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Face aftereffects suggest interdependent processing of expression and sex and of expression and race

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Bruce and Young (1986) proposed that functionally different aspects of faces (e.g., sex, identity, and expression) are processed independently. Although *inter*dependent processing of identity and expression and of identity and sex have been demonstrated previously, evidence for interdependent processing of sex and expression is equivocal. Using a visual adaptation paradigm, we show that expression aftereffects can be simultaneously induced in different directions along anger–fear continua for male and female faces (Experiment 1) and for East Asian and Black African faces (Experiment 2). These findings for sex- and race-contingent expression aftereffects suggest that processing of expression is interdependent with processing of sex and race and are therefore problematic for models of face perception that have emphasized independent processing of functionally different aspects of faces. By contrast, our findings are consistent with models of face processing that propose that invariant physical aspects of faces and changeable social cues can be processed interdependently.

Keywords: Visual adaptation; Emotion; Face processing; Aftereffects; Social cues.

Bruce and Young (1986; see also Le Gal & Bruce, 2002; Young, 1998) proposed that functionally different aspects of faces, such as sex, identity, and

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expression, are processed by independent perceptual systems (i.e., the processing of one face dimension, e.g., expression, is not influenced by processing functionally different dimensions, e.g., identity). In the Bruce and Young model, physical aspects of different face patterns are first encoded in an initial structural encoding stage of the face processing system. Following this initial encoding of face patterns, the face processing system is proposed to split into systems that are specialized for processing functionally different aspects of faces. In other words, after the initial structural encoding stage, functionally different aspects of faces (e.g., identity, expression, lip speech) are proposed to be analysed by discrete mechanisms in the face processing system. Although there is some evidence for this model from neuropsychological studies (e.g., Calder, Young, Perrett, Etcoff, & Rowland, 1996; Humphreys, Donnelly, & Rriddoch, 1993; Tranel, Damasio, & Damasio, 1988; Young, Newcombe, De Haan, Small, & Hay, 1993; but see Calder & Young, 2005, for criticisms of this neuropsychological evidence) and behavioural studies with healthy individuals (e.g., Bruce et al., 1993; Ellis, Young, & Flude, 1990; Young, McWeeny, Hay, & Ellis, 1986), other studies of face perception in healthy individuals (e.g., Atkinson, Tipples, Burt, & Young, 2005; Ganel & Goshen-Gottstein, 2002, 2004) have presented evidence for interdependent processing of functionally different aspects of faces (i.e., evidence that processing of one face dimension, e.g., expression, can be influenced by processing functionally different dimensions, e.g., identity).

More recently, Haxby, Hoffman, and Gobbini (2000) have proposed a distributed model of face perception. According to Haxby et al.'s model different neural mechanisms process invariant aspects of faces and more changeable aspects such as social signals (e.g., gaze direction and expressions). Additionally, however, Haxby et al. suggest that these mechanisms may also interact. In Haxby et al.'s model, physical aspects of different face patterns are thought to be coded by the inferior occipital gyri (see also Rotshtein, Henson, Treves, Driver, & Dolan, 2005) before the different models of face processing (Bruce & Young, 1986; Haxby et al., 2000).

Many behavioural studies have tested for interdependent processing of identity and expression using Garner's selective attention paradigm (e.g., Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Ganel & Goshen-Gottstein, 2004; Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998). The Garner paradigm (Garner, 1974) was originally developed to investigate whether relatively simple stimulus dimensions (e.g., shape and colour) are processed independently or share processing resources. The basic task is to classify stimuli on one dimension while ignoring an irrelevant dimension. This second dimension is either held constant (the baseline condition) or varies independently of the task-relevant dimension. Garner interference is reflected as an increase in stimulus classification latencies in this latter condition relative to the baseline condition. Such interference is interpreted as evidence for interdependent processing of the dimensions, whereas no difference in classification latencies between conditions is interpreted as evidence that the dimensions can be processed independently.

Early studies that tested for Garner interference when processing facial identity and expressions revealed asymmetric patterns of interference (i.e., variation in identity interfered with expression judgements but variations in expression did not interfere with identity judgements, Baudouin et al., 2002; Schweinberger & Soukup, 1998). Although these findings were interpreted as implying a degree of interdependent processing of identity and expression, differences in discriminability between dimensions can produce Garner interference from the more discriminable dimension to the less discriminable dimension that is not necessarily due to interdependent processing of these dimensions (Melara & Algom, 2003). When the effects of differences in the discriminability of identity and expression are controlled for, however, symmetric patterns of Garner interference when processing identity and expression have been observed (Ganel & Goshen-Gottstein, 2004), suggesting that interdependent processing of identity and expression can occur. Furthermore, Garner interference was greater when stimuli were familiar individuals than when stimuli were unfamiliar individuals (Ganel & Goshen-Gottstein, 2004). Collectively, these findings for Garner interference when processing identity and expression are problematic for accounts of face perception that have emphasized the independence of identity and expression processing.

Studies have also demonstrated Garner interference when processing sex and identity of faces (Ganel & Goshen-Gottstein, 2002). In addition to these findings, studies have also shown that sex classification of faces is faster for familiar faces than for unfamiliar faces (Rossion, 2002). Both faster sex classification of familiar than unfamiliar faces and Garner interference when processing sex and identity suggest that sex and identity can be processed interdependently. Although some studies have reported priming effects for identity judgements but not for sex, and have interpreted these findings as evidence that different perceptual systems process sex and identity, other studies have demonstrated that sex judgements can be primed when hairstyle is masked in the stimuli (see Goshen-Gottstein & Ganel, 2000).

Although there is some compelling behavioural evidence for interdependent processing of identity and expression (e.g., Ganel & Goshen-Gottstein, 2004) and identity and sex (Ganel & Goshen-Gottstein, 2002; Goshen-Gottstein & Ganel, 2000; Rossion, 2002), evidence for interdependent processing of expression and sex is equivocal (Atkinson et al., 2005; Le Gal & Bruce, 2002). Le Gal and Bruce (2002), for example, observed no Garner interference when processing sex and expression, and Atkinson et al. (2005) found that expression judgements were influenced by sex. Atkinson et al. also found that sex influenced expression perception using the Simon paradigm (Simon, 1990). Both Atkinson et al. and Le Gal and Bruce emphasized the importance of further tests for interdependent processing of sex and expressions, ideally using different paradigms. In light of this, we tested for interdependent processing of sex and expression using a contingent visual adaptation paradigm.

Visual adaptation to faces influences subsequent face perception and has been identified by many researchers as a useful tool for investigating the processes and mechanisms that underpin face processing (Leopold, O'Toole, Vetter, & Blanz, 2001; Little, DeBruine, & Jones, 2005; Rhodes, Jeffery, Watson, Jaquet, Winkler, & Clifford, 2004; Webster, Kaping, Mizokami, & Duhamel, 2004). Adaptation to faces varying in sexual dimorphism of shape, identity, eye spacing, or feature spacing has been shown to influence subsequent perceptions of the normality and attractiveness of faces such that faces similar to those seen previously are judged more normal and attractive than would otherwise be the case (Little et al., 2005; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Rhodes et al., 2004). Additionally, adaptation to faces varying in expression, sex, race or identity decreases sensitivity to the type of faces viewed (Hsu & Young, 2004; Leopold et al., 2001; Webster et al., 2004). These "face aftereffects" cannot be solely explained by retinotopic adaptation because they are robust to changes in the size and retinal location of the stimuli between adaptation and test phases (Leopold et al., 2001; Leopold, Rhodes, Müller, & Jeffery, 2005).

Using a visual adaptation paradigm, Little et al. (2005) demonstrated that viewing faces of one sex with increased eye-spacing and faces of the other sex with decreased eye-spacing simultaneously induced face aftereffects in different directions for male and female faces. In other words, the manipulation caused increased eye-spacing to appear more normal for female faces seen with increased eye-spacing during adaptation but caused decreased eye-spacing to appear more normal for male faces seen with decreased eye-spacing during adaptation and vice versa. Subsequent research has shown that these sex-contingent face aftereffects reflect adaptation of neural mechanisms that are sensitive to perceptual category and cannot be explained by adaptation of neural mechanisms that are sensitive only to physical aspects of different face patterns (Bestelmeyer et al., 2008). Bestelmeyer et al. (2008) were able to induce contingent aftereffects following adaptation between sex categories (i.e., male and female) but not after adaptation within a sex category (i.e., female and hyperfemale) where the structural differences between the female and hyperfemale groups were mathematically identical to those between male and female groups. Although low-level retinotopic mechanisms may contribute to "simple" (i.e., noncontingent) face aftereffects (e.g., Watson & Clifford, 2003), that Bestelmeyer et al. observed contingent aftereffects following adaptation between, but not within, sex categories suggests that retinotopic adaptation contributes relatively little to sex-contingent aftereffects and, potentially, other category-contingent aftereffects.

Although "sex-contingent aftereffects" have been observed when faces are varied on eye-spacing, we know of no studies that have tested for sex-contingent expression aftereffects. This is noteworthy because sex-contingent expression aftereffects would suggest interdependent processing of sex and expression. Indeed, Winston, Henson, Fine-Goulden, and Dolan (2004) used a contingent adaptation paradigm to test for interdependent processing of expression and identity in a recent neuroimaging study. Winston et al. argued that identity-contingent expression aftereffects would suggest interdependent processing of identity and expression because such effects would demonstrate that processing of facial identity could affect perceptions of facial expressions.

In light of all this, in Experiment 1 we tested if it is possible to simultaneously induce expression aftereffects in different directions along anger–fear continua for male and female faces (e.g., if adaptation to angry male faces and fearful female faces causes angry male faces and fearful female faces to look more neutral). Whereas sex-contingent expression aftereffects would suggest interdependent processing of sex and expression, independent processing of sex and expression would predict that the effects of adaptation to angry and fearful faces would cancel each other out.

Although effects of facial cues to race have been the focus of a large amount of face processing research (e.g., research on the other-race effect, e.g., Ackerman et al., 2006; Michel, Rossion, Han, Chung, & Caldara, 2006), there has been relatively little research into the extent to which processing facial cues of race might affect the processing of functionally different aspects of faces (e.g., expressions). This is somewhat surprising since testing for independent or interdependent processing of race and expressions would also provide insight into the extent to which functionally different aspects of faces are processed by independent or interdependent systems. Ackerman et al. (2006) have shown, however, that facial expressions can modulate the magnitude of the other-race effect in face recognition; the other-race effect was less pronounced when faces were shown with angry expressions than when faces were shown with other expressions. Since race-contingent expression aftereffects would present evidence for interdependent processing of race and expressions, we also tested if it is possible to induce race-contingent expression aftereffects (Experiment 2). Race-contingent aftereffects have previously been demonstrated for faces varying in feature spacing (Jaquet, Rhodes, & Hayward, 2007; Little, DeBruine, Jones, & Waitt, 2008) but have not previously been demonstrated for faces varying in expression. Interdependent processing of race and expression would be indicated by race-contingent expression aftereffects, but race-contingent expression aftereffects would not be expected if race and expression are processed independently.

EXPERIMENT 1

To establish if it is possible to induce sex-contingent expression aftereffects, we tested if viewing either (a) male faces with angry expressions and female faces with fearful expressions or (b) female faces with angry expressions and male faces with fearful expressions shifted categorical judgements of male and female faces with ambiguous expressions in different directions along anger–fear continua. Anger to fear continua were used because it is well established that such continua have a distinct category boundary (i.e., the point on each continuum where the facial expression perceived "switches" from one expression to the other, Calder et al., 1996; Gelder, Teunisse, & Benson, 1997). Previous studies of expression aftereffects have used this method of testing perceptions of ambiguous facial expressions to avoid ceiling and floor effects in emotion perception (e.g., Webster et al., 2004). If it is possible to induce sex-contingent expression aftereffects, adaptation to angry male faces and fearful female faces should cause ambiguous male faces to look less angry (i.e., more fearful) than in the preadaptation test but ambiguous female faces to appear less fearful than in the preadaptation test. Similarly, adaptation to fearful male faces and angry female faces should cause ambiguous male faces to look less fearful than in the preadaptation test but ambiguous female faces to appear less angry (i.e., more fearful) than in the preadaptation test.

Methods

Stimuli. To manufacture ambiguous male and female faces for use in the pre- and postadaptation test phases of Experiment 1, the shape, colour, and texture information from full face photographs of five men with angry expressions and the same five men with fearful expressions were averaged to produce an angry male composite and a fearful male composite. The original face images were randomly selected from the Karolinska Directed Emotional Faces (KDEF) image set (Lundqvist & Litton, 1998). The angry male composite was then morphed in 21 steps (5% each) towards the fearful male composite to create an angry–fearful male continuum. An angry–fearful female continuum was created using the same methods and procedure. For technical details of methods for producing composite faces and morphed continua see Tiddeman, Perrett, and Burt (2001).

To establish which images on the continua were relatively ambiguous in terms of their expression, the 42 images that made up the two continua were presented in a random order to 385 participants (age: $M = 22.43$, $SD = 7.04$ years; 243 female), who were asked to indicate if each face looked angry or fearful. Participants were recruited for an online study of face perception from various lists of online psychology experiments. The face images on the male and female continua that were closest to being judged fearful by 50% of the participants were then identified. They, and the two face images either side of them on each continuum, were used to assess expression perceptions in the pre- and postadaptation test phases. Examples of these images are shown in Figure 1.

Unmanipulated angry and fearful versions of 10 novel male and 10 novel female identities that were different to those identities that had been used to construct the anger–fear continua were randomly selected from the KDEF image set to be used in the adaptation phase of the experiment. These images were resized so their interpupillary distance was 80% that of the composite images. This was done to reduce possible effects of retinotopic adaptation (following Leopold et al., 2001, 2005). Adapting participants to female faces has been shown to produce equivalent aftereffects for judgements of both prototypical (i.e., average) female faces and for judgements of hyperfemale faces (i.e., female faces in which sex-typical cues had been exaggerated), suggesting that the contribution of retinotopic aftereffects to sex-contingent adaptation is relatively slight (Bestelmeyer et al., 2008). All images were converted to greyscale.

Procedure. In the preadaptation test, participants ($N = 56$, 30 female; age: $M = 22.96$, $SD = 7.74$ years) were shown the 10 ambiguous-expression composite faces (5 male and 5 female) in a fully random order and were asked to make a forced choice decision about whether the face looked angry

Figure 1. Examples of male (left) and female (right) composite faces with ambiguous expressions used to assess expression perception in Experiment 1.

or fearful. Twenty-eight of the participants then viewed the 10 angry male faces and the 10 fearful female faces in an adaptation phase where each image was presented for 3 s in a fully randomized order. Participants were instructed to watch the faces closely. The other 28 participants viewed the 10 angry female faces and the 10 fearful male faces in the adaptation phase. Immediately after the adaptation phase, participants repeated the preadaptation test (i.e., completed a postadaptation test). The experiment was run online, with participants recruited from various lists of online psychology experiments. Previous studies of face aftereffects that were also run online have reported similar patterns of results to those obtained in lab-based experiments (DeBruine, Jones, Unger, Little, & Feinberg, 2007; Jones, DeBruine, & Little, 2008).

Initial processing of data. For each participant, the percentage of trials on which faces of the sex that was seen with an angry expression in the adaptation phase were judged to be fearful was calculated separately for the pre- and postadaptation tests (Table 1). Corresponding values were calculated for the sex that was seen with a fearful expression in the adaptation phase (Table 1). These values were then used to calculate change from pretest to posttest (i.e., posttest minus pretest).

TABLE 1
Percentage of trials where ambiguous expressions were categorized as fearful for the sexes seen with angry and fearful expressions in the adaptation phase

Type of face judged, and test phase	*Mean % of trials categorized as fearful*	*Standard error of the mean*
Sex adapted with angry expressions		
Preadaptation test	60.4	3.2
Postadaptation test	64.6	3.0
Sex adapted with fearful expressions		
Preadaptation test	59.0	3.4
Postadaptation test	49.3	3.9

Results

A mixed-design ANOVA (dependent variable: change in the percentage of trials on which the faces were judged to be fearful in the post-adaptation test relative to the preadaptation test; within-subject factor: Type of face judged in test phases [sex seen with angry expression in adaptation phase, sex seen with fearful expression in adaptation phase]; between-subject factor: Sex seen with angry expression in adaptation phase [male, female]) revealed the predicted main effect of type of face judged in test phases, $F = 8.14$, $df = 1, 54$, $p = .006$, partial eta$^2 = 0.13$ (Figure 2) and no other significant effects (all Fs < 0.6, all ps $> .45$, partial eta$^2 < 0.03$).

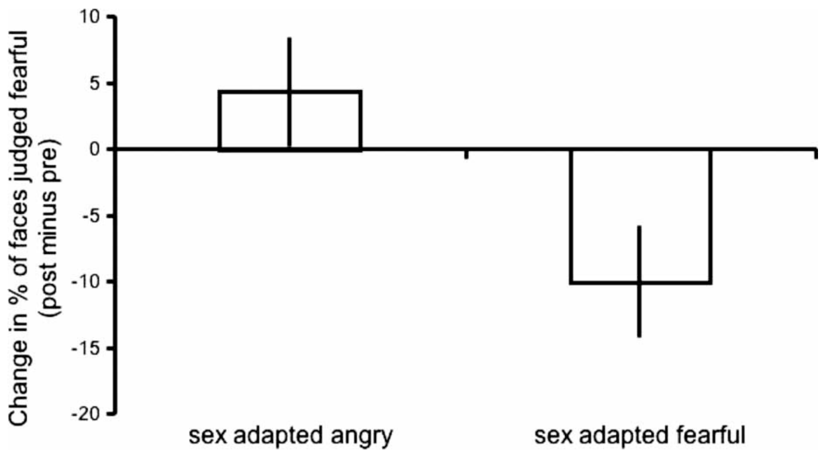

Figure 2. Sex-contingent expression aftereffects in Experiment 1. Participants were less likely to label ambiguous faces as fearful for the sex of face seen with fearful expressions in the adaptation phase but were more likely to label ambiguous faces as fearful for the sex of face seen with angry expressions in the adaptation phase. Bars show means and standard errors of means.

Discussion

Experiment 1 revealed sex-contingent expression aftereffects. Adaptation to angry faces of one sex and fearful faces of the other sex simultaneously caused faces of the first sex to appear less angry and faces of the other sex to appear less fearful in the postadaptation test than in the preadaptation test. These findings complement expression aftereffects that have been observed in previous studies (Hsu & Young, 2004; Webster et al., 2004), since adaptation to expressions biased subsequent expression perception. Furthermore, our findings also complement those of sex-contingent aftereffects following adaptation to faces varied on feature spacing, sexual dimorphism and identity (Little et al., 2005) by showing that analogous sex-contingent aftereffects can also occur when participants are adapted to facial expressions. Furthermore, these findings demonstrate that expression aftereffects are selective for congruency between the sex of the adapting and test faces. This interdependence indicates that expression can be processed in different ways depending on the sex of a face.

Whereas Le Gal and Bruce (2002) observed no Garner interference when processing sex and expression, and interpreted this null finding as evidence that sex and expression are processed independently, our findings for sex-contingent expression aftereffects complement Atkinson et al.'s (2005) findings from Simon and Garner paradigms, which suggested that interdependent processing of sex and expression can occur. Moreover, our findings for sex-contingent expression aftereffects complement previous findings for interdependent processing of identity and expression (e.g., Ganel & Goshen-Gottstein, 2004) and of identity and sex (Ganel & Goshen-Gottstein, 2002; Rossion, 2002). Collectively, these findings are problematic for cognitive models of face perception that propose functionally different aspects of faces are processed independently (Bruce & Young, 1986; Le Gal & Bruce, 2002; Young, 1998).

EXPERIMENT 2

Experiment 1 revealed sex-contingent expression aftereffects, suggesting interdependent processing of sex and expression. Although hairstyles were visible in our stimuli, it is unlikely that our results can be explained solely by processing sex from hairstyle. We note that previous studies of sex-contingent aftereffects for faces manipulated in eye-spacing and identity have found identical results when hairstyles were (Little et al., 2005) and were not visible (Bestelmeyer et al., 2008). Using the same paradigm, in Experiment 2 we tested for race-contingent expression aftereffects. Specifically, we tested if viewing either (a) East Asian male faces with angry expressions and Black African male faces with fearful expressions or (b) Black African male faces with angry expressions and East Asian male faces with fearful expressions shifted categorical judgements of East Asian male and Black African male faces with ambiguous expressions (i.e., those at or near the category boundary on anger to fear continua) in different directions along anger–fear continua.

Methods

Stimuli. The composite male faces with ambiguous fear–anger expressions that were used in the pre- and postadaptation tests in Experiment 1 were again used here. However, these composite faces were transformed in apparent ethnicity using computer graphic methods (see Tiddeman et al., 2001, for technical details of this method). Each of the composite faces was transformed by + 100% of the linear differences in shape, colour, and texture between a prototype White European male face and a prototype East Asian male face to manufacture East Asian versions of these composite faces. To manufacture Black African versions of these composite faces, the ambiguous male faces from the male anger–fear continuum used in Experiment 1 were transformed by + 100% of the linear differences in shape, colour, and texture between a prototype White European male face and a prototype Black African male face. As in Experiment 1, these face images were used to assess expression perception in the pre- and postadaptation tests.

Using the same computer graphic methods, East Asian and Black African versions of the five individual angry and five individual fearful male faces were manufactured. These latter images were used in the adaptation phase of Experiment 2 and examples are shown in Figure 3. Images used in the adaptation, preadaptation, and postadaptation phases of the experiment were masked so that clothing and hairstyle were not visible.

Procedure. In the preadaptation test, participants ($N = 56$, 31 female; age: $M = 27.56$, $SD = 8.80$ years) were shown the 10 ambiguous-expression male composite faces (5 East Asian and 5 Black African) in a fully random order and were asked to make a forced choice decision about whether the face looked angry or fearful. Twenty-seven of the participants then viewed the five angry East Asian male faces and the five fearful Black African male faces in an adaptation phase. Each face image was presented twice, for 3 s on each occasion and in a fully randomized order. The other 29 participants viewed the five fearful East Asian male faces and the five angry Black African male faces in a corresponding adaptation phase. Participants were instructed to watch the faces closely. Immediately after the adaptation phase, participants repeated the preadaptation test (i.e., completed a postadaptation test).

Figure 3. Examples of individual male faces with angry and fearful expressions used in the adaptation phase of Experiment 2. Original White European faces had been transformed to be Black African or East Asian in terms of apparent ethnicity. To view this figure in colour, please see the online issue of the Journal.

TABLE 2
Percentage of trials where ambiguous expressions were categorized as fearful for the races seen with angry and fearful expressions in the adaptation phase

Type of face judged, and test phase	*Mean % of trials categorized as fearful*	*Standard error of the mean*
Race adapted with angry expressions		
Preadaptation test	60.0	2.5
Postadaptation test	66.4	3.1
Race adapted with fearful expressions		
Preadaptation test	56.4	3.3
Postadaptation test	50.4	2.7

The study was run online, with participants recruited from various lists of online psychology experiments.

Initial processing of data. For each participant, the percentage of trials on which faces of the race that was seen with an angry expression in the adaptation phase were judged to be fearful was calculated separately for the pre- and postadaptation tests (Table 2). Corresponding values were calculated for the race that was seen with a fearful expression in the adaptation phase (Table 2). These values were then used to calculate change from pretest to posttest (i.e., posttest minus pretest).

Results

A mixed-design ANOVA (dependent variable: change in the percentage of trials on which the faces were judged to be fearful in the postadaptation test relative to the preadaptation test; within-subject factor: type of face judged in test phases [race seen with angry expression in adaptation phase, race seen with fearful expression in adaptation phase]; between-subject factor: race seen with angry expression in adaptation phase [East Asian, Black African]) revealed the predicted main effect of type of face judged in test phases, $F = 5.47$, $df = 1, 54$, $p = .023$, partial eta$^2 = 0.09$ (Figure 4) and no other significant effects (all Fs < 1.15, all ps $> .28$, all partial eta$^2 < 0.02$).

Discussion

Experiment 2 demonstrated race-contingent expression aftereffects. Adaptation to angry faces of one race and fearful faces of the other race simultaneously caused faces of the first race to appear less angry and faces of the other race to appear less fearful in the postadaptation test than in the

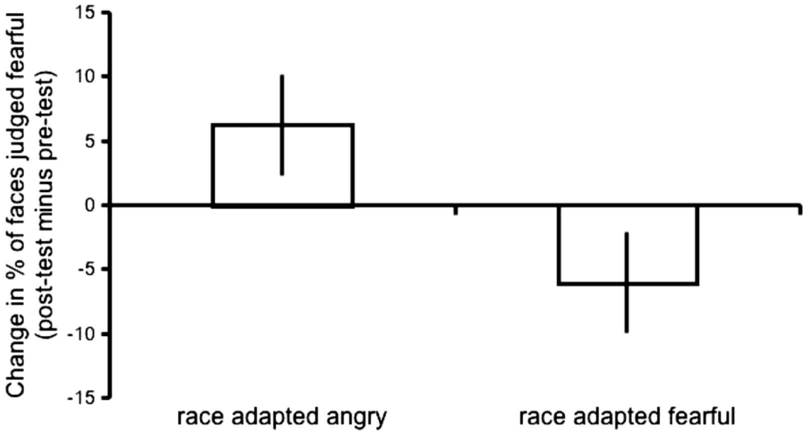

Figure 4. Race-contingent expression aftereffects in Experiment 2. Participants were less likely to label ambiguous faces as fearful for the race seen with fearful expressions in the adaptation phase but were more likely to label ambiguous faces as fearful for the race seen with angry expressions in the adaptation phase. Bars show means and standard errors of means.

preadaptation test. These findings complement previous findings for race-contingent aftereffects following adaptation to faces that had been varied on feature spacing (Jaquet et al., 2007; Little et al., 2008), since we observed race-contingent aftereffects following adaptation to faces differing in facial expressions. Our findings also complement previous studies of expression aftereffects (Hsu & Young, 2004; Webster et al., 2004) by demonstrating that adaptation to expressions can bias subsequent expression perception. Moreover, our findings for race-contingent expression aftereffects demonstrate interdependent processing of race and expression, complementing our earlier demonstration that sex and expression can be processed interdependently.

GENERAL DISCUSSION

Here we demonstrated that it is possible to induce sex-contingent (Experiment 1) and race-contingent (Experiment 2) expression aftereffects. These findings suggest interdependent processing of expression and sex and of expression and race. If the effects of adaptation to expressions that had been presented in conjunction with a particular race or sex affected emotion processing for all races or sexes equally, one would not predict sex and race-contingent expression aftereffects to occur. By contrast, sex- and race-contingent expression aftereffects are a strong prediction of interdependent processing accounts, whereby perceptions of one face dimension (e.g., expression) can be influenced by functionally different dimensions (e.g., identity).

Previous studies have reported evidence for interdependent processing of identity and expression (e.g., Ganel & Goshen-Gottstein, 2004) and of identity and sex (Ganel & Goshen-Gottstein, 2002; Rossion, 2002). However, evidence for interdependent processing of expression and sex from previous studies is equivocal. For example, Le Gal and Bruce (2002) observed no evidence for interdependent processing of these dimensions, whereas Atkinson et al. (2005) found that sex interfered with expression perception. Our findings for interdependent processing of expression and sex complement Atkinson et al.'s findings for Garner and Simon interference when processing expression. Since dissociable processing of male and female faces and faces of different races are prerequisites for interdependent processing of sex and expression and race and expression respectively, our findings for sex- and race-contingent expression aftereffects complement those of previous studies that have interpreted sex-contingent and race-contingent aftereffects for faces manipulated in feature spacing as indicating dissociable processing of male and female faces and of faces of different races (Bestelmeyer et al., 2008; Jaquet et al., 2007; Little et al., 2005, 2008). It is noteworthy that although previous studies have demonstrated interdependent processing of identity and expression (e.g., Ganel & Goshen-Gottstein, 2004), interdependent processing of these dimensions cannot explain our findings for race- and sex-contingent expression aftereffects because we showed that adaptation to expression influences perceptions of faces that were not seen during the adaptation phases.

Although Bruce and Young (1986) proposed that functionally different aspects of faces are processed independently (see also Le Gal & Bruce, 2002; Young, 1998), our findings for interdependent processing of expression and sex and of expression and race contribute to a growing literature suggesting that functionally different aspects of faces can be processed interdependently (e.g., Atkinson et al., 2005; Ganel & Goshen-Gottstein, 2002, 2004; Rossion, 2002). Although interdependent processing of functionally different aspects of faces is problematic for models of face perception that have emphasized independent processing of such dimensions, it is consistent with two alternative models of face perception. These alternative models of face processing are Haxby et al.'s "distributed neural system for face perception" (Haxby et al., 2000; see also Hoffman & Haxby, 2000) and Ganel and Goshen-Gottstein's "structural hypothesis" of expression perception (Ganel & Goshen-Gottstein, 2004; see also Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005).

Haxby et al. (2000) proposed a distributed neural system for face perception whereby different neural substrates are thought to analyse aspects of faces that are invariant within a given individual (e.g., identity, sex, race) and aspects of faces that are changeable within a given individual (e.g., gaze and head direction, expression). Invariant physical aspects of faces are thought to be analysed primarily in the fusiform face area (FFA) and changeable social cues are thought to be analysed primarily in the superior temporal sulcus (STS). Although the neural substrates that are implicated in the processing of invariant and changeable aspects of faces are thought to be dissociable, these neural mechanisms are also thought to interact (Haxby et al., 2000). Indeed, Haxby et al. suggest that the FFA may provide a supporting role for expression perception. Thus, interdependent processing of invariant and changeable aspects of faces is a specific prediction of Haxby et al.'s model. Although the extent to which findings from neuropsychological and neuroimaging studies support dissociable neural systems for processing changeable and invariant aspects of faces has recently been called into question (Calder & Young, 2005; see also Ganel et al., 2005), our findings for sex- and race-contingent expression aftereffects are consistent with interactive processing of functionally different aspects of faces within a distributed neural system.

Haxby et al. (2000) proposed that interdependent processing of changeable and invariant aspects of faces can be achieved if the FFA plays a supporting role in expression perception, but Ganel and Goshen-Gottstein's (2004, see also Ganel et al., 2005) structural hypothesis proposes a different mechanism for interdependent processing of expression and invariant aspects of faces. Ganel and colleagues suggest that expressions are best characterized as dynamic variations from the invariant structure of faces (e.g., identity; Ganel et al., 2005; Ganel & Goshen-Gottstein, 2004). Thus, the manner in which emotions are expressed in faces will be dependent on invariant aspects of face structure (Ganel et al., 2005; Ganel & Goshen-Gottstein, 2004). In other words, Ganel and Goshen-Gottstein (2004; see also Ganel et al., 2005) view processing of structural aspects of faces as an important and necessary component for expression perception. Indeed, Ganel et al. (2005) recently demonstrated that the FFA plays an important role in expression perception that does not appear to be limited to passing information to other brain regions about facial structure alone. Our findings for sex- and race-contingent expression aftereffects are consistent with this notion that expression and invariant aspects of faces (e.g., identity, sex, and race) may be analysed by a common neural substrate. Indeed, previous studies have interpreted contingent adaptation effects as evidence for joint coding of sex and face view (Fang, Ijichi, & He, 2007) and sex and race (Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006).

A limitation of Experiment 2 was that we did not test for an effect of the degree of previous contact with other-race exemplars on race-contingent expression aftereffects. It is important to note here, however, that our intention was simply to establish whether or not race-contingent expression aftereffects can occur, rather than to identify other factors that may modulate the extent to which they occur or that may modulate the circumstances under which they occur. Nonetheless, we acknowledge that investigating the effects of previous contact with other-race exemplars on race-contingent adaptation can shed light on factors that influence face representations and note here that consideration of such factors may provide further insight into the mechanisms and processes that support interdependent processing of diverse facial cues.

In conclusion, the sex- and race-contingent expression aftereffects observed in our experiments, together with previous findings demonstrating interdependent processing of sex and identity (Ganel & Goshen-Gottstein, 2002; Rossion, 2002) and identity and expression (Ganel & Goshen-Gottstein, 2004), are problematic for models of face perception that have proposed that functionally different aspects of faces (e.g., sex, expression, identity) are processed by independent perceptual systems (Bruce & Young, 1986; Le Gal & Bruce, 2002; Young, 1998). By contrast, such findings are consistent with models of face perception that have emphasized the integration of information from different facial cues in person perception (Ganel et al., 2005; Haxby et al., 2000). Further research is needed to establish whether integrating information from different aspects of faces (a) is achieved via interactions among perceptual systems that may be relatively specialized for processing different aspects of faces (Haxby et al., 2000), (b) reflects a common neural substrate for analysing expression and invariant aspects of faces (Ganel et al., 2005), or (c) is achieved by a combination of these processes. Although our findings suggest interdependent processing of sex and expression and of race and expression at a functional level, our findings cannot distinguish between these different accounts of the possible neural mechanisms that underpin such interdependent processing. Studies that directly test these competing explanations for interdependent processing of functionally different aspects of faces will offer important insights into how we combine information from diverse facial cues during social interactions.

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