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Sex-contingent face after-effects suggest distinct neural populations code male and female faces

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Exposure to faces biases perceptions of subsequently viewed faces. Faces similar to those seen previously are judged more normal and attractive than they were prior to exposure. Here we show sex-contingent after-effects following adaptation to eye-spacing (experiment 1), facial identity (experiment 2) and masculinity (experiment 3). Viewing faces of one sex with increased eye-spacing and faces of the other sex with decreased eye-spacing simultaneously induced opposite after-effects for male and female faces (assessed by normality judgments). Viewing faces transformed in identity or masculinity increased preferences for novel faces with characteristics similar to those viewed only when the sex of the faces presented in the adaptation phase and in post-adaptation preference tests were congruent. Because after-effects reflect changes in responses of neural populations that code faces, our findings indicate that distinct neural populations code male and female faces.

Keywords: face space; representation; prototype; adaptation; after-effects; experience

1. INTRODUCTION

Exposure to faces biases subsequent perceptions of novel faces by causing faces similar to those initially viewed to appear more normal than they would otherwise be perceived (Leopold *et al.* 2001; Rhodes *et al.* 2001, 2003, 2004; Webster *et al.* 2004; Leopold *et al.* 2005). For example, adaptation 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; Rhodes *et al.* 2004). Analogous visual after-effects 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), and expression (Webster *et al.* 2004). Adaptation from exposure to faces also influences attractiveness judgments potentially due to the positive association between perceived normality and attractiveness (Halberstadt & Rhodes 2000; Rhodes *et al.* 2001, 2003). Visual after-effects are thought to reflect changes in the responses of neural mechanisms underlying face processing (Leopold *et al.* 2001; Rhodes *et al.* 2003, 2004; Webster *et al.* 2004; Leopold *et al.* 2005; Moradi *et al.* 2005) and cannot be attributed to retinal (i.e. low level) adaptations, as the after-effects are robust to differences in the retinal location and size of faces at exposure and post-exposure testing (Leopold *et al.* 2001; Rhodes *et al.* 2003, 2004; Leopold *et al.* 2005) and are disrupted by binocular suppression during exposure (Moradi *et al.* 2005).

Greater experience with upright than inverted faces causes greater configural processing for upright faces (Yin 1969; Diamond & Carey 1986; Bartlett & Searcy 1993; Moscovitch *et al.* 1997; Hancock *et al.* 2000; Maurer *et al.* 2002). Rhodes *et al.* (2004) found that opposite after-effects could be induced for upright and inverted faces simultaneously, and concluded that distinct neural populations code upright and inverted faces. Distinct neural populations may also code subcategories of faces for which expertise-derived configural processing is equivalent (e.g. male and female faces). Intriguingly, contrasting assumptions about the likelihood that distinct neural populations (or 'face-spaces', Valentine 1991; Leopold *et al.* 2001; Rhodes *et al.* 2003, 2004) code male and female faces have been advanced, but never tested. Johnston *et al.* (1997) state that, 'A single face-space is assumed to represent both male and female faces. Indeed, it is hard to see what alternative could reasonably be suggested', while Rhodes *et al.* (2003) state that, 'Male and female faces differ structurally, so we assume a distinct face-space for each sex'.

In order to test these competing assumptions, we investigated whether visual after-effects cross the salient category of face sex by exposing participants to male and female faces realistically transformed in opposite directions (experiment 1) or transformed faces of a single sex (experiments 2 and 3) and testing for visual after-effects in both male and female novel faces. If distinct neural populations code for male and female faces, we would expect exposure to faces of one sex to affect perceptions of that sex only. On the other hand, if the same neural population codes both male and female faces, we would expect exposure to faces of either sex to affect perceptions of both male and female faces equally. In experiment 1, adaptation was to male and female faces where eye-spacing was increased in one sex and decreased in the other sex. In experiment 2, adaptation was to faces manipulated towards ('plus') or away from ('anti') an individual identity (following Leopold *et al.* 2001) and in experiment 3, adaptation was to faces manipulated in sexual dimorphism

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of shape (following Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Little *et al.* 2001; Little *et al.* 2002).

2. MATERIAL AND METHODS

(a) *Participants*

Participants in experiment 1 were 19 women and 8 men (mean age = 24.5, s.d. = 7.12, range = 16–39). 107 Women and 60 men (mean age = 26.7, s.d. = 8.0, range = 18–45) took part in experiment 2. Experiment 3 participants were 11 women and 10 men (mean age = 21.1, s.d. = 1.7, range = 18–26). Different participants took part in each experiment. All participants were volunteers and of European ethnicity.

(b) *General notes on stimuli construction*

All stimuli were constructed using established (Rowland & Perrett 1995; Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Little *et al.* 2001, 2002; Tiddeman *et al.* 2001) techniques for manipulating the appearance of face images in an objective, systematic manner (for technical details including mathematical algorithms see (Rowland & Perrett 1995; Tiddeman *et al.* 2001). Stimuli in experiments 1 and 3 were manufactured from a set of Canadian Caucasian faces (mean age = 18.9, s.d. = 1.8, range = 17–26 years) and stimuli in experiment 2 were manufactured from a separate set of British Caucasian faces (mean age = 19.6, s.d. = 1.6, range = 17–24).

3. EXPERIMENT 1

(a) *Stimuli*

Eye-spacing was manipulated by transforming all images relative to a pair of composite face images, one original image and one image where the points delineating the eyes and eyebrows had been moved one standard deviation out from the mean position (figure 1*a*). Images of 15 male and 15 female faces were standardized on interpupillary distance. For the adaptation conditions, 10 male and 10 female faces were transformed by increasing and decreasing eye-spacing by 200% of the difference between the composites. For the test conditions, five male and five female faces were transformed by increasing and decreasing by 100% of the difference between the composites. Transformed faces were identical in all other regards. Note that the magnitude of the deviation from average for the wide-set version was identical to the magnitude of deviation from average for the close-set version for each identity used in the adaptation and post-adaptation phases of the experiment.

(b) *Procedure*

The two adaptation conditions consisted of passive viewing of 10 male and 10 female faces. Each face was presented twice and each image presentation lasted for 3 s (a total of 2 min). In one adaptation condition, the 10 male faces were transformed in eye-spacing +200% and the 10 female faces were transformed −200%. In the other adaptation condition, the 10 male faces were transformed −200% and the 10 female faces were transformed +200%. In the test phase, participants were shown five novel male and five novel female pairs of faces and were asked to choose the more 'normal-looking' of the pair. Pairs were of the same identity, one transformed in eye-spacing +100% and one transformed −100%. Participants viewed both adaptation conditions

(*a*) (*b*) (*c*)

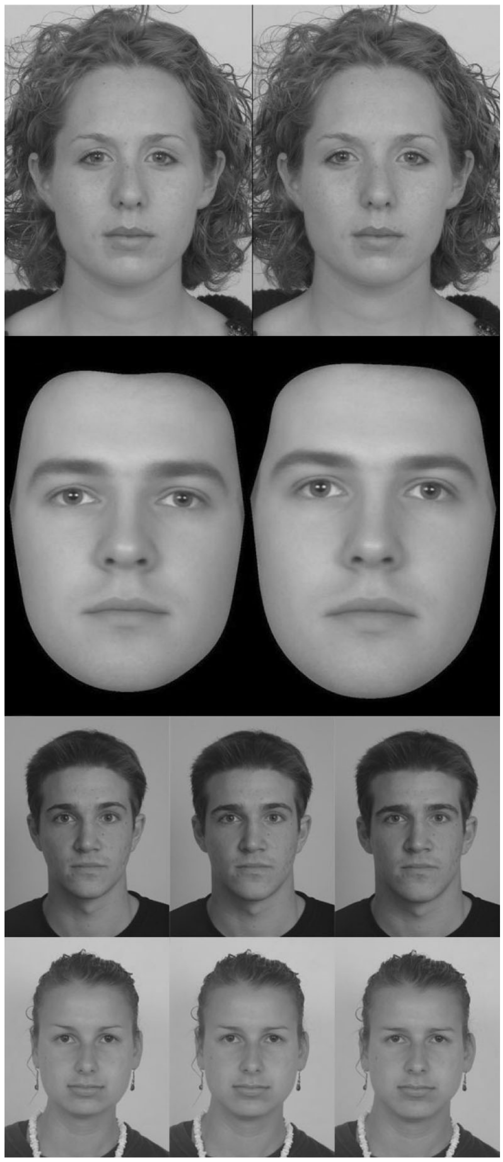

Figure 1. Face images varying in (*a*) eye-spacing, (*b*) identity and (*c*) masculinity. Eye-spacing stimuli were manufactured for experiment 1 by increasing (right) or decreasing (left) the distance between the eye and eyebrow regions of an original image a prescribed distance (100% in this example). Composite faces varying in identity were manufactured for experiment 2 by shifting the shape of a composite face 'plus' (left) or 'anti' (right) the differences in shape between an average male face and an individual male face. Masculinity stimuli were manufactured for experiment 3 by transforming the shape of male and female faces by ±50% of the differences in shape between male and female prototype faces. Feminized (left), unmanipulated (centre) and masculinized (right) faces are shown. All stimuli varied only on the dimension manipulated and did not differ in other regards. See Electronic Appendix A for a high resolution colour version of this image.

(each followed by a test phase) in random order. This procedure and design is analogous to that used by Rhodes and colleagues to test for orientation-contingent adaptation (Rhodes *et al.* 2004).

(c) *Results*

A repeated measures ANOVA (dependent variable: % of trials on which increased eye-spacing was judged as more normal; within-participant factors: test face sex (male,

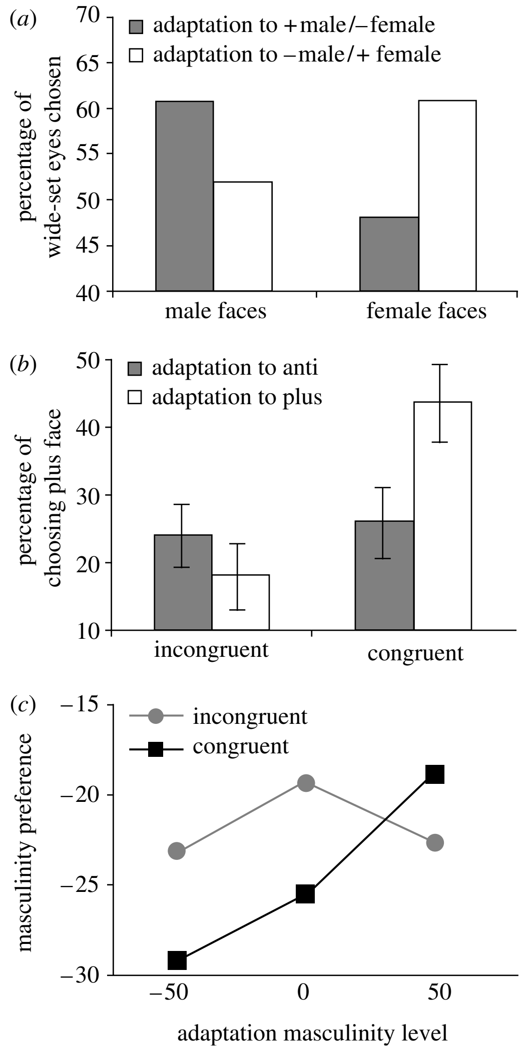

Figure 2. Sex-contingent visual aftereffects following exposure to faces manipulated in (*a*) eye-spacing, (*b*) identity and (*c*) sexual dimorphism of face shape. In experiment 1 (*a*), increased eye-spacing was judged as more normal following the adaptation condition where the congruent sex was presented with increased eye spacing and the incongruent sex was presented with decreased eye-spacing ($F_{1,26}=9.218$, $p=0.005$). In experiments 2 (*b*) and 3 (*c*), preferences for faces similar to those seen in the adaptation phase were stronger when the faces tested were of the congruent sex than when the face tested were of the incongruent sex (experiment 2: $F_{1,158}=7.2$, $p=0.008$; experiment 3: $F_{1,17}=5.02$, $p=0.039$). s.e. is given for between subject comparisons (*b*), but not within subject comparisons (*a*, *c*).

female), adaptation condition (male+200%/female−200%, male−200%/female+200%)) revealed an interaction between test face sex and adaptation condition ($F_{1,26}=9.218$, $p=0.005$, figure 2*a*) such that the image with increased eye-spacing was perceived as more normal after the adaptation condition in which the congruent-sex face was presented with increased eye-spacing than after the adaptation condition in which the congruent-sex face was presented with decreased eye-spacing. No main effects were significant (both $F_{1,26}<0.25$, $p>0.60$).

4. EXPERIMENT 2

(a) *Stimuli*

Twenty-five male and 25 female composite images (either two male or two female images each) were transformed either 30% towards ('plus') or away ('anti') from an individual male face against a composite average male face (50 images), creating 50 images of each type for males and females. In other words, we computed the vector difference between a single male face and an average male face and then used this vector to transform the composites. This method is comparable to that used by Leopold *et al.* (2001) to manipulate facial identity in previous studies of after-effects. A male and a female composite (10 images each) were transformed in the same way, creating two pairs of images for use in the test phase (figure 1*b*). Transforming images 'plus' or 'anti' in this way only changes idiosyncratic features that differentiate the individual face from average and so 'plus' and 'anti' images did not differ in averageness as the transform represents an equal change in difference from the average in opposite directions, that is, the images are equidistant from the average. Changes in masculinity/femininity should be minimal, limited to the variation of our male shape on which the vector is based.

(b) *Procedure*

Participants in experiment 2 were randomly assigned to one of four conditions in the adaptation phase (male 'plus', female 'plus', male 'anti', or female 'anti'). In each condition, participants were asked to rate the attractiveness (on a 7-point scale) of all 25 faces of one sex and identity transformation. After this adaptation phase, participants were presented with two new pairs of face images, one male pair and one female pair, with each pair consisting of one 'anti' and one 'plus' version of the male or female composite. Participants were asked to choose the more attractive face in each pair. All images in the adaptation phase were presented in a random order and in the post-adaptation test phase order and side of image presentation were randomized.

(c) *Results*

A mixed design ANOVA (dependent variable: % choice of plus-face judged as more attractive; within-participant factors: sex congruence between adaptation and test phases (congruent, incongruent); between-participants factors: adapting face sex (male, female), adaptation condition (plus, anti), participant sex (male, female); covariate: age) revealed an interaction between sex congruence and adaptation condition ($F_{1,158}=7.2$, $p=0.008$, figure 2*b*). This demonstrated that visual after-effects (i.e. greater preferences for the 'plus' face in the 'plus' condition than in the 'anti' condition) were only apparent for post-test preferences for faces that were the same sex as in the adaptation phase. No other main effects or interactions were significant (all $p>0.17$). Separate univariate ANOVAs on congruent and incongruent post-test preferences with the same between-participant factors and age as a covariate demonstrated that after-effects only occurred in the congruent condition ($F_{1,158}=5.2$, $p=0.024$) and not in the incongruent condition ($F_{1,158}=0.8$, $p=0.38$). In these analyses, again, there were no other significant main effects or interactions (all $p>0.18$).

5. EXPERIMENT 3

(a) *Stimuli*

Images of 20 individual men and 20 individual women were masculinized and feminized (figure 1*c*) using 50% of the shape differences between a composite average male and female face (20 images each). Masculinity preference stimuli were created in a similar manner, by masculinizing and feminizing the male and female composite faces in 20 steps ranging from 50% feminized to 50% masculinized. These methods have been used in many previous studies assessing preferences for facial masculinity (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Little *et al.* 2001, 2002).

(b) *Procedure*

Participants were first tested for masculinity preferences, as preferences for masculinity are highly variable (Penton-Voak *et al.* 1999; Little *et al.* 2001, 2002) and may affect the extent to which shifts in preference during the adaptation phases could be detected. They viewed both a male and a female face (order randomized) that was randomly chosen from the masculinity preference continuum and were told to move the computer mouse (increasing or decreasing the masculinity of the face) until the image was most attractive. Participants then passively viewed all six adaptation conditions (20 faces that were male or female and feminized, unmanipulated or masculinized, each face presented for 3 s) in random order. After each adaptation phase, participants repeated the masculinity preference task, as described above. The method used in experiment 3 to assess masculinity preference has been used in many previous studies (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Little *et al.* 2001, 2002).

(c) *Results*

A mixed design ANOVA (dependent variable: percentage masculinity preferred; within-participant factors: adaptation face masculinity (masculinized, unmanipulated, feminized), adapting face sex (male, female), sex congruence between adaptation and test phases (congruent, incongruent); between-participants factor: participant sex (male, female); covariates: pre-adaptation % masculinity preferred for male and female faces) revealed a linear interaction between adaptation face masculinity and congruence of face-sex in the adaptation phase and post-adaptation preference test ($F_{1,17}=5.02$, $p=0.039$; figure 2*c*). This interaction was not qualified by any higher-order interactions (all $F_{1,17}<1.34$, $p>0.26$). Although other effects were significant (i.e. pre-adaptation masculinity preferences for male and female faces), these are not relevant to the hypotheses being tested and are not reported in depth here. Further analyses, also with repeated measures ANOVAs, showed that increased adaptation face masculinity only linearly increased masculinity preferences for post-adaptation faces in the congruent condition ($F_{1,17}=14.94$, $p=0.001$) and not in the incongruent condition ($F_{1,17}=0.12$, $p=0.74$).

6. DISCUSSION

Results from all three experiments indicated that visual after-effects occurred only when the sex of the faces at exposure and post-adaptation testing were congruent. Sex-contingent after-effects were observed for a range of face transformations and perceptions. Equivalent effects were observed for adaptation to eye-spacing (experiment 1), identity (experiment 2) and sexual dimorphism (experiment 3) in independent samples of faces using both between- and within-participant designs and were evident in both normality (experiment 1) and attractiveness (experiments 2 and 3) judgements. As previous studies have suggested that after-effects following exposure to faces reflect change in the responses of distinct neural populations that code the stimuli viewed (e.g. the orientation-contingent after-effects observed by Rhodes *et al.* 2004) our findings also suggest that distinct neural populations code male and female faces. The sex-contingent effects observed in all three of our experiments are also further evidence that after-effects due to exposure to faces cannot be explained simply by retinal (i.e. low level) adaptation.

While competing assumptions with regard to the likelihood that distinct neural populations code male and female faces have been advanced in the past (Johnston *et al.* 1997; Rhodes *et al.* 2003), our findings are the first empirical evidence that separate neural populations (or 'face-spaces') code male and female faces. The sex-contingent after-effects observed in all three of our experiments indicate that contingent after-effects, such as those observed for upright and inverted faces (Rhodes *et al.* 2004), are not restricted to comparisons of categories that differ in the extent to which expertise-derived configural processing occurs, but can also occur for categories of faces for which configural processing is equal. This raises the possibility that distinct neural populations may also code other salient subcategories of upright faces (e.g. faces of different ages or ethnicity).

That the after-effects we report are relatively subtle is unsurprising for two reasons. First, the realistic face transformations of the adapting stimuli were themselves subtle (Leopold *et al.* 2001). Second, the duration of the adaptation phases in both studies was relatively brief and after-effects following exposure to faces are known to increase logarithmically as a function of increased duration of the adaptation phase (Leopold *et al.* 2005). Importantly, and as many other researchers have noted, even subtle changes in face preferences may have consequences for a diverse range of social outcomes (Perrett *et al.* 1998; Penton-Voak *et al.* 1999; Langlois *et al.* 2000; Rhodes *et al.* 2003).

Attraction to individuals with parental traits (i.e. imprinting-like effects) has been shown to be specific to faces that are the same sex as the imprinted parent (Perrett *et al.* 2002; Little *et al.* 2003). Additionally, participants' own attractiveness has been shown to be more closely associated with preferences for attractive characteristics in opposite-sex faces than in own-sex faces (i.e. sex-specific condition dependent face preferences, Little *et al.* 2001; Jones *et al.* in press). Our findings suggest that selective adaptation of distinct neural populations that code for male and female faces is a plausible neural mechanism underlying the sex-specificity of these individual differences in face preferences.

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