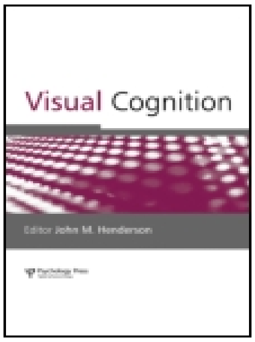

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Adaptation reinforces preferences for correlates of attractive facial cues

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It is generally thought that experience with faces recalibrates preferences to match the population average for recently encountered exemplars. Here, however, we demonstrate that viewing faces biases recalibration of preferences towards characteristics that are common to the more attractive faces that were encountered, rather than characteristics of the unbiased population average. Furthermore, this bias in recalibration of preferences was abolished when participants' attention was directed away from the attractive faces, suggesting it is a consequence of the tendency to look longer and more often at attractive faces than at relatively unattractive faces. These findings suggest a perceptual mechanism that may reinforce directional selection for nonaverage attractive facial characteristics and their correlates, rather than driving stabilizing selection for average traits.

Many studies have demonstrated that recent visual experience influences face perception (Leopold, Rhodes, Müller, & Jeffery, 2005; Little, DeBruine, & Jones, 2005; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003). Exposing participants to faces with a particular configuration (e.g., compressed or expanded features) causes novel faces with this configuration to appear more normal and attractive than would otherwise be the case (Little et al., 2005; Rhodes et al., 2003). Such "aftereffects" are thought to reflect recalibration of perception to match the population average of recently encountered exemplars (Little et al., 2005; Rhodes

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et al., 2003). Recent neuroimaging studies have shown that adaptation to facial identity alters responses in the fusiform face area (Winston, Henson, Fine-Goulden, & Dolan, 2004) and that adaptation to facial expressions and gaze direction alters responses in the superior temporal sulcus (Calder et al., 2007; Winston et al., 2004). These findings suggest face aftereffects reflect changed responses in mechanisms that are relatively specialized for face processing, rather than changed responses in mechanisms that underpin more general aspects of visual perception.

People look longer and more often at attractive faces than unattractive faces (Maner et al., 2003; Shimojo, Simion, Shimojo, & Scheier, 2003). Furthermore, the magnitude of face aftereffects is positively and logarithmically related to the duration of exposure (Leopold et al., 2005). Consequently, perceptual recalibration following exposure to faces may be biased towards physical characteristics that are common to the more attractive faces, rather than matching the unbiased population average for faces that were encountered (DeBruine, Jones, Unger, Little, & Feinberg, 2007). Testing for this bias may reveal a mechanism that could reinforce *directional* selection for nonaverage attractive facial traits and their correlates, rather than driving *stabilizing* selection for average traits (Unger, DeBruine, Jones, Little, & Feinberg, 2006). Indeed, there is compelling evidence that optimally attractive faces deviate systematically from average (DeBruine et al., 2007; Perrett, May, & Yoshikawa, 1994), potentially exerting directional selection pressure on the evolution of human face shape (Perrett et al., 1994). Of course perceptual recalibration is not the only mechanism that may contribute to directional selection for attractive facial traits and their correlates. Both social transmission of face preferences and inherited preferences may also play important roles (Jones, DeBruine, Little, Burriss, & Feinberg, 2007; Laland, Kumm, & Feldman, 1995).

In light of this research, we compared preferences for face shape configurations that had previously been adapted with either attractive or unattractive colour and texture cues. If adaptation biases perceptual recalibration towards characteristics that are common to attractive faces, adaptation should increase preferences for shape configurations adapted with attractive colour and texture more than shape configurations adapted with unattractive colour and texture. Furthermore, if this bias occurs because viewers tend to look longer and more often at attractive than unattractive faces, we predicted that it would be weakened when participants' attention was directed away from the attractive faces during adaptation.

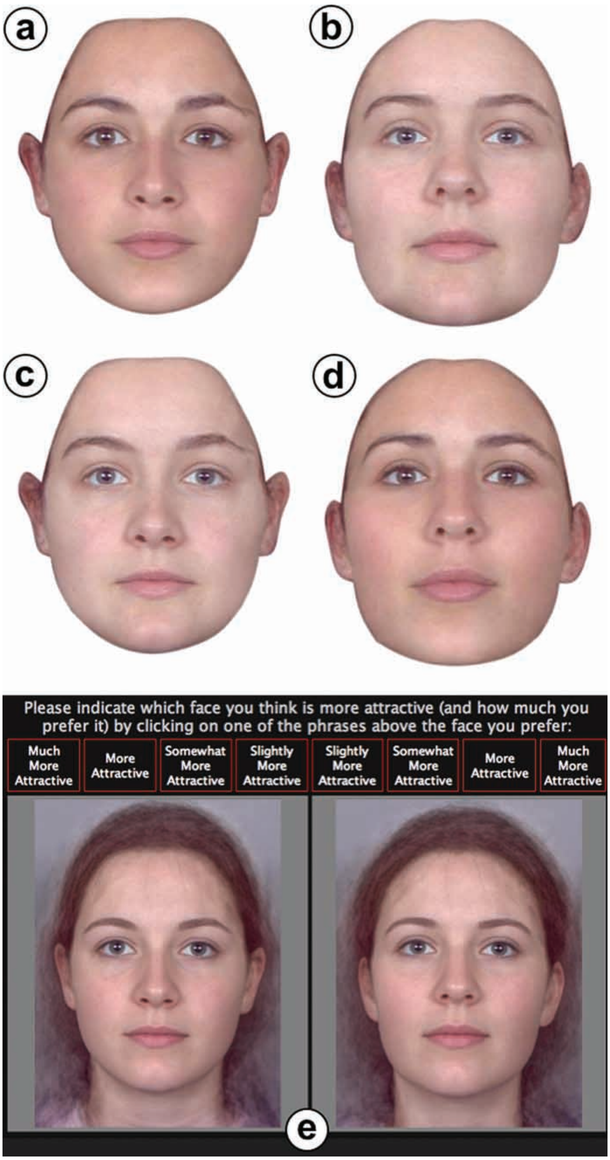

Figure 1. Examples of (a) "plus" shape configuration with attractive colour and texture, (b) "minus" shape configuration with unattractive colour and texture, (c) "plus" shape configuration with unattractive colour and texture, and (d) "minus" shape configuration with attractive colour and texture. Also shown (e) is the interface used to test preferences for the "plus" (left image) vs. "minus" (right image) shape configurations in the pre- and postadaptation tests. To view this figure in colour, please see the online issue of the Journal.

METHODS

Adapting stimuli

Using well-established computer graphic methods described in Tiddeman, Perrett, and Burt (2001), we first manufactured 10 composite faces by averaging the shape, colour, and texture information from face images of 50 White young adult women. Each composite was manufactured from images of five different women.

Next, we used prototype-based image transformation methods (see Tiddeman et al., 2001) to manufacture versions of each composite with particularly healthy-looking colour and texture cues and particularly unhealthy-looking colour and texture cues. This method for systematically manipulating health appearance has been used in many previous studies of preferences, revealing strong attraction to healthy-looking faces (e.g., Jones et al., 2005). Manipulating these colour and texture cues in this way does not alter 2-D face shape.

To confirm that the health manipulation also influences attractiveness judgements, 177 participants (mean age = 23.76, $SD = 5.43$ years; 107 women) were asked to choose the more attractive image in each of the 10 pairs of healthy and unhealthy composites. The side of the screen on which any particular image was shown and the order in which pairs of images were presented were both fully randomized. For each participant, we calculated the percentage of trials on which the healthy image was chosen. Comparing these percentages with what would be expected by chance (i.e., 50%) confirmed that healthy faces were preferred to unhealthy faces: One-sample t-test, $t(176) = 30.30$, $p < .001$, $M = 92.99\%$, $SEM = 1.42$.

Following Little et al. (2005), "plus" and "minus" identity versions of the attractive and unattractive composites were manufactured by adding (to create "plus" versions) or subtracting (to create "minus" versions) 60% of the linear differences in 2-D shape between a female prototype and an individual female identity. Manipulating 2-D shape in this way does not alter colour and texture. The same identity was used to manufacture all "plus" and "minus" images. Forty face images were manufactured in total: "Plus" versions of the 10 attractive composites, "minus" versions of 10 attractive composites, "plus" versions of the 10 unattractive composites, and "minus" versions of the 10 unattractive composites. Masked versions of these images were shown to participants during the adaptation phase of the study (Figure 1a–d).

Test stimuli

A female composite was manufactured by averaging the shape, colour, and texture information from 20 face images (see Tiddeman et al., 2001, for methods). "Plus" and "minus" identity versions were then manufactured by transforming the composite by $+/-30\%$ of the linear differences in 2-D shape between the prototype and identity used to manufacture the adapting stimuli (Figure 1e). Little et al. (2005) have also previously used test stimuli that were manipulated more subtly than adapting stimuli when investigating face aftereffects.

Procedure

Participants ($N = 210$; age: $M = 20.45$ years, $SD = 2.05$; 137 women) first completed a *preadaptation test* where they viewed the pair of test stimuli and indicated which face was more attractive and how much more attractive it was by choosing from the options "much more attractive", "more attractive", "somewhat more attractive", or "slightly more attractive" (Figure 1e). The side of presentation was fully randomized. Test stimuli differed in shape configuration, but had identical colour and texture. Thus, the preadaptation test measured participants' relative preference for the "plus" versus "minus" shape configurations, not for attractive versus unattractive colour and texture.

Next, in the *adaptation phase*, participants viewed a 60 s slideshow of 10 pairs of faces, each pair consisting of the attractive and unattractive versions of one of the 10 adapting stimulus identities. Pairs were shown for 3 s each. Each pair was shown twice, once with the attractive version on the left and once with the attractive version on the right, to control for possible effects of left-side biases in attention (Uttl & Pilkenton-Taylor, 2001) and/or face processing (Burt & Perrett, 1997). The order in which pairs of images were shown was fully randomized. To control for possible effects of retinotopic adaptation, images shown in the adaptation phase were resized to 80% of the size of the test stimuli (following DeBruine et al., 2007).

For half of the participants, the "plus" configuration was shown with attractive colour and texture and the "minus" configuration was shown with unattractive colour and texture. For the other half of participants, the "plus" configuration was shown with unattractive colour and texture and the "minus" configuration was shown with attractive colour and texture. Additionally, half of the participants were told to "Pay particularly close attention to the face with the green square" and all of the unattractive versions were shown with a green square in the upper left corner of the image (the directed attention viewing condition). The other half of the participants was not given this instruction during the slideshow and did not see any images with a green square (the unconstrained viewing condition). These conditions were fully counterbalanced between participants. In other words, 55 participants in the directed attention viewing condition were adapted to attractive “plus” versions and unattractive “minus” versions, 54 participants in the directed attention viewing condition were adapted to unattractive “plus” versions and attractive “minus” versions, 52 participants in the unconstrained viewing condition were adapted to attractive “plus” versions and unattractive “minus” versions, and 49 participants in the unconstrained viewing condition were adapted to unattractive “plus” versions and attractive “minus” versions. Allocation of participants to conditions was randomized.

Immediately after the slideshow, participants completed a *postadaptation test*, which was identical to the preadaptation test.

The study was administered online. Previous studies have demonstrated that online and laboratory tests of face preferences (e.g., Jones et al., 2005) and aftereffects (DeBruine et al., 2007) produce equivalent results.

Initial processing of data

Responses on the pre- and postadaptation tests were coded as the strength of preference for the face shape configuration (i.e., “plus” or “minus”) that was adapted with attractive colour and texture cues using the following scale:

- 0, 1, 2, or 3 = The configuration adapted with *un*attractive cues was judged “much more” (= 0), “more” (= 1), “somewhat more” (= 2), or “slightly more” (= 3) attractive than the configuration adapted with attractive cues.
- 4, 5, 6, or 7 = The configuration adapted with attractive cues was judged “slightly more” (= 4), “somewhat more” (= 5), “more” (= 6), or “much more” (= 7) attractive than the configuration adapted with *un*attractive cues.

RESULTS

A mixed-design ANOVA (dependent variable: Strength of preference for shape configuration adapted with attractive cues; within-subjects factor: Phase [preadaptation test, postadaptation test]; between-subjects factors: Adaptation condition [“plus” configuration adapted with attractive cues, “plus” configuration adapted with unattractive cues], viewing condition [unconstrained, directed attention], participant sex [male, female]) revealed the predicted interaction between phase and viewing condition, $F(1, 202) =$

5.81, $p = .023$ (Figure 2). This interaction was not qualified by any higher order interactions (all $F < 1.4$, all $p > .23$). Preferences for the configuration adapted with attractive cues were stronger at post- than pretest in the unconstrained viewing condition, paired-samples t-test, $t(100) = 2.59$, $p = .011$, but not in the directed attention condition, $t(108) = -0.53$, $p = .599$.

DISCUSSION

Consistent with our predictions, unconstrained visual experience increased preferences for face shapes adapted with attractive colour and texture cues more than face shapes adapted with unattractive colour and texture cues. By contrast, no such bias in recalibration of preferences was observed when participants' attention was directed away from the faces with attractive colour and texture cues. This latter finding suggests that biased perceptual recalibration following unconstrained viewing occurs because participants look longer and more often at attractive than unattractive faces (Maner et al., 2003; Shimojo et al., 2003). One might have anticipated that the effect observed in the directed attention condition would be an inverted version of the effect observed in the unconstrained viewing condition. An inverted effect was not necessarily expected in the directed attention condition, however, since we instructed participants to pay particularly close attention

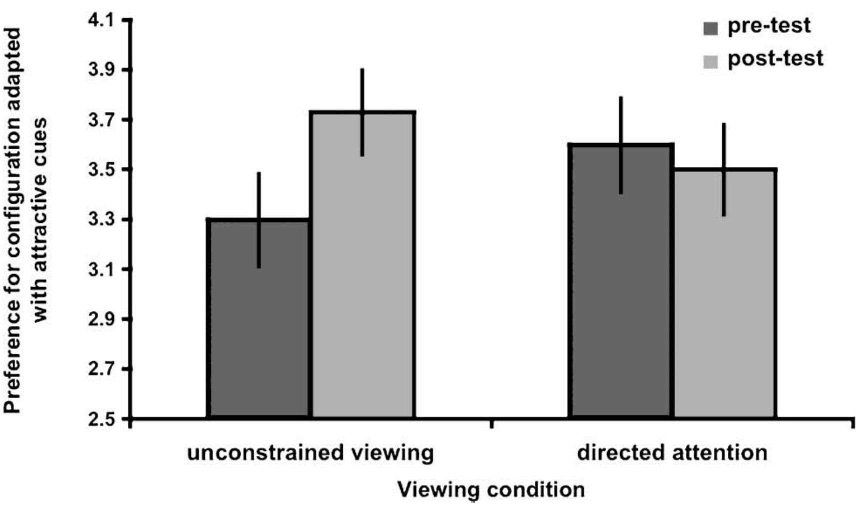

Figure 2. The interaction between viewing condition and phase. Bars show means and SEMs. While adaptation increased preferences for configurations seen in conjunction with attractive cues when viewing was unconstrained, no such effect was observed when participants' attention was directed towards unattractive faces during adaptation.

to the faces that were paired with a green square rather than to attend exclusively to these images.

Previous studies of the effects of visual experience on face preferences have emphasized recalibration of preferences to match the physical characteristics of the population average for the adapting faces (Little et al., 2005; Rhodes et al., 2003). Our findings, however, suggest that adaptation biases preferences towards characteristics common to the more attractive of the seen faces. Importantly, we show that visual experience biases recalibration towards *correlates* of attractive facial cues (e.g., face shape configurations that were paired with attractive colour and texture cues), rather than towards characteristics that are attractive themselves. Thus, our findings are not incompatible with studies showing that increasing experience with extremely attractive faces can decrease their attractiveness by making them appear more normal (e.g., Biederman & Vessel, 2006; DeBruine et al., 2007). Interestingly, selective attention to attractive faces (Waitt, Gerald, Little, & Kraiselburd, 2006) and adaptation of neurons coding visual stimuli (Carandini, Barlow, O'Keefe, Poirson, & Movshon, 1997) have also been observed in nonhuman primates, raising the possibility that recent visual experience might also bias recalibration of nonhuman primates' preferences in a similar way. While we have framed our study in terms of visual adaptation, an alternative mechanism for our findings is learned associations between visible skin condition and 2-D face shape. Further research is needed to investigate this alternative explanation for our findings. Similarly, further research is needed to establish the extent to which our findings for visual experience with face configurations seen with attractive colour and texture cues generalize to configurations seen with attractive 2-D shape cues.

Although our findings suggest a mechanism that reinforces preferences for nonaverage attractive facial characteristics, they do not explain how preferences for such traits initially emerge. Preferences for attractive faces may be present from birth (Slater & Kirby, 1998) and/or reflect learned associations between facial cues and traits that are desirable in partners and associates (Bereczkei, Gyuris, & Weisfeld, 2004). Furthermore, social learning also appears to play an important role in the development of face preferences (Jones et al., 2007; Laland et al., 1995). Perrett et al. (1994) noted that preferences for nonaverage characteristics occur and might exert directional selection pressure on the evolution of human face shape. Here we extend this proposal, suggesting that biased perceptual recalibration following recent visual experience may reinforce directional selection for nonaverage attractive face shapes, rather than driving stabilizing selection for average traits.

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