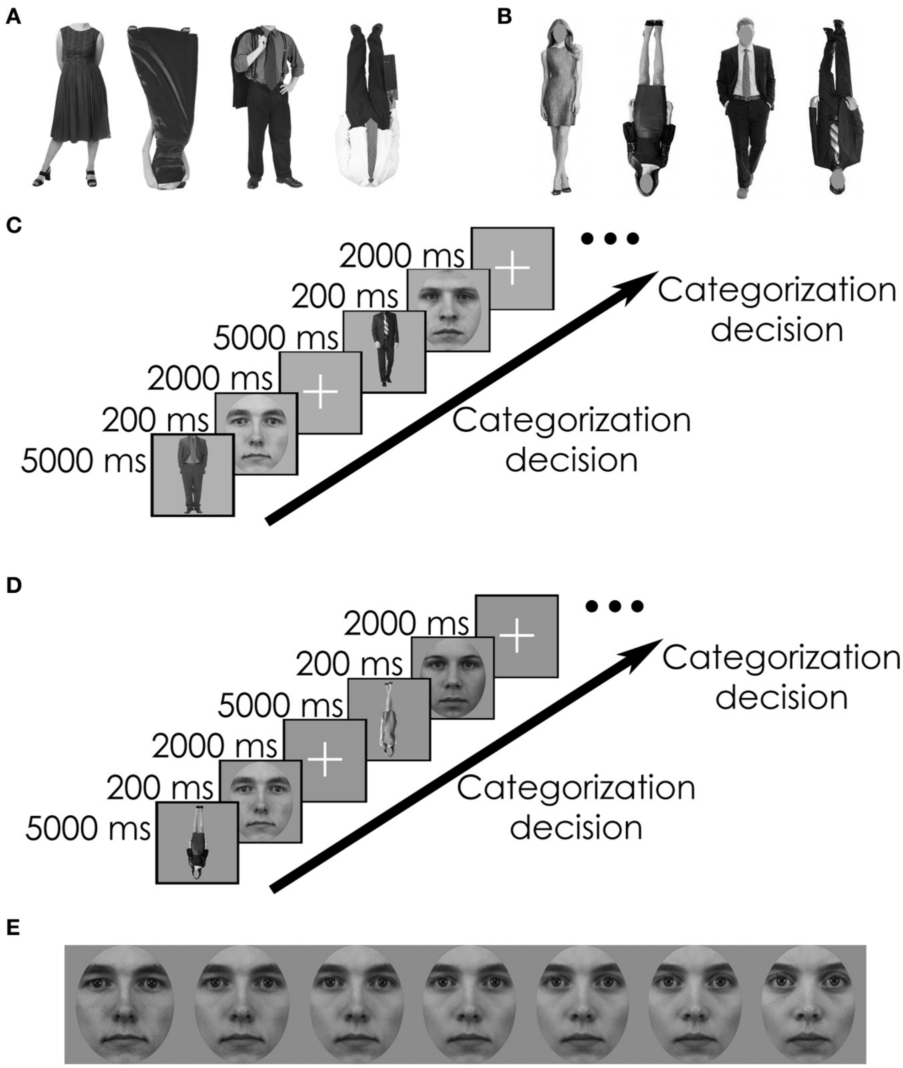

FIGURE 1 | Examples of stimuli and paradigm. (A) Gender-specific bodies from the neck down (Experiment 1). **(B)** Gender-specific bodies with faceless heads (Experiment 2). **(C)** Examples of adaptation trial sequences, adjusted from Ghuman et al. (2010) for both experiments. Each trial consisted of an adapting body [male or female, upright or inverted, with (Experiment 1) or without (Experiment 2) head] for 5000 ms. This was followed by a target face (upright or inverted) for 200 ms. Subjects were asked to make a decision about the gender of the face during the presentation of the fixation cross (2000 ms). **(D)** Examples of adaptation trial sequences using inverted adapting body images. Some trials also included inverted faces. **(E)** Examples of 10, 30, 40, 50, 60, 70, and 90% male-to-female face morphs (target stimuli for both experiments).

never repeated within a block. These blocks were presented in a pseudorandom order, counterbalanced across subjects, so each participant would eventually see every combination of orientations of bodies and faces: upright bodies (↑B) to upright faces (↑F), ↑B to ↓F, ↓B to ↑F, or ↓B to ↓F. Within each block, gender of the body stimuli was also varied pseudorandomly, such that the first half of each block showed bodies of one gender and the second half showed bodies of the other gender. The two halves of each block were separated by a 1-min break. Experiment 2 was identical in structure to Experiment 1, but the adapting body stimuli used here included heads with obscured faces **Figures 1B,D**. In both experiments, the order of the four conditions was counterbalanced across participants.

ANALYSIS

Aftereffect magnitude was defined as the percent of faces endorsed as male following adaptation to female bodies minus the percent of faces endorsed as male following adaptation to male bodies. Only face morph levels where subjects gave a particular response less than 80% of the time, averaged across participants and studies, were used to determine aftereffect magnitude and standard error. This is because aftereffects are known to be minimal for unambiguous stimuli. In practice, this meant that the 90 and 10% face morphs were excluded from analysis of aftereffect magnitude. Had these data been included, all significance determinations would have remained unchanged, but the aftereffect magnitude would have been reduced somewhat. The 30, 40, 50, 60, and 70% face morph levels were used for ANOVAs, *F*-tests and *p*-values, analyzed using MATLAB™ and SPSS™. ANOVAs were three-factor tests with two within-subjects factors ("Face" and "Body") and one between-subjects factor ("Headedness"). The two within-subjects factors were the orientation of the adaptor body and the orientation of the target face, and the between-subjects factor was the presence (or absence) of a head on the body adaptor. The independent variable was the percent endorsed as male in the face categorization decision. In addition, *T*-tests were performed to examine the significance of each of the four within-subject conditions (i.e., orientation of body adaptor and face target).

RESULTS

Consistent with our previous study (Ghuman et al., 2010), we found that adaptation to a body biased the perception of the gender of the target face in the opposite direction [mean aftereffect across all conditions = 8.9%, $t_{(45)} = 4.838$, $p < 0.001$]. The 2 × 2 × 2 (Face × Body × Headedness) ANOVA revealed no significant main effect of body orientation on aftereffect magnitude [mean aftereffect with upright body = 9.5%, inverted body = 7.2%, $F_{(1, 176)} = 1.403$, $p = 0.238$], and no face x body interaction [$F_{(1, 176)} = 0.057$, $p = 0.811$]. These results suggest that the orientation of the body adaptor does not matter, nor does it interact with the orientation of the face target.

The analysis did reveal a significant main effect of face orientation [mean aftereffect with upright face = 5.8%, inverted face = 10.9%, $F_{(1, 176)} = 8.276$, $p = 0.005$]. These results are consistent with previous reports suggesting that face gender adaptation is larger for inverted target faces than for upright target faces (Rhodes et al., 2004; Watson and Clifford, 2006).

Comparing Experiments 1 and 2, we found no main effect of the presence of a head on aftereffect magnitude [**Figure 2**; mean aftereffect with head = 9.3%, without head = 8.8%, $F_{(1, 176)} = 1.057$, $p = 0.305$]. Additionally, there were no interactions of face × headedness [$F_{(1, 176)} = 0.970$, $p = 0.326$], body × headedness [$F_{(1, 176)} = 0.954$, $p = 0.330$], or face × body × headedness [$F_{(1, 176)} = 0.013$, $p = 0.909$]. These results indicate that adaptation to bodies with faceless heads and to bodies without heads are similar.

We then examined the results of the four inversion combinations (↑B to ↑F, ↑B to ↓F, ↓B to ↑F, ↓B to ↓F), shown in **Figure 3A** collapsed across Experiments 1 and 2 due to the lack of significance of headedness on the adaptation effects (see **Figure 3B** for the data from Experiments 1 and 2 separated out). The magnitude of the aftereffect was 6.7% in the ↑B to ↑F condition [$t_{(45)} = 4.850$; $p < 0.001$], 4.8% in the ↓B to ↑F condition [$t_{(45)} = 3.055$; $p = 0.004$], 12.3% in the ↑B to ↓F condition [$t_{(45)} = 6.146$; $p < 0.001$], and 9.5% in the ↓B to ↓F condition [$t_{(45)} = 4.249$; $p < 0.001$].

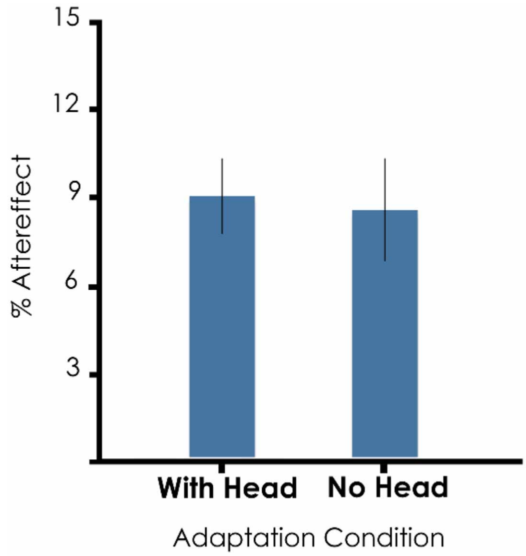

FIGURE 2 | Aftereffect magnitude across experiments. Mean and standard error of aftereffects comparing Experiments 1 and 2. The overall mean aftereffect magnitude was 8.9%, calculated as 9.3% for adapting bodies with heads and 8.8% for bodies without heads.

DISCUSSION

The main objective of this study was to investigate the orientation specificity of the face representations activated by bodies. The aftereffect magnitude for ↑B to ↑F was similar to ↓B to ↑F and ↓B to ↓F was similar to ↑B to ↓F. Therefore, these results support the hypothesis that bodies activate orientation-independent face representations. In addition, we also examined the role of inversion in body-face adaptation when the bodies had heads because the results of previous studies suggest that the presence of a head (with the face occluded) is important to face-body interactions and particularly body inversion (Cox et al., 2004; Brandman and Yovel, 2010; Yovel et al., 2010; Brandman and Yovel, 2012). In this case, we found no significant difference in aftereffect magnitude when comparing the results of the two experiments with regard to the presence of a head. Additionally, we did find a main effect of the orientation of the face, such that larger aftereffects were seen for inverted face targets. This result is in line with previous face–face gender adaptation studies (Rhodes et al., 2004; Watson and Clifford, 2006). Finally, we examined each of the individual conditions and found significant aftereffects in all four body and face orientation conditions. Overall, our results replicate previous reports of body-face adaptation (Ghuman et al., 2010) and extend them by suggesting that bodies activate faces in a relatively orientation-independent manner.

Previous studies suggest that upright and inverted faces are encoded by different populations of neurons(e.g., Watson and Clifford, 2006). Several electrophysiological single-unit studies support this assertion, showing neurons responding differently to upright and inverted cartoon faces (Friewald et al., 2009) and whole bodies (Ashbridge et al., 2000). Based on the result that the perception of individual facial features is invariant to inversion (Searcy and Bartlett, 1996; Leder and Bruce, 1998; Freire et al., 2000), one possibility is neuronal populations that encode these features are broadly tuned with respect to orientation, while neurons that encode holistic properties of faces are more narrowly tuned to upright faces (see Maurer et al., 2002; Watson and Clifford, 2006). From this standpoint, the present results would suggest that bodies primarily activate

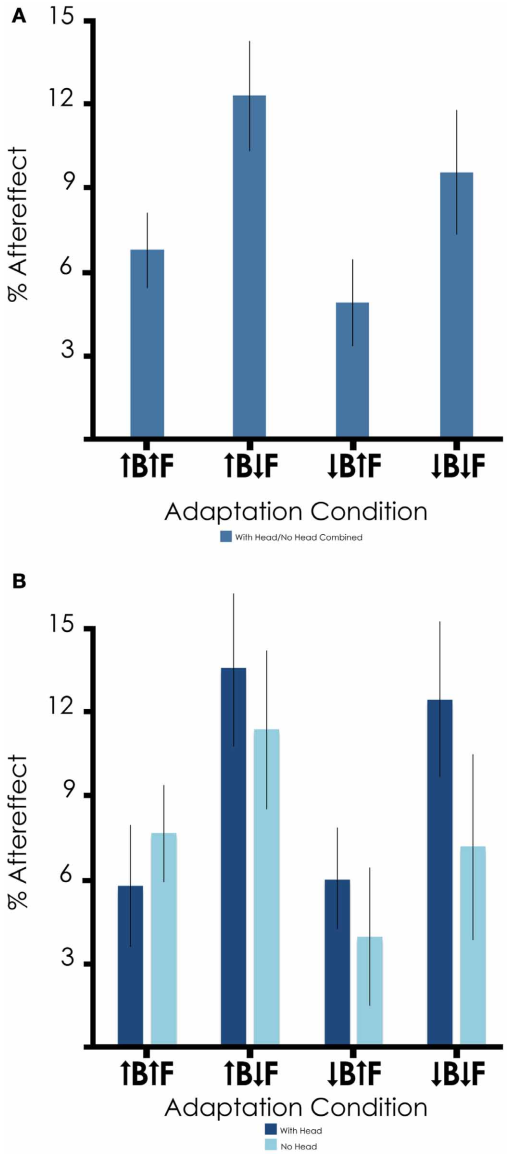

FIGURE 3 | Summary of aftereffect magnitude across adaptation conditions. (A) Results are collapsed across Experiments 1 and 2 due to the lack of significance of headedness on the adaptation effects. Aftereffect magnitudes by condition were 6.7% for ↑B to ↑F, 12.3% for ↑B to ↓F, 4.8% for ↓B to ↑F, and 9.5% for ↓B to ↓F, with overall mean aftereffect 8.9%. **(B)** Results from Experiment 1 (with head) and Experiment 2 (no head) shown separately for comparison.

the orientation-independent representations of individual facial features rather than the orientation-dependent holistic representations. Another hypothesis is that, in addition to neuronal populations tuned to facial features that are inversion-invariant, there are neuronal populations tuned to holistic representations of faces that have two different types of orientation tuning. Specifically, there is a population of narrowly tuned neurons responding to upright faces and a population of broadly tuned neurons responding to upright and inverted faces (Sekuler et al., 2004; Watson and Clifford, 2006). From this perspective, our results would indicate that bodies are primarily activating the broadly tuned, orientation-independent neurons encoding holistic aspects of faces.

Two neural regions that are sensitive to static aspects of faces (as opposed to dynamic properties, such as expression and gaze direction) are potential neural loci for body-face adaptation. The first is the occipital face area (OFA), which is primarily selective for individual facial features (Kanwisher et al., 1997; Liu et al., 2010) and responds similarly to upright and inverted faces (Yovel and Kanwisher, 2005; Pitcher et al., 2011). Neuroimaging studies indicate that the OFA and the extrastriate body area (EBA), which is sensitive to body parts (Urgesi et al., 2004; Chan et al., 2010), both respond more strongly to the presence of both a face and a body than to the presence of a face or body alone (Schmalzl et al., 2012). Thus, they may play a role in combining face and body information. While it would be surprising if bodies activated face information at the level of individual features (e.g., more masculine or feminine facial features) rather than at the level of holistic face representations, the relative orientation invariance of the OFA representation makes this possibility consistent with the current data. A second potential neural locus for body-face adaptation is the fusiform face area (FFA), which has orientation-dependent face representations (Yovel and Kanwisher, 2005) and is influenced by lower-level features and configurations (Chan et al., 2010; Yue et al., 2011) as well as more holistic qualities of faces (Liu et al., 2010; Schiltz et al., 2010; Nestor et al., 2011). The close proximity of the FFA to body-selective regions in the fusiform (Peelen and Downing, 2005; Schwarzlose et al., 2005) along with the superadditive response of face and body information in the fusiform (Schmalzl et al., 2012) support the possibility that this area is a neural basis of face-body adaptation. However, the sensitivity of the fusiform gyrus to inversion of faces and bodies (Yovel and Kanwisher, 2005; Brandman and Yovel, 2010) make this hypothesis unlikely. Indeed, the FFA does not seem to be sensitive to high-level aspects of faces, such as identity (Kriegeskorte et al., 2007; Nestor et al., 2011).

Another potential neural locus for body-face adaptation is body-sensitive neural regions. A recent study suggests that the body inversion effect is mediated by face-specific, rather than body-related, mechanisms (Brandman and Yovel, 2010). Specifically, they found that the FFA was sensitive to body inversion, but the extrastriate body area (EBA) was not. Furthermore, the FFA was only sensitive to body inversion when the body included a visible head (with the face occluded), while the EBA was relatively insensitive to the presence or absence of a visible head. Here we demonstrate that body-face adaptation is not sensitive to body inversion and is not sensitive to the presence or absence of a head, paralleling the neural sensitivity of the EBA. This suggests that body-face adaptation may be governed by body-related processing, potentially in the EBA. A recent study demonstrated that the EBA shows a significant ability to discriminate faces (Chan et al., 2010), suggesting that the EBA may represent some face properties. Thus, one potential hypothesis is that bodies adapt face information in the EBA.

A third hypothesis is that neural regions sensitive to joint body-face properties ("person representations") mediate body-face adaptation. One potential neural locus for person representations and body-face adaptation is the anterior temporal face patch (AT), as it appears important for face individuation and identification (Kriegeskorte et al., 2007; Nestor et al., 2011), responds to whole faces (Nasr and Tootell, 2012), and shows some sensitivity to bodies as well as faces (Pinsk et al., 2009). The orientation sensitivity of AT is difficult to determine as it is downstream of the FFA, and reports of reduced activity in AT for inverted relative to upright faces (Nasr and Tootell, 2012) could be due to the upstream orientation dependence of the FFA rather than orientation sensitivity in AT *per se*. But the evidence that suggests AT is critical for the representation of high-level face information (Kriegeskorte et al., 2007; Nestor et al., 2011) supports the possibility of AT being an important neural locus of face-body adaptation, potentially encoding whole person representations rather than simply face representations. In addition, studies indicate that emotional information from bodies and faces have somewhat overlapping representation (Hadjikhani and de Gelder, 2003; Meeren et al., 2005; Peelen et al., 2010), further emphasizing the relatedness of these representations. If either neural regions sensitive to body or joint body-face properties did underlie body-face adaptation, this would suggest that the cells tuned to this information are involved in the neural representation of the norm-based perceptual face space (Leopold et al., 2001; Webster and MacLeod, 2011).

We found no significant difference between adaptation to bodies with faceless heads and bodies without heads. Previous studies have shown that the presence of a head shape is necessary for many body-face interactions. For example, the body inversion effect has been shown to depend on the presence of a head (Minnebusch et al., 2009; Yovel et al., 2010), the face inversion effect can be induced using bodies with faceless heads (Brandman and Yovel, 2012), and some face and body sensitive regions are activated superadditively in response to bodies and faces (Schmalzl et al., 2012). However, in a visual detection task, the presence of a head did not affect body inversion effects (Stein et al., 2012). Our results seem to indicate that the presence of a faceless head does not modulate body-face adaptation. The reason for this discrepancy between body-face adaptation and the other types of body-face interactions is not entirely clear, but it may be due to the particular face properties being probed. Specifically, many other studies have used facial identity or neural activity as the critical measure of face-body interactions, while ours focused on perceptual adaptation aftereffects of face gender. One potential limitation of the present study is that different body stimuli were used in Experiments 1 and 2. However, the source of the stimuli were similar (websites of clothing retailers; lighting, pose, and orientation of the bodies were similar), so it is unlikely that the lack of a main effect of the presence of a head was driven by the different body pictures used in the two experiments. Our results strongly suggest that bodies with and without visible heads activate and modulate face gender representations equally.

There was a main effect of target face orientation, with larger aftereffects observed for inverted target faces (↑B to ↓F, ↓B to ↓F). While this is consistent with previous studies of face–face adaptation (Rhodes et al., 2004; Watson and Clifford, 2006), the underlying reason is unclear. The simplest explanation is that briefly presented inverted faces are more ambiguous than upright faces, and this ambiguity may result in greater vulnerability to adaptation. Nonetheless, modulation of the aftereffect magnitude by target face orientation demonstrates another similarity between face–face adaptation and body-face adaptation.

A possible explanation for the lack of a significant effect of body orientation is that bodies, regardless of orientation, are specifically activating representations of upright faces rather than activating orientation-independent face representations. Previous studies have shown that upright faces readily adapt the mechanism for perception of inverted faces, eliciting aftereffects of similar magnitude for both upright and inverted face targets (Rhodes et al., 2004; Watson and Clifford, 2006). In contrast, inverted faces cause little adaptation of the mechanism for perception of upright faces (Rhodes et al., 2004; Watson and Clifford, 2006). However, our results show that adapting to bodies produces larger aftereffects for inverted target faces than for upright target faces, which is somewhat inconsistent with the idea that both inverted and upright bodies activate upright faces. While our results do not perfectly align with this idea, it cannot be fully excluded because bodies may activate representations of upright faces that interact with an inverted target face in a way that is unexpected or differs from what occurs when the adaptor is an actual face.

In conclusion, our results confirm that gender adaptation transfers from bodies to faces, and suggest that this effect is invariant to the orientation of the adapting body. The nature of the face representation activated by bodies needs to be clarified by further investigations, such as explorations of retinotopic dependence, size dependence, or other manipulations of visual field properties. Additionally, neuroimaging studies would help elucidate the processing level at which perception of bodies activates face representations. More broadly, body-face adaptation helps demonstrate the overlap between conceptual and perceptual systems, a central tenet of the theory of embodied cognition (Martin, 2007; Barsalou, 2008).

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