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Original Article

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Abstract:

Experience-dependent changes in mate choice preferences may confer an evolutionary benefit by shifting preferences towards traits that are advantageous for specific environments. Previous studies have demonstrated that prolonged exposure to one type of face or body biases perceptions of subsequently viewed faces and bodies, respectively, but only one study has found face after-effects produced by adaptation to body images. We tested whether preferences in facial adiposity (perceptions of weight from the face) were affected by viewing heavy or light bodies. We first assessed facial adiposity preferences by asking Caucasian participants (n=60) to transform three-dimensional female faces along a body mass index (BMI) continuum until they reached optimal attractiveness. Participants then viewed heavy or light body images with their faces cropped out in a distracter task before repeating the face preference task. Participants who viewed heavy bodies shifted preferences toward significantly higher facial adiposity, while those who viewed the light bodies showed no significant overall shift. Findings are discussed in terms of potential neural populations involved in producing after-effects. Specifically, we hypothesise after-effects are unlikely to reflect mechanisms responsible for low-level

sensory mechanisms and instead reflect high-level integration of information relevant to mate choice.

Keywords: adaptation, after-effects, body mass index, 3D faces

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Introduction

Visual adaptation occurs after prolonged exposure to stimuli leads to adaptation of the visual system. Adaptation produces a bias in perceptions of subsequently viewed stimuli, known as a visual after-effect. Basic visual after-effects have been well-documented after adaptation to motion, contrast, spatial frequency, and orientation (Boynton and Finney, 2003; Durgin and Proffitt, 1996) and occur in early visual processing stages, including the retina (Kohn and Movshon, 2003). These 'low-level' visual after-effects are largely specific to the visual parameters, such as size, orientation and retinal position of the stimuli adapted to.

Facial after-effects occur when prolonged exposure to unusual faces leads to biased perceptions of subsequently viewed faces. These effects are relatively invariant to changes in visual stimuli that restrain low-level after-effects. Facial after-effects occur at image area changes of up to 4 octaves (Zhao and Chubb, 2001; Anderson and Wilson, 2005), as well as orientation changes up to 90º (Watson and Clifford, 2003; Rhodes, Jeffery, Watson, Clifford and Nakayama, 2003; Rhodes et al., 2004) and changes in retinal position up to 6º (Leopold, O'Toole, Vetter and Blanz, 2001; Kovács, Cziranky, Vidnyanszky, Schweinberger and Greenlee, 2008).

The strength of facial after-effects can show attenuation with large retinal

differences between the exposure and post-exposure faces (e.g. Zhao and Chubb, 2001). Despite this, the fact that after-effects show any robustness to variation in stimulus patterns demonstrates involvement of neural processing at a later stage in the visual pathways than found in low-level adaptation. The perceptual adaptation of face patterns is often considered to reflect adaptation of neural populations selectively responsive to faces in the occipital and temporal cortex (Kovács et al., 2006, Little, DeBruine and Jones, 2005; Rhodes et al., 2003), such as the fusiform face area (Sergent, Ohta and Macdonald, 1992; Kanwisher, McDermott and Chun, 1997), although the correspondence between perceptual and neural mechanisms is a matter of debate (Sawamura, Orban and Vogels, 2006; Barraclough and Perrett, submitted).

Adaptation to human stimuli is not limited to faces. Winkler and Rhodes (2005) found that viewing heavy bodies biased subsequent perception of body normality and attractiveness. Furthermore, Glauert, Rhodes, Byrne, Fink and Grammer (2009) found that women with higher body dissatisfaction were less prone to after-effects after adapting to heavy bodies. That after-effects in viewing body stimuli are contingent on factors like body satisfaction again suggests that adaptation can involve higher-order neural mechanisms.

Adaptation to faces and bodies may serve an evolutionary function. Face and body attractiveness provide indicators of mate quality (for review see Fink and Penton-Voak, 2002; Rhodes, 2006; Thornhill and Grammer, 1999). Criteria for mate quality differs by culture and environment, though, as is reflected in cross-cultural variation in perceptions of attractiveness. Indeed, masculinity preferences for male faces vary by cultural differences in paternal investment (Penton-Voak, Jacobson and Trivers, 2004) and health (DeBruine, Jones, Crawford, Welling and Little, in press). Likewise, preferences for higher body-mass

index (BMI, a measure of weight scaled to height) are predicted in environments where resources are relatively scarce, as adiposity signals an ability to obtain food. Higher BMI is preferred in resource-scarce cultures, whereas resource-abundant cultures prefer much lower BMI bodies (Swami and Tovée, 2007). Preferences for BMI can be flexible. Tovée, Swami, Furnham and Mangalparsad (2006) found that body preferences among Zulu South Africans living in the UK were lower in BMI compared to Zulus living in South Africa. Such preference shifts would be advantageous for selecting optimal mates for a given environment, and may reflect an evolved plasticity or the impact of learning in mate choice.

Recent studies have found that facial adiposity, or perceptions of weight from faces, plays an important role in perceptions of health and attractiveness. In a British Caucasian sample, Coetzee, Perrett and Stephen (2009) had participants rate faces for weight and found that such facial adiposity ratings correlated with BMI. Facial adiposity also predicted perceived health and measures of real health. These findings demonstrate that facial adiposity is a reliable cue to health and should be considered alongside facial masculinity, symmetry, averageness, and skin texture as a component of face attractiveness. Indeed, adiposity is one of several traits influencing attractiveness that is correlated across the face and body (Hume and Montgomerie, 2001; Thornhill and Grammer, 1999; Gangestad and Thornhill, 2003).

Given the evolutionary hypotheses behind visual adaptation in both faces and bodies, and given the consistency of face and body cues, it is possible that adaptation to one domain may have after-effects on the other. Ghuman, McDaniel and Martin (2010) found that adapting to bodies of a particular sex biased subsequent face perceptions toward the opposite sex. They also found that face after-effects were not produced after adaptation to

stereotypically gender-specific objects (football helmets, purses, etc; Ghuman et al., 2010). Additionally, Kovács et al. (2006) did not find face after-effects after adaptation to human hands. Thus, face after-effects appear to occur after adaptation to bodies, but not after adaptation to hands or inanimate objects. This suggests that cross-adaptation only occurs for mate choice relevant stimuli. Indeed, after-effects in face viewpoint are altered by gaze orientation (Bi, Su, Chen and Fang, 2009), which has been shown to modulate perceptual processing of facial attractiveness (Kampe, Frith, Dolan and Frith, 2001; Jones, DeBruine, Little, Conway and Feinberg 2006).

Functional brain imaging shows that the sight of bodies activates several cortical regions. These include the 'extrastriate body area' of the lateral occipitotemporal cortex (Downing, Jiang, Shuman and Kanwisher, 2001); the ventral 'fusiform body area' (Schwarzlose, Baker and Kanwisher, 2005), and several lateral locations along the superior temporal cortex (STS; Allison, Puce and McCarthy, 2000; Puce and Perrett, 2003). The sight of faces activates neighbouring and, to some extent, overlapping cortical regions (Pinsk et al., 2009, Yovel and Kanwisher, 2004). Indeed, within the STS, 60% of the neurons responsive to sight of the face show additional sensitivity to the sight of the body (with the head occluded from sight; Wachsmuth, Oram and Perrett, 1994; Perrett, Hietanen, Oram and Benson, 1992). To the extent that after-effects involve these neural populations, they may be expected to cross between face and body.

Several studies have evaluated the timecourse of face adaptation. Rhodes, Jeffery, Clifford and Leopold (2007) found a logarithmic build-up and exponential decay for facial after-effects, much like those found in low-level after-effects that last for only a few minutes (Harris and Calvert, 1989; Hershenson, 1989; Krauskopf, 1954). After-effects may

reflect a variety of neural mechanisms lasting over different time scales, from seconds to days (Barraclough and Perrett, submitted). Carbon et al. (2007), however, found that adaptation to distorted familiar faces can produce after-effects more than 24 hours later. Furthermore, they found that these after-effects could generalise to different images of the same person. If visual adaptation serves an evolutionary purpose, we would expect after-effects to last long enough to affect perceptions of subsequent mate choice stimuli.

In the present study, we tested whether or not body size would produce after-effects in preferences (preference after-effects) for facial adiposity. If adaptation occurs at high-order neural mechanisms that integrate mate choice cues, exposure to heavy or thin bodies should produce visual after-effects in the perceived attractiveness of faces with different facial adiposities. Specifically, adaptation to heavy bodies would produce preferences for higher facial adiposity, and adaptation to light bodies would produce preferences for low facial adiposity. We also tested if after-effect strength was affected by the elapsed time between adaptation to bodies and the subsequent face preference task. If adaptation serves a reproductive benefit, we would expect after-effects to be relatively long in duration and to diminish little over time of testing.

Materials and Methods

Participants:

Sixty Caucasian undergraduate students (46 women, mean age = 20.32, SD = 1.80) from the University of St Andrews, Scotland, participated in the study for course credit. All participants gave informed consent.

Stimuli:

We created face stimuli using images of students' faces captured with a three-dimensional face scanner (3DMcranial systems, England), which provides a depth map of the 3-D structure and surface colouration (Figure 1). Once captured, the images can be rotated to show faces from different viewpoints. All photographed individuals posed with their hair pulled back, and were asked to maintain a neutral expression. All photographed volunteers had their heights measured and BMIs recorded with a Tanita SC-330 body composition analyser (Tanita, Holland).

Fifty-eight facial landmarks were manually defined on each captured face image. The facial landmarks were used as a basis for averaging and transforming (using custom built software: Morph-Analyser; Perception Lab) in an equivalent manner to that used for two-dimensional face image processing (see Tiddeman, Burt and Perrett, 2001; Rowland, Perrett, Burt, Lee and Akamatsu, 1997; Blanz and Vetter, 1999).

Individual three-dimensional face shapes can be combined together to create a facial surface representative of a set of individuals. To achieve this, depth maps for each captured face are first re-sampled to a standard face. This step establishes an equivalent number of depth samples between corresponding facial landmarks in any two faces; in effect it establishes the correspondence between locations over the entire surface of all faces in the image collection. Depth values for corresponding loci on the facial surfaces can then be averaged across component individuals. Maps for the colouration of the facial surface can be separately averaged, and wrapped into alignment with the average depth maps.

For the experiment, we first created two faces to use as 'prototypes' (averages of low and high facial adiposity for women) for use in subsequent transformations of target Figure 1.

Figure 1. Three-dimensional face images, shown from centre-view and left and right profiles for faces with low facial adiposity (top row, BMI=18), medium facial adiposity (middle row, BMI=22), and high facial adiposity (bottom row, BMI=26). The faces rotate from side to side, thus participants are able to view the face at all angles.
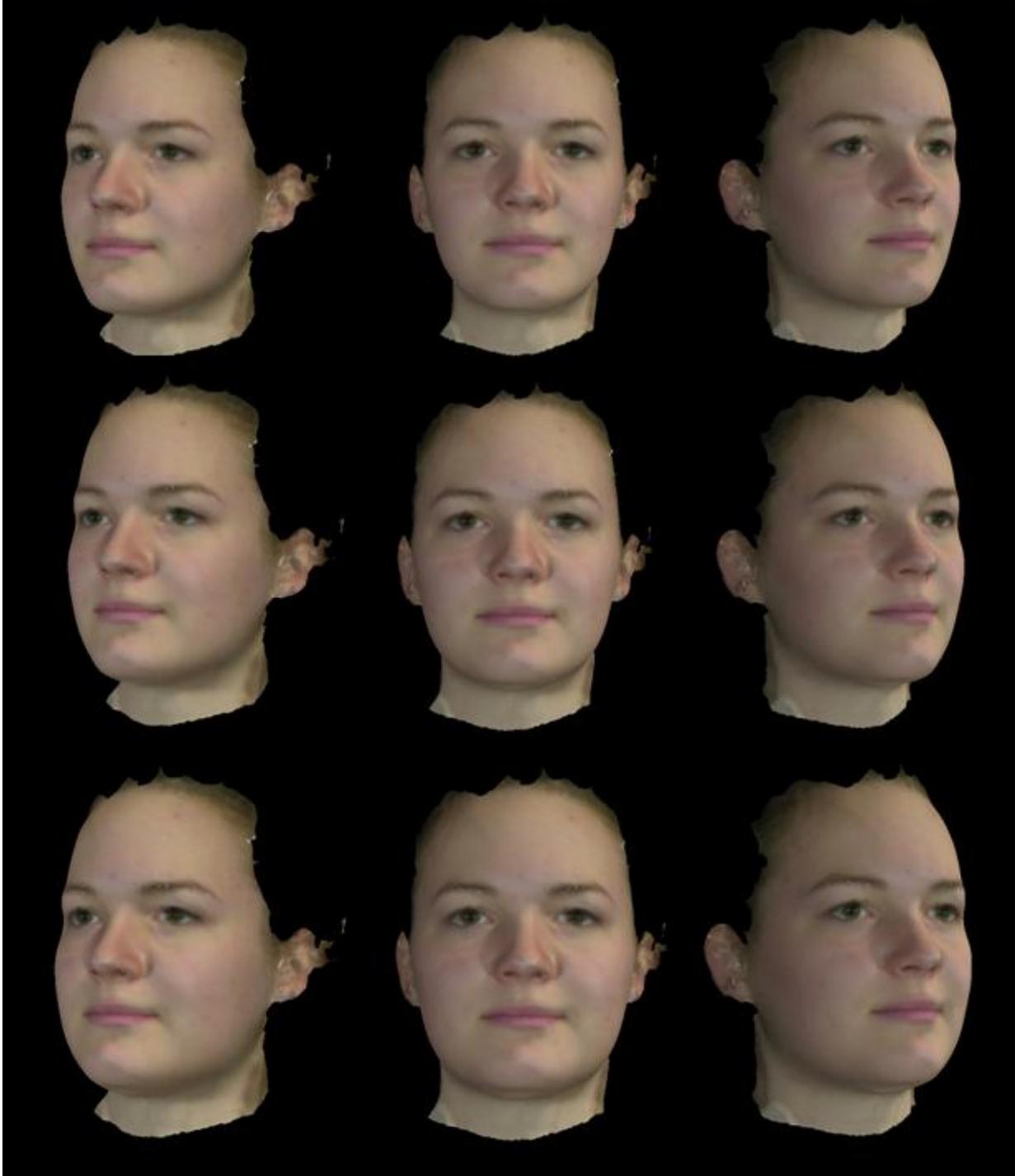
faces. Each prototype was made by averaging 10 individual images. The low-adiposity prototype was made of 10 faces of women with low BMIs (mean = 18.3, SD: 0.37, range:17.8-18.8), and the high-adiposity prototype was made from participants with high BMIs (mean = 29.9, SD: 2.34, range: 27.5-35.1). Next, we created composite images by averaging three same-sex faces of individuals with similar BMIs. The composites of women's faces were created as stimuli to be manipulated by participants in the experiment. Composites were used to eliminate any structural or textural outlier that may be apparent in any individual image, as well as to eliminate the risk of participant recognition of any particular face. The four female composites had average BMIs of 18.0, 21.9, 25.4 and 32.5. Multiple composites were used in the experiment to avoid any confounds that could occur by using one particular stimulus.

To test for facial adiposity preferences, a program was used that allowed participants to manipulate the adiposity of the composite face images. Participants are shown a composite face and can move a slider that transforms the 3-D shape towards one prototype. This occurs by taking the points on the composite face and moving them by the difference of the corresponding points on the prototype faces. This is again similar to the transformation used in two-dimensional face manipulation software (Tiddeman et al., 2001), used in studies of face preferences (e.g. Perrett et al., 1998). To calculate the BMI represented by the facial adiposity chosen as most attractive, the percentage of transformation to the original composite was multiplied by the BMI difference represented by the high and low adiposity prototypes, and then added to the original composite's BMI. The three-dimensional images were rotated 30º from side to side at 25º a second, allowing participants to use motion parallax to perceive the 3-D surface shape of the front and sides

of each face without stereo-viewing glasses (Figure 1).

Images of low- or high-weight women were used for adaptation (Figure 2). The images, originally full length photographs, were cropped so the faces were not shown. Two conditions were created, one showing participants images of 21 heavy bodies (UK body size ~14-16), and the other showing images of 25 light bodies (UK body size ~4-6). Images of bodies were taken from a variety of websites showing heavy- and light-weight models. The images varied in terms of position within frame, posture, perspective view (profile, front), and type of clothing (e.g. – bikini, full-length dress; all models wore some degree of clothing; see Figure 2). All models were oriented with their heads toward the top of the screen (models were standing except two in the heavy condition - one sitting and one lying down). The vertical height of the images ranged from 18º to 72º.

Procedure:

Each of the four composites was shown at the same size (vertical length: 13º) and rate of rotation, and was presented three times in pseudo-randomised order. Each participant saw each composite three times, thus each participant manipulated twelve faces. Participants were presented with composite 3-D faces one at a time and asked to "Please manipulate the face until you think it is most attractive".

Participants then completed the adaptation task in which they viewed either the heavy or light body condition. Thirty-two participants (23 females) viewed the light condition, and 27 (22 females) viewed the heavy condition. The design was between-subjects, as participants viewed only either the heavy or light condition. The light condition consisted of 25 images, and the heavy consisted of 21 images, both repeated twice. Participants were asked to identify whether each body belonged to a person of East Asian

Figure 2. Examples of light bodies (top row) and heavy bodies (bottom row) typical of those used for adaptation. These specific images were not used in the experiment, but accurately represent the types of images used.

(a)

(b)

or Caucasian ethnicity as a distracter task to ensure they were naïve to the purpose of exposure to the body images.

After viewing the body images, participants were asked to repeat the facial adiposity preference manipulation task. Composites were shown at the same size and rotation rate as the first task, and order was again randomised.

Results

We defined preference after-effects (change in facial adiposity preferences before and after adaptation to bodies) as the BMI represented by adiposity preference after adaptation minus the BMI preference before adaptation. Before adaptation, the mean facial adiposity preferred across all evaluators represented a BMI of 19.6 (SD=2.3). Preferences were not significantly different between male and female evaluators [t(57)= -0.64, p=0.52].

Overall, adaptation to bodies produced preference after-effects that were significantly different from zero [t(58)=2.19, p=0.03]. This suggests that exposure to bodies altered subsequent preferences for facial adiposity.

Participants who viewed the heavy condition showed a shift in preferences towards higher facial adiposity, representing an average BMI of 20.1 (SD = 2.7). This is equivalent to a change of 0.4 BMI units after adaptation to heavy bodies. A matched pair t-test showed that the pre- and post-adaptation BMI preference were significantly different [t(26)=-2.26, p<0.03]. The difference between pre- and post-adaptation preferences were not significantly different between sexes [t(25)=-0.40, p>0.69].

Participants who viewed the light condition showed a mean facial adiposity preference that represented a BMI of 19.5 (S.D. = 2.4); a slight but non-significant

reduction from the pre-adaptation preferences [t(31) = 0.80, p>0.43]. The difference between pre- and post-adaptation preferences were not significantly different between sexes [t(30) = 0.93, p>0.34].

An independent-samples t-test was used to test whether preference after-effects were significantly different in the two adaptation conditions. Those who viewed the heavy condition showed significantly greater preference after-effects compared to those who saw the light condition [t(57)=-2.31, p<0.02] (Figure 3).

We wanted to test if the strength of the after-effect was affected by order of presentation. If the after-effects have very short lifespans, there should be attenuation of after-effect strength for faces presented toward the end of the post-adaptation test phase. As there were 12 faces used for post-adaptation adiposity preferences, we grouped testing faces into the first six and last six faces presented after adaptation. A repeated-measures ANOVA found no differences in after-effect size between the first-six and last-six groups in either the heavy [F(1)=0.50, p=0.39] or light [F(1) = 7.50, p=0.83] conditions. Thus, the preference after-effects were not significantly affected by the order of face presentation. This demonstrates that the elapsed time between adaptation and testing did not alter after-effect strength.

Figure 3. Mean preference after-effects after viewing light- and heavy-body conditions.
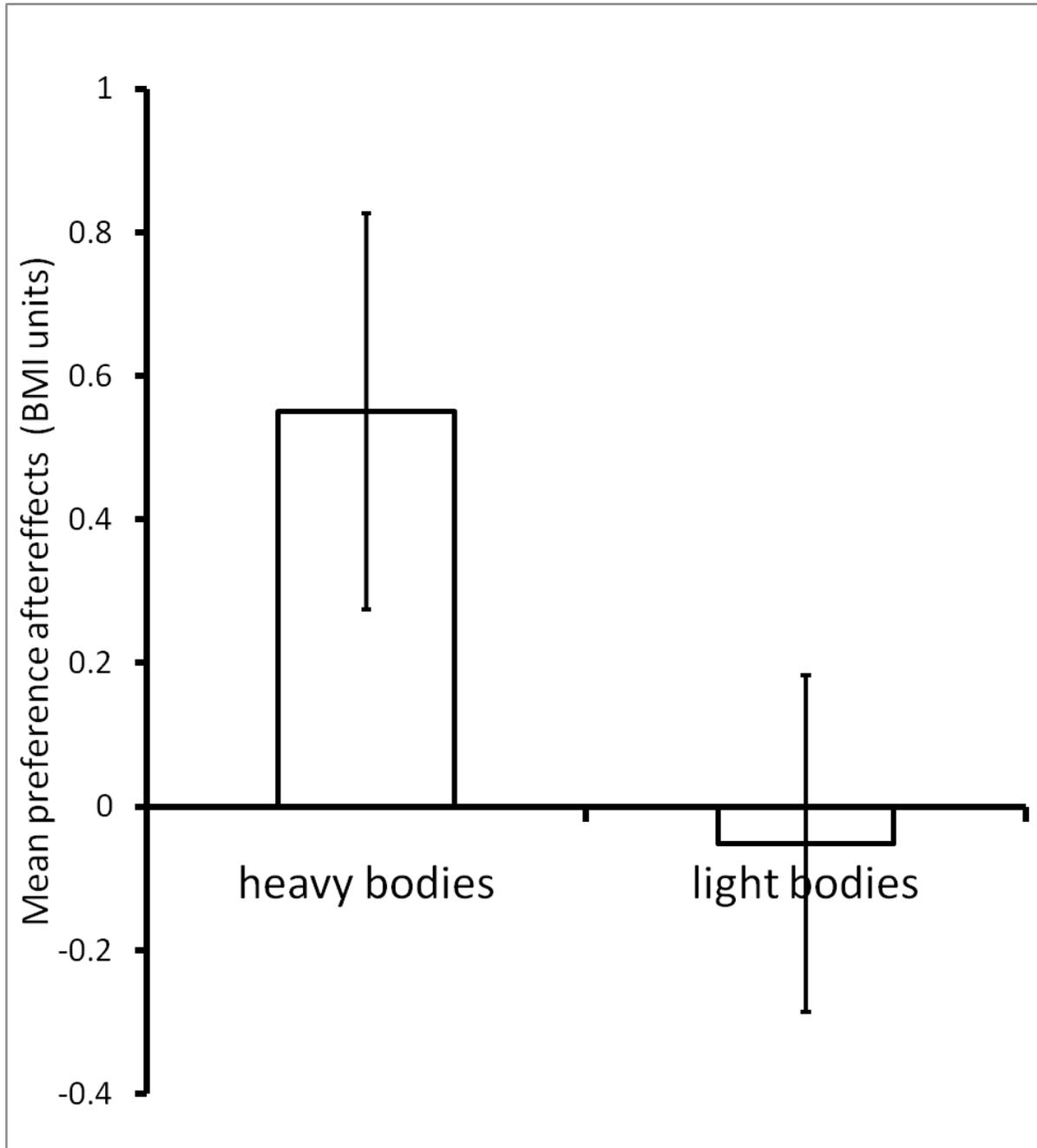
Discussion

The results indicate that viewing bodies can alter attraction to face shape. Participants preferred faces higher in facial adiposity after viewing heavy bodies for approximately 5 minutes. On average, participants preferred faces lower in facial adiposity after viewing light bodies, but this preference after-effect was not significant.

The BMI represented by the mean facial adiposity preference before adaptation (19.6) is in accordance with the optimal BMI of 19-20 found in previous studies of body preferences (Tovée and Cornelissen, 2001; Tovée, Maisey, Emery and Cornelissen, 1999; Tovée, Reinhart, Emery and Cornelissen, 1998). This suggests that facial adiposity in three-dimensional images accurately represented body BMI. The pre-adaptation preferences also agree with other studies of face preferences using two-dimensional face images varying in adiposity (Coetzee et al., 2009; Coetzee, Burt, De Grauw, Tiddeman and Perrett, submitted). The agreement between two- and three-dimensional images is important, as several studies have used three-dimensional bodies (Brown et al., 2008; Smith, Cornelissen and Tovée, 2007), but few have used three-dimensional faces. Results from three-dimensional images that align with those from two-dimensional images helps cross-validate the different techniques and encourages further use of three-dimensional face image technology.

We cannot completely rule out the possibility that the effects found here are due to low-level adaptation. Adaptation to shapes has been shown to produce after-effects on the aspect ratios of test shapes (for example, adapting to a horizontal rectangle may make a subsequently viewed square appear to have a lower width-to-height ratio; Regan and

Hamstra, 1992). These effects have been found to generalise from square to elliptical shapes, and to be resistant to 16-fold changes in shape area (Regan and Hamstra, 1992). It is possible that the heavier bodies used in the current study may have a higher width-to-height ratio than lighter bodies, and adaptation to such a shape may produce preference after-effects for faces with higher width-to-height ratios (faces with higher facial adiposity). Despite this, the variation in body and face images in this study is likely to extend beyond simple shape differences. Our body images not only varied in size, but also body posture, clothing, and view (frontal or side-view). Furthermore, the faces used for the preference task rotated from side to side, thus the shape of the face image changed throughout viewing. The after-effects also spanned from stationary two-dimensional body images to rotating three-dimensional faces. The high degree of variation in both face and body images makes it unlikely that after-effects are due to a low-level adaptation. Even if low-level adaptation is responsible for the after-effects, then such effects should apply to real-world situations and may still reflect neural processes affecting mate choice.

The current study provides evidence that adaptation likely occurs at high-level neural populations where body and face information are integrated. The adaptation effects could involve neural mechanisms conjointly sensitive to body and facial information (e.g. Wachsmuth et al., 1994; Perrett et al., 1992; Ghuman et al., 2010). After-effects spanning face and body cues could reflect mechanisms beneficial to mate choice decisions. Preference after-effects may be useful in selecting desirable traits for a given environment. Preferences for faces (Penton-Voak et al., 2004) and bodies (Swami and Tovée, 2007) change from culture to culture. Indeed, face and body cues often correlate with other cues to mate quality from other domains, such as audition, motion, and odour (Feinberg,

DeBruine, Jones and Little, 2008; Hume and Montgomerie, 2001; Thornhill and Grammer, 1999; Rikowski and Grammer, 1999, Cornwell et al., 2004, but see Peters, Rhodes, and Simmons, 2007).

Interestingly, whereas the heavy-body condition produced significant after-effects, the light-body condition did not. This could be due to the frequent exposure to light female bodies present in Western culture. The female body images used in the light-body condition may have been similar to those frequently shown by the media; it is possible that participants' preferences were already 'tuned' to such bodies before adaptation. One way of testing this explanation would be to run the experiment in a culture not inundated with media portraying light-bodied women. Individuals in such a culture should show aftereffects of viewing light bodies similar to that for heavy bodies found here.

For body to face after-effects to be useful in an evolutionary sense, the adaptation must last long enough to view multiple bodies or faces. Several face (Zhao and Chubb, 2001) and body (Glauert et al., 2009; Winkler and Rhodes, 2005) adaptation studies have presented their adapting stimuli between test trials to maintain after-effects. In the current study, all bodies used for adaptation were shown before subsequent test faces. Face after-effects follow a logarithmic build-up and exponential decay (Rhodes et al., 2007), but short exposures to distorted familiar faces can produce after-effects more than a day later (Carbon et al., 2007). There was no evident decay of after-effect strength during testing in the present study. Such results support the idea that body-face after-effects could be useful in a mating context. Furthermore, in 'real-world' situations, viewing several bodies over time may 'update' adaptation and retain after-effects (Rhodes et al., 2003).

Further studies could assess how robust body-face after-effects are in terms of

mating cues. The current experiment investigates after-effects based on BMI and facial adiposity; it is possible these after-effects could translate to other body-face cues, as well. For example, exposing participants to muscular male bodies (Little, Jones and Burriss, 2007) could produce preference after-effects biased toward facial masculinity, as the two cues are related in terms of underlying testosterone (Penton-Voak and Chen, 2004; Roy et al., 2002; Neave, Laing, Fink, Manning, 2003). Similarly, viewing women with curvaceous bodies could produce after-effects for facial femininity. After-effects may cross modalities and adapting to faces and bodies could affect preference for voice pitch and vice versa (Feinberg et al, 2005; Feinberg, 2008).

Little, DeBruine and Jones (2005) found that face perception after-effects could be built up that were specific to face gender. We exposed participants to images of women's bodies and, congruently, to women's faces. In accordance with Little, DeBruine and Jones (2005), the facial after-effects found here may be reduced if participants had been tested with male faces following exposure to female bodies and vice versa. Indeed, weight preferences for men and women's body are different, perhaps in part due to sex-specific media portrayal of ideals.

In summary, the current study explored changes in facial preference consequent to a visual diet of body images biased to be heavy or light in weight. Participants that viewed heavy bodies showed a subsequent preference for faces of higher adiposity. Hence, these face after-effects appear to reflect processes that integrate distinct types of mate choice relevant information.

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