



Research Report

Did you skip leg day? The neural mechanisms of muscle perception for body parts



Keefe Ip^{a,*}, Nicole Kusyk^a, Ian D. Stephen^b and Kevin R. Brooks^{a,c,d}

^a School of Psychological Sciences, Macquarie University, Sydney, NSW, Australia

^b NTU Psychology, Nottingham Trent University, Nottingham, England, UK

^c Perception and Action Research Centre (PARC), Faculty of Medicine, Health and Human Sciences, Macquarie University, Sydney, NSW, Australia

^d Lifespan Health & Wellbeing Research Centre, Macquarie University, Sydney, NSW, Australia

ARTICLE INFO

Article history:

Received 1 May 2023

Reviewed 12 June 2023

Revised 18 September 2023

Accepted 2 October 2023

Action editor Samuel Schwarzkopf

Published online 3 November 2023

Keywords:

Body image

Body perception

Muscularity

Neural tuning

Visual adaptation

ABSTRACT

While the neural mechanisms underpinning the perception of muscularity are poorly understood, recent progress has been made using the psychophysical technique of visual adaptation. Prolonged visual exposure to high (low) muscularity bodies causes subsequently viewed bodies to appear less (more) muscular, revealing a recalibration of the neural populations encoding muscularity. Here, we use visual adaptation to further elucidate the tuning properties of the neural processes underpinning muscle perception for the upper and lower halves of the body. Participants manipulated the apparent muscularity of upper and lower bodies until they appeared 'normal', prior to and following exposure to a series of top/bottom halves of bodies that were either high or low in muscularity. In Experiment 1, participants were adapted to isolated own-gender body halves from one of four conditions; increased (muscularity) upper (body half), increased lower, decreased upper, or decreased lower. Despite the presence of muscle aftereffects when the body halves the participants viewed and manipulated were congruent, there was only weak evidence of muscle aftereffect transfer between the upper and lower halves of the body. Aftereffects were significantly weaker when body halves were incongruent, implying minimal overlap in the neural mechanisms encoding muscularity for body half. Experiment 2 examined the generalisability of Experiment 1's findings in a more ecologically valid context using whole-body stimuli, producing a similar pattern of results as Experiment 1, but with no evidence of cross-adaptation. Taken together, the findings are most consistent with muscle-encoding neural populations that are body-half selective. As visual adaptation has been implicated in cases of body size and shape misperception, the present study furthers our current understanding of how these perceptual inaccuracies, particularly those involving muscularity, are developed, maintained, and may potentially be treated.

© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

* Corresponding author.

E-mail address: keefe.ip@students.mq.edu.au (K. Ip).

<https://doi.org/10.1016/j.cortex.2023.10.006>

0010-9452/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Estimations regarding one's own body size and shape can be inaccurate – a phenomenon known as body size and shape misperception (BSSM; Brooks et al., 2020; Challinor et al., 2017; Dolan et al., 1987; Fuentes et al., 2013; Longo, 2022). This phenomenon is concerning as it is a risk factor for the development of eating disorders, depression, and other serious health concerns (Caspi et al., 2017; Hasenack et al., 2021; Preston & Ehrsson, 2014, 2016). BSSM also occurs in the context of muscle perception. The misperception that one's muscularity is insufficient, regardless of actual body size, is a central feature of muscle dysmorphia (MD; American Psychiatric Association, 2013) – a form of Body Dysmorphic Disorder associated with severe psychopathology (Phillips et al., 2010). The underestimation of muscularity can result in high levels of body dissatisfaction and the adoption of detrimental behaviours, such as the abuse of performance enhancing drugs (Devrim et al., 2018) or the undertaking of intense physical training routines with extreme caloric restrictions (Grogan, 2010). Although widely presumed to be an almost exclusively male disorder (Phillips et al., 2010), MD prevalence was found to be relatively similar across genders in an Australian adolescent sample, at around 2 % (Mitchison et al., 2022).

To date, socio-cognitive processes have been largely thought to underpin the development and maintenance of BSSM. Specifically, it has been theorised that media and social pressures to be thin or muscular, coupled with social comparison, may result in the internalisation of unrealistic female and male body ideals (Barlett et al., 2008; Rodgers et al., 2015; Shin & Nam, 2015). This proposed mechanism is notable as 56 % of women desire to increase their level of muscularity (Vartanian et al., 2001), potentially reflecting the recent formation of a more athletic female ideal that is both thin and toned (Benton & Karazsia, 2015; Holland & Tiggemann, 2017). This predilection towards a more muscular figure is likewise observed in men as over 49 % of Ghanaian men, 69 % of Ukrainian men, and over 90 % of men from the United States were found to desire a more muscular physique (Frederick et al., 2007). However, these accounts do not provide a neural mechanism for the perceptual processes involved. In seeking a causal explanation for BSSM, perceptual psychologists have postulated that these phenomena may be real-world examples of visual adaptation and its resulting aftereffects (Brooks et al., 2016, 2020, 2021; Challinor et al., 2017; Glauert et al., 2009; Hummel et al., 2012a).

Visual adaptation is the phenomenon whereby prolonged exposure to a visual stimulus with particular properties (the “adaptor”) causes subsequently viewed stimuli (the “test”) to appear distorted in the opposite direction in terms of those visual properties (Barlow & Hill, 1963; Webster, 2011). For example, prolonged fixation on a waterfall, with its continual cascades of downward motion, will result in the perception of upward motion when one's gaze is diverted to nearby stationary objects. This perceptual distortion is known as a visual aftereffect. In addition to low level visual properties such as motion (Barlow & Hill, 1963), line thickness (Blackmore & Sutton, 1969), and colour (Thompson & Burr, 2009), visual aftereffects have been demonstrated for higher level properties including face distortion (Gwinn & Brooks, 2013, 2015; Webster & MacLin, 1999), identity (Leopold et al., 2001) and gender

(Webster et al., 2004), and more recently, body size and shape (Hummel et al., 2012a; Winkler & Rhodes, 2005).

The perceptual bias following adaptation is a result of changes in the response properties of neurons, which serves to facilitate perceptual recalibration (Barlow & Hill, 1963; Clifford & Rhodes, 2005; Leopold et al., 2001). As such, the presence of an aftereffect constitutes evidence of neural mechanisms that encode the adapted property (Thompson & Burr, 2009). By manipulating the characteristics of the adaptor and the test stimuli and examining the presence and strength of the visual aftereffect, it is possible to infer the response properties – the ‘tuning’ – of specific neural populations (Webster, 2011).

One commonly used approach is the simple/cross adaptation paradigm. Simple adaptation is demonstrated when the adaptation and test stimuli are congruent (i.e., they belong to the same stimulus category), while cross adaptation involves adaptors and test stimuli that are incongruent (i.e., belong to a different category). When the magnitude of the aftereffect is the same regardless of whether the adaptation and test stimuli are congruent or incongruent, complete cross adaptation is demonstrated. This would imply that the underlying neural mechanisms process stimuli from either category to the same extent (i.e., are not category selective). For example, Gould-Fensom et al. (2019) showed that adaptation to thin Asian or Caucasian bodies caused equivalent aftereffects regardless of the race of the test bodies, suggesting that the neurons encoding body fat are not selective for race. In contrast, cross adaptation would not be observed if the neural circuits processing the adaptor and test stimuli were completely distinct. For example, Hummel et al. (2012b) demonstrated size aftereffects when the adaptor and test were both human bodies, but no aftereffect when a similar sized rectangle instead served as the adaptor. From this we infer that the body size aftereffect relies on the adaptation of high-level body-selective neurons and cannot be explained by adaptation to lower-level neurons that respond to simple rectangular shapes. If the neural mechanisms encoding the adapted property are partially dissociated for the two categories, then partial cross adaptation should occur, as evidenced by a smaller aftereffect magnitude when the stimuli differ, in comparison to when they are the same. For example, Brooks et al. (2019a) showed that adaptation can be demonstrated with different gendered adaptation and test bodies, but the aftereffects are larger when they are congruent. This suggests that the neurons encoding body size are partially selective for stimulus gender.

This paradigm has been used to demonstrate that aftereffects can transfer between different body parts. Specifically, gender aftereffects can transfer from adaptation stimuli depicting bodies to test stimuli depicting faces (Ghuman et al., 2010), and from faces to bodies (Palumbo et al., 2015), implying that the neural mechanisms encoding gender generalise between faces and bodies. Likewise, identity aftereffects can transfer from bodies to faces (Ghuman et al., 2010), and facial orientation aftereffects can transfer to bodies following adaptation (Cooney et al., 2015), suggesting that identity and orientation are encoded by neural populations that, at least to some extent, respond to both face and body stimuli (Ghuman et al., 2010). The findings from a study measuring perceived

attractiveness were also consistent with cross adaptation for adiposity aftereffects between the face and body (Re et al., 2011). In contrast, Bratch et al. (2021) failed to find evidence of length aftereffect transfer between the leg and arm. However, given that this study was relatively low in power, strong conclusions cannot be drawn from these null results.

While body size adaptation research has historically focused on the dimension of adiposity, recent studies have begun to examine the perception of muscularity. Alongside body fat aftereffects, two studies have demonstrated independent aftereffects following exposure to bodies with relatively extreme levels of muscle mass, revealing separate neural mechanisms that encode muscularity (Brooks et al., 2019b; Sturman et al., 2017). However, whether muscle aftereffects can transfer between different parts of the body, or indeed between any two stimulus categories, remains unknown.

This study will use the simple/cross adaptation paradigm to probe the tuning of the neural mechanisms underlying the perception of muscularity for the upper and lower halves of human bodies. Specifically, two experiments will determine whether the underlying neural mechanisms encoding muscularity are more narrowly tuned, responding only to one particular body-half, or are broadly tuned, responding to both the top and bottom half. Experiment 1 does this in the context of isolated body halves, while Experiment 2 uses full-body stimuli to enhance ecological validity and to test the generalisability of Experiment 1's results.

1. Experiment 1

In this experiment, participants adapted to a set of half body stimuli (upper or lower) with either increased or decreased muscularity. If muscle perception is mediated by cells that are equally responsive regardless of body half, then equivalent aftereffects should be expected irrespective of which body half is used for the test stimuli. If the neural mechanisms underlying muscle perception are body-half selective, then adaptation will only engender a significant aftereffect when testing with congruent stimuli, with no transfer of the aftereffect to incongruent test stimuli. However, if the networks encoding muscularity are partially selective for body half, then some degree of aftereffect transfer should be observed. Hence, aftereffects should be significant when adaptation and test stimuli are congruent and when they are incongruent, but should be smaller in the latter case.

1.1. Method

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

1.1.1. Participants

Two-hundred and eighty-one participants aged between 18 and 40 were recruited for the experiment (87 males, 194 females, $M_{Age} = 20.23$, $SD = 3.58$). Participants were either undergraduate students recruited from Macquarie University

($n = 276$) or friends of the researcher ($n = 5$). The experiment was approved by the Macquarie University Human Research Ethics Committee. All participants were naïve to the experimental hypotheses, had not previously been diagnosed with an eating disorder or MD, had normal or corrected-to-normal vision, and gave written informed consent prior to and following participation. Given the online nature of the study, and the importance of stimulus and response timing in studies of visual adaptation, strict exclusion criteria were employed to ensure experimental rigour. As a result, the results of 180 participants were excluded from the analysis for failing to comply with the instructions or for having internet connectivity issues (refer to Appendix B for exclusion criteria). Hence, a total of 101 participants (33 males, 68 females) were included in the final analyses. Although this exclusion rate would be considered high for a laboratory study, this is in keeping with recent research recommending exclusion of participants demonstrating “careless responding” to improve experimental validity and effect size when conducting experiments through online research platforms (Brühlmann et al., 2020; Oppenheimer et al., 2009).

1.1.2. Design

The experiment employed a 2 (adaptation body half: upper/lower; between subjects) \times 2 (adaptation direction: increased/decreased muscularity; between subjects) \times 2 (test body half: upper/lower; within subjects) mixed design. Participants were randomly allocated to one of four adaptation conditions: increased upper (20 participants), decreased upper (28 participants), increased lower (26 participants), or decreased lower (27 participants). The Point of Subjective Normality (PSN) – the level of muscularity that appeared normal to the participant – was measured for each participant before and after exposure to the adaptation stimuli. The change in PSN for the upper and lower body half test stimuli (Δ PSN) were recorded as the dependent variables. These values were expressed in terms of the percentage of the muscularity level of the adapting stimulus. Positive (negative) Δ PSN scores indicated that the participants selected a more (less) muscular body half following adaptation, implying that the test stimulus appeared reduced (increased) in muscularity, and hence needed to be increased (decreased) in size to appear normal.

1.1.3. Stimuli and apparatus

Stimuli for the study were created using the Genesis 8 male and female models in Daz Studio Version 4.12 (Daz3D, 2000). Eighteen identities were created by applying minor pseudo-randomly generated changes to the models' skin colour, pose, torso and limb lengths, and breast size (for female stimuli). To ensure the male and female stimuli were matched as closely as possible, the same values for these scales were used for both male and female identities.

The muscularity of the models was manipulated via the pre-set whole-body morphing scales – bodybuilder size, bodybuilder detail, and emaciation – to form 25 equidistant muscularity levels. The values were chosen to be evenly dispersed about the point of subjective normality and to be contained within a range of muscularity that was perceived to be realistic by 16 participants (8 male, 8 female) in a pilot study (refer to Appendix A for more details).

The models were clothed in grey underwear and posed in a standard posture (Fig. 1) and rendered at 1080 x 1398 pixels. To produce the upper and lower body half stimuli, the whole-body renders were edited using Krita version 4.1.1 (KDE, 2005). The heads of the stimuli were removed just below the chin and each identity was separated into top and bottom halves at the top of the iliac furrow, above the iliac crest.

The highest and lowest muscularity body half images from each identity were placed on a 1000x1000 pixel grey background and used as the adaptation stimuli. A black border was placed around the grey background to differentiate the adaptation stimuli from the test stimuli. To create the test stimuli, the body half images were centred within a 1000x1000 pixel grey background. The test stimulus images were 67 % the width and height of the adaptation stimuli to reduce the potential influence of low-level adaptation.

Adaptation and test stimuli were created for all 18 male and 18 female identities and were matched to the observer's

gender during the experiment. Two identities were selected to be used in practice trials, while the remaining 16 identities were randomly divided into 2 groups of 8 for use as either adaptation or test stimuli. This separation served to ensure that any measured aftereffect would reflect adaptation to muscularity in general, rather than adaptation to any idiosyncrasies of a particular identity.

The Gorilla Experiment Builder (www.gorilla.sc) was used to create and host our experiment online (Anwyl-Irvine et al., 2020). A body manipulation tool was created within Gorilla using the 25 images from each identity. As these were presented sequentially, the smooth transition gave the illusion that the muscularity of the body half was being manipulated in real time.

1.1.4. Procedure

The experiment consisted of three blocks: practice, baseline test, and adaptation test. For all three phases, participants

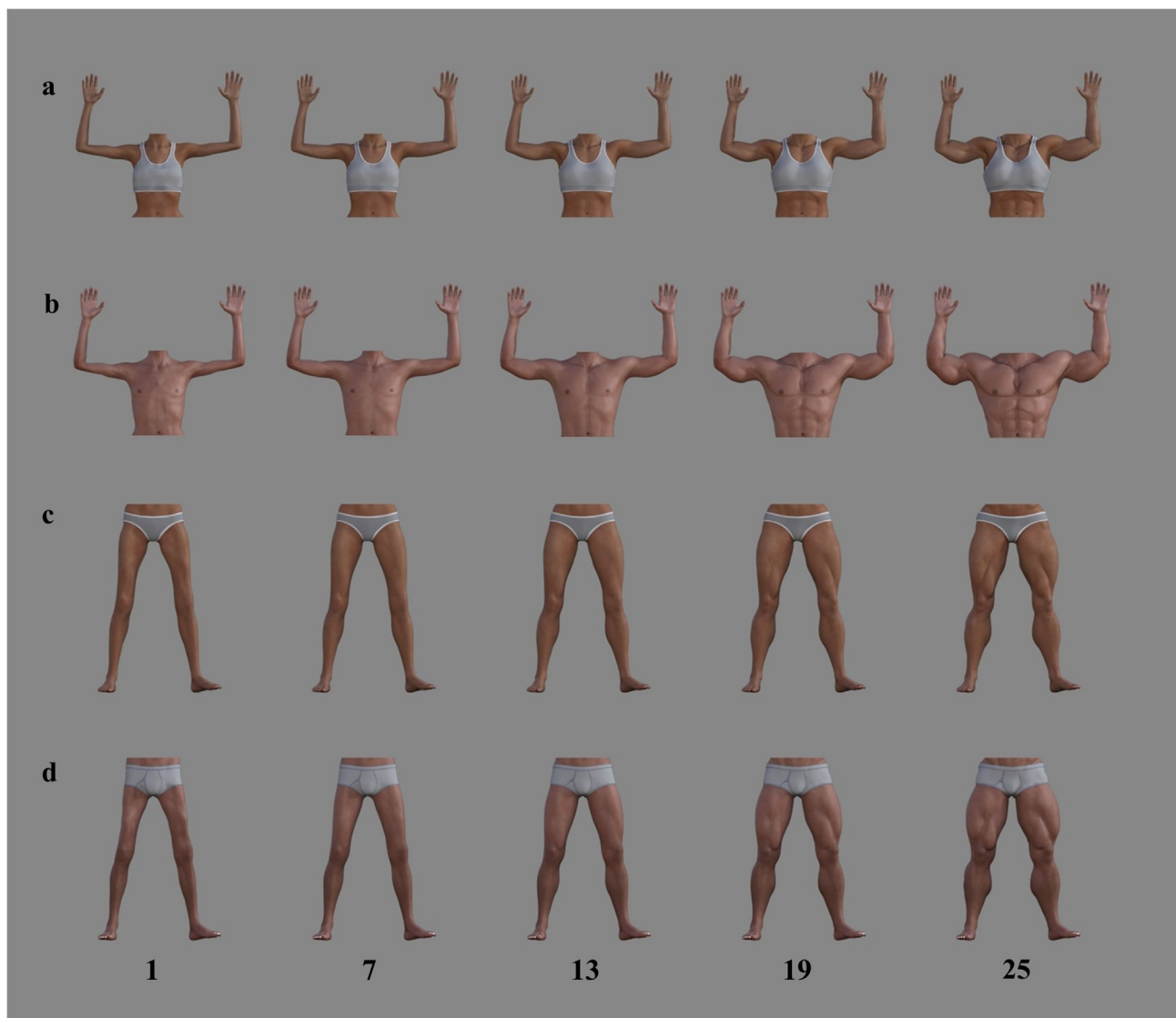


Fig. 1 – Example Male and Female Stimuli

Note. Muscularity levels 1, 7, 13, 19, and 25 for a) Upper female, b) Upper male, c) Lower female, and d) Lower female stimuli. The level 1 and 25 stimuli were also used as adaptation stimuli.

were required to stay in Fullscreen mode to standardise their stimulus displays.

To familiarise themselves with the procedure, participants first completed 4 practice trials, consisting of two trials with upper body halves and two with lower body half stimuli. Data for these practice trials were discarded. For each trial, participants were presented with an upper or lower body image and asked to use the ‘a’ (decrease muscularity) and ‘s’ (increase muscularity) keys on their keyboard to manipulate the apparent muscularity of the body half. The participant was instructed to press the ‘select’ button when the body half appeared ‘normal’, concluding the trial, and recording the muscularity of the onscreen body half as a PSN score ranging from 1 to 25. The definition of normal was left ambiguous to allow participants to use their own criteria. The initial muscularity level displayed in each trial was randomly selected from the possible 25 levels. During the 1 sec inter trial interval, only the blank grey background was visible.

After a short break, the baseline test block commenced. This featured 32 trials, each identical to the practice trials, composed of eight upper and eight lower body half stimuli, presented twice each. The mean PSN baseline scores were calculated separately for the upper and lower body half test stimuli.

The adaptation test phase commenced immediately after the baseline phase. Before the first trial, all eight adaptation identities were presented 8 times sequentially in a random order for 2 sec each, resulting in an initial adaptation period lasting 128 sec. During this period, the participant was instructed to pay attention to the bodies on screen. The centre of each adaptor was positioned at a random location within a 150x150 pixel square at the centre of the grey background to reduce the effects of low-level adaptation (Brooks et al., 2018; Hummel et al., 2012a). Immediately following this, participants completed a second set of 32 test trials. Between each, a 6 sec top-up adaptation was employed, consisting of three randomly selected adaptation stimuli presented for 2 sec each. To ensure the participants were attending during both the initial and top-up adaptation phase, six of the adaptation stimuli were pseudo-randomly selected to display the message “PRESS SPACEBAR NOW” for the duration of the stimulus’ presentation. Participants were instructed to press spacebar when this message appeared. All other details were identical to the baseline phase.

1.2. Results

The analyses were conducted using Stata version 16 and R version 4.2.2. Preliminary analyses found that the assumptions of normality and homogeneity of variance were violated for Δ PSN lower (Shapiro–Wilk $p < .001$; Levene’s test $p = .047$). Hence, the bootstrapped versions of the one-sample t-test, mixed factorial ANOVA and paired t-test were conducted in place of the planned analyses.

The adaptation-induced change in the point of subjective normality for both upper and lower test stimuli are plotted in Fig. 2, expressed as a percentage of the extremity of the adaptation stimulus. From informal inspection, the average Δ PSNs were all positive following exposure to high

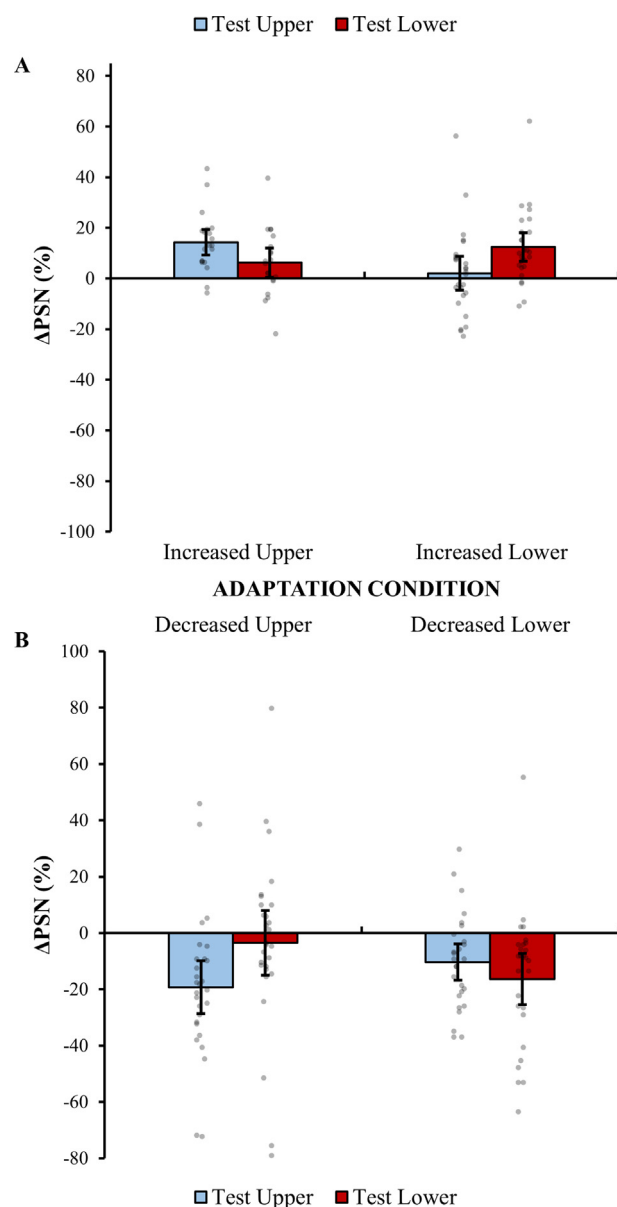


Fig. 2 – Results of Experiment 1

Note. Changes in the point of subjective normality (Δ PSN) for both adaptation and test body half conditions. (A) Adaptation to increased stimuli. (B) Adaptation to decreased stimuli. The grey dots indicate data from individual participants, and the error bars show the 95 % CI from the bootstrapped one-sample t-tests.

muscularity body halves (Fig. 2A) and negative following adaptation to low muscularity stimuli (Fig. 2B). When the body halves for the adaptation and test stimuli were congruent (simple adaptation), the aftereffects had an average distortion level of around 15 % of the muscularity of the adaptation stimuli. Critically, the strength of the aftereffects appears to be weaker when the adaptation and test halves are incongruent (cross adaptation) than when they are congruent.

Formal statistical tests confirmed these preliminary observations. A Bonferroni adjusted critical alpha of .0125 was used for individual comparisons to maintain a familywise

error rate of .05. Bootstrapped one-sample t-tests found statistically significant simple adaptation effects for all congruent conditions (i.e. Δ PSN significantly different from zero); increased upper ($M = 14.27$, 95 % CI: [9.18, 19.36]), $t(19) = 5.37$, $p < .001$, $d = 1.20$, decreased upper ($M = -19.23$, 95 % CI: [-28.61, -9.86]), $t(27) = -4.01$, $p < .001$, $d = .76$, increased lower ($M = 12.46$, 95 % CI: [6.84, 18.08]), $t(25) = 4.33$, $p < .001$, $d = .85$, and decreased lower ($M = -16.34$, 95 % CI: [-25.38, -7.30]), $t(26) = -3.52$, $p < .001$, $d = .68$.

While a statistically significant cross adaptation effect was found for the decreased lower condition ($M = -10.32$, 95 % CI: [-16.73, -3.91]), $t(26) = -3.18$, $p = .002$, $d = .61$, the remaining body-half incongruent conditions failed to reach statistical significance when accounting for the adjusted critical alpha: increased upper ($M = 6.25$, 95 % CI: [.48, 12.02]), $t(19) = 2.11$, $p = .034$, $d = .47$, decreased upper ($M = -3.46$, 95 % CI: [-14.97, 8.05]), $t(27) = -.59$, $p = .556$, $d = .11$, and increased lower condition ($M = 2.04$, 95 % CI: [-4.63, 8.72]), $t(25) = .61$, $p = .549$, $d = .12$.

A 2 (adaptation direction) \times 2 (adaptation half) \times 2 (test half) mixed ANOVA was conducted to compare the strength of the muscle adaptation aftereffects when the adaptation and test halves were congruent versus incongruent, using a critical alpha of .05. The ANOVA showed a significant main effect of adaptation direction, $F(1,97) = 29.31$, $p < .001$, $\eta^2 = .23$, confirming the difference between the aftereffects in the increased and decreased muscle adaptation conditions. In addition, a significant three-way interaction was revealed between adaptation direction, adaptation half, and test half, $F(1,97) = 40.84$, $p < .001$, $\eta^2 = .30$.

To interpret the three-way interaction, two bootstrapped paired t-tests were conducted to compare the Δ PSN upper and Δ PSN lower scores (one for each adaptation condition). A Bonferroni adjusted critical alpha of .0125 was used. Although simple adaptation effects (congruent conditions) were larger than cross adaptation effects (incongruent conditions) in all cases, only three of the four comparisons reached statistical significance; the increased upper ($t(19) = 2.99$, $p = .003$, 95 % CI: [2.77, 13.27], $d = .64$), decreased upper ($t(27) = -4.89$, $p < .001$, 95 % CI: [-22.08, -9.47], $d = .55$), and increased lower adaptation conditions ($t(25) = 3.47$, $p < .001$, 95 % CI: [4.69, 16.15], $d = .65$). In the remaining decreased lower condition, the difference was not significant ($t(26) = -1.85$, $p = .066$, 95 % CI: [-12.43, .39], $d = .29$).

To examine the overall difference between simple and cross adaptation effects across all adaptation conditions, an additional analysis was conducted. For each participant from the decreased adaptation conditions, Δ PSN values were multiplied by -1 and combined with data from the increased adaptation conditions. Further, the Δ PSN upper and Δ PSN lower scores were recoded as Δ PSN congruent (simple adaptation) and Δ PSN incongruent (cross adaptation) depending on the adaptation half (see Fig. 3). Significant aftereffects were observed for both congruent (bootstrapped one-sample t-test: ($M = 15.73$, 95 % CI: [11.85, 19.62]), $t(100) = 7.78$, $p < .001$, $d = .77$) and incongruent conditions (bootstrapped one-sample t-test: ($M = 5.48$, 95 % CI: [1.45, 9.52]), $t(100) = 2.58$, $p = .008$, $d = .26$), with significantly larger simple adaptation effects for congruent conditions (bootstrapped paired t-test: $t(100) = 6.48$, $p < .001$, 95 % CI: [7.10, 13.40], $d = .49$). The cross-

adaptation effect was 34.84 % the size of the simple adaptation effect.

1.3. Discussion

In line with prior research (e.g., Sturman et al., 2017), Experiment 1 demonstrated clear aftereffects of muscularity through simple adaptation, providing evidence for neural populations that encode this dimension of body composition. Further, this study extends previous work by showing, for the first time, a muscularity aftereffect when only parts of bodies are used. In the initial analyses, although results were in the expected direction in each of the incongruent conditions, a significant cross adaptation effect was found in only one of four cases. Subsequent analysis of aggregate data showed a small ($d = .26$) yet significant cross adaptation effect, although this was significantly smaller than the large simple adaptation effect ($d = .77$). These findings suggest that although the muscle encoding neural mechanisms do not show complete selectivity for body half, they do show relatively narrow tuning.

Critically, this experiment only used isolated body halves for stimuli. As natural viewing typically involves whole bodies, with both body halves simultaneously visible, it is unclear whether the results are generalisable to real-world scenarios where observers are often free to fixate on either half of the body. As the duration of fixation on adaptor bodies has been shown to influence the size of visual aftereffects (Stephen et al., 2018, 2019), it is possible that viewing whole body stimuli would produce different results than those demonstrated in Experiment 1. As such, Experiment 2 looked

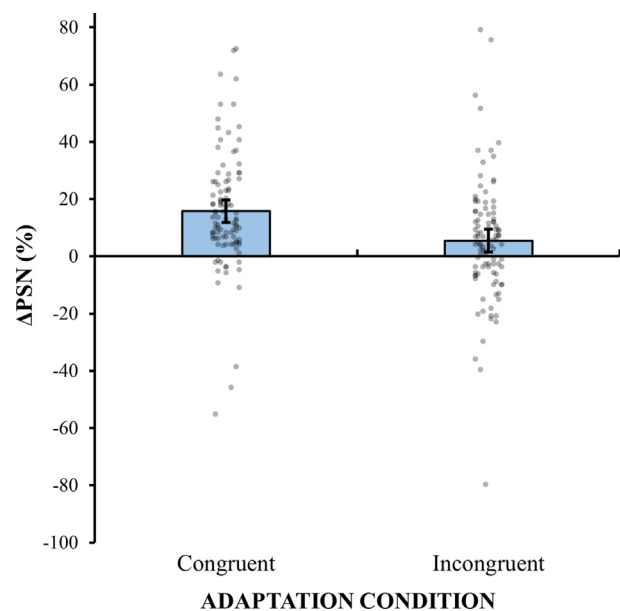


Fig. 3 – Results of Experiment 1: Aggregated Simple and Cross Adaptation Conditions

Note. Results of Experiment 1 aggregated and recoded in terms of congruent and incongruent adaptation conditions. The grey dots indicate individual participants' data, and the error bars show the 95 % CI from the bootstrapped one-sample t-tests.

to replicate the results of Experiment 1 in a more ecologically valid context.

2. Experiment 2

Experiment 2 examined whether no-, partial- or complete-cross adaptation between body halves would occur when observers viewed whole bodies in the adaptation and test phases. Although observers were presented with both halves of the body simultaneously rather than viewing body halves in isolation, adaptation stimuli only showed extreme levels of muscularity (high or low) for one half of the body, the other half having average musculature. During the test phases, participants simultaneously adjusted the muscularity of the top and bottom halves of the body stimulus until it appeared normal. In using full body stimuli, this experiment sought to enhance the ecological validity and test the generality of Experiment 1's results.

2.1. Method

Experiment 2 was identical to Experiment 1, except in the following respects. A total of 222 participants aged between 18 and 40 were recruited (1 non-binary, 64 male, 157 female, $M_{Age} = 21.84$, $SD = 4.39$). Of these, 216 were undergraduate psychology students and six were friends and family of the researcher. One-hundred and thirteen participants (34 male, 79 female) were excluded due to a failure to comply with the instructions, or as a result of the exclusion criteria (see [Appendix B](#)). As in Experiment 1, strict exclusion criteria were necessary to ensure compliance and hence maintain data quality in this online experiment ([Brühlmann et al., 2020](#)). Six participants (5 male, 1 female) were also excluded as they had completed a pilot version of the study. Hence, a total of 103 participants were included in the analyses: 22 in the increased upper, 26 in the increased lower, 29 in the decreased upper, and 26 in the decreased lower condition. Whole-body stimuli were used for both the adaptation (refer to [Fig. 4](#)) and test stimuli, with each stimulus identity being composed of 13 equidistant levels of muscularity. These spanned the same range of muscularity levels as the stimuli in Experiment 1 but omitted every other muscularity level to expedite the recording of responses. Identities one and two were selected to be used in practice trials, while the remaining 16 identities were randomly assigned as adaptation and test stimuli for each participant. A two-dimensional body manipulation tool was created using PsychoPy version 3.0 ([Peirce et al., 2019](#)). This allowed participants to manipulate the muscularity of the upper and lower halves of the bodies simultaneously and independently. While the 'up' and 'down' cursor keys manipulated the upper half, the 'left' and 'right' keys were used to adjust the lower half. A pilot experiment confirmed that adjustments of top and bottom half muscularity took longer than the single adjustments of Experiment 1. To reduce the potential for aftereffect decay during these adjustments, top up adaptation was increased to 12 sec (i.e., double the duration of Experiment 1). The experiment was conducted on the online platform, Pavlovia.

2.2. Results

All analyses were conducted using Stata version 16. Preliminary analyses found that the assumptions of normality and homogeneity of variance were violated for Δ PSN lower (Shapiro–Wilk $p < .001$, Levene's test $p < .001$). As such, bootstrapped one-sample t-tests, a mixed factorial ANOVA, and paired t-tests were employed.

Mean Δ PSN values for all four conditions are plotted in [Fig. 5](#), expressed as a percentage of the extremity of the adaptation stimulus. From informal observation, values for congruent conditions appeared to be positive following adaptation to increased muscularity, and negative following adaptation to decreased muscularity stimuli in line with our expectations. In comparison, the mean Δ PSNs appear to be near zero for all incongruent conditions.

Formal statistical tests confirmed these preliminary observations. A Bonferroni adjusted critical alpha of .0125 was used for individual comparisons to maintain a familywise error rate of .05. Bootstrapped one-sample t-tests found statistically significant simple adaptation effects for all congruent conditions; increased upper ($M = 19.51$, 95 % CI: [8.45, 30.56]), $t(21) = 3.22$, $p = .001$, $d = .69$, decreased upper ($M = -22.38$, 95 % CI: [-29.35, -15.40]), $t(28) = -5.93$, $p < .001$, $d = 1.10$, increased lower ($M = 31.09$, 95 % CI: [17.54, 44.64]), $t(25) = 4.41$, $p < .001$, $d = .86$, and decreased lower condition ($M = -15.02$, 95 % CI: [-21.85, -8.19]), $t(25) = -4.24$, $p < .001$, $d = .83$.

In contrast, there was no evidence of cross adaptation, as all incongruent conditions failed to reach statistical significance; increased upper ($M = -1.33$, 95 % CI: [-8.24, 5.59]), $t(21) = -.36$, $p = .707$, $d = .08$, decreased upper ($M = 2.44$, 95 % CI: [-2.69, 7.57]), $t(28) = .90$, $p = .351$, $d = .17$, increased lower ($M = .08$, 95 % CI: [-8.04, 8.21]), $t(25) = .02$, $p = .985$, $d = .00$, and decreased lower condition ($M = -8.41$, 95 % CI: [-17.20, .38]), $t(25) = -1.86$, $p = .061$, $d = .36$. As such, no further analyses were performed.

A 2 (adaptation direction) \times 2 (adaptation half) \times 2 (test half) mixed ANOVA was conducted to compare the strength of muscle adaptation aftereffects when adaptation and test halves were congruent versus incongruent (critical $\alpha = .05$). The ANOVA showed significant main effects of adaptation direction, $F(1,99) = 33.84$, $p < .001$, $\eta^2 = .25$, and test half, $F(1,99) = 9.97$, $p = .002$, $\eta^2 = .09$, revealing the differences between the aftereffects in the increased and decreased adaptation conditions, and the upper and lower test halves. A significant three-way interaction was also observed between adaptation direction, adaptation half, and test half, $F(1,99) = 85.81$, $p < .001$, $\eta^2 = .46$.

To interpret the three-way interaction, bootstrapped paired t-tests were conducted to compare the Δ PSN upper and Δ PSN lower scores for each adaptation condition. A Bonferroni adjusted critical alpha of .0125 was used. In all conditions, simple adaptation effects were significantly larger than cross adaptation effects; increased upper ($t(21) = 3.52$, $p < .001$, 95 % CI: [10.07, 31.59], $d = .89$), decreased upper ($t(28) = -7.01$, $p < .001$, 95 % CI: [-31.54, -18.10], $d = 1.40$), increased lower ($t(26) = 5.43$, $p < .001$, 95 % CI: [20.27, 41.75], $d = 1.05$), decreased lower ($t(25) = -2.86$, $p = .003$, 95 % CI: [-10.95, -2.28], $d = .32$).



Fig. 4 – Example Full Body Adaptation Stimuli

Note. a) Female and b) male whole body adaptation stimuli. Adaptation conditions from left to right: decreased upper, increased upper, decreased lower, increased lower.

To examine the overall pattern of simple and cross adaptation effects for Experiment 2, an additional analysis was conducted. As in Experiment 1, the data were “rectified” and collapsed into congruent and incongruent conditions (see Fig. 6). While a clear simple adaptation effect was observed for the congruent condition (bootstrapped one-sample t-test: $M = 22.11$, 95 % CI: [16.85, 27.36]), $t(102) = 8.41$, $p < .001$, $d = .83$), for the incongruent condition cross adaptation effects were not significant (bootstrapped one-sample t-test: $M = 1.17$, 95 % CI: [-2.60, 4.95]), $t(102) = .61$, $p = .542$, $d = .06$). The simple adaptation effect was significantly larger (bootstrapped paired t-test: $t(102) = 8.80$, $p < .001$, 95 % CI: [16.21, 25.66]), $d = .90$), with the cross-adaptation effect being only 5.31 % its size.

2.3. Discussion

In this experiment, no evidence of cross adaptation was shown when individuals were presented with whole-body stimuli. Moreover, cross adaptation effects were significantly weaker than simple adaptation. The lack of significant aftereffect transfer, in addition to the significant

difference between the simple and cross adaptation conditions, is most consistent with muscle-encoding neural populations that are completely body-half selective, i.e., are tuned to a particular body half. Although the observation of stronger aftereffects following simple, rather than cross adaptation is broadly consistent with Experiment 1’s findings, the absence of evidence of cross adaptation in Experiment 2 differs.

3. General discussion

The present study is the first to examine the body-half selectivity of the neural mechanisms underpinning muscle perception. By employing the simple/cross adaptation paradigm, inferences concerning the properties of these mechanisms can be made. In Experiment 1 muscle aftereffects were small following cross adaptation, and significantly weaker than following simple adaptation. These findings were broadly corroborated in Experiment 2 as the muscle aftereffects were again significantly weaker for the incongruent condition. However, in this experiment evidence of muscle

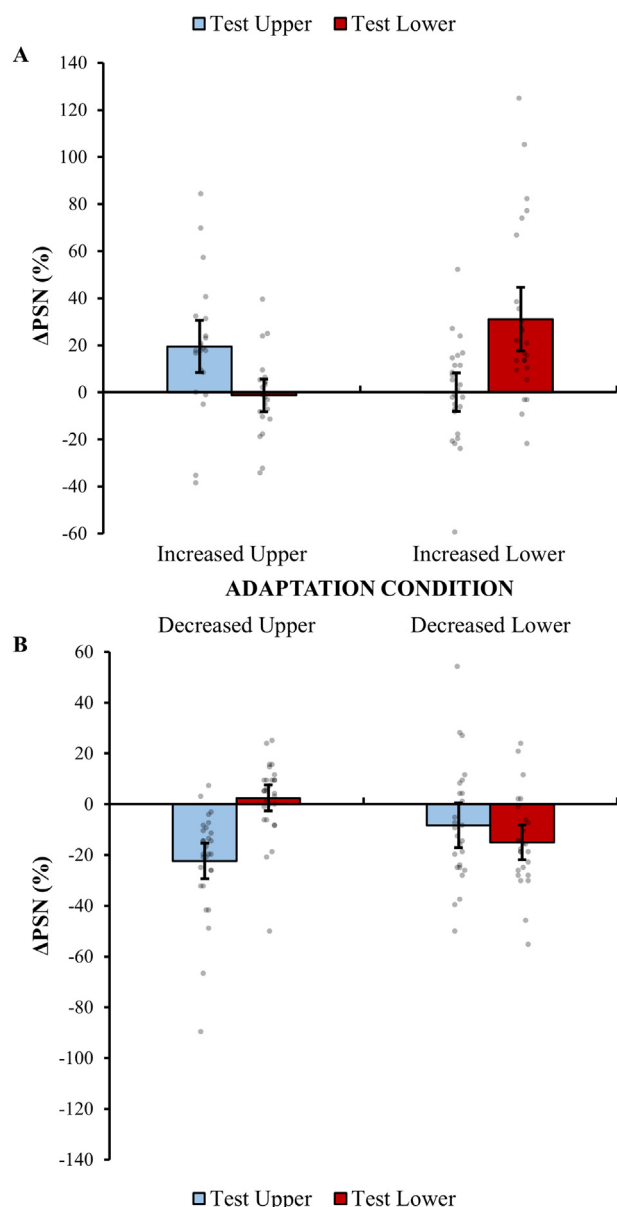


Fig. 5 – Results of Experiment 2

Note. Changes in the point of subjective normality (Δ PSN) for both adaptation conditions and test body half. (A) Adaptation to increased stimuli. (B) Adaptation to decreased stimuli. The grey dots indicate data from individual participants, while error bars show the 95 % CI from the bootstrapped one-sample t-tests.

aftereffect transfer between body halves was entirely absent when participants were presented with whole-body stimuli.

While differences between the patterns of results shown in Experiments 1 and 2 were not hypothesised, we may speculate about the possible cause using insights from historical studies on cross adaptation in binocular vision. Dvorak (1870; cited in Wade et al., 1993) was the first to observe that after adapting one eye to a motion stimulus (with the other eye closed), an aftereffect can still be experienced if the participant closes the adapted eye and opens the non-adapted eye.

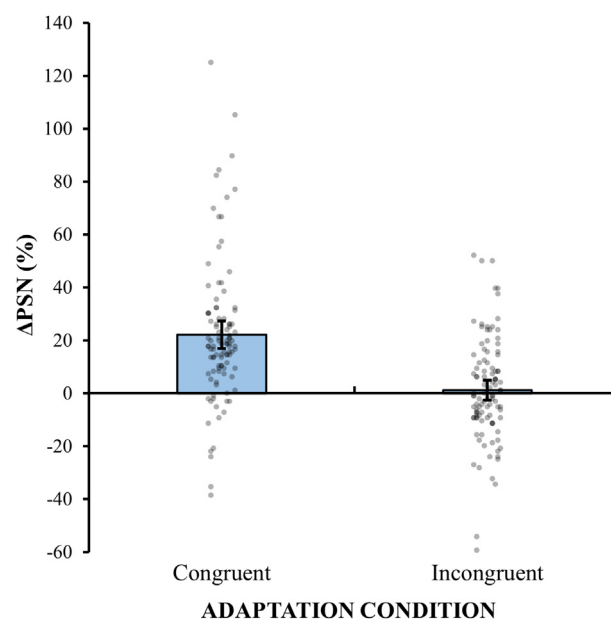


Fig. 6 – Results of Experiment 2: Aggregated Congruent and Incongruent Adaptation Conditions
Note. Results of Experiment 2 aggregated and recoded in terms of congruent and incongruent conditions. The grey dots indicate individual participants' data, while error bars show the 95 % CI from the bootstrapped one-sample t-tests.

This particular brand of cross-adaptation, referred to as interocular transfer, was taken as evidence of the involvement of a binocular “channel” in the motion aftereffect. An elementary model suggested that aftereffect magnitude depends upon the proportion of the channels that are driven during the test phase that have been adapted (Moulden, 1980). This soon led to the proposal that the binocular channels may comprise two sub-types: those with “AND” cells (active only when both eyes were stimulated) and those with “OR” cells (active when either one eye or the other was stimulated; Anstis & Duncan, 1983; Wolfe & Held, 1981). By analogy, it is possible that alongside neurons that process the top half of human bodies and those that process the bottom half, two other body-selective channels exist: those that are active only when both the top AND bottom halves are presented, and those can be activated by the top OR bottom halves of bodies when presented alone. Were this the case, Experiment 1's incongruent test conditions would recruit the “OR” neurons, which would have been adapted, plus neurons selective for the body half that was not used for adaptation. Hence 50 % of the recruited channels would be adapted. However, in Experiment 2, test patterns would instead drive neurons selective for the body half that was not adapted, alongside those in the “AND” channel. Although half of the channels recruited by the test stimulus had been adapted, this case differs from Experiment 1 in that the “AND” neurons will have been stimulated by a body for which only one half was extreme. It seems plausible that this would lead to a smaller degree of cross adaptation in Experiment 2 than 1, potentially rendering the effect undetectable. It is also possible that the proposed

“AND” neurons are far less numerous, or simply do not exist, leading to no cross adaptation at all in Experiment 2. However, it should be remembered that uncovering the details of these channels was not an aim of the present study, and hence the design does not allow confidence in these conclusions. Instead, the study was focused on uncovering any evidence of cross adaptation, finding little.

Previous experiments on cross adaptation between different body parts have shown mixed results. In contrast to studies that have failed to demonstrate arm-leg transfer of limb length aftereffects (Bratch et al., 2021) or face-hand transfer of the gender aftereffect (Kovacs et al., 2006), cross adaptation between body parts has been successful in several studies. This has been shown for identity (Ghuman et al., 2010), gender (Ghuman et al., 2010; Kessler et al., 2013; Palumbo et al., 2015), orientation (Cooney et al., 2015) and adiposity aftereffects (Re et al., 2011). More recently, adiposity cross adaptation has also been demonstrated between images of hands and bodies (Ambroziak et al., 2023). These differences may reflect the particular characteristics of the underlying neural mechanisms. It is noteworthy that each of these studies used isolated body parts as stimuli. In the present study, when similarly isolated stimuli were used (Experiment 1), a small cross adaptation effect was also evident, yet this effect was not apparent when whole body stimuli were used. This raises the question of whether the identity, gender, and adiposity aftereffects cited above would be eliminated if entire bodies were used as stimuli.

Although the effects that have previously been demonstrated imply the presence of face, hand and body networks that are at least somewhat overlapping, the demonstration of little to no cross adaptation within the present study suggests that muscle-encoding neural populations are substantially body-half selective. While we can infer that populations involved in the perception of muscularity for upper body stimuli are not highly responsive to lower body stimuli and vice versa, this does not imply that there are neurons selective specifically for images of half-bodies with the waist as a critical category boundary. It is entirely possible that the neurons in question are actually selective for smaller body parts, such as individual limbs, the chest, the torso, etc.

In the last 20 years, fMRI studies have begun to elucidate the details of the neural representation of bodies. Two body-sensitive regions that have been identified within extrastriate visual cortex are the Extrastriate Body Area (Downing et al., 2007) and Fusiform Body Area (Peelen & Downing, 2005). Within these regions, the neural mechanisms responsible for body part perception appear to be partially overlapping (Bracci et al., 2010, 2015; Orlov et al., 2010). Several studies, using multi-voxel pattern analysis or representation similarity analysis have presented evidence of selectivity for body parts such as these in humans (Vogels, 2022). Clusters of neurons have been identified that are selective for hands in an area that partially overlaps with the left EBA (Bracci et al., 2010), while the EBA was reported to be most highly activated by the upper limbs (Orlov et al., 2010); however, this region also showed substantial activation for lower limbs (see also Bracci et al., 2015). One possibility is that EBA contains individual neurons that are selective for limbs in general (i.e., arms and legs) – the kinds of cells that might underly a cross

adaptation effect such as that shown in Experiment 1. However, it is equally possible that within tight clusters in the EBA, some cells are selective for arms while others are selective for legs – a set-up that would not be expected to facilitate cross adaptation. Clearly, more work on the neural representation of different body parts is required before a clear picture of body part selectivity emerges (Vogels, 2022). Further, it is worth remembering that none of these studies presents any evidence that the neural mechanisms alluded to above have any involvement in the perception of muscularity. Yet given the behavioural data presented in the present study, it seems safe to conclude that the influence of mechanisms that encode muscularity and are activated by body parts both above and below the waist is small, and cannot be detected when whole body stimuli are presented.

The findings of the present study may also have implications for the real-world development and manifestation of BSSM. As suggested previously (Brooks et al., 2020; Challinor et al., 2017), visual adaptation may provide a potential mechanism for the misperception of muscularity, as frequent and prolonged viewing of muscular others may lead to a persistent aftereffect of perceived muscle, such that one's own body, when viewed in a mirror, may appear less muscular than it really is. However, evidence for body-half selectivity in muscularity aftereffects allows for more specific predictions. Under typical everyday scenarios, the upper and lower halves of the body are often simultaneously visible. Yet men, particularly those with high muscle dissatisfaction, tend to fixate more frequently on the chest and shoulders (Porrás-García et al., 2020). This bias is of interest as visual attention has been found to mediate the presence and strength of visual aftereffects (Stephen et al., 2019). The greater fixation on the upper body in men may result in a muscle aftereffect that is largely confined to the upper body regardless of the adaptor's lower body musculature. Thus, when looking at themselves in the mirror, individuals may underestimate the muscularity of their upper halves, but view their lower halves veridically in terms of muscularity, given the lack of cross adaptation. As a result, individuals may work to develop their upper body while comparatively neglecting their lower body, resulting in imbalanced muscular development. To appropriate a popular meme, they may be tempted to “skip leg day”. Muscle imbalances that are facilitated through adaptation may also occur in women but are likely to affect different regions of the body, as their attention is more biased towards the waist, hips, legs, and arms instead of the chest and shoulders (Hewig et al., 2008).

Using the technique of adaptation to uncover the details of perceptual processes has a long history (Thompson & Burr, 2009). It was never doubted that early demonstrations of visual aftereffects of motion, colour and orientation were perceptual in nature, given that their striking effects were retinotopic; that is, they applied only to the adapted region of the retina. Hence clear differences of motion, colour or orientation could be observed between the adapted region and neighbouring stimuli whose perceptual properties remained unchanged. However, high level aftereffects, such as those concerning the more complex properties of faces or bodies, tend to be less conspicuous and are non-retinotopic, affecting all visible stimuli. Effects are subtle, and comparisons

between neighbouring stimuli are not informative. With this in mind, some researchers have raised the possibility that these high level aftereffects are not perceptual in nature, but instead reflect a decisional bias due to a criterion shift (Morgan, 2014; Storrs, 2015). While the “method of adjustment” task used in the present study cannot irrefutably distinguish between these two possibilities, the underlying cause of altered judgements following exposure to extreme stimuli is currently under investigation in our lab. Regardless of the outcome, the implications for real-world instances of BSSM are likely to be equally deleterious. In the context of the present study, when an individual declares themselves to be insufficiently muscular, it may not matter whether this is due to actually seeing a less muscular body in the mirror, or due to a change in one's own standards for what is an appropriate level of muscularity.

The present study used computer-generated (CG) body stimuli. It is noteworthy that one recent study urged caution when using CG images, given that it can produce results that differ from those produced when photographs are used if appropriate manipulation checks are not employed (Alexi et al., 2019). Certainly, this technique is limited in terms of the degree of muscularity that can be simulated while retaining appropriate realism. This limitation was addressed in the present study via the use of extensive piloting to ensure that the stimuli were sufficiently muscular and realistic. Moreover, these pilot ratings were used to ensure that the level of extremity for high and low muscularity stimuli was balanced across both body halves and across stimulus gender. As a result, the strength of the muscle aftereffects observed in the present study are in line with those found in previous studies which used muscularity stimuli created through the manipulation of photographs (Brooks et al., 2019b; Sturman et al., 2017). Although it remains an empirical question, we are confident that our results using CG stimuli would generalise to photographic stimuli.

Although our preference would be to run all studies (especially those involving adaptation) face-to-face, this study was conducted during Australia's prolonged and strict lockdowns when online testing was the only option. We believe that experimental rigour, stimulus control and participant vigilance are crucial, but compliance can be compromised when testing those participating for course credit (many of whom have questionable levels of motivation) without supervision. A core property of adaptation is that the effect decays over time. The rate of decay for body aftereffects, and in particular for muscularity effects, has yet to be established formally. With this in mind, we regarded it as imperative that the adaptation stimuli were displayed without interruption, hence the exclusion criteria regarding internet connectivity problems. Given that adaptation involves viewing many stationary stimuli for a prolonged period without any response being required, we regarded it as likely that participants might fail to attend to the stimuli as instructed, instead leaving the experiment to perform another activity and returning later to make their responses. For this reason, we included simple attention checks. Further, it is important that participants responded promptly as instructed, to avoid prolonged breaks between top-up adaptation stimuli, hence the criteria

regarding average and individual response latencies. A long response latency would cause decay of adaptation and invalidate any PSN responses given from that point onwards. Although this resulted in the exclusion of a relatively large number of non-compliant participants, our exclusion criteria were objective and were established *a priori*, hence it is unlikely that this introduced bias in the data. Importantly, there is no reason to believe that the excluded participants' visual systems are fundamentally different to those of the participants who were included. It seems more likely that, with no supervision and no consequences, they simply did not comply with the task instructions, either deliberately or through inattention.

In sum, despite evidence that cross adaptation between the upper and lower halves of the body is weak when only halves are shown, and non-existent when whole bodies are shown, the present study found clear evidence of muscle aftereffects following simple adaptation, and significantly stronger effects following simple, rather than cross adaptation. Given the subtle differences between the patterns of results when isolated body parts are used compared to whole bodies, this should urge caution about the generality of previous studies showing transfer of adaptation between body parts which use only isolated body parts as stimuli. Regardless, our findings are most consistent with muscle-encoding neural populations that are substantially body-half selective. Moreover, these findings appear to be generalisable to more typical daily scenarios where body halves are viewed simultaneously. Hence, the present study provides a possible explanation of how muscle related BSSM is developed and maintained, whilst further cementing the use of visual adaptation as an effective tool for investigating the neural mechanisms underpinning muscle perception.

Author contributions

Keefe Ip: Conceptualisation, methodology, software, formal analysis, investigation, data curation, writing – original draft, writing – review & editing.

Nicole Kusyk: Conceptualisation, methodology, software, investigation, writing – review & editing.

Ian Stephen: Conceptualisation, formal analysis, writing – review & editing, supervision.

Kevin Brooks: Conceptualisation, methodology, writing – review & editing, supervision.

Open practices section

The study in this article earned Open Data badge for transparent practices. The data used in this study are available at: <https://osf.io/myf28/>

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Public archiving of anonymised study data and experimental stimuli

The anonymised study data for Experiment 1 and 2, and the experimental stimuli have been archived in open science framework (<https://osf.io/myf28/>). No analysis code was used.

Pre-registration

No part of the study's procedures or analyses were pre-registered prior to the research being conducted.

Declaration of competing interest

The authors have no disclosures to report.

Appendix A

Experiment 1: Pilot Study

To establish suitable parameters for the creation of the experimental stimuli, a pilot study was employed. Eight male and female models, each consisting of 11 equidistant levels ranging from extremely low to extremely high muscularity were created using Daz3D. As such, 352 body half stimuli were created for the pilot study. These stimuli were rated by 16 participants (8 male, 8 female) for their muscularity and realism along two symmetrical 11-point

Appendix B

Exclusion Criteria

The present study was conducted online. This is in contrast to prior studies which were typically conducted in highly controlled laboratory settings. To the best of our knowledge, this is the first body adaptation study to be conducted online, along with [Echevarria et al. \(in submission\)](#) and [Mobbs et al. \(in submission\)](#), which were conducted concurrently by other members of our laboratory. The absence of an experimenter to encourage vigilance and prompt responding was potentially problematic. As visual inattention to the adaptation stimuli has been found to significantly reduce the strength of the resulting aftereffects ([Rhodes et al., 2011](#); [Stephen et al., 2019](#)), an attention task was implemented in the adaptation phase to encourage attention to the adaptation stimuli. Moreover, the ability to measure the presence of an aftereffect can be diminished by aftereffect decay ([Rhodes et al., 2007](#)). To address these potential limitations, a strict set of exclusion criteria were enforced.

In Experiment 1, participants were excluded if they had an average trial length above 6 secs (the same as the top-up adaptation duration: $n = 65$) or if any of their trials took longer than 12 secs (double the top-up duration: $n = 116$). Similarly, participants were excluded if they experienced any loading delays due to a poor internet connection ($n = 60$). To

ensure the participants followed instructions, and viewed the adaptation and test stimuli as intended, participants were also removed if they failed any of the Fullscreen checks ($n = 32$). Finally, to ensure that participants attended to the adaptation stimuli as instructed, those who failed to respond to the attention task on more than 10 % of occasions were excluded ($n = 95$). Importantly, these criteria were established before the pattern of PSN responses were inspected. As participants could fail more than one criterion, a total of 180 participants were removed from the final analyses.

In Experiment 2, 41 participants were excluded prior to data collection for meeting one of three exclusion criteria: participant age under 18 or above 40 years, history of ED or MD, and/or vision was uncorrected when undertaking the experiment. Three exclusion criteria were also established a priori for Experiment 2. Participants were excluded if they had an average trial length above 12 secs (again – the same as the top-up adaptation duration: $n = 32$), if any of their trials took longer than 24 secs (again – double the top-up adaptation duration: $n = 16$), or if they failed on more than 10 % of the attention checks (specifically, two or more trials out of 18; $n = 32$). Upon analysis of the data, two further exclusion criteria were implemented. Participants who reloaded and restarted the experiment upon encountering an error were excluded ($n = 5$). A participant was also removed for failing to follow the instructions during the adaptation phase, as they repeatedly pressed the spacebar, regardless of whether the prompt was present, to succeed on the sporadic attention checks. Participants with missing experimental data were also excluded ($n = 18$). As participants could breach multiple criteria, a total of 113 participants were removed from the final analyses.

Despite the relatively high rate of participant exclusion for both experiments, the number of participants per condition in Experiment 1 and 2 was in keeping with prior research that used the simple/cross adaptation paradigm and similar statistical analytical methods (e.g., [Brooks et al., 2019b, 2020](#); [Sturman et al., 2017](#)).

REFERENCES

- Alexi, J., Dommissie, K., Cleary, D., Palermo, R., Kloth, N., & Bell, J. (2019). An assessment of computer-generated stimuli for use in studies of body size estimation and bias. *Frontiers in Psychology*, 2390. <https://doi.org/10.3389/fpsyg.2019.02390>
- Ambroziak, K. B., Bofill, M. A., Azañón, E., & Longo, M. R. (2023). Perceptual aftereffects of adiposity transfer from hands to whole bodies. *Experimental Brain Research*, 241, 2371–2379.
- American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders* (5th ed.). Washington, DC: Author. <https://doi.org/10.1176/appi.books.9780890425596>
- Anstis, S., & Duncan, K. (1983). Separate motion aftereffects from each eye and from both eyes. *Vision Research*, 23(2), 161–169.
- Anwyl-Irvine, A. L., Massoné, J., Flitton, A., Kirkham, N. Z., & Evershed, J. K. (2020). Gorilla in our midst: An online behavioural experiment builder. *Behavior Research Methods*, 52, 388–407. <https://doi.org/10.3758/s13428-019-01237-x>
- Barlett, C. P., Vowels, C. L., & Saucier, D. A. (2008). Meta-analyses of the effects of media images on men's body-image concerns.

- Journal of Social and Clinical Psychology*, 27(3), 279–310. <https://doi.org/10.1521/jscp.2008.27.3.279>
- Barlow, H. B., & Hill, R. M. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature*, 200, 1345–1347. <https://doi.org/10.1038/2001345a0>
- Benton, C., & Karazsia, B. T. (2015). The effect of thin and muscular images on women's body satisfaction. *Body Image*, 13, 22–27. <https://doi.org/10.1016/j.bodyim.2014.11.001>
- Blackmore, C., & Sutton, P. (1969). Size adaptation: A new aftereffect. *Science*, 166(3902), 245–247. <https://doi.org/10.1126/science.166.3902.245>
- Bracci, S., Caramazza, A., & Peelen, M. V. (2015). Representational similarity of body parts in human occipitotemporal cortex. *Journal of Neuroscience*, 35(38), 12977–12985. <https://doi.org/10.1523/JNEUROSCI.4698-14.2015>
- Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural responses to hands and non-hand body parts in human left extrastriate visual cortex. *Journal of Neurophysiology*, 103(6), 3389–3397. <https://doi.org/10.1152/jn.00215.2010>
- Bratch, A., Chen, Y., Engel, S. A., & Kersten, D. J. (2021). Visual adaptation selective for individual limbs reveals hierarchical human body representation. *Journal of Vision* (Charlottesville, Va.), 21(5), Article 18. <https://doi.org/10.1167/jov.21.5.18>
- Brooks, K. R., Baldry, E., Mond, J., Stevenson, R. J., Mitchison, D., & Stephen, I. D. (2019a). Gender and the body size aftereffect: Implications for neural processing. *Frontiers in Neuroscience*, 13, Article 1100. <https://doi.org/10.3389/fnins.2019.01100>
- Brooks, K. R., Clifford, C. W. G., Stevenson, R. J., Mond, J., & Stephen, I. D. (2018). The high-level basis of body adaptation. *Royal Society Open Science*, 5(6), Article 172103. <https://doi.org/10.1098/rsos.172103>
- Brooks, K. R., Keen, E., Sturman, D., Mond, J. M., Stevenson, R. J., & Stephen, I. D. (2019b). Muscle and fat aftereffects and the role of gender: Implications for body image disturbance. *British Journal of Psychology*, 111(4), 742–761. <https://doi.org/10.1111/bjop.12439>
- Brooks, K. R., Mond, J., Mitchison, D., Stevenson, R. J., Challinor, K. L., & Stephen, I. D. (2020). Looking at the figures: Visual adaptation as a mechanism for body-size and -shape misperception. *Perspectives on Psychological Science*, 15(1), 133–149. <https://doi.org/10.1177/1745691619869331>
- Brooks, K. R., Mond, J. M., Stevenson, R. J., & Stephen, I. D. (2016). Body image distortion and exposure to extreme body types: Contingent adaptation and cross adaptation for self and other. *Frontiers in Neuroscience*, 10, Article 334. <https://doi.org/10.3389/fnins.2016.00334>
- Brooks, K. R., Stevenson, R. J., & Stephen, I. D. (2021). Over or under? Mental representations and the paradox of body size estimation. *Frontiers in Psychology*, 12, Article 706313. <https://doi.org/10.3389/fpsyg.2021.706313>
- Brühlmann, F., Petralito, S., Aeschbach, L. F., & Opwis, K. (2020). The quality of data collected online: An investigation of careless responding in a crowdsourced sample. *Methods in Psychology (Online)*, 2, Article 100022. <https://doi.org/10.1016/j.metip.2020.100022>
- Caspi, A., Amiaz, R., Davidson, N., Czerniak, E., Gur, E., Kiryati, N., Harari, D., Furst, M., & Stein, D. (2017). Computerized assessment of body image in anorexia nervosa and bulimia nervosa: Comparison with standardized body image assessment tool. *Archives of Women's Mental Health*, 20(1), 139–147. <https://doi.org/10.1007/s00737-016-0687-4>
- Challinor, K. L., Mond, J., Stephen, I. D., Mitchison, D., Stevenson, R. J., Hay, P., & Brooks, K. R. (2017). Body size and shape misperception and visual adaptation: An overview of an emerging research paradigm. *Journal of International Medical Research*, 45(6), 2001–2008. <https://doi.org/10.1177/0300060517726440>
- Clifford, C. W., & Rhodes, G. (Eds.). (2005). *Fitting the mind to the world: Adaptation and after-effects in high-level vision*, 2. Oxford, England: Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198529699.001.0001>
- Cooney, S., Dignam, H., & Brady, N. (2015). Heads first: Visual aftereffects reveal hierarchical integration of cues to social attention. *Plos One*, 10(9), Article e0135742. <https://doi.org/10.1371/journal.pone.0135742>
- Daz3D. (2000). Daz Studio [Computer software] Version 4.12. <https://www.daz3d.com/>
- Devrim, A., Bilgic, P., & Hongu, N. (2018). Is there any relationship between body image perception, eating disorders, and muscle dysmorphic disorders in male bodybuilders? *American Journal of Men's Health*, 12(5), 1746–1758. <https://doi.org/10.1177/1557988318786868>
- Dolan, B. M., Birtchnell, S. A., & Lacey, J. H. (1987). Body image distortion in non-eating disordered women and men. *Journal of Psychosomatic Research*, 31(4), 513–520. [https://doi.org/10.1016/0022-3999\(87\)90009-2](https://doi.org/10.1016/0022-3999(87)90009-2)
- Downing, P., Wiggett, A., & Peelen, M. V. (2007). Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *The Journal of Neuroscience*, 27(1), 226–233. <https://doi.org/10.1523/JNEUROSCI.3619-06.2007>
- Dvorak, V. (1870). *Versuche über die Nachbilder von Reizveränderungen. Sitzungsberichte der Wiener Akademieder Wissenschaften*, 61, 257–262.
- Echevarria, M. A. J., Stephen, I. D., & Brooks, K. R. (in submission). *Looking round: The viewpoint dependence of body size aftereffects*. School of Psychological Sciences, Macquarie University.
- Frederick, D. A., Buchanan, G. M., Sadeghi-Azar, L., Peplau, L. A., Haselton, M. G., Berezovskaya, A., & Lipinski, R. E. (2007). Desiring the muscular ideal: Men's body satisfaction in the United States, Ukraine, and Ghana. *Psychology of Men & Masculinity*, 8(2), 103–117. <https://doi.org/10.1037/1524-9220.8.2.103>
- Fuentes, C. T., Longo, M. R., & Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica*, 144(2), 344–351. <https://doi.org/10.1016/j.actpsy.2013.06.012>
- Ghuman, A. S., McDaniel, J. R., & Martin, A. (2010). Face adaptation without a face. *Current Biology*, 20(1), 32–36. <https://doi.org/10.1016/j.cub.2009.10.077>
- Glauert, R., Rhodes, G., Byrne, S., Fink, B., & Grammer, K. (2009). Body dissatisfaction and the effects of perceptual exposure on body norms and ideals. *International Journal of Eating Disorders*, 42(5), 443–452. <https://doi.org/10.1002/eat.20640>
- Gould-Fensom, L., Tan, C. B. Y., Brooks, K. R., Mond, J., Stevenson, R. J., & Stephen, I. D. (2019). The thin white line: Adaptation suggests a common neural mechanism for judgements of Asian and Caucasian body size. *Frontiers in Psychology*, 10, Article 202532. <https://doi.org/10.3389/fpsyg.2019.02532>
- Grogan, S. (2010). Promoting positive body image in males and females: Contemporary issues and future directions. *Sex Roles*, 63(9), 757–765. <https://doi.org/10.1007/s11199-010-9894-z>
- Gwinn, O. S., & Brooks, K. R. (2013). Race-contingent face aftereffects: A result of perceived racial typicality, not categorization. *Journal of Vision*, 13(10), 1–11. <https://doi.org/10.1167/13.10.13>
- Gwinn, O. S., & Brooks, K. R. (2015). No role for lightness in the encoding of Black and White: Race-contingent face aftereffects depend on facial morphology, not skin tone. *Visual Cognition*, 23(5), 597–611. <https://doi.org/10.1080/13506285.2015.1061085>
- Hasenack, B., Sternheim, L., Bijsterbosch, J., & Keizer, A. (2021). The link between anxiety and assessment of body attitudes and body size estimation in anorexia nervosa. *Journal of*

- Experimental Psychopathology*, 12(1). <https://doi.org/10.1177/2043808721997632>, 2043808721997632.
- Hewig, J., Cooper, S., Trippie, R. H., Hecht, H. D., Straube, T., & Miltner, W. H. R. (2008). Drive for thinness and attention toward specific body parts in a nonclinical sample. *Psychosomatic Medicine*, 70(6), 729–739. <https://doi.org/10.1097/PSY.0b013e31817e41d3>
- Holland, G., & Tiggemann, M. (2017). “Strong beats skinny every time”: Disordered eating and compulsive exercise in women who post fitspiration on Instagram. *International Journal of Eating Disorders*, 50(1), 76–79. <https://doi.org/10.1002/eat.22559>
- Hummel, D., Grabhorn, R., & Mohr, H. M. (2012b). Body-shape adaptation cannot be explained by adaptation to narrow and wide rectangles. *Perception*, 41(11), 1315–1322. <https://doi.org/10.1068/p7197>
- Hummel, D., Rudolf, A. K., Untch, K. H., Grabhorn, R., & Mohr, H. M. (2012a). Visual adaptation to thin and fat bodies transfers across identity. *Plos One*, 7(8), Article e43195. <https://doi.org/10.1371/journal.pone.0043195>
- KDE. (2005). Krita [Computer software] Version 4.1.1. <https://krita.org/en/>.
- Kessler, E., Walls, S. A., & Ghuman, A. S. (2013). Bodies adapt orientation-independent face representations. *Frontiers in Psychology*, 4, Article 413. <https://doi.org/10.3389/fpsyg.2013.00413>
- Kovacs, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyanszky, Z. (2006). The electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, 16(5), 742–753. <https://doi.org/10.1093/cercor/bhj020>
- Leopold, A. D., O’Toole, J. A., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, 4(1), 89–94. <https://doi.org/10.1038/82947>
- Longo, M. R. (2022). Distortion of mental body representations. *Trends in Cognitive Sciences*, 26(3), 241–254. <https://doi.org/10.1016/j.tics.2021.11.005>
- Mitchison, D., Mond, J., Griffiths, S., Hay, P., Nagata, J. M., Bussey, K., Trompeter, N., Lonergan, A., & Murray, S. B. (2022). Prevalence of muscle dysmorphia in adolescents: Findings from the EveryBODY study. *Psychological Medicine*, 52(14), 3142–3149. <https://doi.org/10.1017/S0033291720005206>
- Mobbs, L. K., Stephen, I. D., & Brooks, K. R. (In submission). Experimental manipulations of visual attention affects muscularity perception. School of Psychological Sciences, Macquarie University.
- Morgan, M. J. (2014). *A bias-free measure of retinotopic tilt adaptation* (pp. 1–9). <https://doi.org/10.1167/4.1.7>. I.
- Moulden, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 290(1038), 39–55.
- Oppenheimer, D. M., Meyvis, T., & Davidenko, N. (2009). Instructional manipulation checks: Detecting satisficing to increase statistical power. *Journal of Experimental Social Psychology*, 45(4), 867–872. <https://doi.org/10.1016/j.jesp.2009.03.009>
- Orlov, T., Makin, T. R., & Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron*, 68(3), 586–600. <https://doi.org/10.1016/j.neuron.2010.09.032>
- Palumbo, R., D’Ascenzo, S., & Tommasi, L. (2015). Cross-category adaptation: Exposure to faces produces gender aftereffects in body perception. *Psychological Research*, 79(3), 380–388. <https://doi.org/10.1007/s00426-014-0576-2>
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93(1), 603–608. <https://doi.org/10.1152/jn.00513.2004>
- Peirce, J. W., Gray, J. R., Simpson, S., MacAskill, M. R., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*. <https://doi.org/10.3758/s13428-018-01193-y>
- Phillips, K. A., Wilhelm, S., Koran, L. M., Didie, E. R., Fallon, B. A., Feusner, J., & Stein, D. J. (2010). Body dysmorphic disorder: Some key issues for DSM-V. *Depression and Anxiety*, 27(6), 573–591. <https://doi.org/10.1002/da.20709>
- Porras-Garcia, B., Exposit-Sanz, E., Ferrer-Garcia, M., Castellero-Mimenza, O., & Gutiérrez-Maldonado, J. (2020). Body-related attentional bias among men with high and low muscularity dissatisfaction. *Journal of Clinical Medicine*, 9(6), Article 1736. <https://doi.org/10.3390/jcm9061736>
- Preston, C., & Ehrsson, H. H. (2014). Illusory changes in body size modulate body satisfaction in a way that is related to non-clinical eating disorder psychopathology. *Plos One*, 9(1), Article e85773. <https://doi.org/10.1371/journal.pone.0085773>
- Preston, C., & Ehrsson, H. H. (2016). Illusory obesity triggers body dissatisfaction responses in the insula and anterior cingulate cortex. *Cerebral Cortex*, 26(12), 4450–4460. <https://doi.org/10.1093/cercor/bhw313>
- Re, D. E., Coetzee, V., Xiao, D., Buls, D., Tiddeman, B. P., Boothroyd, L. G., & Perrett, D. I. (2011). Viewing heavy bodies enhances preferences for facial adiposity. *Journal of Evolutionary Psychology*, 9(4), 295–308. <https://doi.org/10.1556/JEP.9.2011.4.2>
- Rhodes, G., Jeffery, L., Clifford, C. W., & Leopold, D. A. (2007). The timecourse of higher-level face aftereffects. *Vision Research*, 47(17), 2291–2296. <https://doi.org/10.1016/j.visres.2007.05.012>
- Rhodes, G., Jeffery, L., Evangelista, E., Ewing, L., Peters, M., & Taylor, L. (2011). Enhanced attention amplifies face adaptation. *Vision Research*, 51(16), 1811–1819. <https://doi.org/10.1016/j.visres.2011.06.008>
- Rodgers, R. F., McLean, S. A., & Paxton, S. J. (2015). Longitudinal relationships among internalization of the media ideal, peer social comparison, and body dissatisfaction: Implications for the tripartite influence model. *Developmental Psychology*, 51(5), 706–713. <https://doi.org/10.1037/dev0000013>
- Shin, A., & Nam, C. M. (2015). Weight perception and its association with socio-demographic and health-related factors among Korean adolescents. *BMC Public Health*, 15, Article 1292. <https://doi.org/10.1186/s12889-015-2624-2>
- Stephen, I. D., Hunter, K., Sturman, D., Mond, J., Stevenson, R. J., & Brooks, K. R. (2019). Experimental manipulation of visual attention affects body size adaptation but not body dissatisfaction. *International Journal of Eating Disorders*, 52(1), 79–87. <https://doi.org/10.1002/eat.22976>
- Stephen, I. D., Sturman, D., Stevenson, R. J., Mond, J., & Brooks, K. R. (2018). Visual attention mediates the relationship between body satisfaction and susceptibility to the body size adaptation effect. *Plos One*, 13(1), Article e0189855. <https://doi.org/10.1371/journal.pone.0189855>
- Storrs, K. R. (2015). Are high-level aftereffects perceptual? *Frontiers in Psychology*, 6, 157. <https://doi.org/10.3389/fpsyg.2015.00157>
- Sturman, D., Stephen, I. D., Mond, J., Stevenson, R. J., & Brooks, K. R. (2017). Independent aftereffects of fat and muscle: Implications for neural encoding, body space, representation, and body image disturbance. *Scientific Reports*, 7, Article 40392. <https://doi.org/10.1038/srep40392>
- Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, 19(1), R11–R14. <https://doi.org/10.1016/j.cub.2008.10.014>
- Vartanian, L. R., Giant, C. L., & Passino, R. M. (2001). “Ally McBeal vs. Arnold Schwarzenegger”: Comparing mass media, interpersonal feedback and gender as predictors of

- satisfaction with body thinness and muscularity. *Social Behavior and Personality: an international journal*, 29(7), 711–723. <https://doi.org/10.2224/sbp.2001.29.7.711>
- Vogels, R. (2022). More than the face: Representations of bodies in the inferior temporal cortex. *Annual Review of Vision Science*, 8, 383–405.
- Wade, N. J., Swanston, M. T., & de Weert. (1993). On interocular transfer of motion aftereffects. *Perception*, 22(11), 1365–1380. <https://doi.org/10.1068/p221365>
- Webster, M. (2011). Adaptation and visual coding. *Journal of Vision*, 11(5), 1–32. <https://doi.org/10.1167/11.5.3>
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428, 557–561. <https://doi.org/10.1038/nature02420>
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, 6(4), 647–653. <https://doi.org/10.3758/BF03212974>
- Winkler, C., & Rhodes, G. (2005). Perceptual adaptation affects attractiveness of female bodies. *British Journal of Psychology*, 96(2), 141–154. <https://doi.org/10.1348/000712605X36343>
- Wolfe, J. M., & Held, R. (1981). A purely binocular mechanism in human vision. *Vision Research*, 21(12), 1755–1759.