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Brief article

Sex-contingent face aftereffects depend on perceptual category rather than structural encoding

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Abstract

Many studies have used visual adaptation to investigate how recent experience with faces influences perception. While faces similar to those seen during adaptation phases are typically perceived as more 'normal' after adaptation, it is possible to induce aftereffects in one direction for one category (e.g. female) and simultaneously induce aftereffects in the opposite direction for another category (e.g. male). Such aftereffects could reflect 'category-contingent' adaptation of neurons selective for perceptual category (e.g. male or female) or 'structure-contingent' adaptation of lower-level neurons coding the physical characteristics of different face patterns. We compared these explanations by testing for simultaneous opposite after effects following adaptation to (a) two groups of faces from distinct sex categories (male and female) or (b) two groups of faces from the same sex category (female and hyper-female) where the structural differences between the female and hyper-female groups were mathematically identical to those between male and female groups. We were able to induce opposite aftereffects following adaptation between sex categories but not after adaptation within a sex category. These findings

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indicate the involvement of neurons coding perceptual category in sex-contingent face aftereffects and cannot be explained by neurons coding only the physical aspects of face patterns.

Keywords: Categorical perception; Face perception; Contingent aftereffects; Structural encoding

1. Introduction

Visual adaptation has been widely used to investigate the mechanisms that underpin face perception (e.g., Fang & He, 2005; Jenkins, Beaver, & Calder, 2006; Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999). Adaptation to faces manipulated in a particular way decreases sensitivity to the adapted feature (e.g., Fang & He, 2005; Jenkins et al., 2006) and causes novel faces that are physically similar to the adapting faces to appear more normal (e.g., Jeffery, Rhodes, & Busey, 2006; Little, DeBruine, & Jones, 2005). Of particular interest are studies demonstrating 'contingent aftereffects', whereby the effects of adaptation on perceptions are more pronounced when adapting and test faces are matched on dimensions such as sex, identity or race (Jaquet, Rhodes, & Hayward, 2006; Little et al., 2005; Yamashita, Hardy, De Valois, & Webster, 2005). Contingent aftereffects have also been demonstrated by studies that simultaneously induced aftereffects in opposite directions for two different categories, such as male and female, upright and inverted, or White and East Asian (Jaquet et al., 2006; Little et al., 2005; Rhodes et al., 2004). Contingent aftereffects such as these have generally been interpreted as evidence for specialization of neural mechanisms coding perceptual categories such as sex (Jaquet et al., 2006; Little et al., 2005; Rhodes et al., 2004). However, recent neurobiological evidence demonstrating that different neural mechanisms code physical aspects of face patterns and higher-level aspects of faces (Rotshtein, Henson, Treves, Driver, & Dolan, 2005) suggests that these contingent aftereffects could reflect 'structure-contingent' adaptation of lower-level neurons coding the physical characteristics of different face patterns or 'category-contingent' adaptation of neurons selective for higher-level aspects of faces (e.g., perceptual category).

Rotshtein et al. (2005) reported neurobiological evidence for a hierarchical model of face processing whereby different neural substrates code physical aspects of faces and higher-level aspects of faces (e.g., identity). They used computer graphic methods to manufacture continua in which one famous identity was morphed in stages into a different famous identity. From each of these continua, pairs of different morphed faces were selected that were either perceived as the same identity (i.e., were located on the same side of the identity category boundary) or as different identities (i.e., were located on different sides of the identity category boundary). Crucially, the linear physical differences between the faces in 'same' and 'different' identity pairs were mathematically identical. Using a paired-repetition paradigm (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998) to compare the extent to which repeated presentation of stimuli decreased responses in brain regions that have been implicated in face processing (inferior occipital gyrus (IOG), right fusiform gyrus (FFG)) in the 'same' and 'different' identity conditions, Rotshtein et al. (2005) found that the IOG was equally sensitive to physical changes to faces for both 'same' and 'different' identity pairs. By contrast, however, the right FFG was only sensitive to changes that crossed the identity boundary (i.e., 'different' identity pairs). These findings demonstrate that the IOG primarily codes physical aspects of face patterns, but does not code higher-level aspects of faces, and implicate the right FFG in coding higher-level aspects of faces (e.g., identity). Thus, sex-contingent face aftereffects could reflect 'structure-contingent' adaptation of lower-level neurons coding physical characteristics of different face patterns (i.e., sex-typical facial characteristics) or 'category-contingent' adaptation of neurons selective for perceptual category (i.e., male or female).

Using an established paradigm for investigating opposite aftereffects (Jaquet et al., 2006; Little et al., 2005; Rhodes et al., 2004; Watson & Clifford, 2006), here we tested if opposite aftereffects can be induced following adaptation between sex categories (male and female) and also following adaptation within a sex category (female and hyper-female). Following Rotshtein et al. (2005) and other research into categorical perception (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992; Jacques & Rossion, 2006), computer graphic methods were used to ensure that the *physical* differences between male and female faces were mathematically identical to those between female and hyper-female faces. While such linear physical differences are *mathematically* equivalent (Calder et al., 1996; Etcoff & Magee, 1992; Rotshtein et al., 2005), they are not expected to be *perceptually* equivalent (Blanz, O'Toole, Vetter, & Wild, 2000; Calder et al., 1996; Etcoff & Magee, 1992; Rotshtein et al., 2005). Nonetheless, the neural substrate implicated in the structural encoding of physical face patterns (IOG) is sensitive to linear physical differences among digital face images created using computer graphics methods similar to those used in the current study, regardless of whether they cross perceptual category boundaries (Rotshtein et al., 2005). By contrast, the FFG is sensitive to physical differences that cross perceptual category boundaries, but not equivalent physical differences that do not cross perceptual category boundaries (Rotshtein et al., 2005). Thus, comparing the effects of within- and between-category adaptation offers insight to the brain regions involved in visual adaptation to faces.

If the neurons being adapted in sex-contingent aftereffects (Little et al., 2005) are those that code high-level aspects of faces (e.g., sex) and not those that code only physical aspects of different face patterns, it should be possible to induce opposite aftereffects following adaptation to male and female faces (between-sex adaptation condition) but not following adaptation to female and hyper-female faces (within-sex adaptation condition). This would support a 'category-contingent' explanation of sex-contingent aftereffects. However, if the neurons being adapted are those that code physical aspects of face patterns rather than higher-level aspects of faces, it should be possible to induce opposite aftereffects for both the within- and between-sex adaptation conditions. This would support a 'structure-contingent' explanation of sex-contingent aftereffects. Comparing effects in the between-sex and within-sex adaptation conditions is also important in light of Watson and

Clifford (2006) proposal that opposite aftereffects may occur for any two groups of faces that differ systematically in appearance.

2. Methods

2.1. Stimuli

2.1.1. Adapting stimuli

To ensure that the linear physical differences between the female faces and the male versions were identical to those between the female faces and the hyper-female versions, we used a prototype-based transformation method. See Rowland and Perrett (1995) and Tiddeman, Perrett, and Burt (2001) for technical details of this method and a mathematical demonstration that this method can produce image pairs with equivalent physical differences. These prototype-based transformations have been used to manufacture stimuli for many previous studies of face perception (Little et al., 2005; Penton-Voak et al., 1999; Perrett et al., 1998).

Prototype-based transformation alters the properties of a face using the differences between two prototypes. Prototypes are composite images that are constructed by defining a large number of corresponding points on individual faces (e.g., the center of the left pupil, the left corner of the mouth) and using these points to average the shape, color, and texture of a group of faces, such as male or female faces. Prototypes can then be used to transform images by calculating the vector differences in position between corresponding points on two prototype images and changing the position of the corresponding points on a third image by a given percentage of these vectors. The differences between color values at each corresponding pixel can be similarly transformed.

Using this technique, we created male and hyper-female versions of 20 young adult female face images. First, a male prototype was manufactured from face images of 20 white, young adult males and a female prototype was manufactured from face images of 20 white, young adult females. To manufacture the male prototype, 189 landmark points were first marked on each of the 20 male face images. The average *xy* coordinates for each landmark were then calculated and these coordinates were used to calculate the average face shape for the 20 faces. Each individual face was warped into this average shape and the average RGB value for each pixel was then calculated for the sample and applied to the average face shape. A wavelet-based algorithm (Tiddeman et al., 2001) was then used to analyse textural features in the original images and adjust the RGB pixel values so that the composites had realistic texture details that were representative of the constituent faces. The same methods were used to manufacture a female prototype from 20 female face images.

To create male versions of the 20 individual female face images, each original female face was transformed by *subtracting* 100% of the linear differences in shape, color, and texture information between a prototype female face and a prototype male face. To create hyper-female versions of the 20 female face images, each original female face was transformed by *adding* 100% of the linear differences in shape, color, and texture information between a prototype male face and a prototype female face.

We will illustrate this process more specifically by describing the mathematical operations that occur to an original female face (see Table 1). First, we would alter the shape of the face, as we will illustrate using a hypothetical x-coordinate of a single landmark point of this face. We have set the value of this x-coordinate of the original female face to 24, the corresponding x-coordinate of the prototype female face to 22, and the corresponding x-coordinate of the prototype male face to 17. The male version of this original female face would be made by calculating the difference between the corresponding x-coordinates of the prototype female face and the prototype male face [$22 - 17 = 5$] and *subtracting* it from the x-coordinate of the individual female face [$24 - 5 = 19$]. Similarly, the difference between the corresponding x-coordinates of the prototype female face and the prototype male face would be *added* to the x-coordinate of the original female face [$24 + 5 = 29$] to produce the hyper-female version. After repeating these operations for all x- and y-coordinates, the shape of the original female face would be warped into the shape defined by these new x- and y-coordinates using an algorithm described in detail by Benson and Perrett (1991).

Next, we would alter the color of the face. First, the male and female prototype faces would also be warped into this new shape in order to manipulate the color of these new images in a similar manner to the shape manipulations. For the male version of the original female face, we would calculate the difference between the red values of the corresponding pixels of the prototype female face and the prototype male face [e.g., $100 - 80 = 20$] and *subtract* it from the corresponding pixels of the individual female face [e.g., $103 - 20 = 83$]. This would be repeated for the green and blue values of each pixel. Similarly, the difference between the corresponding red, green and blue values of the pixels of the prototype female face and the proto-

Table 1
The mathematical operations for a hypothetical x-coordinate of a single landmark point and red value of one pixel

	Shape (x-coordinate)	Color (red value)
Original female face	24	103
Female prototype	22	100
Male prototype	17	80
Male version	$24 - (22 - 17) = 19$	$103 - (100 - 80) = 83$
Hyper-female version	$24 + (22 - 17) = 29$	$103 + (100 - 80) = 123$
Transforming identity	20	
Plus version of		
Original female face	$24 + (0.5 * (22 - 20)) = 25$	
Male version	$19 + (0.5 * (22 - 20)) = 20$	
Hyper-female version	$29 + (0.5 - (22 - 20)) = 30$	
Anti version of		
Original female face	$24 - (0.5 * (22 - 20)) = 23$	
Male version	$19 - (0.5 * (22 - 20)) = 18$	
Hyper-female version	$29 - (0.5 * (22 - 20)) = 28$	

type male face would be *added* to the corresponding pixels of the original female face [e.g., $103 + 20 = 123$] for the hyper-female version.

Following previous studies of sex-contingent face aftereffects (Little et al., 2005), we then used an identity transformation to generate oppositely manipulated 'anti' and 'plus' versions of the male, female, and hyper-female faces to be used in the adaptation phase of the experiment. An identity transformation alters the shape of a face by a given percentage of the vector differences between the prototype female face and a particular female individual identity (color is not altered). The same female face image (i.e., identity) was used to transform all images. Two versions of each of the 20 male, 20 female and 20 hyper-female faces were made, one transformed by *adding* 50% of these differences ('plus' versions) and one transformed by *subtracting* 50% of these differences ('anti' versions). This created plus versions of faces that were altered in one direction (e.g., decreasing forehead height, decreasing chin roundness, increasing upper lip size, increasing eye openness) and anti versions were altered equally in the opposite direction (e.g., increasing forehead height, increasing chin roundness, decreasing upper lip size, decreasing eye openness; see Fig. 1).

Following the numerical example above, first we would calculate the difference between the x-coordinate in the previous example on the female individual identity used for transformation (i.e., a value of 20) and the corresponding x-coordinate on the female prototype [$22 - 20 = 2$]. To make the plus version of the original female face in the example above, we would *add* 50% of this difference to the corresponding x-coordinate of the original female face [$24 + (0.5 * 2) = 25$]. To make the anti version, we would *subtract* 50% of this difference [$24 - (0.5 * 2) = 23$]. To make plus and anti versions of the male version in the example above, 50% of this same difference would be *added* and *subtracted* from the corresponding x-coordinate of the male version [plus: $19 + (0.5 * 2) = 20$; anti: $19 - (0.5 * 2) = 18$]. The identical manipulation would be applied to the hyper-female version [plus: $29 + (0.5 * 2) = 30$; anti: $29 - (0.5 * 2) = 28$]. Again, after repeating these operations for all x- and y-coordinates, the shape of the original female face, male version, or hyper-female version would be warped into the shape defined by these new x- and y-coordinates. Color was not altered.

Our method of transforming faces applies identical mathematical operations to the defined points of original faces. In this way, we can be sure that the same manipulation applied to different faces results in identical changes relative to the baseline state of the original face. Additionally, we can be sure that pairs of manipulations defined by adding or subtracting identical information (e.g., male and hyper-female or plus and anti) result in changes that are identical in magnitude and opposite in direction.

Although there were multiple steps involved in manufacturing the 'plus' and 'anti' versions of the female, male, and hyper-female faces, importantly the computer graphic software we used to prepare our stimuli records the changed coordinates of every landmark point after each step of the process. Thus, we can be very confident that the mathematical linear differences between plus and anti versions of our stimuli

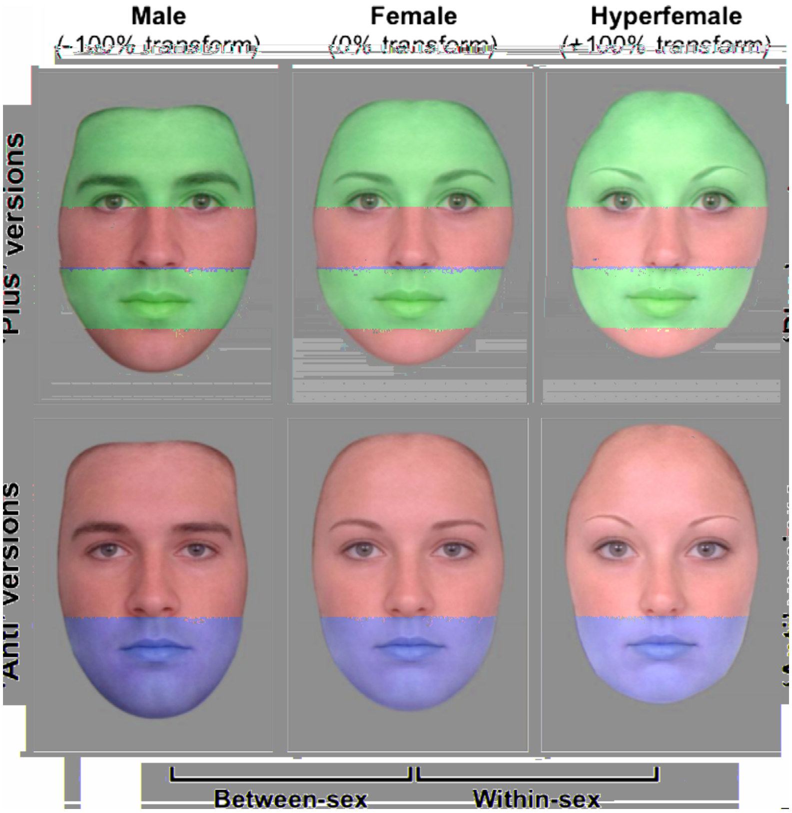

Fig. 1. Test stimuli used in the pre- and post-adaptation tests. The top row shows 'plus' identity versions of male, female, and hyper-female composite faces. The bottom row shows 'anti' versions of these same composites. The magnitude of the physical differences between male and female versions is identical to that between female and hyper-female versions. However, while male and female versions belong to different sex categories, female and hyper-female versions belong to the same sex category. All test and adapting stimuli were masked so that hairstyle and clothing were not visible in the images.

are equivalent in each condition, despite the multiple stages involved in their production.

2.1.2. Test stimuli

For the pre- and post-adaptation tests, composite faces were manufactured by averaging the shape, color, and texture of all 20 individual 'anti' or 'plus' faces separately for each of the male, female, and hyper-female groups. This resulted in the three pairs of composite faces shown in Fig. 1.

2.2. Procedure

In a pre-adaptation test, 118 participants (ages: $M = 25.19$, $SD = 7.74$ years; 59 females) were shown the 3 pairs of 'anti' and 'plus' versions of the composite faces (i.e., the male, original and hyper-female composite pairs). In other words, participants were shown the plus and anti versions of the male composite, the plus and anti versions of the female composite, and the plus and anti versions of the hyper-female composite. Trial order and the side of the screen on which any particular image in each composite pair was shown were fully randomized.

For each trial, participants were instructed to choose the face in each pair that looked more normal. They were also instructed to indicate the magnitude of this perceived difference by choosing from the options 'much more normal', 'more normal', 'somewhat more normal', and 'slightly more normal'.

Next, participants were exposed (i.e., adapted) to 40 individual faces in a fully randomized order for 1.5 s each (totalling 1 min) in one of two adaptation conditions (between-sex adaptation or within-sex adaptation). Sixty participants were randomly allocated to the between-sex condition and 58 participants were randomly allocated to the within-sex condition.

In the between-sex adaptation condition, 29 of the participants were adapted to the 20 'plus' versions of the male faces and the 20 'anti' versions of the female faces. By contrast, the remaining 31 participants in the between-sex adaptation condition were adapted to the 20 'plus' versions of the female faces and the 20 'anti' versions of the male faces. In the within-sex adaptation condition, 30 participants were adapted to the 20 'plus' versions of the female faces and the 20 'anti' versions of the hyper-female faces. The remaining 28 participants in the within-sex adaptation condition were adapted to the 20 'plus' versions of the hyper-female faces and the 20 'anti' versions of the female faces.

Immediately after the adaptation phase, participants repeated the pre-adaptation test. The interpupillary distance of the faces used in the adaptation phase was 80% of the interpupillary distance of the test faces in order to eliminate contributions from retinotopic aftereffects (cf. Leopold et al., 2001; Rhodes et al., 2004).

2.3. Initial processing of data

Responses on the pre- and post-adaptation tests were coded as normality of the plus version using the following 0–7 scale:

0 = anti version judged as "much more normal" than plus version
1 = anti version judged as "more normal" than plus version
2 = anti version judged as "somewhat more normal" than plus version
3 = anti version judged as "slightly more normal" than plus version
4 = plus version judged as "slightly more normal" than anti version
5 = plus version judged as "somewhat more normal" than anti version
6 = plus version judged as "more normal" than anti version
7 = plus version judged as "much more normal" than anti version

For each participant, we then calculated the change in the perceived normality of the plus version from pre-adaptation to post-adaptation test by subtracting the pre-adaptation test score from the post-adaptation test score. This was done separately for judgments of male, female, and hyper-female faces.

3. Results

Opposite aftereffects will be demonstrated by an increase in the perceived normality of the 'plus' version from pre- to post-test for the sex of face that was seen in the 'plus' version in the adaptation phase and a relative decrease in the perceived normality of the 'plus' version for the sex of face that was seen in the 'anti' version in the adaptation phase. The presence of opposite aftereffects in both the between-sex and within-sex adaptation conditions would support a 'structure-contingent' explanation of sex-contingent aftereffects, while the presence of opposite aftereffects in only the between-sex adaptation condition would support a 'category-contingent' explanation of sex-contingent aftereffects.

3.1. Between-category adaptation

Responses were analysed using a mixed-design ANOVA. The dependent variable was the change in perceived normality of the plus face from pre- to post-adaptation test. There was one within-subject factor, *sex of face*, with three levels (male, female, hyper-female). There was one between-subjects factor, *adaptation condition*, with two levels. In the first adaptation condition, male faces were adapted with plus version and female faces were adapted with anti version. In the second adaptation condition, female faces were adapted with plus version and male faces were adapted with anti version.

This analysis revealed the predicted interaction between *sex of face* and *adaptation condition* ($F_{2,116} = 4.50$, $p = .013$, partial $\eta^2 = .072$; Fig. 2) and no other significant effects (all $F<1.11$, all $p > .33$, all partial $\eta^2 < .020$).

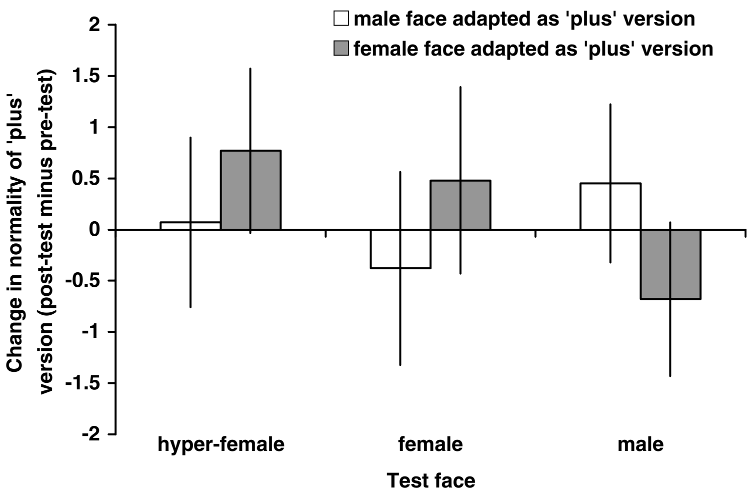

Fig. 2. The significant interaction between sex of face and adaptation condition when participants were adapted to faces from different sex categories. Bars show means and 95% confidence intervals.

We then carried out three additional mixed-design ANOVAs to interpret the significant interaction. The design of these analyses was identical to the main analysis, except that only two sexes of face were compared for each analysis.

The analysis comparing judgments of male faces to judgments of female faces revealed the predicted interaction between *sex of face* and *adaptation condition* ($F_{1,58} = 5.27$, $p = .025$, partial $\eta^2 = .083$) and no other significant effects (all $F_{1,58} < 0.15$, all $p > .70$, all partial $\eta^2 < .004$). The analysis comparing judgments of male faces to judgments of hyper-female faces also revealed an interaction between sex of face and adaptation condition ($F_{1,58} = 5.39$, $p = .024$, partial $\eta^2 = .085$) and no other significant effects (all $F_{1,58} < 1.85$, $p > .17$, all partial $\eta^2 < .032$). The analysis comparing judgments of female faces to judgments of hyper-female faces revealed no interaction between sex of face and adaptation condition ($F_{1,58} = 0.10$, $p = .757$, partial $\eta^2 = .002$) and no other significant effects (all $F_{1,58} < 2.13$, all $p > .15$, all partial $\eta^2 < .036$).

3.2. Within-category adaptation

As for between-category adaptation, responses were analysed using a mixed-design ANOVA. The dependent variable was the change in perceived normality of the plus face from pre- to post-adaptation test. There was one within-subject factor, *sex of face*, with three levels (male, female, hyper-female). There was one between-subjects factor, *adaptation condition*, with two levels. In the first adaptation condition, female faces were adapted with plus version and hyper-female faces were adapted with anti version. In the second adaptation condition, hyper-female faces were adapted with plus version and female faces were adapted with anti version.

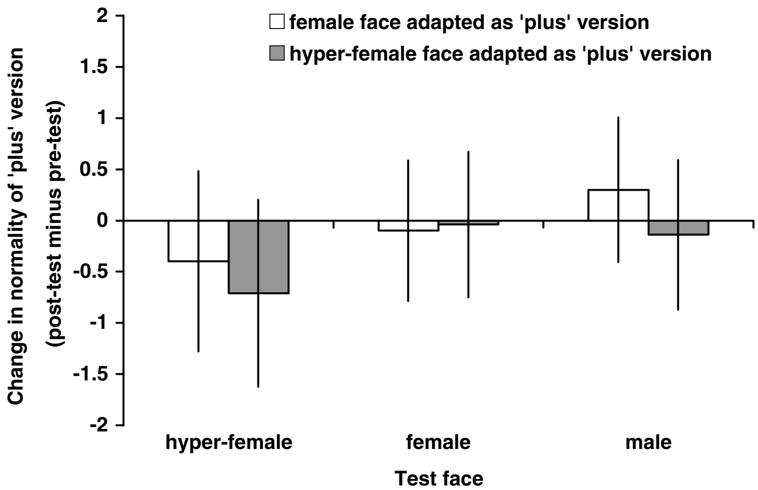

Fig. 3. The nonsignificant interaction between sex of face and adaptation condition when participants were adapted to faces from the same sex category. Bars show means and 95% confidence intervals.

By contrast with our findings for between-category adaptation, this analysis revealed no interaction between *sex of face* and *adaptation condition* ($F_{2,112} = 0.29$, $p = .749$, partial $\eta^2 = .005$; Fig. 3) and no other significant effects (all $F < 1.85$, all $p > .16$, all partial $\eta^2 < .033$).

4. Additional analyses

In order to confirm that the patterns of adaptation for the within-category and between-category conditions are significantly different, we conducted a further mixed-design ANOVA incorporating the data for both category conditions. The dependent variable was the change in perceived normality of the plus face from pre- to post-adaptation test. There was one within-subject factor, face type, with three levels (more masculine adapted type, more feminine adapted type, unadapted type). There were two between-subjects factors, adaptation condition (more masculine faces adapted with plus version and more feminine faces adapted with anti version, more masculine faces adapted with anti version, and more feminine faces adapted with plus version) and category condition (within-category, between-category). A significant three-way interaction was found among face type, adaptation condition, and category condition ($F_{2,228} = 3.60$, $p = .029$, partial $\eta^2 = .031$) and no other significant effects (all $F < 2.06$, all $p > .13$, all partial $\eta^2 < .019$).

In the analysis described above, the unadapted faces are not strictly analogous in the between-category and within-category conditions (i.e., hyper-female faces in the between-category condition are expected to show similar effects to female faces, while male faces in the within-category condition are expected to show no adaptation). Consequently, we repeated the above analysis excluding the unadapted type from the within-subject factor of face type. This analysis also revealed a significant three-way interaction among face type, adaptation condition, and category condition ($F_{1,114} = 4.30$, $p = .040$, partial $\eta^2 = .036$) and no other significant effects (all $F < 1.99$, all $p > .16$, all partial $\eta^2 < .018$). Collectively, these analyses confirm that the patterns of adaptation for the within-category and between-category conditions are significantly different.

5. Discussion

Here we show that it is possible to induce opposite aftereffects for male and female faces, but not for female and hyper-female faces. Adaptation to male faces that had been manipulated in one direction and female faces that had been manipulated in the opposite direction induced aftereffects in opposite directions for male and female prototypes. By contrast, no such pattern of results was seen when participants were adapted to female and hyper-female faces manipulated in opposite directions. Importantly, the use of computer graphic methods to construct these face images ensured that the extent of physical differences between male and female faces was identical to that between female and hyper-female faces. The presence of opposite aftereffects in the between-sex adaptation condition, but not the within-sex adaptation condition, implicates adaptation of neural mechanisms that are sensitive to perceptual category (Földiák, Xiao, Keysers, Edwards, & Perrett, 2003), and cannot be explained by adaptation of neural mechanisms coding only physical aspects of face patterns (see Rotshtein et al., 2005). Furthermore, our findings are evidence against the proposal that it may be possible to induce opposite aftereffects for any groups of faces that differ systematically in appearance (Watson & Clifford, 2006).

Although no opposite aftereffects were observed for the within-sex adaptation condition, the effect of adaptation to female faces in the between-sex adaptation condition generalized to judgments of hyper-female faces. Thus, the absence of an opposite aftereffect in the within-sex adaptation condition cannot be attributed to difficulties in inducing aftereffects in hyper-female faces because of their relative atypicality. Indeed, that adaptation in the between-sex adaptation condition induced equivalent aftereffects for judgments of female and hyper-female faces that were different to those induced for male faces is further evidence that sex-contingent aftereffects reflect category-contingent adaptation rather than structure-contingent adaptation. While our findings show that opposite aftereffects do not occur for within-category pairs that have the same *physical* differences as male and female faces, they do not rule out the possibility that opposite aftereffects could occur for within-category pairs that have the same *perceptual* differences as male and female faces. The extent to which linear physical differences among 2-dimensional images, such as those in our and others' stimuli (e.g., Calder et al., 1996; Little, DeBruine, Jones, & Waitt, 2008; Little et al., 2005; Rotshtein et al., 2005), correspond to differences among 3-dimensional stimuli is also unclear.

Findings from previous studies are equivocal about the extent to which the effect of adaptation to faces reflects adaptation of neural mechanisms implicated in face processing or mechanisms that under pin lower-level analysis of visual stimuli. Previous studies have shown that face aftereffects occur for both upright and inverted faces (e.g., Rhodes et al., 2004), suggesting that face aftereffects may reflect adaptation of neurons that play a general role in processing visual stimuli of any kind rather than adaptation of neurons that are relatively specialized for processing faces (see Yamashita et al., 2005). Other studies, however, have shown that face aftereffects are disrupted by changes to the contrast polarity and spatial frequency of the stimuli and interpreted these effects as implicating face-processing mechanisms (Yamashita et al., 2005). Our findings demonstrating that sex-contingent face aftereffects reflect category-contingent adaptation, rather than structure-contingent adaptation, also suggest that neural mechanisms that are relatively specialized for processing high-level aspects of faces can play an important role in the occurrence of face aftereffects.

Adaptation and categorical perception are thought to reflect specialization of neural machinery (Calder et al., 1996; Etcoff & Magee, 1992; Fang & He, 2005; Jenkins et al., 2006). Our findings therefore indicate neural sensitivity to face categories (Földiák et al., 2003), perhaps at the level of the 'fusiform face area' (Rotshtein et al., 2005), and establish contingent aftereffects as an effective tool for studying the coding of high-level properties of faces.

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