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**Experience-dependent reshaping of body processing: from  
perception to clinical implications**

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## *Summary*

Starting from the moment we come into the world, we are compelled to pay large attention to the body and its representation, which can be considered as a set of cognitive structures that have the function of tracing and coding our state (de Vignemont, 2010). Although it may appear trivial, having a correct representation of our body is necessary to carry out many simple activities. To reach an object, for example, it is necessary that our brain makes a correct representation of how long our arm is; also, to understand where a sound comes from, it is essential for us to consider the distance between the two ears. Surely, a correct representation of the body schema is necessary in situations of calculating distances and metrics. However, we cannot consider body aside from its image, which can determine the way we emotionally perceive ourselves and other people as well as the way we experience the world. With a brief look to the body, we can identify a persons' identity, thus catching distinctive elements such as her age or gender; further, by means of body posture and movements we can understand the affective state of others and appropriately shape our social interaction and communication. Several socially significant cues can be detected and provided through the body, but this thesis principally aims to increase the knowledge about how we perceive gender from bodily features and shape. Specifically, I report on a series of behavioral studies designed to investigate the influence of the visual experience on the detection of gender dimension, considering the contribution of brain networks which may also have a role in the development of mental disorders related to body misperception (i.e. Eating Disorders; ED).

In the first chapter, I provide evidence for the interdependence of morphologic and dynamic cues in shaping gender judgment. By manipulating various characteristics of virtual-human body stimuli, the experiment I carried out demonstrates the association between stillness and femininity rating, addressing the evolutionary meaning of sexual selection and the influence of cultural norms (D'Argenio et al., 2020).

In the second chapter, I present a study that seeks to define the relative role of parvo- and magnocellular visual streams in the identification of both morphologic and dynamic cues of the body. For these experiments, I use the differential tuning of the two streams to low- (LSF) and high-spatial frequencies (HSF) and I test how the processing of body gender and postures is affected by filtering images to keep only the LSF or HSF (D'Argenio et al., submitted).

The third chapter is dedicated to a series of experiments aimed at understanding how gender perception can be biased by the previous exposure to specific body models. I utilize a visual adaptation paradigm to investigate the mechanisms that drives the observers' perception to a masculinity or femininity judgement (D'Argenio et al., 2021) and manipulates the spatial frequency

content of the bodies in order to account for the contribution of parvo- and magnocellular system in in this process.

The fourth chapter explores the role of cortical connections in body gender adaptation by means of Transcranial Magnetic Stimulation (TMS), with the aim to investigate neural correlates of dysfunctional body perception. Here, I briefly report the preliminary results emerging from a cortico-cortical Paired Associative Stimulation (cc-PAS) experiment.

In conclusion, the fifth chapter represents the intent to explain, at least partially, body misperception disorders by applying adaptation paradigms to ED clinical population.

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## 1. How motion and gender-type features interact in the perception of human bodies

### 1.1 Introduction

Gender is one of the most significant constructs in human social organization. Humans can rapidly differentiate between male and female conspecifics, relying on a heightened sensitivity to the biological commonalities that make an individual a male or a female. The evolution of this ability has been likely driven by the reproductive necessity to recognize the natural features of a potential mate. Even when primary sex characteristics are not visible, other morphological features of the body can easily mark sexual dimorphism. Among these features, the *waist-to-hip ratio* (WHR), is considered an important body cue to accurately discriminate men from women (K. D. Johnson, 2004; K. L. Johnson et al., 2012; Lippa, 1983). After puberty, women accumulate more fat on the hips than men and, over the years, the similarity in WHR between boys and girls decreases (Singh, 1993). Another sexually dimorphic feature is the *shoulder-to-hip ratio* (SHR), a distinction that tends to be higher in men than in women (Hugill et al., 2011). Accordingly, eye-tracking studies have shown that, while men spend more time examining the waist area of women's bodies, women focus their attention on the upper body of men (Dixson et al., 2011, 2014), suggesting that the use of WHR and SHR might be more important for evaluating female and male bodies, respectively.

Not only the morphological appearance of the body, but also its dynamicity, may identify gender, particularly when morphological features provide ambiguous information, such as when people are seen heavily dressed and/or from a considerable physical distance (Johnson & Tassinari, 2005). Since men and women move differently, gender judgement is tightly linked to body movement perception (Kerrigan et al., 1998; Kozlowski & Cutting, 1977; Mather & Murdoch, 1994). Accordingly, people can accurately detect gender from mere point-light displays of walking figures (Kozlowski & Cutting, 1977; Mather & Murdoch, 1994). Indeed, while walking with more hip translations (sway) is judged as more feminine, walking with more shoulder translations (swagger) is judged as more masculine. Further, McDonnell and colleagues (2007) have demonstrated that motion *per se* can guide gender judgement when morphological cues are ambiguous, as in the case of androgynous bodies. When typical feminine or masculine walking kinematics is applied to a neutral body figure, gender judgement follows the applied walking kinematics (McDonnell et al., 2007). Thus, there is evidence that people consider both morphologic and dynamic cues as reliable information on which to construct their gender assessments.

Interestingly, the compatibility between morphological and dynamic cues of gender categorization leads to greater aesthetic appreciation of a body, with swaying female bodies and swaggering male bodies being judged as more attractive (K. L. Johnson et al., 2007). From an evolutionary perspective,

body attractiveness plays a key role in sexual selection, as it is the main vehicle to appeal to a partner and prompt reproductive behaviour. However, since the factors regulating health and reproductive capabilities cannot be directly observed, sexual selection may have favoured psychological adaptations to attend to bodily features that are correlated with a greater procreative value (Sugiyama, 2004; Symons & Buss, 1994). Within this framework, studies have shown that different bodily features signal procreative value in men and women. For example, a man can increase his reproductive success by choosing a woman who is highly fecund, thus attending more to morphological body features (e.g. WHR) that signal female fertility. Indeed, WHR has been documented as a strong indicator of female fertility (Singh, 1993) as well as a reliable measure in the judgment of women's body attractiveness (Grammer et al., 2003; Singh & Singh, 2011) in a consistent way across many populations regarding men's preferences (R. C. Brooks et al., 2015; Dixon et al., 2007; Sorokowski & Sorokowska, 2012). Conversely, women may be more prone to choose a male mate with greater competitive drive (Archer, 2009) in order to provide resources to raise her offspring. This is consistent with data showing that women rate taller and more muscular men (Mautz et al., 2013) as more attractive. Also, body composition in men is not related to sperm motility, an indicator of male fertility (Fejes et al., 2005), but rather with physical strength (Windhager et al., 2011). Further, women seem to infer the health and strength qualities of a man through their active displays of the body, such as in dance (Hugill et al., 2009, 2010; Neave et al., 2011). Physical manifestations can be viewed as an important part of male courtship (Sheets-Johnstone, 2005). This is in keeping with the special role of body movements in communicating men's formidability (i.e., fighting ability and resource-holding potential).

The pressure of sexual selection within survival values of men and women has blended into stereotypical expectations about gender-specific features that men and women are encouraged to exhibit in given socio-cultural contexts. Indeed, society not only shapes personality and behaviour, but also the way in which the body appears (Nicholson, 1994). Applying undeniable societal pressure towards a thin-ideal shape for girls (Blaivas et al., 2002; Grabe et al., 2008; Hawkins et al., 2004) and an increased muscular body for boys (Daniel & Bridges, 2010; Hawkins et al., 2004), mass media reinforces gender-role norms. For example, it has been documented that men use physical activity to showcase their masculinity, since it helps to emphasize muscularity and, consequently, to be identified as a stronger individual (Drummond, 2008). Women have challenged the myth that sport is a prerogative of men, but the over-representation of male athletes in the media is still persistent; over 94% of athletic coverage is dedicated to men (Hovden & von der Lippe, 2019). As well, sports achievements of male athletes are regarded as more important than those of female athletes, who are rarely mentioned for their physical attractiveness. While morphological cues are emphasized for the

judgement of women (Tolman et al., 2006), masculine gender-type features are more related to performance and activities, including personal attributes of power, strength and efficacious (McCreary et al., 2005; Mishkind et al., 1986).

To summarize, both evolutionist and socio-cultural studies have provided numerous clues about the association between specific forms and movements of a body and the perception of its femininity/masculinity. These studies show that morphological and dynamic cues may influence the aesthetic appreciation of a male or female body. What is unclear, however, is whether and how much form and movement cues influence one another. Cazzato, Siega, & Urgesi (2012) showed not only that thinner and more dynamic bodies receive more positive aesthetic appreciation, but also that the perception of the size of a body is influenced by its dynamicity. The same body is judged thinner when displayed in a dynamic rather than a static posture.

This paper investigates how variations of gender-type morphological features (e.g., WHR) and dynamicity (static vs moving posture) influence each other in guiding gender judgement and aesthetic appreciation of a body.

To this aim, I created a pool of 3-D rendered images of bodies, offering a variety of sex-specific morphological features and implied movement. Participants were asked to rate the femininity and masculinity qualities (Exp. 1) and to rate the dynamism and attractiveness (Exp. 2).

## **1.2 Experiment 1**

### **1.2.1 Materials and methods**

#### **1.2.1.1 Participants**

A sample of 30 students (17 female) from the University of Udine (Italy) took part in the experiment in return for course credits. They were aged 18–35 years (mean= 26.63, sd= 5.15) and reported normal or corrected to normal visual acuity in both eyes. No participants reported any current neurological or psychiatric disorders. Written informed consent was obtained from each participant. The study procedures were approved by the institutional ethics review board (Commissione di Garanzia per il rispetto dei principi etici nell'attività di ricercar sugli esseri umani, Department of Language and Literature, Communication, Education and Society, University of Udine, Italy; Study Protocol CGPER-2019-12-09-02) and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. Participants were not informed to the aims and hypothesis of the experiment and a study debriefing was conducted at the end of the experiment. All participants were right-handed as ascertained with standard handedness inventory (Oldfield, 1971). The sample size required was

determined with the G\*power software (Faul et al., 2009), using the “as in SPSS” option. The expected effect size was set at  $f = 0.3$  based on a previous study of influence of motion and form on aesthetic body perception (Cazzato et al., 2012), alpha-level at 0.05, and desired power (1-beta) at 90%.

### **1.2.1.2 Stimuli**

To systematically control for the masculinity/femininity traits and implied motion of our body stimuli, I used the software Character Creator 3.0 (Reallusion, San Francisco, CA, USA). Four virtual-human models (two female and two male models) were previously selected from the default database. By using the software function to manipulate the percentage of masculinity/femininity traits embodied by a neutral body, I produced two different versions of each model, setting the amount of gender typicality traits at 60% or 90%. This allowed us to obtain more or less masculine/feminine bodies for each identity. Each body was rendered in ten typical daily poses, five static (e.g., standing, open, idle, and turned postures) and five moving poses (e.g., running, walking, jumping, dancing, moving), selected from the default folders of static and dynamic poses available in Character Creator (see Fig. 1). Bodies could be viewed from a frontal or three-quarter view and were pictured against a black background. In total I had two female and two male models depicted in 2 different versions (60% or 90% gender typicality) and rendered in 10 different postures for a total of 80 different body images. Furthermore, pictures were imported into GIMP 2.10.8 (GNU Image Manipulation Program, Berkeley, CA, USA) in order to produce a mirrored version of each image and thus obtain a pool of 160 different body stimuli. It is important to note, the head, pectoral and pelvic areas were blurred in order to mask primary sexual characteristics, however enough morphological information to visually convey the sexual phenotype was maintained (see Fig. 1).

### **1.2.1.3 Procedure**

The experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA). During the experimental session, participants sat 60 cm away from a 19-in PC monitor (resolution:  $1360 \times 768$  pixels; refresh frequency: 60 Hz), on which  $600 \times 600$  pixels images were presented one at a time at the centre of the screen. In different blocks, participants were asked to provide two different judgements about the bodies. For example, “How feminine is this body?” in Italian “*Quanto ritieni che questo corpo sia femminile?*” or How masculine is this body?”, in Italian “*Quanto ritieni che questo corpo sia maschile?*”). Each trial started with the appearance of the body image with a 1-7 Likert-scale below, which remained on the screen until a response was given. Participants rated the two attributes for each body by using 1 (not at all) to 7 (very much) keyboard keys with both hands. After the participants response, the image disappeared and the next trial was

presented. The same stimuli were randomly presented once in the Femininity block and once in the Masculinity block. The order of presentation of each block was counterbalanced across the participants.

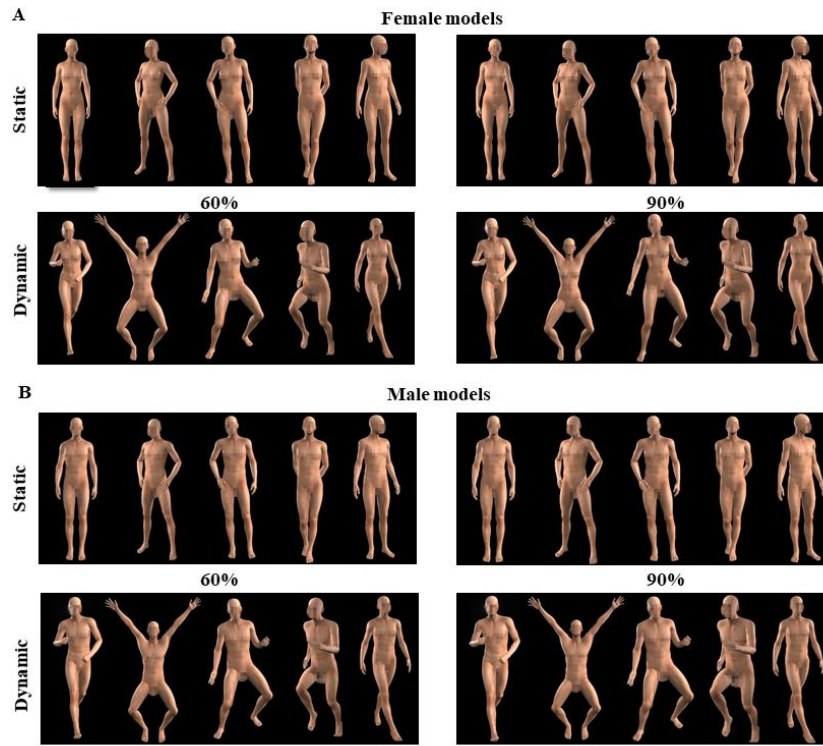


Figure 1. Examples of female and male virtual models used in the study. The examples depict the body sex-typing variation of either static or dynamic female (A) and male (B) models.

### 1.2.1.4 Data handling

The analyses were performed using ANOVA designs implemented in STATISTICA software (Stat Soft, version 10, StatSoft Inc, Tulsa, OK). For each experimental block (i.e., Femininity and Masculinity), individual rating values were collected and separately submitted to 3-way ANOVA with Posture (static vs. dynamic poses), Gender (male vs. female stimuli) and Typicality (60% vs. 90% gender traits) as within-subject variables and Gender group (male vs. female observers) as a between-subjects variable. Significant interactions were explored with the Tukey post-hoc test to correct for multiple comparisons. Significance threshold was set at  $p < 0.05$ . Effect size were estimated with partial eta squared ( $\eta_p^2$ ). Judgment values are shown as mean  $\pm$  standard error (SE).

## 1.2.3 Results

### 1.2.3.1 Femininity judgments

The ANOVA on femininity judgments (Fig. 2A) showed significant main effects of Gender [ $F(1,29) = 326.98$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.919$ ] and Typicality [ $F(1,29) = 5.68$ ;  $p = 0.024$ ;  $\eta_p^2 = 0.164$ ], that were

further qualified by a significant Gender x Typicality interaction [ $F(1,29) = 134.17$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.822$ ]. Tukey post-hoc tests [mean square error (MSE) = 0.06525,  $df = 29$ ] showed that femininity judgments increased from the 90% male stimuli, judged as the least feminine bodies, to the 90% female stimuli, judged as the most feminine bodies (all  $ps < 0.001$ ). Importantly, I also found a main effect of Posture [ $F(1,29) = 10.67$ ;  $p = 0.003$ ;  $\eta_p^2 = 0.2690$ ], showing a higher level of femininity for static rather than dynamic poses. The Posture x Gender x Typicality interaction [ $F(1,29) = 4.587$ ;  $p = 0.04$ ;  $\eta_p^2 = 0.1365$ ] was significant, showing that the effect of posture was different for body figures with varying degrees of feminine/masculine typicality. Tukey post-hoc comparisons [MSE = 0.02869;  $df = 29$ ] revealed that both 60% ( $p = 0.017$ ) and 90% ( $p = 0.019$ ) male stimuli received higher femininity judgments when displayed in static rather than dynamic poses. The same effect of posture, however, was only obtained for the 60% ( $p < 0.001$ ), but not the 90% ( $p = 0.525$ ) female stimuli. Femininity judgements increased with higher feminine typicality and with lower masculine typicality, independently from postures (all  $ps < 0.001$ ). However, the 60% static female stimuli received comparable feminine judgements to the 90% dynamic ones ( $p = 0.289$ ), suggesting that a static posture increased the feminine judgements of a low-typical body up to the level of a dynamic typical female body (or that a dynamic posture reduced the feminine judgments of a typical female body to the level of a static low-typical body). No significant main effect or interaction of Gender group was obtained but a Gender group x Gender interaction [ $F(1,28) = 6.053$ ;  $p = 0.02$ ;  $\eta_p^2 = 0.1777$ ], which showed that the difference between female and male models tended to be higher for female than male participants; however, post-hoc test did not reveal any significant between-group difference (all  $ps > 0.27$ ).

### **1.2.3.2 Masculinity judgments**

The ANOVA on masculinity judgments (Fig. 2B) showed significant main effects of Gender [ $F(1,29) = 303.36$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.913$ ] and Typicality [ $F(1,29) = 26.338$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.476$ ] as well as a significant 2-way Gender x Typicality interaction [ $F(1,29) = 171.994$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.856$ ]. Tukey post-hoc tests [MSE = 0.0592,  $df = 29$ ] showed a symmetrical pattern of results compared to femininity judgements: 90% female stimuli were judged as the least masculine bodies. 90% male stimuli were judged as the most masculine bodies (all  $ps < 0.001$ ). Again, I found a main effect of Posture [ $F(1,29) = 32.85$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.531$ ], which revealed higher judgements of masculinity for dynamic than static poses and was qualified by a significant Posture x Typicality interaction [ $F(1,29) = 8.74$ ;  $p = 0.006$ ;  $\eta_p^2 = 0.232$ ]. Tukey post-hoc tests [MSE = 0.02808,  $df = 29$ ] showed that dynamic poses led to higher masculine judgments independently from gender typicality, even if the effect of posture was higher for the 60% (dynamic vs static pose difference,  $0.694 \pm 0.115$ ) than for



the 90% (dynamic vs static pose difference,  $0.439 \pm 0.1$ ) bodies [planned comparison,  $F(1,29) = 8.74$ ,  $p = 0.006$ ]. No significant main effect or interaction of Gender group was obtained (All  $F < 2.928$ ,  $ps > 0.1$ )

### **1.2.6 Discussion**

The results of Experiment 1 showed that implied motion modulated the perception of feminine gender-typing morphological features, since the same low-typical bodies received lower feminine and higher masculine judgements when displayed in dynamic than static poses. This points to an association between stillness and femininity. Importantly, the effects of implied motion on femininity and masculinity judgements were comparable between the male and female observers, since the effect of posture was not modulated by gender group. From this pattern of results, it is not possible to discern whether gender-typing feminine forms may also modulate the perception of implied motion conveyed by a static picture of a body. It is also unclear whether the compatibility between two seemingly associated body cues, namely stillness and femininity affect body aesthetic appreciation, as shown for gender-typing bodies moving in a gender-typical way (Johnson & Tassinari, 2007).

To address these issues, I implemented a second experiment testing a subset of participants who took part to Experiment 1 by agreeing to complete a second session.

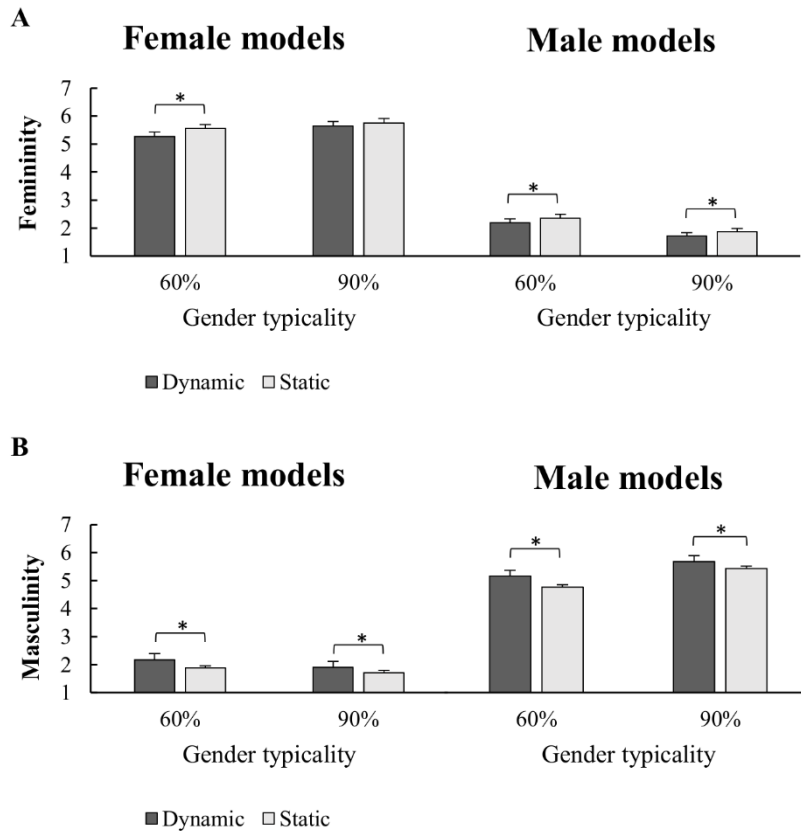


Figure 2. Mean and standard error of mean for Femininity (A) and Masculinity (B) judgments of Female and Male models as a function of implied motion (static/dynamic) along the two categories of sex-typing traits expressed (60%/90%).

## 1.3 Experiment 2

### 1.3.1 Materials and methods

The same stimuli, procedure and data handling approach as in Experiment 1 were used, but participants (N = 21, 11 women) aged 19-34 years (mean = 26.75, SD = 4.82) were asked to judge, in separate blocks, the dynamism (“How much do you think this body is dynamic?”; in Italian “*Quanto ritieni che questo corpo sia dinamico?*”) and the pleasantness (“How much do you like this body?”; in Italian “*Quanto ti piace questo corpo?*”) of the stimuli. The order of block presentation was balanced for all participants. The same repeated-measure variables (Posture x Gender x Typicality) as in Experiment 1 were tested, but the Gender group was not tested since it did not modulate the effects of implied motion on masculinity/femininity judgments in Experiment 1 in spite of greater sample size.

### 1.3.2 Results

#### 1.3.2.1 Dynamism judgments

The 3-way Posture x Gender x Typicality repeated-measures ANOVA on dynamism judgments (Fig. 3) showed a significant main effect of Posture [ $F(1,20) = 211.22$ ;  $p < 0.001$ ;  $\eta_p^2 = 0.914$ ], with higher dynamism judgements for dynamic than static poses. Interestingly, the ANOVA revealed also a significant main effect of Gender [ $F(1,20) = 6.16$ ;  $p = 0.02$ ;  $\eta_p^2 = 0.236$ ], demonstrating that female stimuli were judged as less dynamic than the male ones, even if displaying the same poses. However, a significant Posture x Gender x Typicality interaction [ $F(1,19) = 7.51$ ;  $p = 0.01$ ;  $\eta_p^2 = 0.283$ ] indicated that the dynamism judgements of female and male stimuli were modulated not only by the displayed body posture but also by gender typicality. Tukey post-hoc comparisons [MSE = 0.01886;  $df = 20$ ] showed that female bodies were judged less dynamic than male bodies only when they were displayed in a dynamic posture and with a 90% gender typicality ( $p = 0.005$ ); conversely, no between-gender differences were obtained for the other figure types (all  $ps > 0.84$ ). Furthermore, dynamic poses received higher dynamism judgments than static poses for all stimuli (all  $ps < 0.001$ ), while for either male or female models the 60% figures received comparable dynamism judgements to the 90% ones (all  $ps > 0.45$ ).

### **1.3.2.2 Pleasantness judgments**

The ANOVA on the pleasantness judgment values (Fig. 4) showed a significant main effect of Typicality [ $F(1,20) = 8.55$ ;  $p = 0.008$ ;  $\eta_p^2 = 0.299$ ], further qualified by a Gender x Typicality interaction [ $F(1,20) = 10.74$ ;  $p = 0.004$ ;  $\eta_p^2 = 0.349$ ]. Tukey post-hoc test [MSE = 0.05433;  $df = 20$ ] revealed the 90% male stimuli were judged more pleasant than the 60% ones ( $p < 0.001$ ), while no typicality modulation of the pleasantness judgments was obtained for the female stimuli ( $p = 0.822$ ). Furthermore, less typical (i.e., 60%) female stimuli were liked more than less typical male stimuli ( $p = 0.026$ ), while no between-gender difference was found for the 90%-typicality stimuli ( $p = 0.444$ ). Importantly, I found a significant Posture x Gender interaction [ $F(1,20) = 9.59$ ;  $p = 0.006$ ;  $\eta_p^2 = 0.324$ ], showing that also posture modulated the pleasantness judgements of male and female bodies. Tukey post-hoc test comparisons [MSE = 0.020789;  $df = 20$ ] indicated that female models were judged more pleasant in static than dynamic poses ( $p = 0.002$ ), while no significant difference between static and dynamic poses for male models was found ( $p = 0.50$ ).

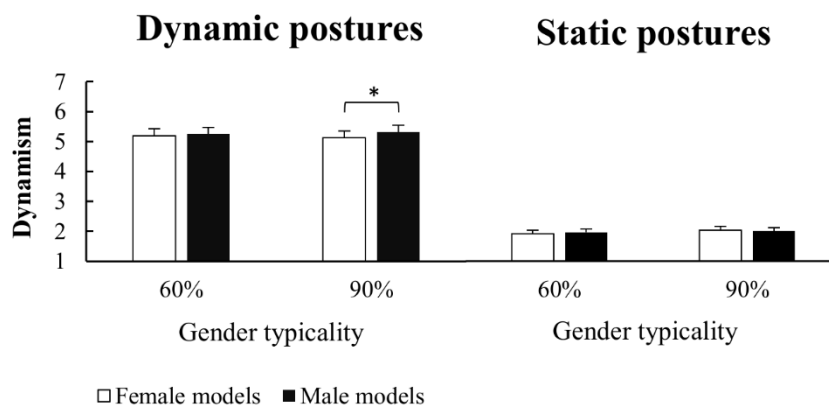


Figure 3. Mean and standard error of mean for Dynamism judgment of Dynamic and Static postures as a function of gender (female/male) along the two categories of sex-typing traits expressed (60%/90%).

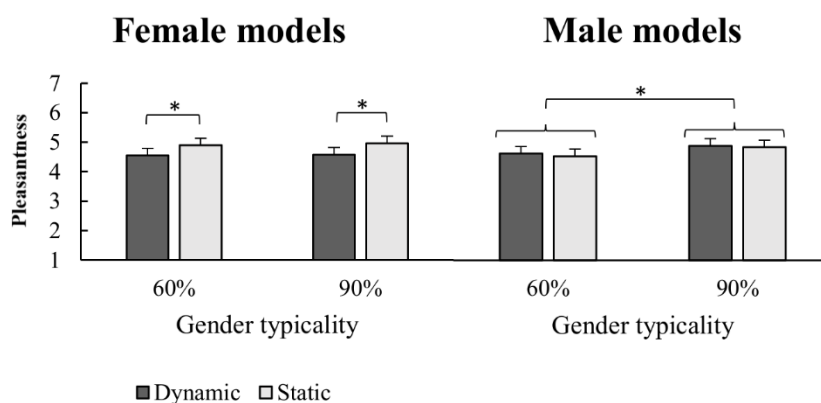


Figure 4. Mean and standard error of mean for Liking judgment of Female and Male models as a function of implied motion (static/dynamic) along the two categories of sex-typing traits expressed (60%/90%).

### 1.3.3 Item Analysis

To further explore the relationship between gender typicality, dynamism and aesthetic appreciation, I switched the data from the participant into the stimulus space, averaging for each of the 180 stimuli the dynamism, pleasantness or gender judgments across the 21 participants who took part to both Experiments 1 and 2. Female and male stimuli were analyzed separately, considering the femininity judgments for female stimuli and masculinity judgments for male stimuli. A series of bivariate correlation analyses was performed within the two sets of stimuli. Within the female stimuli, the bivariate correlation analysis showed a significant positive correlation between Femininity and Pleasantness judgments [ $r(80) = 0.58, p < 0.001$ ], but a negative correlation between Dynamism and Pleasantness judgments [ $r(80) = -0.35, p = 0.002$ ]; furthermore, a negative correlation between Femininity and Dynamism judgments was also found [ $r(80) = -0.22, p = 0.047$ ]. Within the male stimuli, results showed a significant positive correlation of Masculinity judgments with either

Dynamism [ $r(80) = 0.23, p = 0.04$ ] or Pleasantness [ $r(80) = 0.65, p < 0.001$ ] judgments, while dynamism did not significantly correlate with the aesthetic appreciation of male bodies [ $r(80) = -0.072, p = 0.527$ ]. In sum, the correlation analysis revealed that, for both male and female figures, greater gender typicality was associated with greater pleasantness judgments. However, while dynamism was associated with greater masculinity judgments for male stimuli, more dynamic female stimuli were judged less feminine and less pleasant.

Considering the trine reciprocal correlation between femininity, dynamism, and aesthetic appreciation of female bodies, we conducted a mediation analysis in order to assess the relative role of femininity or dynamism in mediating the influence of the other variable on Pleasantness judgments of female stimuli. Thus, we used established methods of mediation analyses to understand whether the effect of the independent variable (IV) on the dependent variable (DV) could be explained by a mediator (M) (MacKinnon et al., 1995). In particular, in two separate models we tested whether the femininity or the dynamism could mediate the influence on pleasantness judgment, exerted respectively by the dynamism or the femininity variables (Fig. 5). Mediation effects were tested using the Sobel test by applying the Goodman correction (Goodman 1960 MacKinnon 1995). One-tailed effects were tested since the direction of the mediation was predicted. In the first model (A), we speculated that the level of Femininity (M) could mediate the impact of the Dynamism (IV) expressed by a female body on its Pleasantness (DV). Inserting Femininity as mediator, the model provided evidence for an indirect effect of Dynamism on Pleasantness judgments, since the negative relation between Dynamism and Pleasantness was significantly affected by the inclusion of Femininity as a mediator ( $z = -1.91, p = .05$ ). Conversely, no evidence of mediation was obtained ( $z = 1.65, p = 0.1$ ) in a second model (B), considering that the Dynamism (M) conveyed by a body could mediate the effect of Femininity (IV) and on its Pleasantness (VD). Thus, mediation analyses suggested that more static female bodies were judged more feminine leading to a more positive aesthetic appreciation.

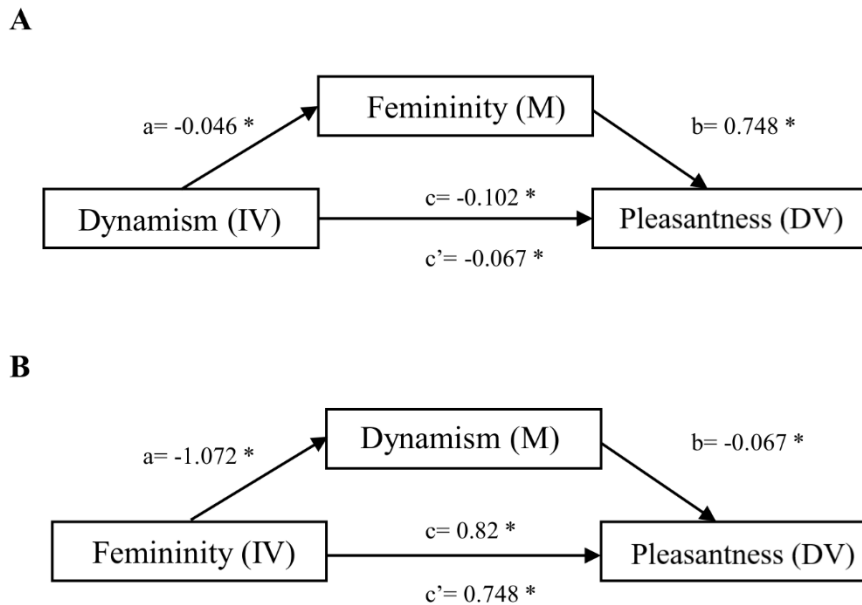


Figure 5. Path diagrams illustrating the two mediation models. The first model (A, upper panel) tested whether Femininity could mediate the influence of Dynamism (IV) on Liking judgements. The second model (B, lower panel) tested whether Dynamism could mediate the influence of Femininity (IV) on Liking judgements. For each path, values correspond to the unstandardized path coefficients for the association between variables. Namely, path a represents the relationship between IV and M, path b represents the relationship between M and DV (controlling for IV). Path c represents the direct effect between IV and DV. Lastly, the indirect effect of the mediator, path c', was quantified as the difference between the unstandardized path coefficients of the direct effect between the independent and the dependent variable (path c), and the product of the unstandardized path coefficients, a and b. Asterisks denote significant ( $p < 0.05$ ) regression coefficient. Significant differences between the direct and the indirect effects resulted from Sobel test in model A, indicating that the negative relationship between Dynamism and Liking judgement is mediated by Femininity.

### 1.3.4 Discussion

The aim of Experiment 2 was to investigate how gender typicality influences the perception of implied motion and how these two body cues interact in shaping the aesthetic appreciation of a human body. For this reason, participants rated male and female bodies varying in gender typicality for their level of dynamism and pleasantness. The results showed that gender typicality influences the perception of motion implied by a body posture. Female bodies with 90% typical gender-typing morphological features were judged as less dynamic than male bodies even if they had the same postures. Notably, this gender asymmetry was not found for the low-typical (i.e. 60% typicality) body figures, demonstrating the crucial impact of the salience of sex-specific traits in perceiving the motion evoked by body postures. This further strengthens the association between stillness and femininity.

Experiment 2 also showed that the compatibility between morphological and motion cues to the perception of body gender influenced the aesthetic appreciation of bodies. The more typical, 90% models were liked more than the less typical, 60% bodies, confirming that typicality of body forms is associated with greater pleasantness (Johnson & Tassinary, 2007). This effect, however, appeared

stronger when people were asked to judge a male model, indicating that the salience of gender-type attributes may be more important in the appreciation of male beauty. I found that female models in static poses were judged more pleasant with respect to female models in dynamic poses. Since appreciation of a body increases with the capability to express gender-specific features (Johnson & Tassinari, 2007), the higher scores for static female bodies seems to be consistent with the idea that stillness could enhance femininity appearance. This finding was corroborated by an item-level mediation analysis showing that more static female bodies were judged more feminine, leading to a more positive aesthetic appreciation.

#### **1.4 General discussion**

The present study aimed to investigate how the manipulation of gender-specific morphological features and implied motion of a body interact in making a judgment. For Exp 1, participants were asked to rate the masculinity and femininity. For Exp 2, participants were asked to judge dynamism and pleasantness. Both experiments used a series of pictures depicting male and female bodies expressing varying degrees of gender-type features (60% vs. 90% typicality) in static or dynamic postures.

Participants assigned a higher value of masculinity and femininity to more gender-typical male and female bodies, respectively. However, the most interesting finding was that implied motion influenced the gender judgment of body figures, at least when they were displayed with less gender-typing features (i.e., 60% typicality). Participants tended to perceive low-typical female bodies as more feminine when displayed in static rather than dynamic poses and to perceive low-typical male bodies as more masculine in dynamic rather than static poses. Not only implied motion influenced the perception of the gender-typing features of a body figure; gender typicality also influenced the perception of motion conveyed by a body posture. Models with typical female-typing features were evaluated as less dynamic than models with typical male-typing features, even with the same pose.

This pattern of results suggests that gender-type morphological cues and implied motion interact in shaping the perception of body gender. When morphological cues are not clear, the perception of static or dynamic postures pushes gender perception toward female or male, respectively. Similarly, when the motion conveyed by a body is fuzzy (e.g., implied motion in body pictures), the perception of female- or male-type features pushes motion perception toward stillness or dynamism, respectively.

Importantly, I found, at both subject and item level analyses, that the association between stillness and femininity influences the aesthetic appreciation of a body. Bodies with more gender-type features

(i.e., 90% typicality) were liked more than less-typical bodies (60% typicality). This is in line with the notion that the stereotypical representation of the body according to its gender has implications for its aesthetic appreciation (McCreary et al., 2005), reflecting a correlation between gender-type features and the impression of a good-looking body (Grammer et al., 2003; R. A. Johnstone, 1994; Singh & Singh, 2011).

Within female figures, the models in static poses were evaluated as more pleasant than those in dynamic poses. This may seem in contrast with studies showing that more dynamic dance poses are liked more (Calvo-Merino et al., 2008; Cross & Ticini, 2012; Kirsch et al., 2016) and that implied motion enhances the aesthetic appreciation of human bodies (Cazzato et al., 2012), in terms of either attribution of intrinsic perceptual properties to the stimulus (i.e., beauty) or the observer's attitude to it (i.e., enjoyment or attractiveness). Albeit gender-typical features were less salient in previous studies, implied motion was found to be a better predictor of the aesthetic appreciation of male more than female bodies (Cazzato et al., 2012). Static and dynamic stimuli in the judgment of female physical attractiveness has been reported in adult actresses, showing that more feminine WHRs and larger breasts are considered desirable traits in static photographs whereas more androgynous body shapes are considered appropriate in stars that perform in movies (Voracek & Fisher, 2006). The current experiments found that static postures increased the aesthetic appreciation of female bodies. This effect could be due to a direct negative effect of implied motion on the appreciation of female attractiveness or be indirectly mediated by a masking of female-typical physical traits.

The item mediation analysis allowed us to better delineate the relationship between femininity perception, stillness and aesthetic appreciation. I tested two models, based on the hypothesis that either stillness increased the perceived femininity of a female body and thus increased its pleasantness (Model A) or that femininity reduced the implied motion of a female body and thus reduced its pleasantness (Model B). The results provided evidence in favor of the first model, since perception of femininity was a key mediator of the negative relation between implied motion and liking. The effect of implied motion on positive appreciation of female bodies was better explained by an indirect effect mediated by femininity than by a direct effect of implied motion on liking. This supports the claim that stillness increases the aesthetic appreciation of a female body at least partially because it increases gender typicality, facilitating the perception of feminine-type features. Our data suggests that femininity and stillness, as well as masculinity and dynamism are associated features in body representation, confirming clues from both sexual-selection and socio-cultural frameworks.

In a sexual-selection evolutionist framework, perceiving a static female body vs. a dynamic male body may boost the salience of gender-type physical traits, such as WHR for women and muscularity



for men. Numerous studies have shown that a female body is strongly defined by the WHR. This is most likely related to objective gender-specific qualities such as the levels of sex hormones (e.g., estradiol; De Ridder et al., 1990; Mondragón-Ceballos et al., 2015), the accessibility to fat resources suitable for fetal neurodevelopment (Lassek & Gaulin, 2008), and the more general capacity to sustain pregnancy (Singh, 1993). WHR may serve as a proxy for covarying bodily traits that shape the entire body phenotype and co-determine the judgment of body attractiveness (Brooks et al., 2015). Selecting these qualities on the basis of visual cues increases the reproductive success of the species; the body shape of a woman could be considered as the best way to rapidly infer her femininity, meant as a set of biologically determined attributes. Since WHR is based on the computation of the waist and hips proportions, it is plausible that movements may affect its estimation altering shape and size perception. A body in motion can provide misleading information about shape, for instance, producing overlaps of body parts (i.e. arms that cover hips while running). As shown in a recent eye-tracking study (Pazhoohi et al., 2019), WHR is widely view-dependent and movement pattern can cause variation in WHR detection, even if body proportions remain constant. Dynamism may hinder the expression of femininity in women by obscuring salient shapes as compared to staying in canonical static poses.

As in many animal species, humans show sex differences in body composition and the amount of muscle mass appears to be greater in men than in women (Wells, 2007). Performing actions may accentuate the perception of body muscularity, thus biasing gender perception toward masculinity. Males tend to disclose their masculinity through movement (Darwin, 1871), as demonstrated by some species that use dance as a signal of neuromuscular condition (Maynard Smith, 1956) or flight ability (Williams, 2001). In humans, men's bodily symmetry reflects the developmental stability of an organism (Moller & Swaddle, 1997; Polak, 2003) and preservation from morbidity and mortality (Stevenson, 2000) and strongly correlates with their dance ability (Brown et al., 2005) and running performance (Manning & Pickup, 1998). This suggests that movements, rather than shape, may be a better predictor of men's functional effectiveness.

As a legacy of sexual selection, the stereotypical association between femininity/stillness and masculinity/dynamism is reflected in socio-cultural norms, based on how people think men and women should differ. A domain in which this distinction is quite tangible is represented by sports. Studies have suggested that, in most of Western countries, girls and women are less encouraged to participate in sports than boys and men (Eccles & Harold, 1991; Hartmann-Tews, I. ; Pfister, 2003). Even in physical activities where women are predominant, such as ballet, performance seems to be judged on the basis of aesthetic features than body capability (Klomsten et al., 2005). Media images

in sports endorses the stereotyped view of men's and women's bodies, emphasizing strength and physical abilities in the case of male athletes but featuring female performers in terms of a sexualized body (Von Der Lippe, 2002). This is in line with the present finding that perception of femininity appears to be intensified by a static body pose.

Studies about 'woman objectification', which refers to the tendency to perceive a woman's worth based on bodily appearance and sexual function, have demonstrated that the identification of the female body as an object available for satisfying the needs of men may diminish her attribution of agency (Cikara et al., 2011) and underline her passive condition. Interestingly, recent researchers have shown that images of female bodies are processed as a recollection of body parts rather than a whole figure (Bernard et al., 2012, 2015), a fragmentary process that is generally observed in the recognition of objects. This pattern of visual perception occurs independently from the gender of the observer, demonstrating that such objectification of the female body involves women themselves. The well proved association between femininity and object-related features could easily explain why static postures make bodies to appear more feminine. At the same time, men are encouraged to display their features in keeping with contemporary masculine norms, that consider increased muscle mass as more masculine (McCreary et al., 2005; Mishkind et al., 1986). This may explain why men tend to express their gendered body through exercising and practicing physical activity. Accordingly, a study aimed at exploring the association between levels of exercise and patterns of masculinity in men undergoing androgen deprivation therapy has recently revealed that men who are aerobically active have higher levels of self-reported masculinity than those who are inactive (Langelier et al., 2018), highlighting the intersection of masculinity and physical activity. Also women seem to judge masculinity through body movements, since they assess a men's physical strength and attractiveness on the basis of his gait (Fink et al., 2016).

The conclusions that can be drawn from this study need to be weighed in the light of important limitations. First of all, I investigated the effects of dynamic cues in body perception by using static pictures of bodies with implied motion. This allowed controlling for the amount of body views offered in videos of a moving or still person, but obviously limits the salience and naturalness of body movements. Nevertheless, there is evidence for common neurocognitive representation of actual and implied body movements (Cazzato et al., 2014,2016; Urgesi et al., 2006). Second, the limited sample size prevented us from examining differences between male and female observers and to generally explore the role of individual differences in body related processes on the association between stillness, femininity and aesthetic appreciation of bodies. In keeping with previous findings (Bernard et al., 2015; Bernard et al., 2012), our analyses showed overlapping pattern of results in male and

female participants, at least in Experiment 1 where the effects of implied motion on masculinity/femininity perception were explored. Further studies with larger sample are required to appropriately test for gender effects in body perception.

Furthermore, I found overlapping results not only when data were treated at the subject level but also at the item level. This directs us to generalizing the results at a wider population of male and female bodies. The use of a limited number of variations in gender typicality (i.e., 60% vs. 90%) prevents us from describing the effect of implied motion on female and male bodies along the continuous of gender typicality. Future studies, thus, need to test larger sample and use different type of stimuli (e.g., videos of real rather than computer generated bodies in movements) with greater variations of gender typicality and greater ecological validity in order to shed light on whether the association between stillness and femininity concerns mostly perceptive mechanisms or the stereotypical meaning assigned to men and women.

## 2. Spatial Frequency tuning of body gender and posture

### 2.1 Introduction

Classical models of object perception claim a separation of labour for the dorsal and ventral visual streams. The former is involved in object motion processing and the latter in object identity recognition (M. A. Goodale et al., 1991; Melvyn A. Goodale et al., 1994). These two pathways are biased toward different spatial frequencies in the scene that are conveyed by magnocellular or parvocellular signals and are better qualified to support the processing of large spatial differences or analysis of local features, respectively. The anatomical mapping of magnocellular and parvocellular regions has revealed a preference of the dorsal pathway for low spatial frequency (LSF) information (Denison et al., 2014), which is more critical when people are asked to make spatial coordinate judgements of stimuli. Concurrently, high spatial frequency (HSF) information seems to dominate the ventral information flowing, which is more efficiently exploited when the observers need to integrate fine details in order to categorize objects (Kosslyn et al., 1992; Michimata et al., 2011; Saneyoshi & Michimata, 2015). It has been shown that high-order areas of the dorsal stream are more sensitive to the processing of LSF images (Kauffmann et al., 2014), while the ventral areas that are generally dedicated to object recognition, such as the ventral part of the lateral occipital cortex, respond more strongly to HSF than LSF content (Valerie Goffaux et al., 2011).

However, the processing of human faces and bodies engages special perceptual processes and neural mechanisms (Dailey & Cottrell, 1999; Minnebusch & Daum, 2009). Faces and bodies seem to be preferentially processed with a configural strategy, for which the detection of specific spatial relations among features is more relevant than the single features per se (Sergent, 1984; Tanaka & Farah, 1993; Young et al., 1987). This tendency is further reflected by peculiar perceptual effects that do not occur, at least at the same extent, for objects (Tanaka & Farah, 1993). For example, it has been largely demonstrated that people exhibit impaired recognition of faces and bodies that are presented upside down with respect to their canonical orientation (Reed et al., 2003, 2006; Yin, 1969). This so-called “inversion effect” shows that changing the spatial configuration of a face or a body heavily disrupts its processing, even though both upright and inverted stimuli convey the same amount of local information. Inversion prevents the otherwise favoured engagement of configural mechanisms and leaves only inspection of single details (Bullier, 2001; Flevaris & Robertson, 2011; Hegdé, 2008; Watt, 1987).

Previous studies have provided mixed evidence on whether configural processing of faces is mainly contributed by LSF information (Goffaux, 2009; Goffaux & Rossion, 2006) or involves both LSF and HSF (Cheung et al., 2008). Even if the face inversion effect can be detected at a behavioural level

either using HSF or LSF visual information (Boutet et al., 2003; Gaspar et al., 2008), an electrophysiological marker of early-stage face processing, namely the N170, has been found to be less affected by face inversion for HSF than LSF or broadband faces (Flevaris et al., 2008; Valérie Goffaux et al., 2003; Halit et al., 2006). This may point to a dynamic coarse-to-fine mode of face processing, in which the early stages of visual processing of faces mainly rely on LSF to detect face configuration, while HSF are later processed to identify local details (Goffaux, 2009). In keeping with this model, Goffaux et al. (2011) found that short or long presentations of faces led to a preference of face selective areas in the occipito-temporal cortex to LSF or HSF, respectively.

Less is known about the contribution of visual scene bands to configural processing of bodies. A coarse-to-fine mode of body processing, like the one reported for faces (Goffaux, 2009), may point to the priority of LSF over HSF information also for configural body perception. Accordingly, Canario and colleagues (2016) showed that both face and body-selective areas in the occipito-temporal cortex are more activated by LSF than by HSF images of their preferred stimulus (i.e., a face or a body, respectively). This hints at a preferential involvement of configural processing embedded in magnocellular channels. Similarly, the neural activation of body-selective occipito-temporal areas was reported to be greater in response to whole bodies rather than in response to individual body parts (Taylor et al., 2007) or to a scrambled assembly of the same body parts (Brandman & Yovel, 2016). This points to a preferential response to body configurations.

A neurostimulation study by Urgesi et al. (2007a) used broadband body stimuli and assessed the body inversion effects after interferential stimulation of areas within the dorsal or the ventral streams, namely the ventral premotor cortex and a body-selective occipito-temporal area (i.e., extrastriate body area, EBA), respectively. Results of this study showed that, while interference with the ventral premotor cortex reduced the accuracy in matching upright body postures that diminished the body inversion effect, the interference with EBA impaired the matching of inverted bodies and enhanced the body inversion effect. Based on this evidence, the authors proposed the existence of two independent cortical routes involved in human body processing. The first is a route deputed to the configural process of whole bodies and housed in dorsal system areas (such as ventral premotor cortex). The second is a route specialized in the process of local body features and housed in ventral system areas (such as EBA).

The discrepancies between these previous studies in highlighting the involvement of ventral and dorsal stream areas to body configural processing can reflect the relative contribution of these streams to the processing of different aspects of the body. Ventral areas seem to be more engaged when steady aspects of the body are processed, such as body form. Dorsal areas come into play when an observer

treats more changeable attributes, such as body postures and movements (Gandolfo & Downing, 2020; Giese & Poggio, 2003; Urgesi, et al., 2007b). According to the Flexible Usage Hypothesis (Oliva & Schyns, 1997), initial categorization of a stimulus may influence early perception so that identical visual inputs may prompt the preferential use of LSF vs HSF information. Perception may use LSF more efficiently for configural processing and HSF for featural processing (Goffaux et al., 2005). Both configural and featural sources of information can be differently obtained from broadband spatial scale ranges (Cheung et al., 2008; Goffaux et al., 2005), according to the type of perceptual categorization that is required for the task. Face perception studies have shown that varied scales of frequencies can support a range of categorization tasks, with discrimination of steady (e.g., identity) and dynamic (e.g., expressions) aspects of face recognition that rely on HSF or LSF (Dailey & Cottrell, 1999; Oliva & Schyns, 1997; Rosenblum et al., 1996; Schyns et al., 2002).

(Based on these findings and exploiting the differential tuning of ventral and dorsal pathways to HSF and LSF, respectively, I hypothesized that processing body gender, as a proxy to body form, may rely more on the activity of ventral areas and be biased to HSF information). In contrast, processing body posture, as a proxy to body dynamics, may rely more on dorsal areas and be biased to LSF information.

To test this hypothesis, I administered a delayed matching-to-sample paradigm in which participants were given two probe bodies and asked which one matched a previously presented body sample. The match could differ by gender (with the same posture) or posture (keeping gender constant). The sample and probe stimuli could be presented either upright or inverted and could contain all spatial frequencies or be filtered to retain only HSF or LSF bands. I aimed to test the relative contribution of LSF and HSF to the body inversion effect (BIE) and, thus, configural processing of body gender and posture. Previous studies showed a deficit of configural body processing (Reed et al., 2007) and a bias for local rather than global processing of visual information (Booth & Happé, 2018; Happé & Booth, 2008) in individuals with autism. To investigate this further, I tested the dependence of LSF vs. HSF for configural body processing in relation to the distribution of autistic traits in our non-clinical sample.

## **2.2 Methods**

### **2.2.1 Participants**

Seventy-two students (forty-five women, mean age 24.3, SD 6.76 years) recruited at the University of Udine took part in the present study. Written informed consent was obtained from all participants. The procedures were approved by the local ethics committee (Institutional Review Board,

Department of Languages and Literatures, Communication, Education and Society, University of Udine, Study Protocol CGPER-2019-12-09-02) and conformed with the Helsinki Declaration. Participants were right-handed as ascertained with standard handedness inventory (Oldfield, 1971) and reported normal or corrected vision. They were naïve to the purpose of the experiment and a detailed debriefing was provided only after the whole experiment was completed.

The sample size required for our 2 x 3 x 2 repeated-measures ANOVA design (Task x SF x Orientation) was determined with the G\*power software (Faul et al., 2009), using the “as in SPSS” option. The expected effect size was set at  $f = 0.3$  based on a previous study of SF modulation of face inversion effect (Boutet et al., 2003), alpha-level at 0.05, and desired power (1-beta) at 90%.

### **2.2.2 Stimuli**

I used the Character Creator 3.0 software (Reallusion, San Francisco, CA, USA) to generate a set of virtual-human body stimuli. The stimuli were constructed selecting four virtual-human models (two females and two males) from the software default database (i.e., F1, F2 and M1, M2). In order to increase stimuli variation, I produced four different versions of each model by setting the amount of gender traits at 80% or 100% and the amount of body fat at 0% or 10%. I generated more or less masculine/feminine and fatter/thinner bodies, thus obtaining a set of 16 different bodies. Each body was rendered in four different daily poses (e.g., standing, idle, walking, moving) selected among the default postures available in Character Creator. The images were then imported into Adobe Photoshop CS6 (Adobe Systems, San Jose, CA) to manipulate the SF content by using a Gaussian blur filter with a 6-pixel kernel for low-pass filtering (LSF) and the high-pass filter application set to a radius of 0.9 pixels for the high-pass filtering (HSF). In addition to the intact one, I obtained an HSF and a LSF version of each image, for a total of 192 different stimuli. All the grey-scale bodies were pictured from a frontal view and against a black background. For all images, the head, pectoral and pelvic areas were blurred to mask facial and primary sexual characteristics while keeping enough morphological information to visually convey sexual phenotype (Fig. 6).

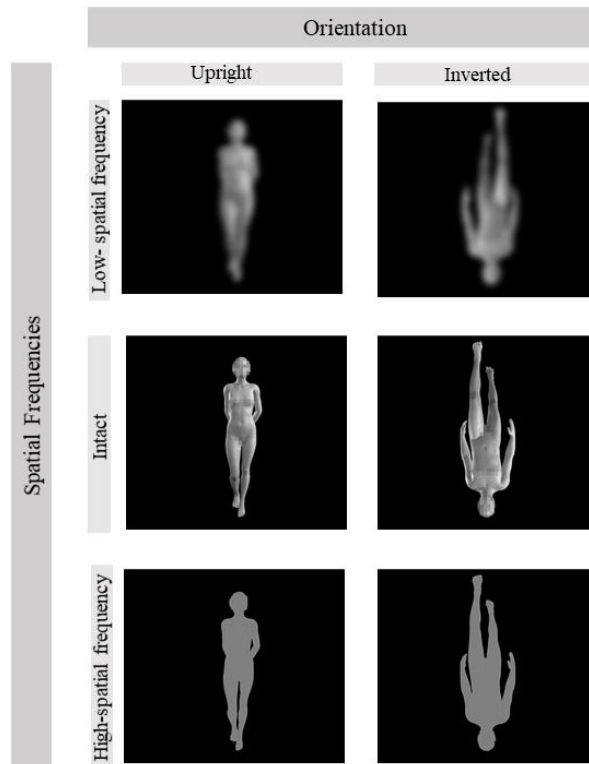


Figure 6. Examples of female and male virtual models used in the study as stimuli. The figure depicts the variation in orientation (upright vs inverted) and spatial frequency (high-spatial frequency vs intact vs low-spatial frequency).

### 2.2.3 Procedure

The experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA). The participants were tested individually (at their house) using a laptop PC with the E-prime Subject Station installed; they were advised to work in a quiet room and sit in front of their computer screen (refresh rate, 60 Hz) at a distance of 60 cm. Stimulus size was adapted to cover approximately a  $10^{\circ} \times 5^{\circ}$  area for all participants. Due to Covid-19 restrictions, the experimenter was not present, and this must have posed risks in terms of respected homogeneity of conditions. In two different sessions, participants were asked to perform two identical matching-to-sample tasks, with the exception of identifying the models to be used as stimuli (F1 and M1 in one session and F2 and M2 in the other session). Each session lasted approximately 40 min. Participants were administered in 8 blocks of 96 trials, with random presentation of upright and inverted stimuli in the intact, LSF and HSF conditions and required the discrimination of either gender or posture. For both sessions, participants were administered for a total of 1,536 trials (128 trials per cell).

Each trial started with the appearance of a white central fixation cross (500 ms) presented on a black background and followed by the sample body that lasted 150 ms. Soon after the image offset, a scrambled mask was presented for 500 ms. Then, participants were presented with two probes,



positioned one next to the other at the side of the screen center, and asked to identify the body that matched the target. To give their responses, they used the left or right index finger to press the “Z” or “M” key on their QWERTY keyboard; each key corresponded to one of the two positions on the screen on which the probes were randomly presented. The two probes stayed on the screen until a response or for a maximum of 3,000 ms, after which a new trial was presented (Fig. 7). The two probes could differ either for gender or for posture. All body stimuli could be shown with an upright or inverted orientation, with the orientation of the probes consistent with that of the sample.

In addition, participants filled in a computerized version of the Autistic Quotient (AQ; Baron-Cohen et al., 2001). This is a 50-items self-report questionnaire that is largely used to estimate the presence of autistic traits in a non-clinical population measuring impairments related to either cognitive functions (i.e., attention switching, attention to detail, and imagination) or social skills (i.e., communication and social skills) that characterize the autistic profile (Ruzich et al., 2015).

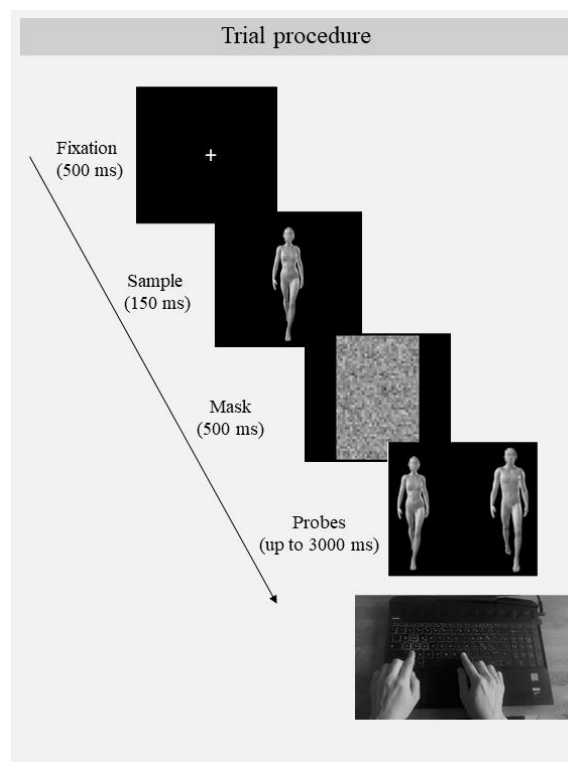


Figure 7. Trial procedure. A representation of the events constituting the structure of a single trial of the matching-to-sample task. Each trial began with the fixation cross, followed by the target picture. Soon after the mask presentation, a frame with the two probes remained on the screen until a response was recorded or for a maximum of 3,000 ms.

#### 2.2.4 Data handling

Analyses were performed using Analysis of variance (ANOVA) designs and HSD Tuckey post-hoc test for multiple comparisons implemented in the STATISTICA 7 software (Stat Soft, Tulsa, OK). Individual performance in the matching-to-sample task was expressed as percentage of correct

responses (Accuracy, %) and mean Reaction Times (RTs, in ms) of correct responses for each individual and condition. I excluded, from both accuracy and RTs analyses, trials that resulted two standard deviations (SD) above or below the individual RTs mean. Accuracy and RTs were entered as dependent variables in two separated RM ANOVAs Task (2 levels), SF (3 levels), and Orientation (2 levels) as repeated measures.

We calculated a BIE index, for both Accuracy and RT for each participant and condition. To obtain the Accuracy BIE score, I subtracted the accuracy for inverted bodies from the accuracy for upright bodies within the same condition. To obtain the RTs BIE score, I subtracted the mean RTs for upright bodies from the mean RTs for inverted bodies within the same condition. For both Accuracy and RTs, the greater the BIE, the larger the drop of performance for inverted vs. upright bodies and the larger the use of configural body processing. I performed planned comparisons between the strength of the BIE across the three spatial frequency conditions using paired dependent sample t-test (two tailed) with Bonferroni correction to control for multiple (6) comparisons. Individual BIEs for each condition (i.e., gender HSF, gender LSF, gender INTACT, posture HSF, posture LSF and posture INTACT) were correlated with the AQ total score. The significance of the Pearson's  $r$  coefficient was tested with a Bonferroni correction procedure to control for multiple (6) correlations. Significance threshold was set at  $p < 0.05$  for all analysis. Effect sizes were estimated with partial eta squared ( $\eta^2$ ). Values are reported as mean  $\pm$  standard error of the mean (SEM).

## **2.3 Results**

### **2.3.1 Accuracy**

The 2 Task x 3 SF x 2 Orientation ANOVA on Accuracy yielded significant main effect of SF [ $F(2,132) = 57.55$ ;  $p < 0.001$ ;  $\eta^2 = 0.466$ ], which revealed that bodies were matched better for HSF ( $88.2 \pm 0.7\%$ ) than for Intact ( $86.1 \pm 0.8\%$ ) and LSF ( $84.5 \pm 0.8\%$ ; all  $p < 0.001$ ) stimuli. Also, performance for the LSF stimuli was significantly lower than for the Intact ones ( $p < 0.001$ ). A significant main effect of Orientation [ $F(1,66) = 140.2$ ;  $p < 0.001$ ;  $\eta^2 = 0.679$ ] emerged, confirming that body discrimination was easier for upright ( $88.2 \pm 0.8\%$ ) rather than inverted ( $84.3 \pm 0.7\%$ ) images. The ANOVA showed significant Task x SF [ $F(2,132) = 57.82$ ;  $p < 0.001$ ;  $\eta^2 = 0.467$ ] and Task x Orientation interactions [ $F(1,66) = 96.52$ ;  $p < 0.001$ ;  $\eta^2 = 0.594$ ], further qualified by the Task x SF x Orientation interaction [ $F(2,132) = 4.45$ ;  $p = 0.013$ ;  $\eta^2 = 0.063$ ]. All other effects were not significant (all  $F < 1.7$ ,  $p > 0.19$ ,  $\eta^2 < 0.02$ ). Tuckey HSD post-test revealed that, for upright bodies, the gender task was performed better than the posture task in the Intact and HSF conditions (all  $p < 0.001$ ). As well, a better performance in the posture than in the gender task was shown for the LSF condition ( $p = 0.006$ ). For inverted bodies, the gender task was more difficult than the posture

task in all SF conditions (all  $p < 0.012$ ). This pattern reflected a worsening of the gender discrimination performance with either inversion or LSF manipulations.

Considering modulations within the gender task, for both upright and inverted bodies, participants' accuracy was significantly lower in the LSF than in the HSF and Intact conditions (all  $p < 0.001$ ), which in turn did not differ (all  $p > 0.48$ ). Upright bodies were matched better than inverted bodies in all SF conditions (all  $p < 0.001$ ; Fig 8a). With respect to the Accuracy BIE scores, planned t-tests comparing the three SF conditions (Intact:  $7.69 \pm 0.913\%$ ; HSF:  $7.45 \pm 0.552\%$ ; LSF:  $6.73 \pm 0.824\%$ ) did not reveal any difference (for all comparisons,  $t(66) < 1.1$ ; Bonferroni corrected  $p > 0.99$ ).

Concerning the Posture task, post-hoc tests showed that upright bodies were not matched as well for Intact than for HSF and LSF stimuli (all  $p < 0.001$ ), which in turn did not differ ( $p = 0.99$ ). Performance for inverted bodies was comparable for all SF conditions (all  $p > 0.39$ ). Comparing upright and inverted showed no significant difference in SF conditions (all  $p > 0.23$ ; Fig 8c). Planned t-tests on the Accuracy BIE revealed that the difference between upright and inverted bodies did not differ for SF conditions (Intact:  $-1.16 \pm 0.913\%$ ; HSF:  $1.15 \pm 0.668\%$ ; LSF:  $1.78 \pm 0.661\%$ ; all  $t(66) < 2.166$ , Bonferroni corrected  $p > 0.059$ ).

### **2.3.2 Reaction Times (RTs)**

The 2 Task x 3 SF x 2 Orientation ANOVA performed on the RTs showed a significant main effect of Task [ $F(1,66) = 29.80$ ;  $p < 0.001$ ;  $\eta^2 = 0.311$ ], revealing that participants were overall more rapid in matching the bodies for their gender ( $733.56 \pm 15.35$  ms) than for their posture ( $771.22 \pm 15.61$  ms). A main effect of SF was also found [ $F(2,132) = 27.349$ ;  $p < 0.001$ ;  $\eta^2 = 0.293$ ], which revealed that bodies were matched faster in the HSF ( $734.37 \pm 14.49$  ms) than Intact ( $754.94 \pm 14.72$  ms,  $p < 0.001$ ) and LSF ( $767.86 \pm 16.61$  ms;  $p < 0.001$ ) conditions; also, responses in the LSF condition were significantly slower than in the Intact one ( $p < 0.01$ ). A significant main effect of Orientation [ $F(1,66) = 60.66$ ;  $p < 0.001$ ;  $\eta^2 = 0.478$ ] was found, thus attesting that body recognition was faster for upright ( $727.97 \pm 14.01$  ms) rather than inverted ( $776.82 \pm 16.67$  ms) images. The ANOVA on RTs also showed significant Task x SF [ $F(2,132) = 20.70$ ;  $p < 0.001$ ;  $\eta^2 = 0.239$ ], Task x Orientation [ $F(1,66) = 127.69$ ;  $p < 0.001$ ;  $\eta^2 = 0.659$ ], and SF x Orientation [ $F(2,132) = 17.08$ ;  $p < 0.001$ ;  $\eta^2 = 0.205$ ] interactions, further qualified by the Task x SF x Orientation interaction [ $F(2,132) = 19.99$ ;  $p < 0.001$ ;  $\eta^2 = 0.232$ ]. The Tuckey HSD test reported that, in all SF conditions, participants discriminated more rapidly the gender than the posture of upright (all  $p < 0.001$ ), but not inverted (all  $p < 0.43$ ), bodies.

Considering the modulations in the Gender task, for upright bodies, participants' performance was significantly slower for the LSF than the HSF and Intact stimuli (all  $p < 0.001$ ), which in turn did not

differ ( $p = 0.602$ ). For inverted bodies, performance for the HSF stimuli was significantly faster than that for the LSF stimuli ( $p < 0.001$ ) and tended to be faster than that for Intact stimuli ( $p = 0.062$ ); RTs for LSF and Intact stimuli did not differ ( $p = 0.938$ ). Upright bodies were matched faster than inverted bodies in all SF conditions (all  $p < 0.001$ ; Fig 8b). Comparing the drop of performance for the inverted as compared to upright bodies for the three SF conditions revealed that the RTs BIE was much smaller in the LSF condition ( $60.10 \pm 84.79$  ms) than in the Intact ( $107.63 \pm 80.56$  ms;  $t(66) = -5.97$ ; Bonferroni corrected  $p < 0.001$ ) and HSF ( $101.24 \pm 77.29$  ms;  $t(66) = -4.51$ ; Bonferroni corrected  $p < 0.001$ ) ones, which in turn did not differ ( $t(66) = 0.85$ ; Bonferroni corrected  $p > 0.9$ ).

For the Posture task, post-hoc tests showed that upright bodies were matched faster for HSF than for LSF and Intact stimuli (all  $p < 0.001$ ), which in turn did not differ ( $p=0.13$ ). The performance for inverted bodies was comparable in the three SF conditions (all  $p > 0.99$ ). Only the HSF stimuli performance was better for upright rather than inverted bodies ( $p < 0.001$ ). The LSF and Intact conditions performance for upright and inverted bodies was comparable (all  $p > 0.12$ ; Fig. 8d). Planned t-tests on the RTs BIE scores showed that the difference between upright and inverted bodies was higher in the HSF ( $38.55 \pm 7.29$  ms) than in the Intact ( $-17.73 \pm 8.99$  ms;  $t(66) = 5.44$ ; Bonferroni corrected  $p < 0.001$ ) and LSF ( $3.31 \pm 6.86$  ms;  $t(66) = 3.93$ ; Bonferroni corrected  $p = 0.001$ ) conditions, which in turn did not differ ( $t(66) = -2.2$ ; Bonferroni corrected  $p = 0.187$ ).

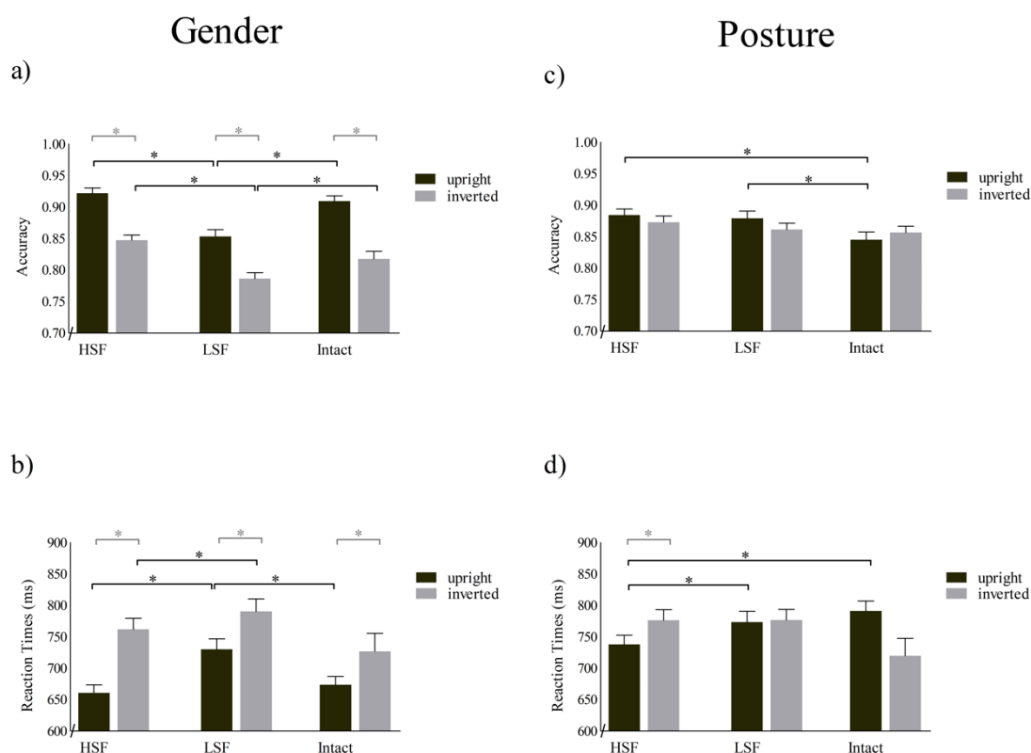


Figure 8. Participants' performance in the matching-to-sample task under the different spatial frequency conditions (i.e., intact, LSF, and HSF) of upright and inverted bodies. Mean and standard error of mean for Accuracy and Reaction Times

(RTs) in the Gender task are reported in panels a) and b), respectively. Mean and standard error of mean for Accuracy and RTs in the Posture task are reported in panels c) and d), respectively. Asterisks indicate significant comparison ( $p < 0.05$ ) between SF condition (black brackets) and orientation (grey brackets).

### 2.3.3 Correlations

Concerning the correlations between the AQ and the BIE indexes for each SF and task condition, I obtained only a significant negative correlation with the Accuracy BIE for HSF bodies in the posture task [ $r(67) = -0.38$ , Bonferroni corrected  $p = 0.01$ ], which suggested that participants with higher level of autistic traits were less sensitive to BIE when detecting body posture from parvo-biased stimuli (Fig. 9). No other correlations were significant (all Bonferroni corrected  $p > 0.15$ )

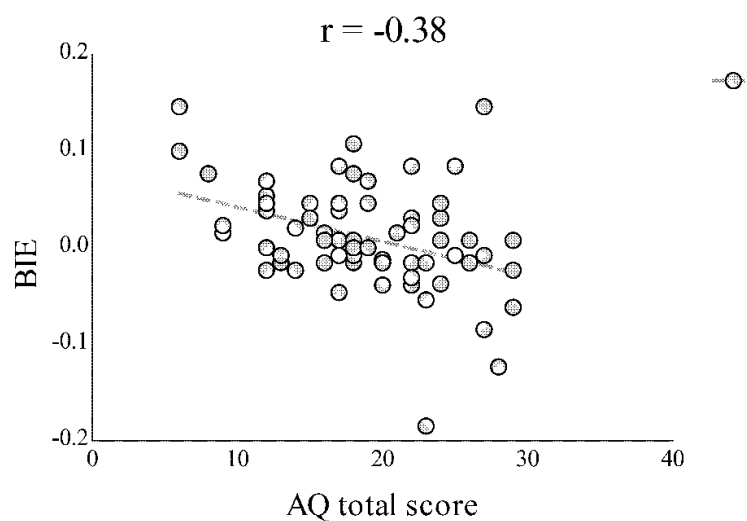


Figure 9. Correlation between the Body Inversion Effect (BIE) calculated as the difference between the Accuracy of upright bodies and the Accuracy of inverted bodies, and the Total Score of the Autistic Quotient (AQ). The relationship indicates that the higher is the participant's level of autistic traits, the lower is the difference between posture recognition ability of upright and inverted high-filtered bodies.

## 2.4. Discussion

The present study aims to test the contribution of HSF and LSF to the configural processing of body gender and posture. To do so, I present upright and inverted bodies either broadband or filtered to only HSF or LSF and require participants to discriminate bodies that differ for gender or posture. Based on knowledge regarding relative preference of ventral and dorsal visual stream areas for HSF and LSF (Denison et al., 2014) and their relative involvement in the processing of form or motion aspects of human bodies (Urgesi et al., 2007a), I expected better performance and greater BIE for the HSF than LSF body images in the gender discrimination task and for the LSF than HSF images in the posture discrimination task.

In keeping with these expectations, I found that filtering out HSF information from body images disrupted the discrimination of body gender, with lower accuracy and slower RTs for LSF rather than

intact and HSF stimuli. This preference for HSF is in line with the notion that perceiving body gender may require diagnostic information about morphology and proportions among body parts (Johnson et al., 2010; Johnson & Tassinari, 2005; Hughes & Gallup, 2003). These steady aspects of the body may be better conveyed through ventral- parvocellular rather than dorsal-magnocellular channels and may preferentially engage occipito-temporal areas (i.e., EBA) (Gandolfo & Downing, 2020; Giese & Poggio, 2003; Urgesi et al., 2007b). Nevertheless, gender judgement of faces has not revealed a compelling dominance of HSF or LSF, with studies supporting either a bias for LSF (Deruelle & Fagot, 2005) or HSF information (Koyama et al., 2010), providing evidence for a contribution of both spatial scales (Jeantet et al., 2019; Schyns et al., 2002; Schyns & Oliva, 1999; Vuilleumier et al., 2003). The contribution of HSF and LSF to gender perception from bodies and faces, however, might depend on the specific type of gender-typing features. Here, I used 3-D body renderings and, even if primary sexually-dimorphic cues (i.e., breast and genitals) were blurred, male and female bodies differed not only for their global figure (i.e., width of shoulder, torso and hip and their relationship, such as the waist-to-hip ratio), but also for their internal secondary sexually-dimorphic cues (i.e., musculature, body fatness), which may characterize gender perception from either bodies or faces (Skomina et al., 2020). This might have facilitated the discrimination of gender based on HSF information in our study and in previous studies highlighting HSF preference for face gender perception (Koyama et al., 2010).

A partially different pattern of findings was obtained for the posture discrimination task, with improved performance after filtering images to keep only HSF or LSF information. Discrimination of upright body postures was facilitated for HSF rather than Intact images in terms of both accuracy and speed of response. In a slightly different way, discrimination of LSF upright postures was facilitated in terms of accuracy, but not of speed of response, compared to discrimination of intact images. No effects of SF were obtained for inverted body postures. The effects of SF manipulation for the gender and the posture discrimination tasks extends to body processing evidence in favor of the Flexible Usage Hypothesis (Schyns & Oliva, 1997), by documenting a change of preference for different sources of information depending on the type of body features relevant for the task. However, in contrast with our expectations, body posture discrimination was not mainly affected by LSF but involved both HSF and LSF sources of information. This contrasts with a prominent role of magno-biased, dorsal stream areas to the processing of dynamic features of the body (Urgesi et al., 2007a) and supports the contribution of parvo-biased occipitotemporal body areas in encoding body shape and posture, integrating them in a perceptual framework (P. E. Downing & Peelen, 2011). The joint contribution of LSF and HSF to body posture perception might reflect a coarse-to-fine temporal dynamics of LSF and HSF processing in ventral body-selective areas, as proposed for faces (Goffaux,

2009). The precedence of LSF over HSF information may reflect fast- vs. slow-acting feedback connections operating within primary and secondary visual cortices during visual perception of a stimulus (Bullier, 2001). Manipulation of the two frequency bands may affect the correctness of the final response or its speed differently (Morrison & Schyns, 2001), a possible explanation to why accuracy and speed of responses were differently affected by the removal of HSF and LSF information in our study.

A coarse-to-fine/fast-to-slow progression of the contribution of magno- and parvo-cellular pathways has been proposed for general object recognition (Bar, 2003). According to this model, LSFs are quickly extracted and conveyed by the magnocellular pathway in order to trigger preliminary predictions about object identity; HSFs would take part in the process activating the matching visual representations in the ventral temporal cortex (Bar et al., 2006). This model has been recently extended to body action perception (Amoruso et al., 2020) based on evidence showing that LSF-based, magnocellular information about actions may not only be processed in the dorsal action observation network, but it may exert, through fast connections between the occipital and prefrontal cortex, feedback impact on later processing in both ventral and dorsal areas. These fast and slow connections may sustain the mixed contribution of both HSF and LSF to body posture discrimination in our study.

While gender and posture discrimination rely differently on HSF and LSF information, configural body processing showed a preference for HSF in both tasks. When I compared the amount of BIE across the SF conditions of the gender task, we found a reduction of the RT BIE, but not of the Accuracy BIE, for the LSF stimuli as compared to both HSF and intact stimuli. This suggests that removing HSF affected gender discrimination because it slowed down configural body processing. Still, a significant body inversion effect was found for all SF conditions, suggesting that configural processing of body gender involves both HSF and LSF information, with a preference, however, for HSF. The BIE for posture discrimination was less reliable than the one for gender discrimination and it only reached significance in the HSF condition. In the posture task, a reliable BIE, again limited to RTs, was found for the HSF only and not for LSF or intact images. This suggests that limiting visual information to HSF facilitated configural processing of body posture, while no evidence of configural processing was found for LSF (and Intact) images. To summarize, a greater configural processing was found for HSF rather than LSF images in both gender and postures discriminations, pointing to an overall preference of configural body processing for parvo-biased, HSF information.

The preference for body configural processing of HSF seems to diverge from the dynamic coarse-to-fine mode of processing proposed for faces, which should prioritize configural processing of LSF

(Goffaux & Rossion, 2006; Goffaux, 2009). However, other studies have questioned this notion, by documenting comparable face inversion effects for different spatial frequencies (Boutet et al., 2003; Gaspar et al., 2008). Although human faces and body shapes are both biological stimuli relevant for social communication, their visual structure is inherently different and may trigger configural processing at different levels. Several authors have described a configural processing continuum in which different types of processing mechanisms can be distinguished, starting from the part-based processing up to the holistic processing of the whole stimulus (Maurer et al., 2002; Reed et al., 2006). As addressed by Minnebusch & Daum (2009), mechanisms for face and body perception may share the earlier stages of this continuum, namely first-order relational information and structural information, while dissociations might take place at later stages, at the level of holistic processing. While studies converge in showing comparable inversion effects, and configural processing for faces and bodies (Reed et al., 2003, 2006), there is inconsistent evidence for holistic body processing (Bauser et al., 2011). This suggests that body forms might not be processed as integrated representations at the same extent as faces are. Similarly, there is evidence supporting that configural representations of face and body may differ in the hierarchy of representational space. Harris and colleagues (2016) showed that bodies might be represented in a configuration not only at the level of the whole body structure, but also at the finer-scale organization of basic parts (e.g. arm), resulting in multiple configural processing of body schema components. I argue that ventral- HSF information may be more appropriate to elicit configural processing at the level of the within-part organization of body structure.

A noteworthy outcome came from the correlation between the AQ score and the BIE. Although the difference in accuracy between HSF upright and inverted bodies in the posture task was not significant, I found that participants with a higher level of autistic traits showed less Accuracy BIE when asked to make posture discrimination of HSF bodies. Thus, higher autistic traits prevented exploiting HSF information for configural processing of body postures. Participants with the highest autistic traits were facilitated in local processing of inverted postures compared to the configural processing of upright bodies (i.e., negative BIE scores) when dealing with HSF images. This keeps with previous studies that have tested BIE in autism spectrum disorder (ASD) and have provided evidence of weak configural processing of body postures (Reed et al., 2007). This impairment in configural body processing could be partially ascribed to a deficit in interpreting and emulating body movements (Blake et al., 2003). Accordingly, individuals with ASD are characterized by a cognitive style biased toward local details at the expense of global processing of visual information (Booth & Happé 2016; Happé & Booth 2008) and seem to gain advantage in processing stimuli containing HSF information (Deruelle et al., 2004; Vanmarcke et al., 2017). Together, data coming from previous



research and the correlation I observed in the current study suggest that people with high autistic traits may adopt distinctive strategies of body visual processing with a bias toward exploiting HSF for local processing of body part details.

The conclusions I can draw from this study need to be weighted in light of its limitations. First, I did not take into account the temporal dynamics characterizing SF processing (Goffaux et al., 2011). As well, the relatively long presentation time (i.e., 150 ms) I used might have hindered the earlier contribution of LSF. Preference of occipito-temporal areas for LSF peaked at 75 ms after stimulus presentation and decayed at 150 ms (Goffaux et al., 2011). Thus, future studies need to test whether a greater contribution of LSF might be detected at earlier stages of stimulus processing, by reducing the presentation timing. Also, using static body representations of different postures, can only partially define SF influence on motion processing, since dynamic stimuli may elicit greater contribution of the magnocellular system. Thus, future studies exploring body motion perception should include the presentation of moving stimuli (i.e., videos) to clarify to what extent the bias of configural processing for HSF information in our study was due to the presentation of implied rather than actual movements. Lastly, the dorsal and ventral pathways preferentially receive inputs from the magnocellular and parvocellular systems, respectively, but our behavioural results can just theoretically reveal the major involvement of the one route or the other. Parvo- and magno- systems are not completely segregated in the cortex and there is evidence of inter-transmissions between them in visual processing (Sincich & Horton, 2005). Future studies might combine this behavioural paradigm with electrophysiological, neuroimaging or neurostimulation techniques to explore the involvement of ventral and dorsal areas to the processing of HSF and LSF information about body gender and posture.

### **3. Exposure as a variable in reshaping of body gender perception**

#### **3.1 Introduction to body gender adaptation paradigm**

Consider the description of the Waterfall illusion. You look at a waterfall and suddenly direct your eyes on the rocks results in the illusory perception of the rocky surface moving upwards (Addams, 1834). Many psychophysical studies have targeted such visual aftereffects. This perceptive experience occurs after a prolonged exposure to an adaptor stimulus, which biases the perception of the ones that follow toward the opposite pole of the adaptor. Over the years, what is observed as motion (Anstis et al., 1998) has been proven as basic properties of visual stimuli, like orientation (Gibson & Radner, 1937; He & MacLeod, 2001) and colour (Dodwell & Humphrey, 1990; von Helmholtz, 2001). Research arising from these early paradigms mainly conceived aftereffects as retinotopic, since they appeared to be confined to the field of the retina that was exposed to the adaptor (Knapen et al., 2009). However, evidence that similar aftereffects can be present even when adaptor and test stimuli appear in different retinal regions have supported a spatiotopic explanation (Turi & Burr, 2012), especially for more complex stimulus dimensions. Aftereffects reflect a recalibration of the perceptual system according to a changing surrounding (Thompson & Burr, 2009), likely due to firing adaptation in populations of neurons coding for a specific stimulus feature (Barlow & Hill, 1963).

Studies have demonstrated face aftereffects along various semantic and social continua (Webster et al., 2004), such as identity (Clifford & Rhodes, 2005; Leopold et al., 2001), expression (Butler et al., 2008; Ying & Xu, 2017), ethnicity (Webster et al. 2004) and gender (Kloth et al., 2010; Webster et al. 2004). These effects occur in changes of size and location (Rhodes et al., 2003; Yamashita et al., 2005; Zhao & Chubb, 2001), suggesting the involvement of high-level coding mechanisms. Nevertheless, evidence of reduced aftereffects when the adapting and testing faces differ for ethnicity (Gwinn & Brooks, 2013, 2015; Jaquet & Rhodes, 2008), gender (Little et al., 2005), and age (Yang et al., 2011) suggests that face aftereffects involve neural populations specifically tuned to these aspects of facial identity. Similarly, greater face-gender aftereffects occur when the orientation of the adapting and testing faces is congruent compared to when the faces are in opposing orientations, pointing to a partial orientation-tuning of the neural populations encoding face gender (Rhodes et al., 2004; Watson & Clifford, 2006).

More recently, aftereffects for human bodies, mainly related to body size and body shape, have been demonstrated (Brooks et al., 2019). As faces, these body aftereffects likely reflect high-level coding, as they occur in free-viewing conditions where the testing and adapting stimuli occupy different retinal positions (Brooks et al. 2019). They transfer, with a variation of magnitude, in a range of

orientation (Brooks et al., 2018), identity (Brooks et al., 2016; Hummel et al., 2012), gender (Brooks et al. 2019) and ethnicity (Gould-Fensom et al., 2019) when adapting and testing stimuli. Therefore, visual adaptation has been proposed as one of the mechanisms that is involved in the internalization of body-ideals in the general population (Burke et al., 2010; Challinor et al., 2017; Robinson & Kirkham, 2014) and the development of body misperception and disordered eating (K. R. Brooks et al., 2019; Griffiths et al., 2018). Adaptation to idealized body images presented by the media may shift our point of subjective normality by influencing the way we actually perceive bodies (Bould et al., 2018; Brooks et al., 2016, 2018; Hummel et al., 2012; Mele et al., 2013; Winkler & Rhodes, 2005). Accordingly, an altered adaptation-related reshaping of body perception has been reported in patients with Eating Disorders (EDs; Cazzato et al., 2016; Mohr et al., 2016).

Other researchers have investigated properties of the human body that can be sensitive to visual adaptation, such as gender. Compared to shape and size dimensions, which are susceptible to recurrent changes by their nature, gender can be considered a naturally stable feature of a body. A rapid processing of conspecifics' gender plays a significant role in social interactions since it is at the root of mate selection and reproductive behaviour (Darwin, 1871; Singh & Singh, 2011; Windhager et al., 2011). Despite this inherent need of accurate discrimination and its stability, gender perception has been shown to be susceptible to aftereffects. By using silhouettes of headless human models, Palumbo and colleagues (2013) demonstrated that prolonged exposure to a distinctively male or female body leads to gender-specific aftereffects on the perception of an androgynous one. Interestingly, stronger effects were found, for either male or female participants, when they were adapted to silhouettes of their own sex, pointing to a high-level modulation of body aftereffects according to the meaning of the stimulus for the observer. Body-gender aftereffects related to high-level stimulus dimensions has been also corroborated by findings of cross-categorical (i.e., body-to-face) aftereffects, where exposure to a faceless body biases the perception of the gender and identity of faces (Ghuman et al., 2010). The opposite direction of cross-category aftereffects (i.e., face-to-body) has been also demonstrated (Palumbo et al., 2015). Cross-categorical gender aftereffects for faces and bodies point to a common, high-level representation of the gender conveyed by facial and bodily cues. Cross-category studies, such as those testing the influence of gender-specific voices (Kloth et al., 2010) or hands (Kovács et al., 2006) on face perception, have failed to find adaptation effects. This suggests a closer relationship between body and face representations as compared to other gender-specific stimuli.

The perception of faces and bodies seems to involve, more than other objects, configural processing, where a stimulus is encoded on the basis of the relations among its parts in the context of the entire

stimulus space, and not only feature-based mechanisms, where the stimulus is encoded on the basis of the details of its single parts (Bartlett & Searcy, 1993; Carey, 1992; Freire et al., 2000; Leder & Bruce, 2000). Faces and bodies share a common template configuration that is shaped by repeated exposure to various exemplars of these two categories. This template representation is used to perceive individual face and body stimuli, at least when they are presented in a canonical, upright orientation, which is compatible with those stimuli that have contributed to the formation of the category template. Consequently, a configural processing mechanism may be used only for upright stimuli, explaining the disproportioned drop of perceptual performance when faces and bodies are presented upside-down, with respect to the canonical upright orientation - the so-called inversion effect (Maurer et al., 2002; Reed et al., 2003). Aftereffects for upright and inverted faces have been attributed to specific adaptation of configural and local processing mechanisms, respectively (Rhodes et al., 2004; Watson & Clifford, 2006; Webster & MacLin, 1999). Interestingly, abnormal aftereffects for (upright) faces have been reported in children with autism (Pellicano et al., 2007), who have deficits in configural processing (Behrmann et al., 2006; Rondan & Deruelle, 2007), in their relatives (Fiorentini et al., 2012), and in typical developing men with high autistic traits related to social skills (Rhodes, Jeffery, Taylor, et al., 2013).

Both configural and local processing mechanisms are involved in the processing of upright faces, but only the latter may be involved for inverted faces. Adaptation to upright faces has been shown to readily transfer to the perception of inverted faces, while the opposite transfer of effects is negligible (Watson & Clifford, 2006). The configural and local face-coding mechanisms can be contingently adapted since opposite size and gender aftereffects were induced simultaneously for upright and inverted faces by adapting to opposite distortions in each orientation, an evidence of contingent aftereffects (Rhodes et al., 2004). It is unclear, however, whether the same orientation-specificity of gender aftereffects also occurs for human bodies. A recent study showed that upright and inverted bodies have comparable aftereffects on the gender perception of upright and inverted faces, despite larger aftereffects were observed for the latter stimuli (Kessler et al., 2013). This finding suggests that bodies adapt to an orientation-independent representation of faces, likely mediated by local processing mechanisms, involved for both upright and inverted faces processing.

In this study, I aim to investigate the identity- and orientation-tuning of body-gender aftereffects, whilst evaluating the potential modulation of personality traits associated to body misperceptions and autistic traits. In three distinct experiments, I used a body adaptation paradigm, in which participants were exposed to a series of distinctively male or female adapting bodies and then asked to categorize the gender of androgynous testing bodies. To control for low-level stimulus features, renderings of

computer avatars were manipulated to appear more or less feminine (see Chapter 1, Section 1.2.1.2), leaving intact low-level visual features, like colour, luminance and size.

Experiment 1 manipulated the individual body characteristics of the adapting and testing bodies to investigate body-gender aftereffects as identity-specific or transfer to different characters. Body identity here refers to those individual body characteristics (e.g., physique, skin texture and colour, etc.) that characterize individuals independently from their gender.

Experiments 2 and 3 also manipulated the orientation of the adapting and testing bodies, asking participants to categorize the gender of both upright and inverted androgynous bodies after adaptation to upright (Experiment 2) or upright and inverted (Experiment 3) gender-typical bodies. Generally, I expected that adaptation to male or female bodies would produce aftereffects in the perception of androgynous bodies, making them to appear more feminine after male exposure and more masculine after female exposure). Evidence of identity tuning and orientation independence of body-gender aftereffects would call for high-level, object-based mechanisms involved in the processing of individual body characteristics. Their identity independence and orientation tuning would call for lower-level mechanisms involved in the processing of body form cues. Concerning the influence of specific individual traits, I expected a modulating role of autistic traits (Pellicano & Burr, 2012), body misperceptions (Bould et al., 2018; Brooks et al. 2016; Stephen et al. 2018; Mele et al. 2013; Mohr et al. 2016) and gender (Palumbo et al. 2013).

### **3.1.1 Experiment 1**

I tested whether body-gender aftereffects are specific for the individual characteristics of the adapting body or generalize across different characters. Gender distinctiveness of two different adapting avatars were manipulated to appear highly (90%) or less (60%) masculine/feminine. The masculine or feminine versions of both characters were presented as adapting bodies during a body-pose categorization (i.e., static vs. dynamic) task, while the androgynous versions of the same characters were later presented as testing bodies in a body-gender (male vs. female) categorization task. The experiment investigated the aftereffects for the high- and low-adapted characters.

#### **3.1.1.1 Materials and methods**

##### **3.1.1.1.1 Participants**

A sample of 30 students (15 female, mean age = 23.22, SD = 4.54 years) from the University of Udine participated in the experiment in return for course credits. They reported normal or corrected vision and had no current neurological or psychiatric disorders as assessed with the Symptom Checklist 90

(SCL-90; Derogatis et al., 1973). Written informed consent was obtained from all participants. The procedures were approved by the local ethics committee (Commissione di garanzia per il rispetto dei principi etici nell'attività di ricerca sugli esseri umani, Department of Languages and Literatures, Communication, Education and Society, University of Udine; Prot. N. CGPER-2019-12-09-04) and conformed with the Helsinki Declaration. Participants were right-handed as ascertained with standard handedness inventory (Oldfield 1971).

### **3.1.1.1.2 Stimuli**

Character Creator 3.0 software (Reallusion, San Francisco, CA, USA) was used to generate a set of virtual-human body stimuli systematically controlling for their individual characteristics and masculinity/femininity traits. The adapting stimuli were constructed selecting two pairs of male-female virtual-human characters from the software default database (i.e., M1-F1 and M2-F2). The male and female character in each pair shared individual bodily characteristics (i.e., those bodily features that make an individual unique independently for gender) but were extremized to along the gender-typing features. Two versions of each character were produced setting the amount of gender traits at 60% or 90%, while leaving neutral the remaining 40% or 10% traits, in order to obtain more or less masculine/feminine bodies (Fig. 10A). Each resulting body stimulus was rendered in ten daily poses, five static (e.g., standing, open, idle, and turned postures) and five dynamic poses (e.g., running, walking, jumping, dancing, moving), selected among default postures available in Character Creator. The grey-scale bodies could be viewed from a frontal or three-quarter view and were pictured against a black background. Overall, we had two pairs of male-female characters (M1-F1 and M2-F2) expressing two levels of gender-typicality (60% or 90% of embodied masculinity or femininity traits) rendered in ten postures. Images were imported into GIMP 2.10.8 (GNU Image Manipulation Program, Berkeley, CA, USA) to produce a mirrored version of each image. A total of 80 male and 80 female adapting bodies were obtained. For all images, the head, pectoral and pelvic areas were blurred to mask facial and primary sexual characteristics while keeping enough morphological information to visually convey the sexual phenotype.

To create the testing stimuli, the same four characters were used for the adapting stimuli. However, to manipulate the percentage of female and male traits expressed by each body, two pairs of female and male characters were combined. F1 was mixed with M1 and F2 was mixed with M2. Each pair of characters was applied in a continuous variation from 20% male and 80% female (20M/80F) up to 20% female and 80% male (80M/20F). This led to the creation of androgynous stimuli that, beyond containing different levels of gender-typing features, could contain the individual body characteristics of either the M1-F1 or the M2-F2 pair of virtual characters. A total of 7 different percentages of

male/female features for each pair of characters (M1/F1 and M2/F2; Fig. 10B) was obtained. All 14 androgynous body figures (2 character pairs x 7 percentages of male/female features) were rendered in the same neutral pose, which was different as compared to those used for the adapting stimuli, and were presented in their original and mirrored versions, for a total of 28 testing bodies.

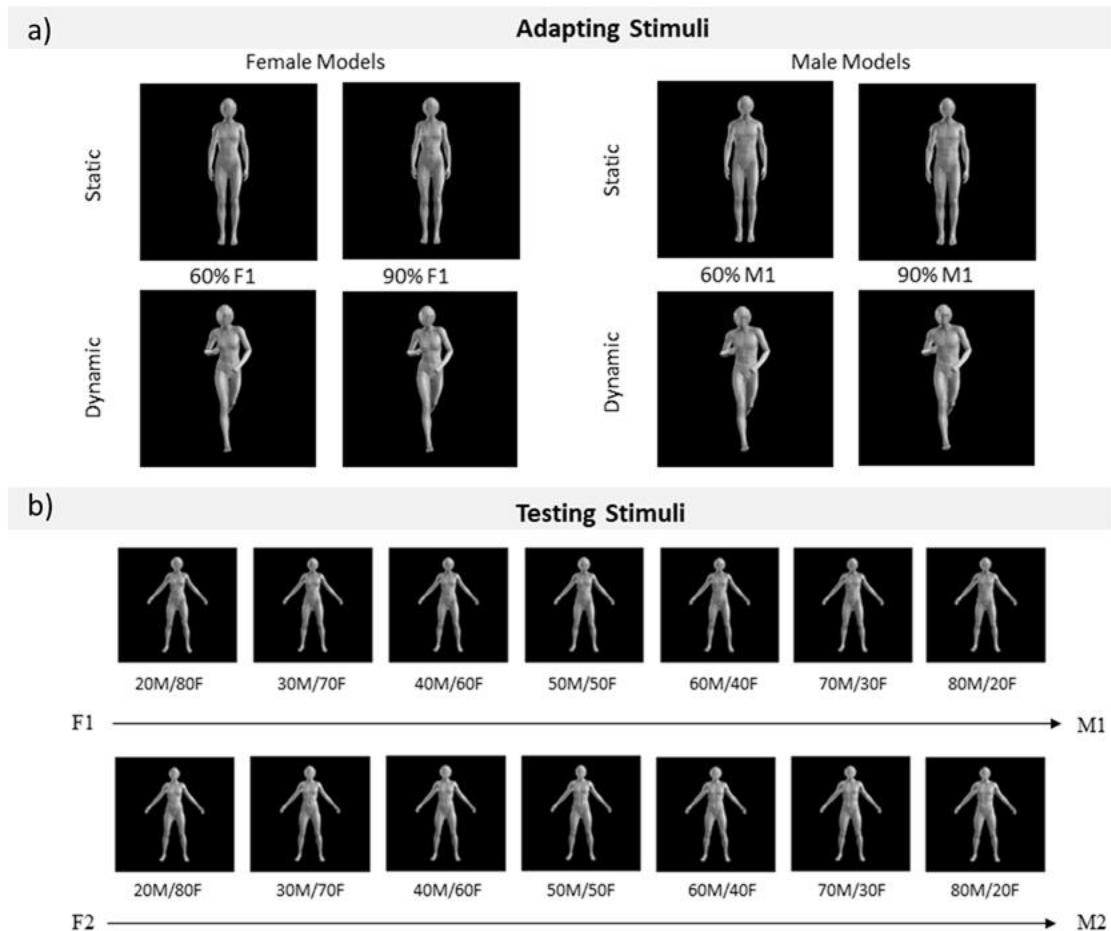


Figure 10. Examples of stimuli used in the study. A) Examples of female and male virtual models used as Adapting stimuli. The figure depicts the body sex-typing variation (60% vs. 90%) of either static or dynamic female and male models (Identity 1). B) Androgynous virtual models presented as Testing stimuli. The figure depicts the continuous % variation from 20 male-80 female up to 80 male-20 female for both identities.

### 3.1.1.1.3 Procedure

The experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA). Participants sat 60 cm away from a 19-in PC monitor (resolution:  $1360 \times 768$  pixels; refresh frequency: 60 Hz) and looked at the  $450 \times 450$  pixels body images presented one at a time at the centre of the screen. Each participant was asked to perform two experimental sessions, one with adaptation to Female models and the other with adaptation to Male models. The order of the two sessions was counterbalanced between participants and a short break was allowed between sessions. Each session was composed of two identical blocks, each one including an adaptation phase

and an immediately consecutive test phase. The test phase was identical in all conditions, while the adaptation phase differed across sessions according to whether male or female adapting stimuli were used (Fig. 11).

Each adaptation block comprised 160 trials (i.e., two presentations for each male or female adapting stimulus) and lasted about 8 minutes. One pair of characters (i.e., F1 /M1 or F2/M2) was presented with a high gender-typicality figure (i.e., 90) while the other was presented in a low gender-typicality figure (i.e., 60). Each adaptation trial started with the appearance of a white central fixation cross (500 ms) presented on a black background and followed by a body image lasting 2,000 ms. Soon after the image offset, the Italian words “Statico” and “Dinamico (Static and Dynamic in English) appeared on the bottom of the screen and the participant was asked to report the correct response by pressing the “Z” or “M” key on a QWERTY keyboard. The high- vs. low-adapted identities and the response-key associations were counterbalanced across participants.

Shortly after each adaptation block, a test phase block was administered and lasted about 5 minutes. The 28 androgynous bodies were presented six times each for a total of 168 trials per test block. 336 test trials were administered in each experimental session (i.e., 24 trials per cell). In each test trial, a central fixation cross (500 ms) was followed by an androgynous body, which was presented until response or for a maximum of 1,500 ms. Participants were asked to report the gender (male or female) of the body stimulus by pressing as soon as possible the key “Z” or “M”. Response-key association was counterbalanced across participants.



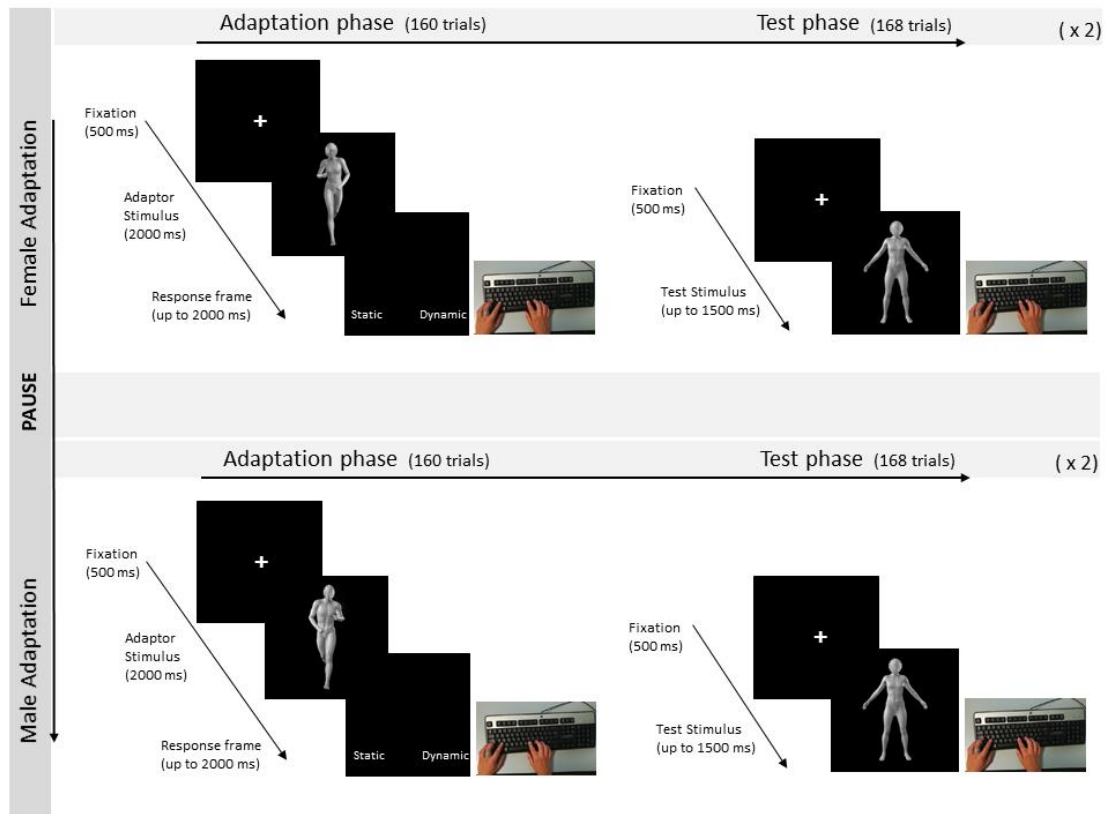


Figure 11. Experimental session and trial procedure. A representation of the timeline of a single Experimental session and a depiction of the events constituting the structure of a trial in the adaptation and test phases. For both Female and Male exposures, two adaptation- and two test-phase blocks were performed.

### 3.1.1.1.4 Data handling

Analyses were performed using Analysis of variance (ANOVA) designs implemented in the STATISTICA software (Stat Soft, Tulsa, OK). The performance in the adaptation phase was not considered in the analysis since it only served to capture participants' attention to the adapting stimuli. For the test phase, the proportion of male responses at each level of gender typicality of the androgynous bodies was calculated separately for the male and female adaptation sessions and for the high and low adapting identities. Individual proportions of male responses were fitted as a function of male/female features with a logistic function. Then, for each participant and condition, I calculated the Point of Subjective Equality (PSE), which represents here the level of gender typicality of a stimulus that is equally likely to be judged as a male or a female. Individual PSE were entered into a mixed ANOVA design with Exposure (Male or Female) and Character (High or Low adapting) as within-subject variables and Gender group (Male vs. Female observers) as a between-subjects factor. Significant interactions were explored with the Duncan's post hoc test for multiple comparisons), which has been developed to reduce the risk of false negative (Type II) error when correcting for multiple comparisons (IJSMI, 2016) by reducing the size of the critical difference depending the number of steps separating the ordered means. This procedure is optimal for testing in

the same design effects that may have different sizes (Duncan, 1955; Dunnett, 1980; McHugh, 2011). A significance threshold was set at  $p < 0.05$  for all analysis. Effect sizes were estimated with partial eta squared ( $\eta^2$ ). Values are reported as mean  $\pm$  standard error of the mean (SEM).

The sample size required for our 2 (Exposure)  $\times$  2 (Character)  $\times$  2 (Group) mixed within the ANOVA design was determined with the G\*power software (Faul et al. 2009), using the “as in SPSS” option for estimating effect size from  $\eta^2$  and setting the  $\alpha$  level at 0.05 and the desired power ( $1 - \beta$ ) at 95%. The expected effect size was set at  $f(U) = 0.71$  based on the effect size ( $\eta^2 = 0.33$ ) of the interaction between exposure and observer’s gender in a previous body-gender-adaptation study (Palumbo et al., 2013).

### **3.1.1.2 Results and Discussion**

The ANOVA on the PSE scores revealed a significant main effect of Exposure [ $F(1,28) = 6.66$ ;  $p = 0.015$ ;  $\eta^2 = 0.192$ ]. That is, PSE was lower after Female exposure ( $48.34 \pm 1.67$ ) than after Male exposure ( $53.49 \pm 2.13$ ), on average. This suggests that participants needed higher amounts of feminine features to judge an androgynous body as female after exposure to feminine bodies than after exposure to masculine bodies. The data revealed body-gender aftereffects, in which exposure to a specific gender leads the judgment of androgynous bodies towards the opposite gender, keeping with Palumbo and colleagues (2013). However, the Character main effect [ $F(1,28) = 1.38$ ;  $p = 0.248$ ;  $\eta^2 = 0.047$ ] and the Exposure  $\times$  Character interaction [ $F(1,28) < 0.01$ ;  $p = 0.936$ ;  $\eta^2 < 0.001$ ] were not significant, revealing that participants’ responses were comparably adapted for the High and Low adapting characters (Fig. 12). This is in keeping with previous studies showing the transfer of body size and shape aftereffects across different bodies (Brooks et al. 2016; Brooks et al. 2019; Gould-Fensom et al. 2019; Hummel et al. 2012). Nevertheless, the comparable amount of body-gender aftereffects for both characters contrasts with the findings of a reduction of body size aftereffects when the adapting and testing bodies had different characteristics (Hummel et al. 2012; Brooks et al. 2016; Brooks et al. 2019). This reveals that body-gender aftereffects involve populations of neurons that do not code the specific individual characteristics of the observed body. In contrast with the findings of Palumbo et al. (2013), no significant main effect or interaction of Gender group was obtained (all  $F < 3.24$ ,  $p > 0.08$ ). Thus, participants’ gender of the observer was not further considered.

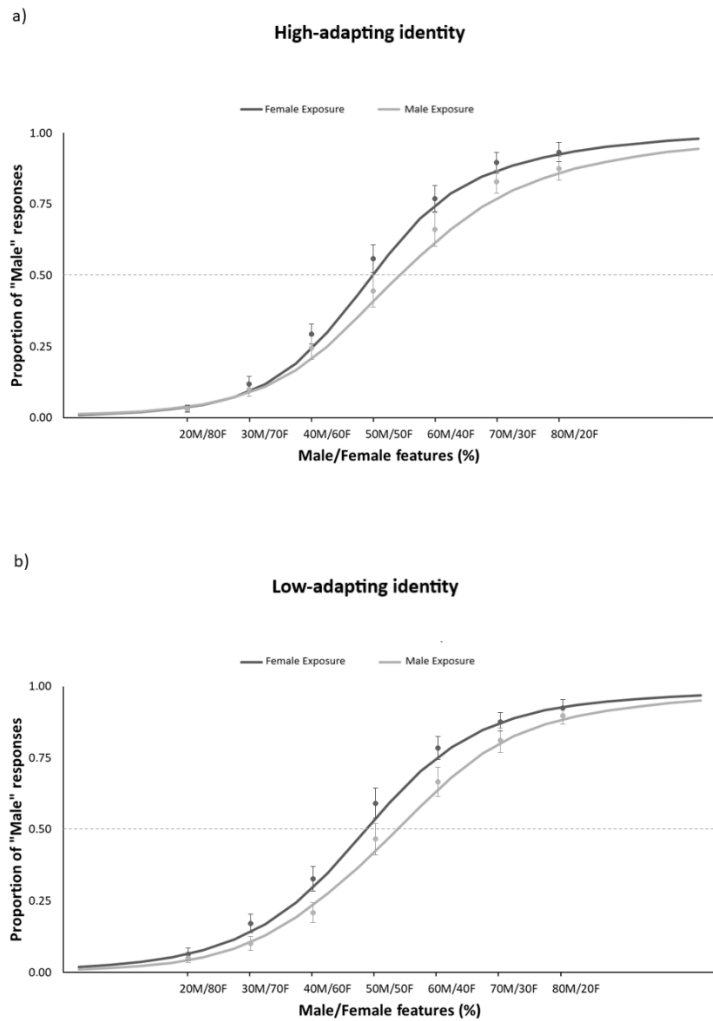


Figure 12. Group data showing the psychometric function of the mean proportion of "male" responses, after adapting to Female or Male bodies, according to increasing % of Male/Female features embodied by the androgynous stimuli used during the test phase in Experiment 1. Vertical bars denote standard error of the mean. Results are presented separately for the high-adapting (a) and low-adapted (b) identities

### 3.1.2 Experiment 2

Previous studies showed that aftereffects for face distortions (Watson et al. 2003; Webster & MacLin 1999; Watson et al. 2006) and body size (Brooks et al. 2018) transfer from upright adapting stimuli to inverted testing stimuli. Similarly, body-to-face gender aftereffects transfer stimulus orientations (Kessler et al. 2013). In Experiment 2, I tested whether body-to-body-gender aftereffects transfer from upright to inverted bodies or whether they are specific for the configural processing of (canonical) upright bodies. I adapted participants to female or male upright bodies and tested the aftereffects on the processing of androgynous upright and inverted bodies. If body-gender adaptation selectively involves only upright configural-processing mechanisms, inverted bodies should be adapted. Conversely, if body-gender adaptation affects local processing mechanisms, I expected

comparable aftereffects for upright and inverted bodies, since the local processing mechanisms can be used for both upright and inverted bodies. If both configural and local processing mechanisms are involved, aftereffects should occur for both upright and inverted testing bodies, but they should be lower for the latter.

### **3.1.2.1 Materials and methods**

Twenty participants (16 women, mean age = 22.2, SD = 4.34 years) were recruited. Seven participants participated to Experiment 1 several weeks before. The same stimuli, procedure and data handling approach as in Experiment 1, were used in this experiment, with the exception that upright and inverted androgynous bodies were randomly presented in the testing phase. The 28 testing bodies were presented eight times each, four times with an upright orientation and four times with an inverted orientation, for a total of 224 trials per block; 448 test trials were administered in each experimental session (i.e., 16 trials per cell). In addition to the repeated-measure variables of Exposure and Character, the effect of the Orientation (upright vs. inverted) of the testing bodies was also tested. The sample size required was 2 (Exposure)  $\times$  2 (Character)  $\times$  2 (Orientation) repeated-measure. ANOVA design was determined by setting the expected effect size set at  $f(U) = 0.92$  based on the effect size ( $\eta^2 = 0.46$ ) of the interaction between exposure and orientation in the only previous study in the orientation-tuning of body size aftereffects (Brooks et al. 2018).

### **3.1.2.2 Results and Discussion**

The ANOVA on the PSE values revealed a significant main effect of Orientation [ $F(1,19) = 7.26$ ;  $p = 0.014$ ;  $\eta^2 = 0.28$ ], showing lower PSE for inverted ( $44.02 \pm 3.01$ ) rather than upright stimuli ( $52.18 \pm 2.35$ ). This suggests that inverted androgynous bodies looked more masculine, since they needed fewer masculine features to be judged as male with respect to their upright counterparts. This unexpected result, however, can reflect a side effect of the exposure procedure, where the adapted upright bodies could be judged as more masculine than the newer inverted bodies.

Even though the effect of Exposure was not significant [ $F(1,19) = 0.15$ ;  $p = 0.7$ ;  $\eta^2 = 0.008$ ], I found a significant Exposure  $\times$  Orientation interaction [ $F(1,19) = 6.88$ ;  $p = 0.017$ ;  $\eta^2 = 0.265$ ], which indicated that the effect of adaptation was different for upright and inverted testing bodies (Fig. 13).

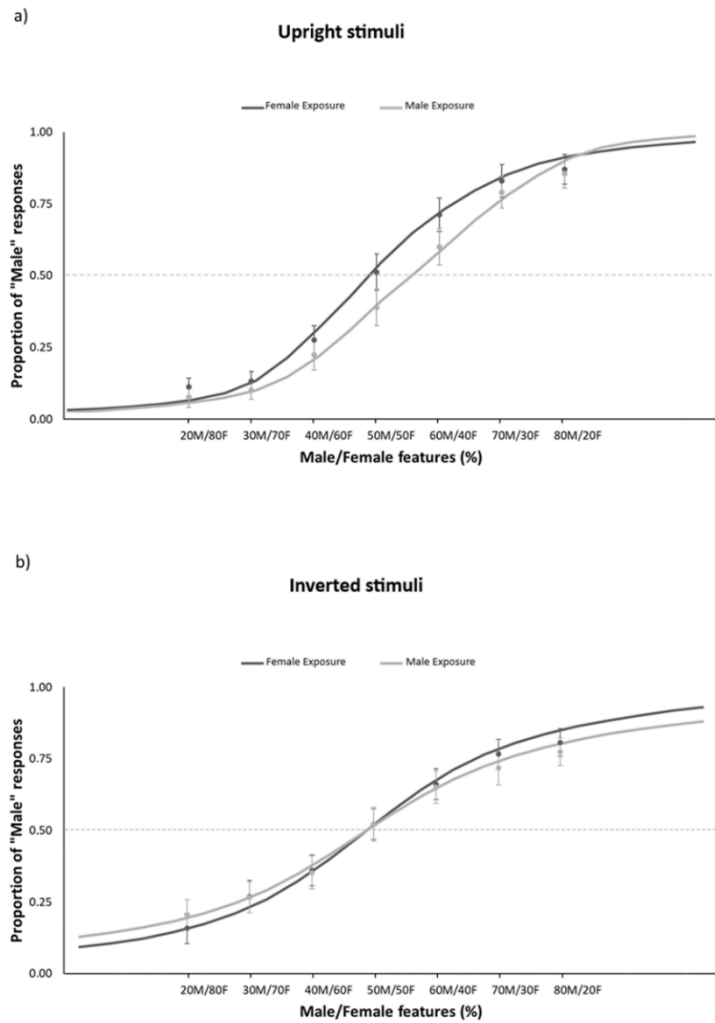


Figure 13. Group data showing the psychometric function of the proportion of "male" responses, after adapting to Female or Male bodies, according to increasing Male/Female features embodied by the androgynous stimuli used during the test phase in Experiment 2. Vertical bars denote standard error of the mean. Results are presented separately for upright (a) and inverted (b) testing stimuli

First of all, Duncan post-hoc comparisons [MSE = 55.092 df = 19] revealed that, in keeping with the main effects of Orientation, PSE scores were significantly lower for inverted rather than for upright bodies after both Female ( $p = 0.037$ ) and Male ( $p < 0.001$ ) exposures. Upright stimuli had lower PSE scores after Female ( $50.17 \pm 2.61$ ) than Male exposure ( $54.20 \pm 2.54$ ;  $p = 0.025$ ). Inverted bodies showed no effect of exposure ( $p = 0.21$ ). In contrast with body size aftereffects (Brooks et al. 2018) and body-to-face gender aftereffects (Kessler et al., 2013), body-to-body-gender aftereffects did not transfer from upright to inverted bodies.

There are two potential explanations of this finding. First, body-gender adaptation may involve populations of neurons that are tuned to the specific orientation of the body, different for faces that are completely object-based. Second, it is possible that body-gender adaptation selectively involves

configural-processing mechanisms, such that only the processing of upright bodies can be adapted. In keeping with Experiment 1, no main effect or interaction of Character was found (all  $p > 0.434$ ).

### **3.1.3 Experiment 3**

Here I aimed to qualify the results of Experiment 2 by further investigating the orientation-tuning of body-gender aftereffects. I required participants to recognize the gender of both upright and inverted androgynous models after adaptation to both upright and inverted bodies. The same type of exposure for both male and female was used for the upright and inverted bodies, since we were not looking at evidence of contingent aftereffects with the orientations (Rhodes et al. 2004). Instead, the testing regarded the effects of adapting to inverted as well as upright bodies as in Experiment 2. If body-gender adaptation is strictly orientation-tuned, exposure to both upright and inverted bodies is expected to comparably adapt the gender discrimination of upright and inverted androgynous bodies. Conversely, if body-gender adaptation exclusively involves the use of configural processing mechanisms, then we should observe, as in Experiment 2, body-gender aftereffects for only upright, not inverted androgynous bodies even after the adaptation involved in inverted body perception.

#### **3.1.3.1 Materials and methods**

Twenty participants (10 women, mean age = 23.3, SD = 4.78 years) were recruited for this experiment. 2 participants also took part to Experiment 1. The same stimuli, procedure and data handling approach as in Experiments 2 were used, but participants were exposed to both upright and inverted distinctively female or male bodies in the adaptation phase. Thus, each of the 80 male or female adapting stimuli was presented once in an upright orientation and once upside-down, for a total of 160 trials.

#### **3.1.3.2 Results and Discussion**

In Experiment 3, a significant main effect of Orientation [ $F(1,19) = 7.18$ ;  $p = 0.014$ ;  $\eta^2 = 0.28$ ] was found, highlighting lower PSE for inverted ( $M = 50.68$ ,  $SEM = 3.11$ ) rather than upright ( $56.49 \pm 2.33$ ) stimuli. A similar result was found in Experiment 2. This rules out that the difference between the perceived masculinity of upright and inverted bodies was a side effect of exposure to only upright bodies. A significant main effect of Exposure [ $F(1,19) = 4.94$ ;  $p = 0.038$ ;  $\eta^2 = 0.27$ ] revealed, for all orientations, lower PSE following Female exposure ( $50.83 \pm 2.77$ ) not following Male exposure ( $56.34 \pm 2.85$ ). Crucially and differently from Experiment 2, the interaction between Exposure and Orientation was not significant [ $F(1,19) = 1.73$ ;  $p = 0.203$ ;  $\eta^2 = 0.08$ ]. Exposure to both upright and inverted bodies comparably adapted the gender discrimination of both upright and inverted

androgynous bodies, suggesting the orientation-tuning of body-gender aftereffects (Fig. 14). As in Experiments 1 and 2, no main effect or interaction of Character was found (all  $F < 1.36$ ,  $p > 0.2$ ,  $\eta^2 < 0.002$ ), showing that the same pattern of orientation-dependent adaptation was obtained for both the highly and lowly adapting identities. This points to the identity-independence of the neural populations adapted by both upright and inverted bodies.

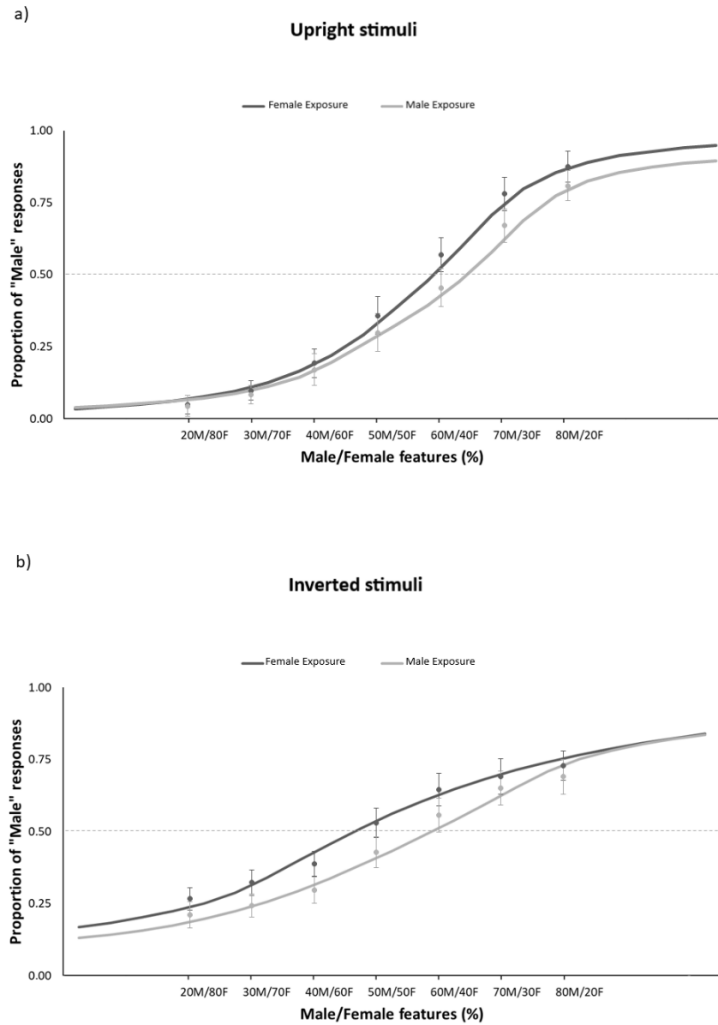


Figure 14. Group data showing the psychometric function of the mean proportion of "male" responses, after adapting to Female or Male bodies, according to increasing male/female features embodied by the androgynous stimuli used during the test phase in Experiment 3. Vertical bars denote standard error of the mean. Results are presented separately for upright (a) and inverted (b) testing stimuli

### 3.1.3.3 Regression Analysis

In Experiments 2 and 3, I asked participants to fill out three questionnaires in a counterbalanced order at the end of the second experimental session. These questionnaires were the Body Uneasiness Test (BUT) that evaluates body misperceptions (Cuzzolaro et al., 2006), the Autistic Quotient (AQ) that provides a measure of participants' autistic traits (Baron-Cohen et al. 2001) and the Bem Sex Role

Inventory (BSRI; Bem, 1974) that measures a participant's level of masculinity and femininity. The BUT is a 71-item self-report questionnaire that consists of two parts, one evaluating 6 dimensions related to self-body perception (weight phobia, body image concerns, avoidance, compulsive self-monitoring, detachment and depersonalization) and the other concerning body part concerns. Here I considered the Positive Symptom Total score (PST), which provides a global measure of a participant's body satisfaction. The AQ consists of 50 items divided into five subscales measuring social (i.e., imagination, communication and social skills) and cognitive (i.e., attention to detail and attention switching) aspects of autistic traits (Hoekstra et al., 2008; Warrier et al., 2019). Finally, the BSRI consists of two 20-items subscales measuring masculinity and femininity plus 20 neutral items, aimed at measuring the internalization of different aspects of gender traits.

Using these psychological measurements, I aimed to test the influence of individual differences in body perception, autistic traits and internalization of gender role on body-gender aftereffects. Previous studies showed that body size aftereffects are modulated by body misperception in healthy volunteers (Bould et al. 2018; Stephen et al. 2018) and are altered in individuals with eating disorders (Mohr et al. 2016; Mele et al. 2013). Thus, I expected higher aftereffects in individuals with higher levels of body misperceptions. Face aftereffects have been shown to be altered in individuals with autism (Pellicano et al., 2007), in particular in those with more severe deficits in the areas of socialization, communication, and restricted and/or repetitive interests (Pellicano et al. 2007), and in healthy individuals with high autistic traits related to social interactions (Fiorentini et al., 2012; Rhodes et al., 2013). A diminished sensitivity to adaptation from the participants with higher autistic traits, reflecting weaker ability in using prior experience to modulate perceptual experience (Pellicano & Burr 2012) was considered. Experiment 1 showed, in contrast with the findings of Palumbo et al. (2013), no modulation of observer's gender as a categorical variable. But it would still be possible that internalized gender role may modulate differential gender body adaptation in men and women. It has been widely shown that the degree of masculinity/femininity, rather than biological sex, is a better predictor of body perception and body satisfaction (Cella et al., 2013). A recent study showed that gender identification, more than biological sex, explains individual differences in autobiographical memory (Compère et al., 2021) and also modulates the initial perceptual processing responses of male and female observers to same vs. opposite gender faces (Domen et al., 2020).

Accordingly, a standard multiple regression analyses with two partially independent measures of social autistic traits (i.e., Social skills and Communication; Austin, 2005) was used along with a measure of cognitive autistic traits (i.e., Attention to details), the PST of the BUT, and the Masculinity and Femininity scores of the BSRI. The dependent variable was an individual measure of the



magnitude of body-gender aftereffects, calculated as the difference between the PSE after Male exposure and the PSE after Female exposure. The greater the PSE aftereffect index, the greater the repulsion of PSE between the two exposure conditions and the greater the body-gender aftereffects. To obtain more consistent aftereffects measurements in the experiments, only responses for upright stimuli were taken into account, since the adaptation for inverted bodies was different in Experiments 2 and 3.

Multicollinearity statistics confirmed that the regression assumption was not violated (Tolerance > 0.65). The entire model was significant (adjusted R<sup>2</sup> = 0.195; F(6,33) = 2.57; p = 0.037), confirming that the variables considered in the model pointed to a clear prediction regarding the amount of individual body-gender aftereffects. The AQ Communication subscale (r(44) = -0.31; p = 0.018) and the Masculinity scale (r(61) = -0.41; p = 0.037) were significant predictors. All other scale scores were non-significant (all ps > 0.3). Keeping with the finding of aftereffect alterations for face identity coding in individuals with autism (Pellicano & Burr 2012) and high autistic traits (Fiorentini et al. 2012; Rhodes et al., 2013), evidence of a modulating role of Communication deficits was shown on body-gender adaptation. Communication deficits are social aspects of autistic traits (Hoekstra et al., 2008; Warrier et al., 2019). Greater communication deficits in receiving and providing information (i.e., higher Communication subscale scores) were associated with weaker body-gender aftereffects (Fig. 15A). Individuals with higher internalization of a male gender role (i.e., higher Masculinity) also showed weaker body-gender aftereffects (Fig. 15B).

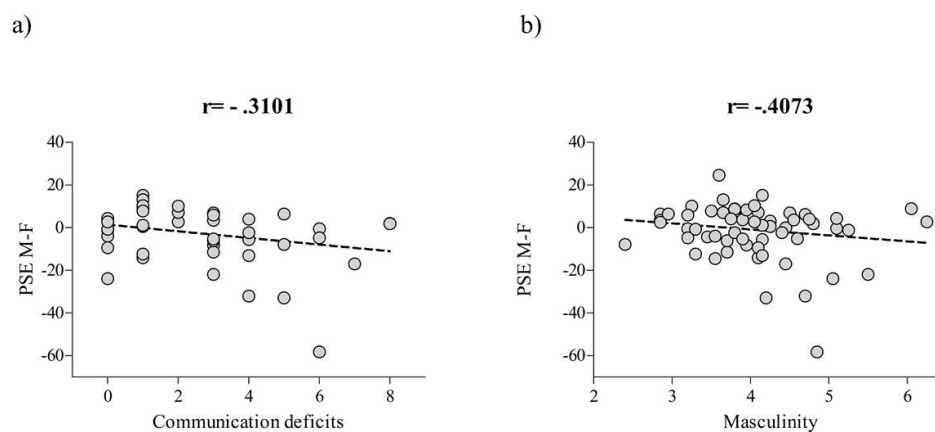


Figure 15. Correlations between the body-gender aftereffects index (calculated as the difference between the Point of Subjective Equality (PSE) after Male exposure and the PSE after Female exposure) and individual scores at the (a) Communication subscale of the Autistic Quotient or (b) Masculinity scale of the Bem Sex Role Inventory

### 3.1.4 General discussion

Identity- and orientation-tuning of the mechanisms involved in body-gender adaptation were investigated. Participants were exposed to a prolonged vision of distinctively female or male bodies and then asked to detect the gender of a series of androgynous bodies. In line with previous research (Palumbo et al. 2013), exposure to gender-distinctive body models biases the perception of androgynous bodies towards the opposite gender. Differently from the study by Palumbo and co-workers (2013), participants' judgments on androgynous stimuli after several minutes of exposure to a series of adapting bodies was collected. A long-lasting adaptation effects after cumulative perceptual experience was demonstrated, approaching in a more ecological way the mechanisms of adaptation to body models in everyday life (Brooks et al. 2019).

Building on past knowledge, body-gender aftereffects were shown to be independent of the specific individual characteristics of the model, transferring the various body characters. Adaptation to only upright bodies biased the perception of upright but not of inverted bodies (Experiment 2). Adaptation to both upright and inverted bodies biased the gender perception of both, thus proving the orientation tuning of body-gender aftereffects (Experiment 3). In contrast with previous evidence (Palumbo et al. 2013) no effect of the observer's gender was found. Individuals with higher autistic traits and higher internalization of a male gender role displayed less body-gender aftereffects. No effect was found for individual differences in body dissatisfaction. The findings point to identity independence and orientation tuning of body-gender adaptation mechanisms associated with individual differences in autistic traits and gender identity.

Body-gender adaptation is identity -independent

Research on visual adaptation has suggested that the gender of faces or bodies is represented mainly by two distinct neuronal channels that are broadly tuned (Ghuman et al., 2010; Winkler & Rhodes, 2005). The coding of gender follows an entirely symmetrical norm-based system, with male and female faces and bodies represented as opposite poles along the gender dimension and the androgynous body represented as its average value. The representation of body identity follows the line of norm-based coding (Rhodes et al. 2013a). Adaptation to a specific body (i.e., "Rose") biases perception toward the character with opposite features (i.e. "anti-Rose"), implementing a sort of opponent coding system. Gender distinctiveness of two different characters was modulated based on global shape (i.e., height/width ratio and curvature) and internal details (e.g., skin texture) during the experiments. One character was adapted with a high gender distinctiveness, while the other was adapted with a low gender distinctiveness. Thus, neural populations that adapted based on a gender exposure code for individual character features, body-gender aftereffects would be stronger for the

highly- adapting character. In all experiments adaptation to body gender acted regardless of character. The amount of aftereffects for highly- and lowly- adapting characters suggests that, the two body dimensions are processed at different levels of body representations. This finding was discovered despite the identity and the gender of the body being susceptible to similar adaptation mechanisms and following similar norm-based coding,

This points to a hierarchical organization of body representation, similar to what has been proposed for faces (Bruce & Young, 1986; Haxby et al., 2000; Rhodes et al. 2013a). Body gender is coded preliminarily to other dimensions such as body size and individual characteristics through the adoption of a male or a female body template. In keeping with the view that gender is a low-level dimension on which other relevant cues of the body are grounded, a study on selective-attention demonstrated that gender can be processed independently from body size. The latter cannot be detected independently from the former (Johnstone & Downing, 2017). Accordingly, evidence of contingent body-size aftereffects for male and female bodies (Brooks et al. 2019) suggests that the body size of male and female bodies is coded by separate populations of neurons that are engaged after the access to a male or female template. This hierarchical organization of body processing may also explain the discrepancy between the transfer of body-gender aftereffects regarding character and the partial identity- tuning of body-size aftereffects. Brooks et al. (2016) investigated the transfer of body-size aftereffects from self- to other- and showed that, moderate body size aftereffects occurred regarding identity. The effects were larger when the adapting and testing stimuli depicted the same person.

Our findings of an identity-independent adaptation of gender perception are in keeping with the response properties of areas in the lateral (extrastriate body area; Downing & Kanwisher, 2001) and medial (fusiform body area; Schwarzlose et al., 2005) occipito-temporal cortex associated to the processing of body form cues (Moro et al., 2008; Peelen & Downing, 2005; Urgesi et al., 2004; Urgesi, Calvo-Merino, et al., 2007). The fMRI adaptation studies (Kable & Chatterjee, 2006; Wiggett & Downing, 2011) showed that neural activation of these areas during action observation was not adapted with the repetition of the same actor. This suggests that the processing of body form cues in these areas might be used to distinguish individual bodies only at later stages (Downing & Peelen, 2016; Hodzic et al., 2009). Accordingly, our body-gender aftereffects may stem from adaptation of neural firing in these “low-level” body processing areas, rather than in those involved in person coding in more anterior temporal cortex (Kriegeskorte et al., 2007; Nestor et al., 2011).

## Body-gender adaptation is orientation-tuned

Results from Experiments 2 and 3 suggested that body-to-body-gender aftereffects are orientation tuned. It was necessary to perceive the adaptor and test stimuli in the same orientation to obtain significant body gender aftereffects. Orientation-independency of aftereffects is held as a marker of the involvement of high-level object-based processing (Brooks et al. 2018; Watson & Clifford 2006). Thus, our finding of an orientation tuning of body-gender aftereffects does not support the involvement of fully object-based mechanisms in body-gender adaptation. This is in contrast with the findings of a transfer regarding orientation of face-to-face (Watson et al. 2003; Webster & MacLin 1999, Watson et al. 2006) and body-to body (Brooks et al. 2018) shape aftereffects. More importantly, a previous study (Kessler et al. 2013) documented orientation transfer of body-to-face gender aftereffects, wherein upright or inverted bodies adapted the gender perception of both upright and inverted faces. This finding suggests that gender cues conveyed by the body activate orientation invariant representations of face gender. Conversely, in MY study, I found that perception of body gender activates orientation-tuned representations of body gender. The discrepancy between the body-specific and cross-categorical aftereffects may point to the involvement of different levels of gender coding. This involves a conceptual and independent coding from the specific person cues, either facial or body (Gaetano et al., 2014), and another more perceptual coding, specifically tuned to the specific stimulus template (Kovács et al., 2006). This keeps to the evidence of contingent face-to-face gender aftereffects for upright and inverted faces (Rhodes et al. 2004), which may reflect selective adaptation of configural and local processing mechanisms of face perception. Our results suggest that body-gender adaptation selectively engages neural populations that are tuned to the processing of upright or inverted bodies and are involved in configural and local processing of bodies, respectively.

Brooks and co-workers (2018) found that a significant, still weakened, transfer of body-size and -shape aftereffects can be obtained when the adaptor and test stimuli tilted 90° away. The mechanisms mediating body shape and size aftereffects operate within an object-centered frame of reference. However, the body stimuli used in this previous study were tilted at a +45° or -45° angle, a manipulation that reduces retinotopic contributions. but cannot disentangle the engagement of configural and local processing. It is likely that ±45°-tilted bodies involve a mix of configural and local processing. It is possible that body gender and body size are encoded at different levels of body representations, as demonstrated by opposite body-size aftereffects contingent on the gender of the stimuli (Brooks et al. 2019b) above. Our findings are in line with a hierarchical organization between body gender and size coding, wherein gender processing is driven by low-level, identity-independent,

and orientation-tuned mechanisms. Body size processing involves high-level, object-based mechanisms, that are, at least partially, tuned to the individual characteristics of the body (Brooks et al. 2016) and independent from its orientation.

Body-gender adaptation is associated to masculinity and autistic traits.

Despite men and women adapted by models of either gender, a previous study reported that aftereffects were stronger after adaptation to a model of the same gender (Palumbo et al. 2013). This was explained as the enhancement of perceptual attributes of gender after a prolonged vision of one's own gender and was qualified as an attentive advantage for mate selection. However, I did not find any difference between men and women. This finding might relate to the type of gender features adapted in the two studies. Palumbo et al. (2013) used body silhouettes and only manipulated the distinctiveness of the global male and female figures (i.e., shoulder, torso, and hip width). I used 3-D body renderings in which primary sexually-dimorphic cues (i.e., breast and genitals) were blurred. I manipulated not only the global body figure (i.e., width of shoulder, torso and hip and their relationship, such as the waist-to-hip ratio), but also the internal secondary sexually-dimorphic cues (i.e., musculature, body fatness), that characterize gender perception from faces (Skomina et al. 2020). A gender-contingent perceptual asymmetry has not emerged in the case of face gender adaptation, even though faces appear to be more relevant than bodies for the evaluation of attractiveness (Currie & Little, 2009).

I found a significant effect of the individual internalization of a male gender role on the amount of body-gender aftereffects. Individuals with higher self-reported masculinity showed weaker aftereffects. Masculinity/ femininity on prevalence body dissatisfaction and ED behaviours have been previously reported (Johnson et al., 1996; Murnen & Smolak, 1997; Sitnick & Katz, 1984). A negative correlation between masculinity and EDs has been documented, independently from biological gender (Cella et al., 2013), evidence that masculinity is a protective factor against the development of EDs in both men and women.

Our finding of a negative association between masculinity and body gender aftereffects may shed a new light on how masculinity may protect from body dissatisfaction and EDs. Stronger male-gender internalization may be associated with weaker reshaping of body perception, lower influence of body ideals and, consequently, less body misperception. Even though I did not find a reliable association between the amount of body-gender aftereffects and body dissatisfaction, measured with BUT, it is possible that other aspects of ED traits and symptoms are more strongly associated to atypical body adaptation (Mele et al. 2016; Cazzato et al. 2016).

In this regard, I found that higher autistic traits related to communication deficits, but not those related to attention to details and predicted weaker body-gender aftereffects. This result supports the findings of reduced face aftereffects in individuals with autism (Pellicano et al. 2007) and in their relatives (Fiorentini et al. 2012) as well as in individuals with higher autistic traits (Rhodes et al. 2013b). Rhodes and colleagues (2013b) found that the amount of face-identity aftereffects was negatively associated with the social aspects of autistic traits in only male undergraduate students. No effect was documented for the attention-to-detail scale. Our results extend to the aforementioned studies by showing that alterations of face and body adaptation mechanisms may be an endophenotype for autism. The reduced body adaptation in individuals with higher autistic traits may also inform aspects of EDs that are associated to altered body adaptation mechanisms. The increased interest on the neurocognitive profile of individuals with EDs has shed light on a conceivable association between autistic traits and anorexia nervosa symptoms (Roberts et al., 2011; Tchanturia et al., 2013). Our result agrees with the hypothesis that deficits in social communication, which are shared by patients with EDs and with autism, may influence the perceptual phenomenon of visual adaptation and body perception. Future studies are needed to substantiate the alterations of body gender adaptation in clinical populations with EDs or autism.

Inverted bodies are perceived as more masculine

Unexpectedly and independently from adaptation, inverted bodies were judged as more masculine than upright bodies. This result is in contrast with the finding for face gender discrimination (Rhodes et al. 2004), where inverted faces were judged as more feminine than upright faces. It appears also to be in contrast with the sexualized-body inversion hypothesis, which claims there is a reduced use of configural processing for female bodies, revealed by lower inversion effects for female models (Bernard et al. 2012, 2015). Inverted bodies should appear more feminine but I found the opposite. However, this effect has been attributed to an object-like processing of female bodies portrayed in sexualized clothes and poses in which typical inversion effects have been observed for personalized representation of either men and women (Cogoni et al., 2018), and may not apply to our virtual-human models presented in neutral postures. Rather, the fact that I found a tendency to report a male body for inverted stimuli may reflect the emergence of a general male decision bias that occurs when gender decision is particularly difficult, as in the case of inverted bodies. This bias has been demonstrated for several gender cues, including faces (Wild et al., 2000), body shapes (Gandolfo & Downing, 2020; Johnson et al., 2012) and biological motion displays (Troje & Szabo, 2010)).

### **3.1.5 Limitations and future directions**

First participants' judgment of androgynous bodies without previous exposure was not tested. Instead, only the difference between the two exposure conditions was considered. The aim was to reduce the repetition of judgments of the participants and did not allow for the exclusion of pre-existing decision biases in reporting the presence of male and female bodies. The difference between inverted and upright bodies, independently from exposure, might point to these biases.

Secondly, the results could be limited to the specific type of stimuli used, namely human-like avatars, and a different pattern of results may be driven by the use of silhouettes and photographs of real person bodies. A relatively long exposure time during the test phase (i.e., 1,500 ms) was used, but did not control the strategies adopted by participants during visual inspection (e.g., Cogoni et al. 2018).

Finally, the effect of adaptation was compared only to upright or to both upright and inverted bodies, not to the effect of exposure to only inverted bodies. Thus, the effects of adapting was not isolated from feature-based mechanisms on body gender perception. Future studies are needed to further elucidate the characteristics of body-gender adaptation and to deepen our knowledge on how we extract information on the gender of conspecifics based on bodily cues.

Our study, instead, qualifies the description of body gender perception. It highlights experience-dependent reshaping based on mechanisms that are independent from the person's characteristics but tuned to be used with configural or local processing. Hints to understanding how alterations of the malleability of body perception may be associated to individual difficulties in social interactions were given.

### **3.2 Spatial frequency tuning of Body Adaptation**

To explore mechanisms involved in visual processing, cognitive psychologists look for non-invasive methods that allow human perception to be tested. As previously discussed, the visual adaptation paradigm has been largely approved and, thanks to the property to be a window into neural plasticity, it has earned the title of "psychophysicist's microelectrode" (Frisby, 1979).

Today, beside the evidence that watching a stimulus in motion makes a subsequent fixed stimulus moving toward the opposite direction, we can report a series body aftereffects which drive visual perception toward stimuli with the opposite structural characteristics of the adapted ones (Brooks et al., 2018; Challinor et al., 2017; Leopold et al., 2005; Rhodes et al., 2003; Rhodes & Jeffery, 2006).

As in the case of adaptation, the function of spatial frequencies (SFs) in visual perception has made them a remarkable tool to indirectly investigate how we process visual objects. Indeed, examining the scale usage during recognition and categorization of specific stimuli came in handy to understand both hierarchical representation of distinct features and the relative contribution of dorsal and ventral pathway in the processing of visual stimuli. Studies using SF manipulation are still scarce. By combining a visual adaptation task with a spatial-frequency manipulation, the aim has been to better understand the difference of the two channels in body perception, focusing on gender dimension. The three experiments investigated the parallel, cross-transfer and contingent aftereffects of body gender adaptation. In Experiment 1, both filtered and un-filtered gendered body stimuli effects on gender recognition of a set of non-filtered androgynous models was tested. Experiment 2 tested the aftereffect ability to transfer across different bandwidths. Experiment 3 tested participants for contingent aftereffects of LSF and HSF channels to find a dominance of one or another pathway. Here the results to help clarify how mechanisms engaged in body gender perception are structured among ventral and dorsal visual systems.

### **3.2.1 Experiment 1**

In “Experiment 1”, participants were tested for the parallel aftereffects of body gender adaptation across different band widths of spatial frequencies, namely HSF and LSF. Four adapting avatars (2 male and 2 female) were manipulated and presented non-filtered or containing only HSF or LSF information.

#### **3.2.1.1 Participants**

A sample of 30 students (26 female, mean age = 22.43, SD = 3.26 years) from the University of Udine took part in the experiment in return for course credits. They reported normal or corrected vision and they were right-handed as ascertained with standard handedness inventory (Oldfield 1971). Written informed consent was acquired from all participants. The procedures were approved by the local ethics committee (Commissione di garanzia per il rispetto dei principi etici nell’attività di ricerca sugli esseri umani, Department of Languages and Literatures, Communication, Education and Society, University of Udine) and conformed with the Helsinki Declaration.

#### **3.2.1.2 Stimuli**

All virtual-human body stimuli presented within the three experiments were created with the use of Character Creator 3.0 software (Reallusion, San Francisco, CA, USA). To generate the testing stimuli, we started from four models (2 female and 2 male) and we manipulated the percentage of female and male traits expressed by each body by mixing the two pairs of female and male models in



a continuous variation from 20% male and 80% female up to 20% female and 80% male (Fig. 1B), as already described in our previous study (D'Argenio et al., 2021). A total of 40 male and 40 female bodies were selected from the pool of bodies used in a previous study (D'Argenio et al., 2021) and imported into Adobe Photoshop CS6 (Adobe Systems, San Jose, CA) in order to produce high- and low- spatial frequency version of each image (Fig. 1A). Spatial frequency content of images was manipulated by using a Gaussian blur filter with a 6-pixel kernel for low-pass filtering (resulting in images low-pass filtered at  $\approx 2$  cycles per image, LSF) and the high-pass filter application set to a radius of 0.9 pixels for the high-pass filtering (resulting in images filtered at  $\approx 90$  cycles per image, HSF). A non-filtered as well as a high-/ low-frequency version of each image was produced (Fig.16).

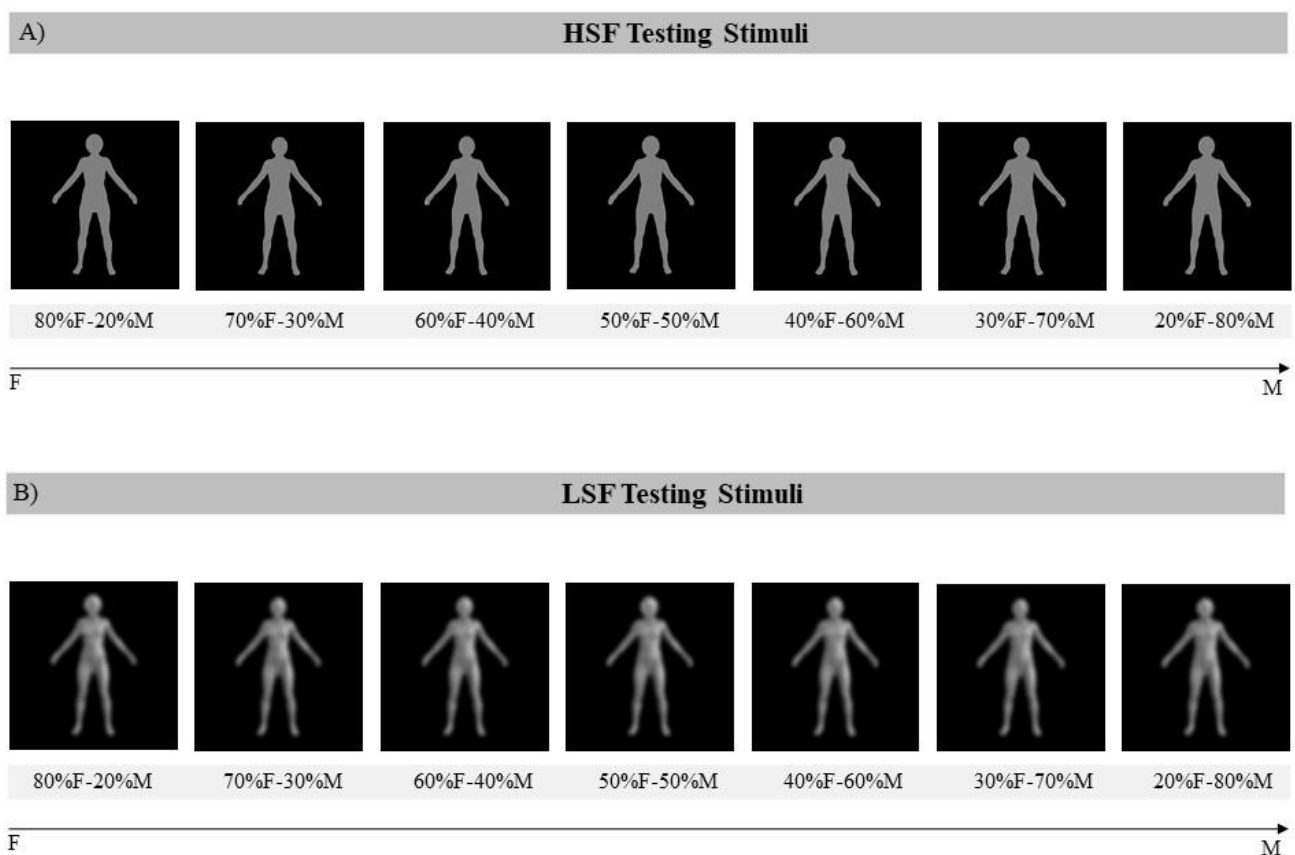


Figure 16. Androgynous virtual models presented as Testing stimuli. The figure depicts the continuous % variation from 20 male-80 female up to 80 male-20 female for both A) high-spatial frequency and B) low-spatial frequency.

### 3.2.1.3 Procedure

The experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA) and participants were tested individually from their home, by means of the

Subject Station supplied by the software. They were recommended to stay in a quiet room and seat in front of their computer screen (refresh rate, 60 Hz) at a distance of 60 cm. All participants were asked to perform two experimental sessions consisting of two blocks, each one including an adaptation phase and a subsequent testing phase. The adaptation phase changed across the two experimental sessions, with one containing only Female models and the other one containing only Male models, even though participants were not aware of gender manipulation. Each participant took part, in three different days, to three experimental conditions, which varied in the spatial frequency content of the adapting bodies presented in both sessions, which could be non-filtered, HSF-filtered or LSF-filtered. The test phase remained always the same even though the adaptation phases differed across sessions and conditions according to the gender and the SF of the adapting stimuli (Fig. 2),

Each adaptation block contained 160 trials (i.e., two presentations for each male or female adapting body) and lasted about 8 minutes. They started with a white central fixation cross (500 ms) appearing on a black background and followed by a body image lasting 2,000 ms. The image then disappeared and the two alternative “Statico” and “Dinamico (“Static” and “Dynamic” in English) were displayed on the bottom of the screen. The participant was asked to press the button (i.e. “Z” or “M” key on a QWERTY keyboard) that spatially corresponded to the correct answer. After each adaptation block, a test phase block was administered and lasted about 6 minutes. The 28 possible androgynous bodies were presented eight times each for a total of 224 trials per test block. 448 test trials were administered in each experimental session (i.e., 32 trials per cell). The test trial started with a central fixation cross (500 ms) followed by an androgynous body that lasted on the screen until a response was given or for a maximum of 1,500 ms. Participants were asked to report the gender (male or female) of the body stimulus by pressing as soon as possible the key “Z” or “M”. The response-key associations in both adapting and testing phase as well as the order of both the experimental sessions and conditions were counterbalanced for all participants.

### **3.2.1.4 Data handling**

All statistical analyses were calculated with STATISTICA software (Stat Soft, Tulsa, OK) by using Analysis of variance (ANOVA) designs. The adapting stimuli were used to capture participants’ attention on body stimuli. The participants’ performance in the adaptation phase was not considered for the analysis. Individual proportion of male responses for each of the 7 points of gender typicality of the androgynous bodies was tested, in order to estimate the increase of male responses according to the increasing amount of specific gender characteristics. Two experimental sessions (Male vs Female adaptation) and the three experimental conditions (intact vs HSF vs LSF) were taken into account separately. For each subject, the proportions of male responses were fitted as a function of

male/female features with a logistic function. The Point of Subjective Equality (PSE) was calculated. This corresponded to the level of gender typicality of a stimulus to which the judgement of male or female identity is equally likely to occur. Individual PSE were entered into a mixed ANOVA design with Exposure gender (Male or Female) and Spatial Frequency (intact vs HSF vs LSF) as within-subject variables. Significant interactions were explored using Duncan's post hoc test for multiple comparisons. The test has been developed to reduce the risk of false negative (Type II) error when correcting for multiple comparisons (Ijzmi 2016) by reducing the size of the critical difference depending on the number of steps separating the ordered means. This procedure is optimal for testing in the same design effects that may have different sizes (Duncan, 1955; Dunnett, 1980; McHugh, 2011). Significance threshold was set at  $p < 0.05$  for all analysis. Effect sizes were estimated with partial eta squared ( $\eta^2$ ). Values are reported as mean  $\pm$  standard error of the mean (SEM). The sample size required for our 2 (Exposure gender)  $\times$  3 (Spatial Frequency) ANOVA design was determined with the G\*power software (Faul et al. 2009), using the "as in SPSS" option for estimating effect size from  $\eta^2$  and setting the  $\alpha$  level at 0.05 and the desired power ( $1 - \beta$ ) at 95%. The expected effect size was set at  $f = 0.3$  based on our previous study of body gender adaptation (D'Argenio et al., 2021), alpha-level at 0.05, and desired power (1-beta) at 90%.

### **3.2.1.5 Results and discussion**

The 2-way ANOVA performed on the PSE scores showed a significant main effect of Exposure gender [ $F(1,29) = 10.73$ ;  $p = 0.001$ ;  $\eta^2 = 0.27$ ], revealing a lower PSE after Female exposure ( $49.9 \pm 1.49$ ) and ( $53.72 \pm 1.36$ ) after Male exposure. Protracted exposure to female or male bodies made subsequent androgynous bodies to appear as more masculine or feminine, respectively. A contrast aftereffect occurred independently from the SF content of the adapting stimuli since the SF manipulation did not yield a significant effect [ $F(1,29) = 0.317$ ;  $p = 0.73$ ;  $\eta^2 = 0.011$ ; Fig.17]. Both high- and low- SF adaptation influenced the judgment of intact androgynous bodies towards the opposite gender. This result may suggest the existence of a parallel aftereffect involving both parvo- and magnocellular systems.

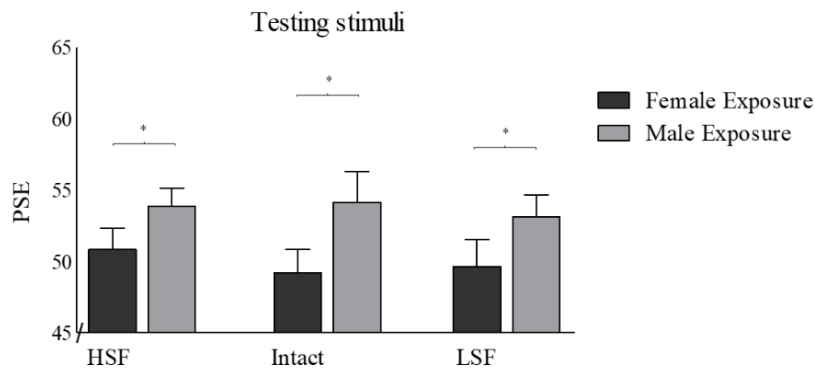


Figure 17. Mean and standard error of mean for PSE after female and male exposure in the three spatial frequency conditions. Asterisks indicate significant comparison ( $p < 0.05$ ) between SF condition and gender exposures.

### 3.2.2 Experiment 2

In “Experiment 2”, the aftereffect of body gender was investigated regarding the transfer to different band widths. As in Experiment 1, participants were separately adapted to HSF or LSF bodies, depending on the experimental condition, and to female or male bodies, depending on the experimental session. Throughout all the test phases, participants were presented with both HSF and LSF androgynous bodies.

#### 3.2.2.1 Materials and methods

Thirty naïve participants (25 women, mean age = 22.17, SD = 5.21 years) were recruited and the same adapting stimuli were used. The same procedure and data handling approach was used as in “Experiment 1”. However, this time, the 28 testing bodies were presented in their high- and low-filtered versions and participants were not exposed to the intact experimental condition. The 28 testing bodies were presented eight times each, four times high-filtered and four times low-filtered, for a total of 224 trials per block; thus, 448 test trials were administered in each experimental session (i.e., 16 trials per cell). This time, Individual PSE were entered into a 3-way ANOVA with Exposure gender (Male or Female), Exposure SF (HSF vs LSF) and Testing Stimuli SF (HSF vs LSF) as within-subject variables.

### 3.2.2.2 Results and discussion

The 3-way ANOVA performed on the PSE scores revealed, as in Experiment 1, a significant main effect of Exposure gender [ $F(1,29) = 9.70$ ;  $p = 0.004$ ;  $\eta^2 = 0.25$ ], with a lower PSE after Female exposure ( $50.76 \pm 2.16$ ) rather than after Male exposure ( $57.77 \pm 2.36$ ). A main effect of Testing Stimuli SF [ $F(1,29) = 4.942$ ;  $p = 0.03$ ;  $\eta^2 = 0.146$ ], indicating that LSF stimuli appeared more feminine ( $58.80 \pm 3.05$ ) than for HSF ( $49.73 \pm 2.59$ ). This data seemed at first to point to a bias concealed in LSF bodies which should make them less effective at adapting to male features and consequently driving to weaker aftereffects than with their HSF counterparts. But with more analysis, as shown in the graph (Fig. 5), there is no evidence that effects obtained with LSF stimuli are misleading. The Exposure SF main effect [ $F(1,29) = 0.024$ ;  $p = 0.87$ ;  $\eta^2 = 0.0008$ ] as well as the Exposure gender  $\times$  Exposure SF [ $F(1,29) = 2.369$ ;  $p = 0.13$ ;  $\eta^2 = 0.075$ ], the Exposure SF  $\times$  Testing Stimuli SF [ $F(1,29) = 0.554$ ;  $p = 0.46$ ;  $\eta^2 = 0.018$ ] and the Exposure gender  $\times$  Exposure SF  $\times$  Testing Stimuli SF [ $F(1,29) = 2.932$ ;  $p = 0.1$ ;  $\eta^2 = 0.091$ ] interactions were not significant (Fig. 18). This gives evidence that the SF content of adapting stimuli to distinctive gender exposures influenced the perception of both high- and low- SF stimuli. These results demonstrate a spatial-frequency transcoding suggesting that gender exposure aftereffects may transfer to different band widths.

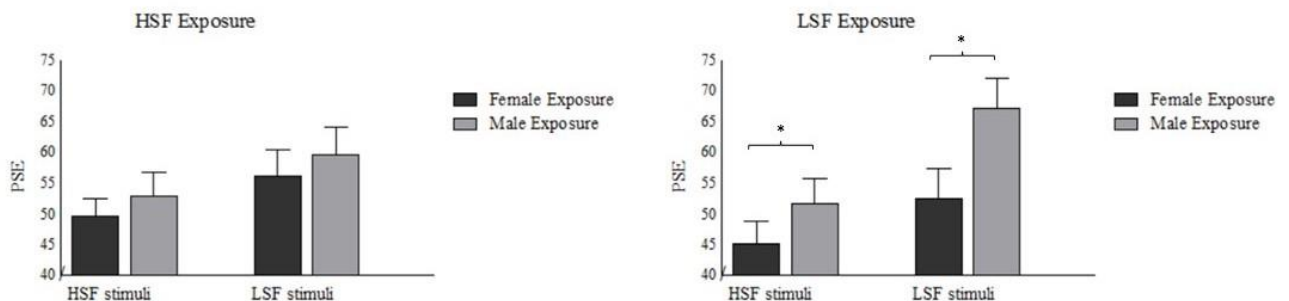


Figure 18. Mean and standard error of mean for PSE after High-spatial frequency male and female exposures (on the left) and Low-spatial frequency male and female exposures (on the right). Asterisks indicate significant comparison ( $p < 0.05$ ) between SF condition and gender exposures.

### 3.2.3 Experiment 3

The aim was to qualify the results of the previous experiments by investigating the contingent aftereffects of body gender adaptation. For this, opposite gender-typing features in the two SF channels within the same experimental condition were presented.

### 3.2.3.1 Materials and methods

Thirty naïve participants (20 women, mean age = 23.87, SD = 5.23 years) took part in the “Experiment 3”. The same stimuli and data handling approach as in Experiment 2 were used. This time, the procedure consisted of two experimental conditions, performed within the same session with a pause in between. Participants were exposed to one condition showing high-pass filtered males and low-pass filtered females and another condition showing high-pass filtered females and low-pass filtered males as adapting stimuli. The testing phases were conducted, as in “Experiment 2”, so that the 28 testing bodies were presented in both their high- and low- filtered versions for a total of 224 trials per block (448 test trials in each experimental condition; 16 trials per cell). Individual PSE were entered into a 2-way ANOVA with Exposure SF (HSF vs LSF) and Testing Stimuli SF (HSF vs LSF) as within-subject variables.

### 3.2.3.2 Results and discussion

The 2-way ANOVA performed on the PSE scores showed again a significant main effect of Testing Stimuli SF [ $F(1,29) = 6.426$ ;  $p = 0.016$ ;  $\eta^2 = 0.18$ ], with lower PSE for LSF ( $49.83 \pm 2.59$ ) than the HSF ( $61.23 \pm 3.02$ ) stimuli, confirming that LSF bodies appear more feminine than their HSF counterpart. A significant Exposure SF  $\times$  Testing Stimuli SF [ $F(1,29) = 7.309$ ;  $p = 0.011$ ;  $\eta^2 = 0.201$ ] interaction was found, revealing a partial contingent aftereffect in accordance to the gender exposure (Fig. 19). The significant interaction was explored with the Duncan’s post hoc test for multiple comparisons [MSE = 168.66 df = 29]. For HSF Testing stimuli, the PSE scores were significantly lower after HSF-female ( $45.15 \pm 3.08$ ) rather than after HSF-male exposure ( $54.53 \pm 2.5$ ;  $p = 0.009$ ). For LSF Testing stimuli, the PSE scores after both LSF- female ( $59.51 \pm 2.98$ ) and -male ( $62.95 \pm 4.19$ ) exposures were comparable ( $p = 0.31$ ). This result seems to suggest that gender aftereffect can transfer from HSF to LSF stimuli, pointing to a body gender adaptation effect that is mainly driven by high spatial frequencies.

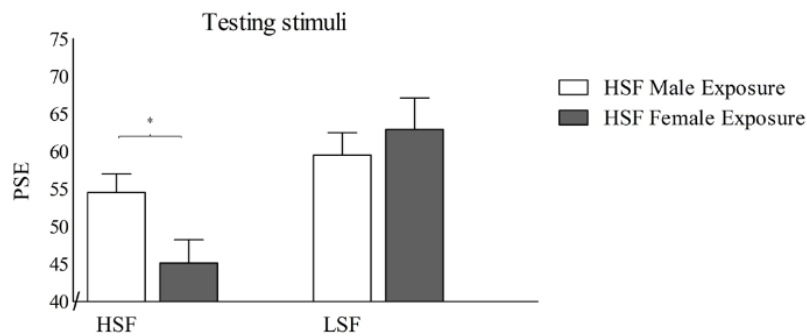


Figure 19. Mean and standard error of mean of the PSE for high-spatial frequency and low-spatial frequency testing stimuli, after high-male/low-female exposure (white columns) and high female/low male exposure (grey columns). Asterisks indicate significant comparison ( $p < 0.05$ ) between exposures.

### 3.2.4 General discussion

The present study aimed to better understand the relative contribution of magno- and parvocellular channels in gender body perception. How the manipulation of spatial-frequency content of bodies could influence visual adaptation to their gender was investigated. In line with the study reported in Section 3.1 (D’Argenio et al., 2021), an investigation of how adapting participants to gender-distinctive body model biases perception of intact androgynous bodies towards the opposite gender was performed. Results show that perception is affected by the set of bodies we are exposed to. They also show that this effect occurs independently from the spatial frequency content of the adaptors. The greater contrast aftereffect has been shown when adaptors and test stimuli were both non-filtered. The exposure to only HSF- or LSF- filtered bodies have revealed a robust reshaping of the judgement of intact androgynous bodies as well.

This result can be fairly interpreted as the evidence of a parallel aftereffect, which seems to suggest the efficiency of both parvo- and magnocellular channels in conveying body gender information. A non-filtered body can be considered a sum of different ranges of bandwidths blended into a single visual representation; exposure to an individual band of SF may have exerted its influence on the analogous frequency component embedded in the intact image, leading to neural habituation of either parvocellular (i.e. after HSF exposure) or magnocellular (i.e. after LSF exposure) channel. The information supporting a fine-detailed processing of the body and the information used for the development of its holistic shape should be considered sufficient to detect gender distinctive features that adapt our perception. The findings appear to support studies exploring gender processing of faces

which have frequently supported the contribution of both spatial scales (Jeantet et al., 2019; Schyns et al., 2002; Schyns & Oliva, 1999; Vuilleumier et al., 2003). With the extension of SF manipulation to adapting bodies introduced in Experiment 2, clarification of how the two channels may be implicated in the phenomenon was considered. To do this, testing for the actual separation of the aftereffects or a possible transcoding across bandwidths was undertaken. The results revealed that, regardless the SF content used during adaptation phases, distinctive gender exposures influenced the perception of both high- and low- SF testing stimuli, indicating that adaptation aftereffects are not frequency-tuned. The processing of body gender might not be ascribed to either parvo- or magnocellular system but, rather, to the integration of information originating from both channels. Regarding dorsal and ventral contributions, high-level perceptual mechanisms were proposed based on the interaction between the two pathways. The same was introduced for general object recognition (Bar, 2003) and action perception (Amoruso et al., 2020), which may support a continuing exchange of HSF and LSF information between ventral and dorsal body areas. However, the ventral visual stream receives both magnocellular and parvocellular inputs (Ferrera et al., 1992) and may be the most qualified route to support the non-diagnostics of spatial frequencies in gender body adaptation since it can flexibly respond to both SF components. To deeply explore this hypothesis in Experiment 3, a paradigm aimed at unveiling the preference for a specific range of SF when both high- and low-SF gendered bodies were available was developed. Opposite gender-type features were presented in the two SF channels within the same block and results definitively claimed a dominance of HSF over LSF. A partial contingent aftereffect on HSF testing stimuli in accordance with adaptors gender of the same SF band was found. LSF stimuli did not show a significant contrast aftereffect.

For perceptual preference for HSF exposure to body gender to be explained, it is assumed that neural populations implicated in the analysis of HSF content may be segregated and, thus, influenced only by the consistent SF. Those implicated in the encode of LSF content could not exclusively be dedicated to this range of SF, leading to mutually exclusive aftereffects. This view seems to follow the notion of a “coarse-to-fine” mode of processing face stimuli (Goffaux, 2009; Goffaux & Rossion, 2006), in which LSF global information are processed before HSF local ones. Along the same channel there are neurons, supposedly, that respond firstly to LSF information of the body and, in a second stage, to HSF ones, to progressively compute a finer analysis. Thus, when LSF and HSF information do not compete with each other, as in Experiment 2, adaptation aftereffects can be observed for both ranges of spatial frequency, since both channels are sensitive to adaptation. Instead, creating conflictual conditions, HSF exposure reveals to be better suited because of its dedicated channel. Based on this data, since any perceptual responses driven by HSF should be indicative of inputs coming from the ventral visual pathway, it is fair to suggest that the ventral is the most qualified route



to convey gender information from body stimuli. Accordingly, the fact that both SF bands can be effective in producing perceptual aftereffects in absence of conflictual conditions seems to be in accordance with the major involvement of the pathway that can process both magno- and parvocellular inputs.

Unexpectedly, in both Experiment 2 and 3, LSF bodies were generally judged as more feminine than HSF bodies. Although this bias was not indicative of the efficiency of LSF bodies in adapting to male gender, it can realistically be a matter of discussion. Surely, it appears in contrast with studies supporting the objectification theory (Fredrickson & Roberts, 1997) proposing that female bodies are recognized in a piecemeal way (Bernard et al., 2012, 2015), a processing mode that should be favored by HSF bands. However, as addressed in the study reported above (D'Argenio et al., 2021), virtual-human models presented with blurred primary sexually-dimorphic cues may not be processed as typical sexualized bodies are. So, rather than looking for conceptual account of body sexualization, a perceptual bias that is more related to participants' general attention could be proposed. LSF content allows the recognition of the body that refers almost exclusively to its shape since it conveys coarse information about the global form of a visual stimulus. As widely demonstrated, the waist area of a body is considered an important indicator to categorize female bodies, while the judgment of males is more related to their upper part (Dixson et al., 2011, 2014). Due to the fixation cross and the relative short time of stimuli presentation, it seems plausible that participants were not able to entirely explore the figure, thus paying attention primarily to the core, namely the waist and hip area. So, the attention focuses on waist shape, in absence of other clues other than global form, may have biased participants perception towards a female judgment.

Overall, the above experiments offer novel data about the contribution of different spatial frequencies in visual body processing, finally suggesting the major involvement of the ventral visual stream. This is the first study concerning the relationship between visual adaptation to body stimuli and their spatial frequency content, so the conclusions can be weighed in light of critical limitations. First, there is the relative involvement of the ventral and dorsal visual streams in body gender adaptation to be explored by means of an empirical research method (i.e. the manipulation of spatial frequency). This cannot directly verify a specific channel role. Instead, the method allowed for testing participants from their house during the COVID-19 pandemic, but obviously future studies should include the introduction of brain stimulation protocols, for example Transcranial Magnetic Stimulation, to clarify to what extent the preference for HSF information was due to the contribution of ventral rather than dorsal pathway. Further, due to the nature of the study, temporal dynamics characterizing high vs low- spatial frequency processing have not been considered. An adaptation paradigm requires the

prolonged exposure to stimuli which cannot disentangle the earlier vs later contribution of LSF and HSF, respectively (Goffaux et al., 2011).

To conclude, this study lays the foundation for future exploration of the neural mechanisms involved in body gender perception, giving critical support to models of visual adaptation that are based on a spatial frequency analysis.

## **4. Brain mechanisms of body adaptation: a ccPAS study**

### **4.1 Introduction**

In the general population, body perception can be reshaped by previous experience as documented by visual aftereffects following prolonged exposure to a body with a specific feature (see Chapter 3). Alterations of these aftereffects could play a role in body misperceptions since patients with ED show reduced effects to body exposure. It is well known that regions of the lateral (extrastriate body area; EBA) and medial (fusiform body area, FBA) occipito-temporal cortex are dedicated to body processing, showing a greater activity evoked by the visual presentation of body and body parts with respect to other objects and faces (Peelen & Downing, 2007). Alterations of these areas as in the case of patients with occipito-temporal injury (Moro et al., 2008) or their functional alteration by means of Transcranial Magnetic Stimulation (TMS; Urgesi et al., 2004; Urgesi, et al., 2007a; 2007b) have shown to induce a selective impairment in the recognition of non-facial body stimuli. Several neuroimaging studies have documented functional and structural alterations of the occipito-temporal areas in patients with ED (Suchan et al., 2013; Uher et al., 2005). Further, some neuroscientists have studied the functional connectivity (i.e. the strength of the connections between different areas) of the individual occipito-temporal areas involved in the perception of the body, in both healthy controls and AN patients (Suchan et al., 2013). Their results have documented a reduced connectivity between EBA and FBA in the left hemisphere of patients with AN with respect to controls, thus suggesting that patients with AN may be characterized by a weaker flow of information between lateral and medial areas of the occipito-temporal cortex during body observation.

The cortico-cortical paired associative stimulation (cc-PAS) is a TMS protocol based on hebbian spike-timing-dependent plasticity (STDP). According to this principle, the strength of synapses increases when presynaptic and postsynaptic neurons are constantly activated at predetermined intervals. A suitable interstimulus interval (ISI) should reflect the timing of information transfer between regions. When a fitting ISI is selected, the spikes that are induced over time by couples of TMS pulses applied on two cortical regions empower their connectivity, thus leading to neurophysiological and behavioural changes. At first, PAS protocols have been conceived with the intent to modulate motor system excitability, by pairing electrical stimulation of the median nerve with a TMS pulse on the contralateral primary (M1) or sensory (S1) motor cortex (Stefan et al., 2000; Wolters et al., 2005). Over the years, the association of a peripheral and a cortical stimulus has been replaced by a couple of two cortical stimuli aimed at inducing temporary and reversible associative plasticity between human cortical regions. The studies conducted so far have mainly focussed on the investigation of motor cortices connectivity and the relative effect of cc-PAS on motor performance

(Arai et al., 2011; Buch et al., 2011; Rizzo et al., 2009, 2011). However, some authors targeted more complex components of human cognition, such as fluid intelligence (gf), showing that cc-PAS applied on fronto-parietal nodes can enhanced cognitive tasks performance (Momi et al., 2019; Santarnecchi et al., 2019). Importantly, both motor and cognitive studies reported that 15 minutes of cc-PAS can induce effects lasting around 30-60 minutes after the end of stimulation. Further, these studies have shown that the order in which TMS pulses are delivered is crucial in determining cortical plasticity changes.

Considering the relation between body adaptation mechanisms and dysfunctional body visual experience, it appears useful to better investigate the role of cortical areas dedicated to body adaptation and the connections between them. Here, I tailored a cc-PAS protocol to study the role of feed-forward and reentrant connections within the occipito-temporal cortex in body gender adaptation, whereby exposure to a distinctively female or male body makes androgynous bodies appear as more masculine or feminine, respectively.

## **4.2 Participants**

Thirty-four healthy individuals (18 females; mean  $\pm$  standard deviation (SD), 25.43 years  $\pm$  3.69) were recruited at the University of Udine. All participants reported normal or correct-to normal vision, no past history of neurological or mental illness, and were negative for the risk factors of TMS (Rossi et al., 2009). Informed consent forms were signed by all subjects before taking part to the experiment. The study was approved by the local ethics committee (*Commissione di garanzia per il rispetto dei principi etici nell'attività di ricerca sugli esseri umani*, Department of Languages and Literatures, Communication, Education and Society, University of Udine) and conformed with the Helsinki Declaration.

## **4.3 Stimuli and behavioural task procedure**

The stimuli utilized to build the behavioural task were the same used in previous adaptation experiments (see Section 3.1). Again, the experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA). The task consisted of an Adaptation Phase, in which participants were exposed to male or female sex-typing virtual-human bodies, followed by a Test phase in which they were asked to discriminate the gender of a series of androgynous bodies. They performed the entire task two times. The test phase was identical in the two sessions, while the adaptation phase differed according to whether male or female adapting stimuli were used (Fig. 2). The order of the two sessions was counterbalanced between participants and a short break was allowed between sessions (Fig. 20).

Differently from the behavioural experiment, the adaptation block comprised a total of 160 trials and lasted about 8 minutes while in the test phase the 28 androgynous bodies were presented for a total of 280 trials, lasting about 5 minutes.

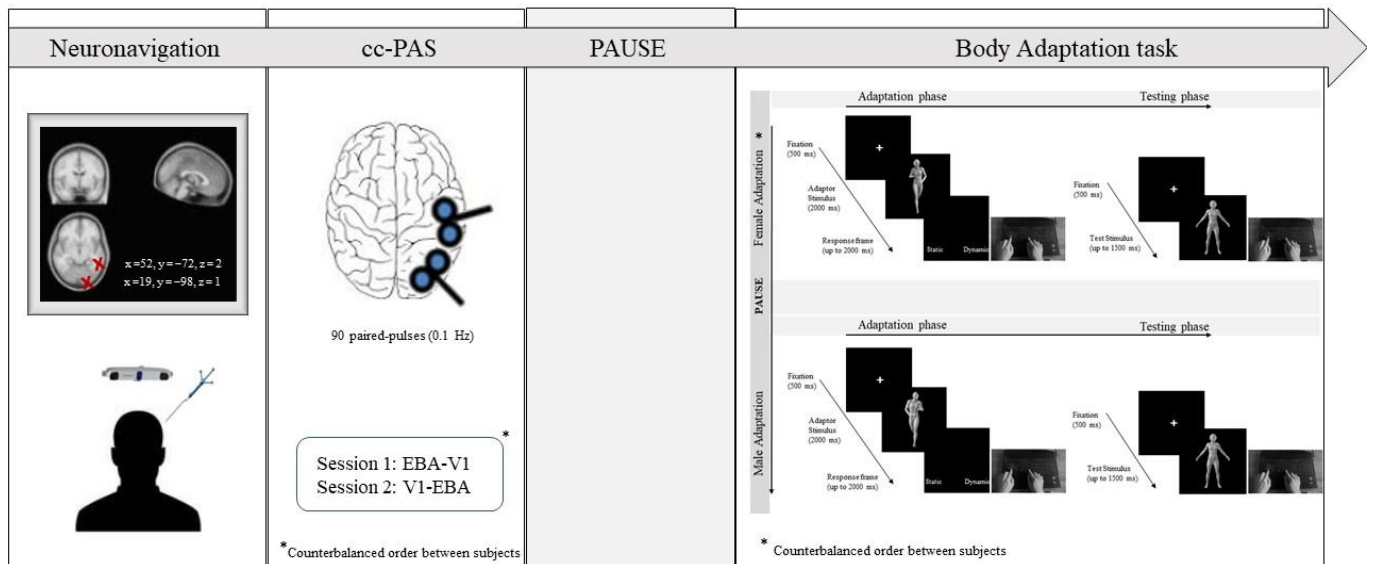


Figure 20. Experimental session design. After individual target areas localization (Neuronavigation), participants underwent a 15-minutes brain stimulation (cc-PAS), followed by 15 minutes of rest (PAUSE). Then, participants were asked to perform a behavioral task, which consisted of two different adaptation phases (i.e. female adaptation and male adaptation) and two identical testing phases (Body Adaptation task). Each participant took part to two experimental sessions, in which a different cc-PAS protocol (i.e. V1-EBA or EBA-V1) was applied. The order of cc-PAS protocol was counterbalanced between participants.

#### 4.4 Neuronavigation system

To localize target cortical areas for each subject, a SofTaxic Optic neuronavigation system (Electro Medical Systems, Bologna, Italy; [www.softaxic.com](http://www.softaxic.com)) was used. Four skull landmarks (i.e. nasion, inion, and two preauricular points) and 23 points providing a uniform representation of the participants' scalp were digitized by means of a Polaris Vicra optical tracking system (Northern Digital, Inc., Waterloo, Ontario, Canada). Then, the system automatically estimated the coordinates in standard space from an MRI-constructed stereotaxic template, in which Talairach coordinates (Talairach & Tournoux, 1988) of EBA and V1 were marked. The coordinates of the stimulation sites for right EBA were  $x = 52, y = -72, z = 2$ , taken from previous TMS studies investigating the role of right EBA in visual body perception (Cazzato et al., 2014; Urgesi et al., 2004, 2007), while the coordinates for V1 were  $x = 19, y = -98, z = 1$ , as in the study of Serino and colleagues (2011).

#### **4.5 cc-PAS protocol**

cc-PAS protocol consisted of 90 paired TMS pulses delivered over right EBA and V1 by means of two figure-of-eight coil connected to a Magstim 200 stimulator. The couples of pulses were delivered every 10 s (0.1 Hz) with an ISI of 20 ms, so the intervention lasted about 15 minutes. Both the conditioning (first TMS pulse) and the test stimulus (second TMS pulse) were applied to subjects at an intensity of 60% of the maximum output of the TMS machine. Neuronavigation system allowed to monitor online the position of the coils focus over the target positions during stimulation. The coil was placed over the two target areas and securely held tangentially to the scalp by means of two coil holders. Participants underwent two cc-PAS sessions in two different dates. In one session (V1-EBA), I boosted feedforward connections by applying TMS first over V1 and then, after 20 ms, over EBA; in the other session (EBA-V1), I boosted reentrant connections by applying TMS first over EBA and then, after 20 ms, over V1. The order of cc-PAS stimulations was counterbalanced between participants.

#### **4.6 Data handling**

Analyses were performed using Analysis of variance (ANOVA) in the STATISTICA 7 software. For the test phase, the proportion of male responses was calculated separately for the male and female adaptation sessions and for the EBA-V1 and V1-EBA cc-PAS protocols. Then, for each participant and condition, I calculated the PSE. Individual PSE were entered into a mixed ANOVA design with Exposure (Male or Female) and cc-PAS (EBA-V1 or V1-EBA). A significance threshold was set at  $p < 0.05$  for all analysis. Effect sizes were estimated with partial eta squared ( $\eta^2$ ). Values are reported as mean  $\pm$  standard error of the mean (SEM).

#### **4.7 Results**

In keeping with the behavioural experiment, the 3-ANOVA performed on the PSE values revealed a significant main effect of Exposure [ $F(1,33) = 24.49$ ;  $p < 0.001$ ;  $\eta^2 = 0.425$ ], with lower PSE after Female exposure ( $45.86 \pm 1.60$ ) than after Male exposure ( $51.68 \pm 1.79$ ), on average. Further, a main effect of Orientation was founded [ $F(1,33) = 14.46$ ;  $p < 0.001$ ;  $\eta^2 = 0.305$ ], showing lower PSE for inverted ( $45.11 \pm 2.38$ ) rather than upright stimuli ( $52.42 \pm 1.13$ ). Again, this data revealed that inverted androgynous bodies looked more masculine with respect to their upright counterparts.

Crucially, I found a significant ccPAS  $\times$  Exposure interaction [ $F(1,33) = 4.30$ ;  $p = 0.045$ ;  $\eta^2 = 0.115$ ], which indicated that the effect of gender adaptation was different depending on the TMS intervention. Duncan post-hoc comparisons [ $MSE = 48.948$   $df = 33$ ] revealed that, in keeping with the main effects of Exposure, PSE scores were significantly lower for female rather than for male exposure after both

EBA-V1 ( $p = 0.001$ ) and V1-EBA ( $p < 0.001$ ) stimulation. However, while PSE scores after Male exposures remained similar after both EBA-V1 ( $51.18 \pm 1.85$ ) and V1-EBA ( $52.17 \pm 2.27$ ;  $p = 0.41$ ) cc-PAS, PSE scores following female exposure was significantly lower after V1-EBA ( $44.60 \pm 2.01$ ) than EBA-V1 ( $47.13 \pm 1.72$ ;  $p = 0.04$ ) cc-PAS (Fig. 21). This result suggests that adaptation effects were boosted after V1-EBA as compared to EBA-V1.

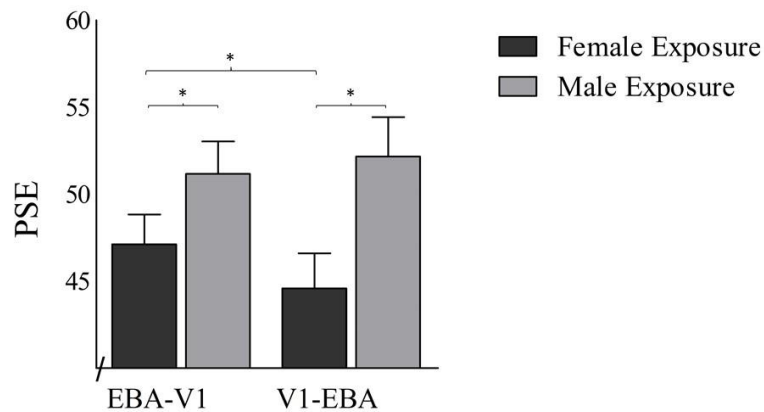


Figure 21 Mean and standard error of mean of the PSE after male (grey column) and female (black column) exposure for both EBA-V1 and V1-EBA cc-PAS conditions. Asterisks indicate significant comparison ( $p < 0.05$ ) between exposures and ccPAS conditions.

#### 4.2.6 Discussion

In keeping with the behavioral studies, these results provided evidence of contrast aftereffects for body gender adaptation. Importantly, they revealed for the first time that the empowerment of feed-forward projection from V1 to EBA boosted body gender adaptation. It is well known that, within the visual network, feed-forward connections convey signals from lower- to higher-order areas to reach full visual awareness. This observation is consistent with the idea that the coding of body gender features relies on cortical connectivity granting a fair level of perceptual consciousness. Exploring more closely the findings, we can observe that V1-EBA cc-PAS exerted the greater effect on female exposure aftereffects. This result can be certainly explained on the light of the male bias, which reflects the predisposition to assume maleness in the case of high perceptual ambiguity (Gaetano et al., 2012). Indeed, it has been demonstrated that, when people are required to judge others' gender, the "female" response is less frequent than the "male" one, since the former needs the presence of additional perceptual signals to be selected. In other words, we are set on a default "male" reference. On this view, it seems easier to boost and bring out perceptual effects inducing male perception of the body.

Taken together, our behavioral and TMS experiments bring to light clinical implications of feed-forward cortical connectivity between V1 and body-specific cortical areas in the occipito-temporal cortex. It can be fairly assumed that alterations of these pathways may underlie dysfunctional body adaptation in patients with eating disorders, which could be restored by boosting feed-forward connectivity in the occipito-temporal cortex.



## 5. Clinical implications of body adaptation paradigm

### 5.1 Introduction

Current diagnostic conceptualisations of Eating Disorders (ED) agree in recognize their multifactorial aetiology. Alongside the most cited psychological and socio-cultural factors, such as traumatic experiences and emotional dysregulation (Brustenghi et al., 2019; Groth et al., 2020; Hansson et al., 2017) or the internalisation of the “thin ideal” (Aparicio-Martinez et al., 2019; Stice et al., 2017), researchers and clinicians have identified some purely cognitive aspects that must be considered. Several studies have reported impairments in set shifting functions in anorectic patients (Roberts et al., 2007; Tchanturia et al., 2005). Notably, such impairments seems to manifest in a variety of forms, namely as rigidity in perceptual domain (Tchanturia et al., 2002), stringent approaches to problem-solving (Tchanturia et al., 2012) and perseverative/obsessive practices (Zucker et al., 2015). Hence, it has been suggested that these patients may be characterized by a general rigid thinking style promoting a series of maladaptive behaviours. Not rarely, patients with ED exhibit a distorted image of their body, especially regarding size and shape features. In the last years, some authors have interpreted the empirical evidence related to the distorted representations of the body using the O’Shaughnessy’s long-term body image hypothesis (LTB; Gadsby, 2017; O’Shaughnessy, 1998; Riva & Gaudio, 2018). This model predicts the existence of an almost stable mental representation that contains spatial information about the body. Yet, this static information is constantly combined with more dynamic ones, which can change rapidly based on the sensory inputs received from the environment. In other words, the LTB should store body size content and this information should be used to generate a variety of context-specific body representations. Some neuroscientists have hypothesized that AN patients may have a distorted LTB and that it can be due to an inefficiency of body memory: they could get stuck in an allocentric<sup>1</sup> memory of their own body that is not updated during the life course, thus contrasting the self-centered representations guided by perception (Allocentric Lock Theory; Riva & Gaudio, 2018). As emerged from neuropsychological and neuroimaging studies, the alterations observed in several cortical areas of AN patients, and specifically in their corticolimbic circuitry, might suggest the involvement of both cognitive impairments and dysfunctional interoceptive processes in developing an inaccurate perception of the body (Gaudio et al., 2014, 2016; Serino et al., 2015).

Through the previous chapters, I deeply explained the perceptive event occurring after a prolonged visual exposure. This phenomenon shows the influence exerted by the previous experience gained

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<sup>1</sup> The allocentric memory refers to a third-person representation of the body (observer perspective)

with stimuli defined as “adaptors” on the perception of the subsequent ones. This aftereffect has the role to facilitate human behaviour in complex environments by reducing the visual system’s response to invariable stimuli whilst improving sensitivity to the changeable ones (Pestilli et al., 2007). On the basis of my previous studies (see Chapter 3) I can affirm that, in the general population, the protracted exposure to female (male) bodies causes strongly biased perception of ambiguous bodies as being male (female). In addition, some authors have reported evidence of body size overestimation (underestimation) aftereffects induced by visual exposure to contracted (expanded) figures (Brooks et al., 2016, 2018; Winkler & Rhodes, 2005). Interestingly, results emerged from a body size adaptation study have revealed that ED patients are not as sensitive to body images exposure as non-clinical participants are (Mohr, 2016). In more details, a group of patients has been asked to rate manipulated pictures of their own bodies after prolonged exposure to thin or fat body pictures. In contrast to the control group, EDs have showed to be only affected by the view of fat body pictures, while thin body exposure did not determine any perceptual aftereffect. As addressed by the authors, the Allocentric Lock Theory may explain the phenomenon calling into play a memory lock on negative fat body image which would have induced perceptual adaptation through the top-down modulation of specific neurons. On the other hand, also visual attention has been proposed as a variable that may mediate the occurrence of body size and shape aftereffects: patients with ED may be characterized by an attentional bias to specific stimuli (e.g. pictures of thin models) thus causing a pre-existing, long-lasting adaptation to thin body shapes which prevented newer perceptual aftereffects. In keeping with the attentional hypothesis, it has been demonstrated that people experiencing high levels of body dissatisfaction have a general reduced ability to shift their attention between different types of visual information (Lang et al., 2014; Roberts et al., 2013), showing difficulties in recalibrate perception according to environmental information. Despite the several hints about the mechanisms on which clinically relevant body image disturbance may be grounded, many questions still remain open. First, the relative role of perceptual, cognitive and affective components is not clear. Although many studies have shown that a relevant number of women with AN tend to overestimate their body size (Collins, 1987; Cornelissen et al., 2013; Gardner & Bokenkamp, 1996; Steiger et al., 1989; M J Tovée et al., 2000; Martin J Tovée et al., 2003; Williamson et al., 1993), thus suggesting a perceptual distortion, the emotionally relevant charge linked to body size and shape can hardly be separated by purely perceptual and cognitive mechanisms. Further, body size adaptation tasks which have showed that patients cannot normally modulate their own body image on the basis of previous experience did not investigate whether adaptation to non-self-bodies was atypical as well. Despite the several hints about the mechanisms on which clinically relevant body image disturbance may be grounded, many questions remain open. First, the relative role of perceptual, cognitive and

affective components is not clear. Although many studies have shown that a relevant number of women with AN tend to overestimate their body size (Collins, 1987; Cornelissen et al., 2013; Gardner & Bokenkamp, 1996; Steiger et al., 1989; Tovée et al., 2000; Tovée et al., 2003; Williamson et al., 1993), thus suggesting a perceptual distortion, the emotionally relevant charge linked to body size and shape can hardly be separated by purely perceptual and cognitive mechanisms. Further, body size adaptation tasks that have shown that patients cannot normally modulate their own body image on the basis of previous experience did not investigate whether adaptation to non-self-bodies was atypical as well. To what extent the alteration of the body representation in EDs derives from affective influences or from primarily perceptual alterations? Also, does ED patients exhibit abnormal adaptation for all bodies or just their own? To answer these questions, it seems necessary moving the attentional focus from the size to other dimensions of the body and, at the same time, testing if adaptation aftereffects are also present for non-self-bodies. Trying to delineate at which level bodily misperception is established, in this experiment a gender adaptation task was administered to both healthy and AN subjects, using body stimuli picturing others' bodies.

## **5.2 Participants**

We recruited a total of 32 women: 16 patients with a diagnosis of AN and 16 healthy volunteers. The ED patients (mean age = 23.81, SD = 4.9 years) were recruited at the 'Centro Unico per il Trattamento dei Disturbi del Comportamento Alimentare (CUDICA), Udine. Our inclusion criteria were an IQ > 85, evaluated by means of the Raven Standard Progressive Matrices test, and diagnosis of AN restrictive (AN-R) or purge-binge (AN-PB) type, according to DSM-V. Patients reporting a history of a different type of ED, such as Binge Eating Disorder (BED) or Bulimia Nervosa (BN), were excluded from this study. Control participants (mean age = 23.2, SD = 4.22 years) were recruited among students of University of Udine. Exclusion criteria for controls included history of any type of ED, being under medication at the time of testing, no history of psychiatric disorders as determined with the screening section of Symptom Checklist-90 (SCL-90), no history of alcohol or substance abuse or dependence, and no current major medical condition. Written informed consent was obtained from all participants. The procedures were approved by the local ethics committee (*Commissione di garanzia per il rispetto dei principi etici nell'attività di ricerca sugli esseri umani*, Department of Languages and Literatures, Communication, Education and Society, University of Udine) and conformed with the Helsinki Declaration.

## **5.3 Stimuli and Procedure**

The stimuli and the experiment procedure were the same used in our previous adaptation study (see Section 3.1). Both controls and patients were asked to perform two experimental sessions, one with

adaptation to Female models and one with adaptation to Male models, with the order of the two sessions counterbalanced across participants. Each session was composed of two identical blocks, which included an adaptation phase and a test phase consecutively performed. The test phase was identical in all conditions, while the adaptation phase differed across sessions according to whether male or female adapting stimuli were used.

Individual PSE values were entered into a mixed ANOVA design with Exposure (Male or Female) and Orientation (Upright or Inverted) as within-subject variables and Group (AN vs. Controls) as a between-subjects factor.

#### 5.4 Results

The ANOVA on the PSE scores revealed a significant main effect of Exposure [ $F(1,30) = 12.78$ ;  $p = 0.001$ ;  $\eta^2 = 0.299$ ], which showed that, on average, PSE was lower after Female exposure ( $50.07 \pm 2.07$ ) than after Male exposure ( $56.32 \pm 2.02$ ). Similarly to our previous experiments, this result confirmed that, after exposure to feminine (masculine) bodies, participants required greater amount of feminine (masculine) features to conclude that an androgynous body is a female (male). Crucially, we observed a significant Exposure  $\times$  Group interaction [ $F(1,30) = 4.68$ ;  $p = 0.04$ ;  $\eta^2 = 0.135$ ]. The significant interaction was explored with the Duncan's post hoc test for multiple comparisons [MSE = 134.22 df = 42], showing that, while in the control group PSE scores were significantly lower after female ( $49.48 \pm 2.93$ ) than after male exposure ( $59.52 \pm 2.86$ ;  $p < 0.001$ ), AN patients presented comparable PSE scores after female ( $50.65 \pm 2.93$ ) and male ( $53.12 \pm 2.86$ ) exposures ( $p = 0.33$ ), suggesting a failure in adapting them to specific gender of the body (Fig. 20).

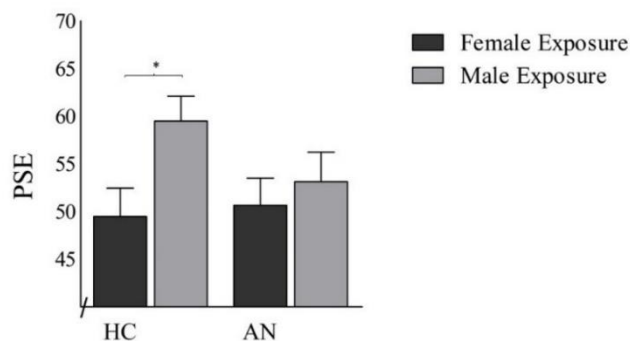


Figure 20 Mean and standard error of mean of the PSE after male (grey column) and female (black column) exposures for both healthy control (HC) group and Anorexia Nervosa (AN) patients. Asterisks indicate significant comparison ( $p < 0.05$ ) between exposures.

#### 4.1.4 Discussion

In line with previous findings, healthy participants exhibited a typical contrast aftereffect, with exposure to gender-distinctive bodies biasing the perception of androgynous ones towards the opposite gender. Conversely, patients with AN did not exhibit a significant modulation of gender detection after the prolonged exposure to specific body models since their responses remained similar between the two sessions. In other words, our preliminary results indicate that AN patients were not susceptible to distinctive body gender exposure, as already demonstrated for thin body exposure (Mohr, 2016). This data suggests a lack of flexibility in shaping the model of the body that could involve body features going beyond the emotionally relevant ones (i.e. size and shape). In ecological conditions, by adjusting the sensitivity of specific body neurons to the prolonged stimulation, people can encode which is the “normal” background and, thus, correctly shape a reliable body canon. Importantly, this canon can regularly be updated based on the different input which characterizes visual experience. If these perceptual mechanisms do not work properly, however, the individual cannot revise the construction of the model, thus remaining anchored to a top-down modulation. So far, we gained many clues about the difficulty of ED patients in generating new body models by using experience-dependent information. With respect to previous experiments, however, this study suggests that such dysfunctional body adaptation mechanisms extend to different body dimensions, pointing to a more general body representation impairment.

A longstanding literature consistently supports the association between anorexia diagnosis and a poor ability to flexibly adapt to changing environmental demands and switching between different tasks and mental sets (Monsell, 2003; Robbins et al., 2012). Accordingly, our result can be interpreted within the context of a weak cognitive flexibility, that could be detached from the affective component. Further, our experiment provided new elements in favour of a broader perceptual impairment for self- and non-self-bodies. Indeed, the body stimuli used in this task did not depict the participant in first person but different characters, thus revealing that ED patients have reduced adaptation effects for all bodies, not just their own. Taken together, our results point to a longer-range phenomenon regarding body misperception, which may be based on a weak cognitive flexibility. Future extension of this preliminary study should focus on the possible link between body adaptation dysfunction and specific personality traits.

## **Concluding remarks**

The value that people attribute to the visual representation of the body is extremely huge. The image that we see in the mirror has the power to affect our thoughts and behaviors, thus influencing the quality of our life. The modern society still emphasizes this behavior by imposing body canons that inevitably shape our perception. Although we are inclined to think of body as a whole, it is important to consider it as a multidimensional concept in which single elements can be conveyed and extracted. Surely, distorted self-perception and dissatisfaction with body image mainly involves social characteristics such as size and shape. However, body misperception seems to be more complex than just the difference between two body sizes, rather involving top-down cognitive mechanisms that may bias the representation of other bodily features. Gender is one of the components that must be included in the study of the perceptual experience of the body, especially because it relies on physical cues linked to body shape. By means of a series of experiments, this thesis aimed to examine how different visual experiences may specifically affect the perception of body gender, trying to identify to what extent this factor may be implicated in the distorted representation of the body.

Firstly, I demonstrated that the judgment of masculinity and femininity depends on the interplay between different bodily characteristics, crucially proving a stereotypical association between femininity and static bodies. Indeed, I found that, when morphological cues are not clear, the perception of static or dynamic postures drives perception toward female or male response, respectively. Similarly, when the motion conveyed by a body is ambiguous, the perception of female- or male-type features drives motion perception toward stillness or dynamism, respectively. Further, I demonstrated that the association between stillness and femininity has a positive impact on the aesthetic appreciation of a body. My findings may be relevant to further explore the woman objectification theory, giving additional evidence about the less sense of agency attributed to the woman and her consequent devaluation.

In a second step, I analyzed the contribution of high- and low-spatial frequency to gender perception. A greater configural processing was found for HSF rather than LSF images in both gender and postures discriminations, pointing to an overall preference of configural body processing for parvo-biased, HSF information. On the basis of the anatomical mapping of magnocellular and parvocellular regions, this result defines the role of the ventral visual stream in the configural processing of body gender.

In the next phase, I developed a series of experiments grounded on a body gender adaptation paradigm. It helped us to prove the experience-dependent reshaping of body gender perception, by assessing that also gender recognition can be easily manipulated through a brief exposure to specific

body models. Interestingly, my studies highlight that the phenomenon is based on mechanisms that are independent from the specific person's characteristics. Also, according to previous experiments, these series of results suggest that body adaptation to gender is tuned to configural or local processing of the body and that it may rely on parvo-cellular visual channels.

Finally, I applied the well-established body gender adaptation paradigm with a twofold purpose, that is exploring the neural connectivity underlying body adaptation mechanisms and testing the possibility of a dysfunction of this process in EDs. Data coming from the TMS study pointed to a key role of feed-forward cortical connectivity between V1 and EBA, suggesting that its alterations may underlie dysfunctional body adaptation. Concurrently, the preliminary results obtained on AN patients revealed their lack of flexibility in shaping the model of the body on the basis of gender features. Together, these results may support the use of V1-EBA ccPAS protocol as a treatment to enhance the malleability of body adaptation in AN patients.

Overall, the present thesis aimed to outline the hierarchical organization of body gender processing, providing hints to the understanding of how the alterations of the malleability of body perception may be associated with individual difficulties in social interactions and personality traits characterizing Anorexia Nervosa.

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