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RUNNING HEAD: Hand and Body Adaptation

Perceptual aftereffects of adiposity transfer from hands to whole bodies

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Abstract

Adaptation aftereffects for features such as identity and gender have been shown to transfer between faces and bodies, and faces and body parts, i.e. hands. However, no studies have investigated transfer of adaptation aftereffects between whole bodies and body parts. The present study investigated whether visual adaptation aftereffects transfer between hands and whole-bodies in the context of adiposity judgments (i.e., how thin or fat a body is). On each trial participants had to decide whether the body they saw was thinner or fatter than average. Participants performed the task before and after exposure to a thin/fat hand. Consistent with body adaptation studies, after exposure to a slim hand participants judged subsequently presented bodies to be fatter than after adaptation to a fat hand. These results suggest that there may be links between visual representations of body adiposity for whole bodies and body parts.

Along with faces, bodies are among the most fundamental sources of information we have about other people (Minnebusch & Daum, 2009; Peelen & Downing, 2007). Neuroimaging studies in both monkeys (C. Fisher & Freiwald, 2015; Pinsk et al., 2005, 2009; Tsao et al., 2003) and humans (Chan et al., 2010; Downing et al., 2001; Downing & Peelen, 2011; Saxe et al., 2006) have revealed regions of the visual system which appear specialised for perception of bodies and body parts. In humans, these areas include the extrastriate body area (Downing et al., 2001) and the fusiform body area (Peelen & Downing, 2005; Schwarzlose et al., 2005). Psychophysical studies have also revealed that bodies are susceptible to sensory adaptation, with prolonged exposure to extreme body types producing perceptual aftereffects in the opposite direction (Brooks et al., 2016; Glauert et al., 2009; Hummel, Rudolf, et al., 2012; Winkler & Rhodes, 2005). Together, these results demonstrate the existence of specialised mechanisms in the visual system for perceiving human bodies.

We frequently see both entire bodies as well as individual body parts. There is evidence from patient studies that semantic knowledge of the body is a distinct domain which can be selectively impaired or spared following brain damage (Capitani et al., 2003; Coslett et al., 2002; Kemmerer & Tranel, 2008). Traditionally, knowledge about the body has been proposed to be organised into a structure called a 'partonomy', in which different parts of the body are hierarchically organised into progressively larger units (Brown, 1976; McClure, 1975). There is some evidence, however, that the visual system may treat whole bodies and body parts in more qualitatively different ways. For example, Taylor and colleagues (2007) found that the EBA and FBA show very different response patterns to whole bodies vs. body parts. They showed participants both individual body parts and larger portions of the entire body. The EBA showed a progressive increase of blood oxygen level-dependent (BOLD) response the more of the body was shown, suggesting that it maintains distinct representations of different parts and the more parts are shown, the stronger the BOLD response will be. Notably, the EBA responded even to very small body parts such as fingers. In striking contrast, the FBA showed a step-like increase of activation when large portions of the body were shown, showing no response at all to small parts like fingers.

Another recent study (Harry et al., 2016) found that a region in the anterior temporal lobe showed integrated representations of faces and whole-bodies, whereas more posterior regions such as EBA and FBA did not, consistent with other recent studies (C. Fisher & Freiwald, 2015; Kaiser et al., 2014). Critically, however, there was no evidence for integrated representations of faces and individual body parts, suggesting that they are not bound into more holistic representations of personal identity in the way that whole bodies are. Other behavioural experiments have found that whole bodies and body parts are differentially affected by inversion (Reed et al., 2006; Walsh et al., 2018). One study suggested that the body-specific responses in the regions like the EBA may be embedded in a much larger, somatotopic map of the body across wide regions of the posterior visual cortices (Orlov et al., 2010), while another study suggested that there may be interesting semantic structure underlying the representations of different body parts in the occipito-temporal cortex (Bracci et al., 2015). Together, this body of research suggests that there are important differences in the way the visual system codes whole bodies and body parts.

One particularly interesting body part is the hand. Within the somatosensory system, the hand has among the highest levels of cortical magnification given its obvious importance for skilled action (Penfield & Boldrey, 1937; Sur et al., 1980). There is also evidence that hands are unusually important for the visual system as well. Early single-unit studies of the infero-temporal cortex of monkeys reported neurons with highly-selective responses to specific categories of stimuli, notably including faces and hands (Desimone et al., 1984; Gross et al., 1969, 1972). While such responses to faces have resulted in a vast body of research, the hand-specific responses have been comparatively ignored. There is some evidence, however, that there may be hand-specific visual representations. Bracci and colleagues (2010) identified a region in the left extrastriate cortex which showed highly-selective responses to hands compared to other body parts, which they argued was at least partly distinct from the EBA. In a subsequent study, this group replicated this result and showed that the representations of hands in this area are highly similar to representations of tools (Bracci et al., 2012). There is also neuropsychological evidence that semantic knowledge about limbs (if not about hands specifically) may be selectively impaired or spared following brain damage (Laiacona et al., 2006). One patient, though impaired at naming many categories of everyday object, was incredulous at the suggestion that she might have analogous difficulty identifying hands, "everyone knows what a hand is" (Shelton et al., 1998). Intriguingly, a recent study which put head-mounted cameras on young infants showed that hands become a dominant visual input during the second year of life (Fausey et al., 2016).

One approach to investigating overlap of processing between stimuli or domains is to look at the extent to which adaptation aftereffects transfer between them. Several studies have reported that adaptation to a stimulus in one sensory modality can transfer to other modalities, for example between vision and touch (Konkle et al., 2009; Matsumiya, 2013) and audition and vision (Kitagawa & Ichihara, 2002; Pye & Bestelmeyer, 2015). Within vision, other studies have identified transfer of adaptation aftereffects between faces and whole bodies (Cooney et al., 2015; Ghuman et al., 2010; Kessler et al., 2013; Palumbo et al., 2015), consistent with the evidence mentioned above for the existence of integrated whole-person representations in the visual system (C. Fisher & Freiwald, 2015; Harry et al., 2016). Two studies have investigated transfer of aftereffects between hands and faces, reaching opposite conclusions. Kovács and colleagues (2006) reported clear adaptation aftereffects on perceived sex for both faces and hands. Critically, however, they found no evidence of transfer of adaptation between these categories (i.e., adaptation to a female face did not affect the perceived sex of subsequently presented hands). In contrast, Lai and colleagues (2012) did find transfer of adaptation between hands and faces for judgments of age. One other recent study showed partial transfer of adaptation to altered length from legs to arms (Bratch et al., 2021). To our knowledge, no studies have investigated transfer of adaptation between hands and whole bodies.

The present study investigated whether visual adaptation aftereffects transfer between hands and whole-bodies in the context of adiposity judgments (i.e., how thin or fat a body is). Numerous recent studies have demonstrated large and systematic adiposity aftereffects for whole-body stimuli (Brooks et al., 2016; Challinor et al., 2017; Glauert et al., 2009; Hummel, Grabhorn, et al., 2012; Hummel, Rudolf, et al., 2012; Mohr et al., 2016; Winkler & Rhodes, 2005). We asked whether such adaptation would be found if the adapting stimulus was a fat or a thin hand. Participants made judgments of whether presented whole-body stimuli were fatter or thinner than an average body both before and after visual adaptation to a fat or a thin hand. If adiposity aftereffects transfer between hands and whole-bodies, the body stimuli judged as most average should be shifted in the direction of the adapting hand stimuli at post-test. In contrast, if adaptation affects distinct representations of hands and whole-bodies, then no such differences should be found.

Methods

Participants

Twenty female volunteers in London between 20 and 39 years of age (*M*: 25.7) participated after giving informed consent. Participants had normal or corrected-to-normal vision. The procedures were approved by the Department of Psychological Sciences ethics committee at Birkbeck.

Our sample size was chosen to be in line with our previous study using a similar paradigm with visual body stimuli (Ambroziak et al., 2019). A sample-size weighted average of the effect sizes in the three experiments of that study gave a mean of d_z = 2.225, a very large effect size. A power analysis using G*Power 3.1 software (Faul et al., 2007) using this effect size and alpha of .05 showed that only 4 participants were needed for power of .95. Indeed, our sample size would give power of more than .95 even if the effect size for hand-to-body adaptation was only half that we found for body-to-body adaptation in our earlier study.

Stimuli

The test stimuli were a set of 89 images of female bodies which varied parametrically in body-mass index (BMI), from a BMI of 13 (i.e., emaciated) to 35 (i.e., obese) in a biologically-realistic way, as shown in Figure 1. Stimuli were created using the Genesis 2 Model in Daz Studio 4.8 software. In order to approximate the BMI of each avatar, we used the formula proposed by Cornelissen and colleagues (2009) which relates waist-to-hip ratio (WHR) to BMI for white British women of reproductive age based on data from the 2003 Health Survey for England: WHR = (2.057*BMI + 29.67) / (1.842*BMI + 56.004). This formula allowed us to adjust WHR to produce avatars of a continuous range of BMI values between 13 and 35. The waist and hip circumference of avatars was manipulated using the Universal Sizing Apparatus (Rocketship Technologies Inc., http://rocketship3d.com/). The height of each avatar was kept constant at 170 cm. The bodies were displayed from a frontal perspective and with the head removed.

Note that the BMIs given to the avatars are approximations and may not align exactly with real BMIs in the physical world. Indeed, we believe that these virtual BMIs are somewhat overestimated when compared to real bodies. Critically, however, this is irrelevant in the present study as we do not compare the BMI values of our participants with those of the avatars, and hence, the BMI values are simply a useful nomenclature for labelling the continuum of body shapes.

The adapting stimuli were a very thin and a very fat hand, also created using Daz Studio 4.8. The hand was taken from a default avatar provided by the software: model "Genesis female 3", and adjusted to create the thin (Figure 1, right top) and the fat (Figure 1, right bottom) hand in Daz by adjusting the adiposity parameters to be maximally low and high respectively. Stimuli were presented in the centre of a 24-inch monitor. The height of each image was approximately 18 cm (20.4° visual angle).

Figure 1: *Left*: The test stimuli consistent of a continuum of 89 female bodies which varied from emaciated (BMI=13) to obese (BMI=35) in a biologically-realistic way. Seven of the bodies are shown here as examples. *Right*: The adapting stimuli consisted of thin (top) and fat (bottom) hands.

To confirm that the hand stimuli were actually perceived as differing in how thin and fat they were, we obtained ratings from an independent group of nine women (*M*: 35.2 years). For each hand stimulus, ratings were obtained for two questions: (1) "How thin or fat does this hand look?", and (2) "Think about the person whose hand this is. How thin or fat would you think they are?" Ratings were made using a 1-10 scale with 1 labelled "Extremely thin" and 10 labelled "Extremely fat".

The results clearly show that the hands are perceived as dramatically different. Ratings were substantially higher for the fat hand than the thin hand, both for the first question about how fat the hand itself was (7.7 vs. 1.9), $t(8) = 9.34$, $p < .0001$, $d_z = 3.11$, and for the second question about how fat the person was (8.0 vs. 1.7), $t(8) = 10.97$, $p < .0001$, $d_z = 3.66$.

Procedures

Participants sat at a table approximately 50 cm in front of the monitor. Head movements were unrestricted. Stimuli were presented using the Psychtoolbox (Brainard, 1997; Pelli, 1997) in MATLAB (Mathworks, Natick, MA).

There were four blocks in total, a *Baseline* and an *Adaptation* block for each of the two adapting stimuli (a fat and a thin hand). The adaptation blocks were always preceded by a baseline block. Within each block, there were 80 trials. On each trial, participants were shown one of the body test stimuli and asked to judge whether the body was thinner or fatter than an average body of a woman of the participant's own age in the UK. At the start of the session, the experimenter explained that "average" in this context means the most common or typical body for someone of their age and sex in the UK. Participants responded by pressing either the left (thinner than average) or right (fatter than average) arrow keys on the keyboard using their right index and middle fingers, respectively.

The point of subjective equality (PSE; i.e., the stimulus which the participant judged as exactly average) was estimated using the QUEST Bayesian adaptive staircase method (Watson & Pelli, 1983). Each block included two independent QUEST staircases each including 40 trials, which were randomly interleaved.

During the baseline blocks, each trial began with a 250 ms blank screen, and then the test stimulus appeared for 1000 ms. The test stimulus was chosen on each trial by QUEST from the set of 89 stimuli based on the history of responses within that staircase. After the test stimulus disappeared, the screen remained blank until the participant responded. The response was followed by a black fixation cross in the centre of the screen for 500 ms.

Each adaptation block began with an initial exposure period in which the participant viewed either the thin or the fat hand. During this period, the hand was shown for 2 min 21 sec (i.e., the image was presented for 4.5 seconds followed by a 200 ms blank screen, repeated 30 times). Before each test stimulus, the adapting stimulus was shown again for 4 seconds in order to “top up” the adaptation and ensure that it was sustained throughout the entire block, followed by a one second fixation cross. The rest of the trial was identical to the baseline blocks.

The order of the two adaptation blocks was counterbalanced across participants. After the first adaptation block, participants took a 10 minute break before starting the next baseline block in order to allow adaptation to the previous adaptor to dissipate.

Raw data are included as electronic supplemental material.

Analysis

The PSEs from the two QUEST staircases in each block were averaged. The PSE represents the body size for which the participant would be equally likely to judge the body as being thinner or fatter than an average body. We can thus think of this value as the body size which the participant sees as average. Changes in the PSE as a result of adaptation can be counterintuitive to understand. For example, suppose the PSE is 25 at baseline and 23 after adaptation. Though this is a shift in the 'thinner' direction, it corresponds to a bias to judge individual stimuli as fatter. A stimulus of 24 would be judged as thinner than average at baseline, but as fatter than average after adaptation. According to the standard logic of contrastive adaptation aftereffects, adaptation to a thin hand should make bodies look fatter and thus shift the PSE to a lower value. Conversely, adaptation to a fat hand should make bodies look thinner and thus shift the PSE to a higher value.

PSE values were analysed with a 2x2 repeated-measures analysis of variance (ANOVA) with factors block type (baseline, adaptation) and adaptor type (thin, fat). Planned t-tests compared the effects of adaptation (i.e., baseline vs. adaptation) separately for each of the two adaptor types, and also the difference between the two adaptor types separately for baseline and adaptation blocks.

As measures of effect size, we report η_p^2 for F-statistics and Cohen's d_z for paired t-tests.

Results

The results are shown in Figure 2. An ANOVA revealed a significant interaction between block type (baseline, adaptation) and adaptation type (thin, fat), $F(1, 19) = 8.95$, $p < 0.01$, $\eta_p^2 = 0.32$. There were no significant main effects of block type, $F(1, 19) = 0.35$, $p > 0.50$, $\eta_p^2 = 0.02$, nor of adaptor type, $F(1, 19) = 2.71$, $p > 0.10$, $\eta_p^2 = 0.13$.

There was a clear PSE difference in the adaptation blocks, between the thin (*M*: 23.92) and fat (*M*: 25.01) conditions, $t(19) = 3.26$, $p < 0.005$, $d_z = 0.73$. Importantly, this difference was not observed in the baseline blocks (*M*: 24.43 in the thin condition and *M*: 24.28 in the fat condition), $t(19) = 0.41$, $p > 0.50$, $d_z = 0.09$. A comparison between baseline and adaptation blocks revealed an effect of adaptation for the fat adaptor, $t(19) = 3.00$, $p < 0.01$, $d_z = 0.67$, while the effect did not reach significance for the thin adaptor, $t(19) = 1.60$, $p = 0.125$, $d_z = 0.36$.

To compare the magnitude of aftereffects induced by adaptation to the two adaptors, we multiplied the difference between post-test and pre-test PSEs in the thin condition by -1, so that for both types of adaptors, a positive value indicated an aftereffect in the predicted direction. The magnitude of aftereffects did not differ significantly between the two adapting stimuli, $t(19) = 0.59$, $p > 0.20$, $d_z = 0.133$.

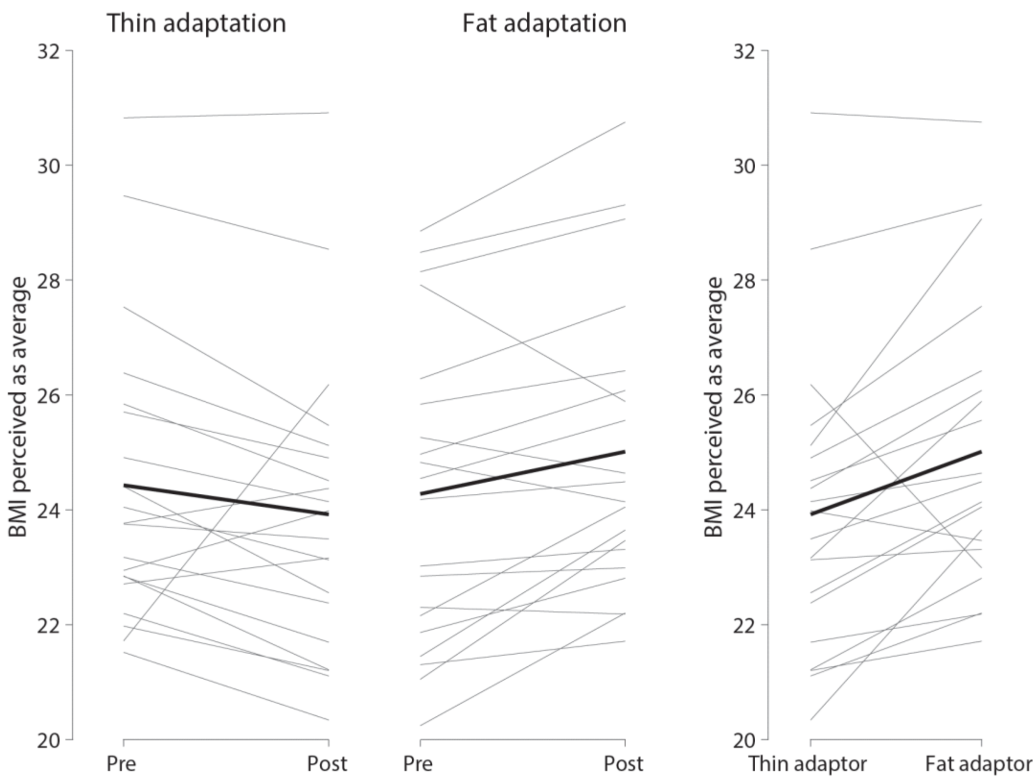

Figure 2: The grey lines indicate individual subjects and the mean is shown in black. *Left panel:* there was no significant effect of adaptation as compared to

baseline in the thin condition (p = 0.125). *Middle panel*: there was a clear effect of adaptation as compared to baseline in the fat condition ($p < 0.01$). *Right panel*: Direct comparison between adaptation phase for thin and fat adaptor showed clear effect of adaptation ($p < 0.005$).

Discussion

Adiposity aftereffects transfer between hands and whole bodies. Adaptation to extremely fat and thin hands produced classical aftereffects on judgments of perceived adiposity of whole-body stimuli. These results suggest that hand adiposity is a feature coded by the visual system and which is susceptible to sensory adaptation, and that a common representation may underlie perception of adiposity in whole-bodies and hands.

A few recent studies have found transfer of adaptation aftereffects between faces and whole bodies for a range of characteristics, including gender (Ghuman et al., 2010; Palumbo et al., 2015), identity (Ghuman et al., 2010), and orientation (Cooney et al., 2015). These results converge with neuroimaging results showing that higher-level regions of the visual system maintain integrated whole-person representations, abstracting across faces and whole bodies (Cox et al., 2004; C. Fisher & Freiwald, 2015; Harry et al., 2016; Kaiser et al., 2014). Previous studies have reached mixed conclusions about transfer of adaptation between hands and faces, with one study finding such transfer (Lai et al., 2012) and another not finding it (Kovács et al., 2006). To our knowledge, this is the first study to investigate transfer of adaptation between hands and whole bodies.

It is also important to situate the successful transfer of adaptation between hands and bodies in the context of other cases in which transfer does not seem to occur. For example, in the study by Cooney and colleagues (Cooney et al., 2015) orientation aftereffects transferred from faces to bodies, but not in the opposite direction from bodies to faces. Similarly, Lai and colleagues (Lai et al., 2012), while finding transfer from hands to faces for age judgments, found no such transfer from voices to faces. Several other studies on face aftereffects have found high levels of specificity with at least partial independence of adaptation across stimuli depicting individuals differing in sex, race, age, or species (Bestelmeyer et al., 2008; Jaquet & Rhodes, 2008; Little et al., 2008; Schweinberger et al., 2010). The degree of such specificity has been found to be modulated by the way in which stimuli are labelled (Little et al., 2011), suggesting that transfer is not based only on the degree of overlap between categories in visual representations, but relates to higher-level conceptualisation of the stimuli. In the present study, we made no explicit comment to participants about the relation between the identity of the hand and body stimuli, though they were of similar skin colour and were compatible in terms of sex and age. It would be interesting in future studies to manipulate such characteristics to investigate how the effects we observe are similarly modulated. It is notable in this context that studies of adiposity aftereffects for whole bodies have found clear transfer across identity, for example between images of the participant themselves and a stranger (Brooks et al., 2016; Hummel, Rudolf, et al., 2012). Other studies have demonstrated analogous transfer between bodies in different orientations (Brooks et al., 2018), of different genders (Brooks et al., 2019), and of different races (Gould-Fensom et al., 2019).

As discussed in the introduction, there is a range of evidence that body parts and whole-bodies may be distinctly represented by the visual system. For example, the EBA and FBA appear to code for body parts and whole bodies, respectively (Taylor et al., 2007), and hands appear to have their own distinct representation in extrastriate cortex (Bracci et al., 2010, 2012). The present results showing transfer of adaptation between hands and whole bodies emphasises the functional links between parts and whole in body perception. In particular, these results suggest that visual representations of body adiposity may be shared between whole-bodies and body parts.

One important issue concerns how specific the reported effects are to hands as adapting stimuli, or whether they might result from low-level features of the adapting stimuli, such as the overall aspect ratio of the images. Multiple pieces of evidence suggest that the effect is not due to the aspect ratio of the stimuli. First studies of both face adaptation (Bestelmeyer et al., 2008; Jaquet & Rhodes, 2008; Little et al., 2008; Schweinberger et al., 2010) and body adaptation (Brooks et al., 2019) have found that aftereffects are larger when adapting and test stimuli match in features such as sex, race, and age. Second, Hummel, Grabhorn, and colleagues (2012) showed that adaptation to rectangles differing aspect ratio did not affect judgments of how fat or thin subsequently viewed bodies were. Finally, it is also worth noting that the thin and fat hand stimuli in our study did not differ substantially in overall aspect ratio. Looking at the ratio of length to width of the smallest rectangle each of the hand images would fit into gives values of 1.34 for the thin hand and 1.40 for the fat hand. Not only is this difference quite small, it also goes in the opposite direction as would be needed to account for our results. That is, the bounding rectangle of the fat hand is actually taller and thinner than that of the thin hand. While this is counterintuitive, it is related to the fact that we did not create the fat and thin stimuli by simply stretching an image in opposite directions, but manipulate the apparent adiposity of the hands in a subtler and more biologically-realistic way.

One limitation of the present study is the fact that the whole-body test stimuli we used included hands. This raises the possibility that the aftereffects we report could results hand-to-hand effects, rather than hand-to-body ones. We consider this possibility unlikely given that the hands in the whole-body stimuli are very small, and are shown in profile, making them poor cues to body size, particularly in comparison to the very salient cues in the rest of the body. Another limitation is the use of a single identity for each adiposity level for hand and body stimuli. While the body stimuli form a clear continuum from thin to fat, it is possible that there are idiosyncratic features of these stimuli that might be unrepresentative of effects with other stimuli.

Another limitation concerns whether adaptation affects perception of stimuli themselves or merely the decisions participants make about those stimuli (cf. Storrs, 2015). The psychophysical methods used in this paper do not allow interpretations in terms of changes in low-level sensory representations or in terms of higher-level perceptual decisions to be distinguished. The same is true, however, for nearly all studies investigating "high-level" aftereffects related to stimuli such as faces and bodies. It will be important for future research to distinguish these potential underlying mechanisms across the wide range of face and body aftereffects reported in the literature.

The perception of body size in whole-bodies has been widely studied given its obvious importance for both judgments of attractiveness (Brierley et al., 2016; Singh, 1993; Tovée et al., 1998) and body image concerns (Becker & Hamburg, 1996; Bruch, 1978). Some recent research has investigated the perception of facial adiposity, which has been linked to overall attractiveness (Currie & Little, 2009; Peters et al., 2007; Re & Perrett, 2014) and perceived health (Coetzee et al., 2009, 2011; C. I. Fisher et al., 2014). Comparatively little research, however, has investigated perceived hand adiposity and attractiveness. One study did find that ratings of hand 'fattiness' were a significant negative predictor of hand attractiveness, among several others such as femininity, typicality, and skin healthiness (Koscinski, 2012). In the present study, participants were not asked to make any judgments at all about the hand stimuli, which as adaptor stimuli were passively viewed. The clear adaptation aftereffects we report demonstrate, however, that hand adiposity is a feature coded by the visual system and which is susceptible to sensory adaptation.

Conflict of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data Availability Statement

Raw data are included as electronic supplemental material.

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