The functional body: Does body representation reflect functional properties?

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Abstract

There is a growing interest in the distortions of body representation in healthy population and most studies have focused their attention on specific parts of the body, such as the hands. Only three studies have considered the representation of the body as a whole. Findings, acquired by different means of assessment methods, are partially contrasting, leading to different interpretations. The present study aims to investigate which aspects of body representation can be preserved regardless of the method adopted and whether current and previous findings can be explained by a unique theoretical model. In Experiments 1a and 1b we adopted a modified version of the Body Image Task to investigate body representations in real scale and the relationship of its parts. Participants judged the location of body landmarks by pointing on their own silhouette imagined on a wall in front of them. In Experiment 2 we investigated i) whether the pattern of distortions observed in the first experiment are maintained across different methods by asking participants to estimate the veracity and proportionality of the length of their own body parts; and ii) whether similar distortions can be generalized to stereotypical representations. Overall, we observed a consistent pattern of distortions, whereby upper body limbs are underestimated and lower parts of the body are overestimated across all experiments and conditions. These findings are then interpreted as the result of a functional relationship between body parts and daily actions, which underlie a close modulation of body schema and body image. This interpretation offers a reconciliation of seemingly contradictory findings in the literature and supports to the *co-construction model* (Pitron et al., 2018).

Introduction

The notion of body representation has changed and developed throughout the years, and yet the very nature of this concept remains difficult to delineate. The description of body representation is based on the distinction, originally proposed by Head and Holmes (1911), between a dynamic representation of current body posture (postural schemata) and a map of the body surface that mediates localisation of touch (superficial schema). There is a common agreement on the existence of at least two mental representations of the body: body image and body schema. Although these two terms have often been used by different authors in different manners, sometimes even with opposite meanings (Gallagher, 2005; 1986), the literature offers a consistent body of evidence that supports a dyadic model of body representation based on the functional role of these two components. The body *image* is a multidimensional construct that refers to the person's conscious perception and experience of the physical self in terms of its size, shape, and physical composition (Longo, 2016; Gallager 2005). Evidence has shown that the *body image* consists of two distinct components. At a more conceptual level, the *body semantics* provides a description of the functional purpose of body parts and their categorical relationship. At a perceptual level, the visual and somatic information provides a structural description of the body (visuo-spatial body map) that metrically and spatially describes the relationships between body parts (Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). This representation dissociates from a more dynamic, action-based representation of body posture and configuration: body schema (Buxbaum & Coslett, 2001; Head & Holmes, 1911). Crucially, body schema is mainly based on kinematic and proprioceptive feedback that provides a representation of the body at each given moment during movement.

The concepts of *body schema* and *body image* have been used also in a temporal context. *Body image* is generally considered a relatively long-term stable representation compared to the *body schema*, which is instead characterized by a short-term plasticity and reorganization due to posture and orientation changes of the body in space (Dijkerman & de Haan, 2007; Longo, 2016). From this

point of view, body configuration and metrics appear to be long-term properties of the body representation as, in 'normal' conditions, these properties tend to be rather stable with relatively slow changes over time. However, it should be taken into consideration, that there is not a clear-cut definition that provides a full account of the relationship between the different body representations (de Vignemont, 2010). Research on tool use has shown that, although the objective length of the upper limbs remains stable, the subjective length of these body parts can be modulated following motor training (Pitron, Alsmith & de Vignemont, 2018). For example, Cardinali and colleagues (2009a) observed that after the use of a mechanical grabber, participants performed grasping movement (without the tool) as if their arms were longer. The authors suggested that the kinematic consequences of tool use lead to somatosensory changes in the *body schema* (Cardinali et al., 2009a). Interestingly, the effect of tool use did not just modify the kinematic of the grasping movement, but also the subjective perception of the arm's length. When participants were asked to localize touches delivered on their elbow and middle fingertip, before and after tool use, the distance between the two landmarks increased, as if the arm was perceived as longer after tool use (Cardinali et al., 2009a). Similarly, other studies have shown that the use of tools, as well as specific manipulations of body parts mobility, modulates the internal representation of body parts size (Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino & Serino, 2013; Sposito, Bolognini, Vallar & Maravita, 2012; Bassolino, Finisguerra, Canzoneri, Serino & Pozzo, 2015; Romano, Uberti, Caggiano, Cocchini & Maravita, 2018). Furthermore, even in the absence of tools, extensive training can shape the metrics of the body representation. Cocchini and colleagues (2018) showed that magicians, using sleight of hand, are considerably better than naïve-to-magic controls in estimating their own finger lengths in a localization task. This evidence, along with some well-known body illusions (e.g., Pinocchio illusion; Lackner, 1988; Ramachandran & Hirstein, 1998), highlight that, under specific circumstances, the body image is rather malleable. It is therefore clear that subjective body metrics do not rely on a unitary mechanism, but rather it is the combination of various factors. Afferent signals provide information about body posture and limb configuration; however, these signals do not relate directly to the actual length and width of specific body-parts. It follows that the current body state must be inferred by stored representations of the body's metric properties (Berlucchi & Aglioti, 2010; Longo Azañón, & Haggard, 2010; Longo, 2016).

Although some studies showed that, under some circumstances, *body image* and *body schema* can be dissociated (e.g., Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Botvinick & Cohen, 1998; Anema et al., 2009), these components are usually both impaired in the neuropsychopathological population (de Vignemont, 2010). These observations seem to suggest that a dialectic relationship between these two representations is essential for the successful interaction with the external environment; so that there is some coherence between the body, as we perceive it (i.e. *body image*) and the actions that we perform with it (i.e. *body schema*). According to the *coconstruction model* (Pitron et al., 2018; Pitron & de Vignemont, 2017), *body schema* (for action) and *body image* (for perception) interact and reshape each other. This model claims that information coming from different sensory modalities determines the construction of body representation. However, this information is compared within a probabilistic model where one type of input may be predominant over another depending, for example, on the context or task demands.

Different factors can play different roles in determining the final representation and its related distortions (i.e., Sadibolova, Ferrè, Linkenauger & Longo, 2019; Cocchini et al., 2018; Ambroziak, Tamè, & Longo, 2018; Tamè, Bumpus, Linkenauger, & Longo, 2017; Linkenauger et al., 2015; Fuentes, Longo, & Haggard, 2013a; Longo & Haggard, 2010, 2012a, 2012b; D'Angelo, di Pellegrino, Seriani, Gallina & Frassinetti, 2018). The majority of these studies shed light on different mechanisms involved in the representation of the hand or the face, which are very special parts of the body (Bruce & Young, 1998; Brozzoli, Ehrsson & Farnè, 2014). It remains unclear how to extend these findings to the representation of the body as a whole, which has been the focus of interest of very few studies. Fuentes and collaborators (2013a) presented scaled body parts (e.g., the head) on a computer screen and asked participants to judge the relative location of the other parts. The authors found that the width of their shoulders and the length of their upper arms were overestimated, while the lengths of

forearms and lower legs were underestimated. A different pattern of distortions has been found in more recent studies (Linkenauger et al., 2015; Sadibolova et al., 2019) where participants showed an overall overestimation when asked to judge body parts' length by inferring how many times a metric standard (an object or a body part) would fit into the body segment they were asked to estimate.

Therefore, while there is some evidence that supports that even healthy population tends to hold a distorted and malleable body representation, there are contrasting results which pose the question of why different patterns of distortion may arise. It has been suggested that the method adopted, either "metric" or "depictive", may lead to different types of representation due to implicit or explicit (metric and depictive, respectively) access to the *body image* (Longo & Haggard, 2010).

The present study aimed investigating the role of different factors affecting the body metric representation. By means of a modified version of the Body Image Task (BIT), we attempted to enhance the correspondence between real and represented body parts' location and measures by asking participants to perform the task in real scale in order to investigate whether localization distortions can imply intrinsic functional properties of body parts (Experiments 1a and 1b). We then explored whether bodily distortions are consistent across different methods (metric and depictive) and whether the effect is individual-specific or more generalized to a prototypical body (own and avatar).

Experiment 1a. Localization of body landmarks on real scale (metric task)

Method and Procedures

Participants

Sample size was determined by an a priori power analysis run with G* Power (Faul, Erdfelder, Buchner & Lang, 2009), which considered the type of analyses required to assess: i) differences between real and represented body measures by means of t-tests; and ii) differences between represented body measures among different conditions by means of analysis of variance. We also

considered previous studies on body representation adopting a localization task that reported an averaged effect size for one sample t-test of 0.8 (i.e., Ganea & Longo, 2017; Mora, Cowie, Banissy & Cocchini, 2018).

The power analysis for one sample t-test with an effect size of d = .8, $\alpha = .05$, and power = .95 indicated an adequate sample of 23 participants.

We also calculated the sample size for a repeated measures design with two conditions and 12 body parts to estimate with an $\eta_{partial}^2 = .1$, $\alpha = .05$ and power of .95. The average effect size reported in previous studies assessing differences in length estimation across body parts was $\eta_{partial}^2 = .3$ (Linkenauger et al., 2015; Sadibolova et al., 2019). The analysis suggested a sample of 12 participants to obtain an appropriate effect.

Twenty-eight participants (16 females) took part in the first experiment; their age ranged from 20 to 26 years, with a mean of 23.6 years (SD = 3.5). All participants were right-handed (Edinburgh Inventory mean score = 0.95; SD= 0.11). The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

Body Image Task (BIT)

The experiment consisted of a modified version of the Body Image Task (BIT; Fuentes et al., 2013a, 2013b). Participants were asked to imagine their silhouette with their arm aligned with the body, as if they were standing against a white wall at 2 meters in front of them (see Figure 1). To create some mismatch with the represented silhouette, participants performed the task while seating on a chair. Two conditions were considered. In the first condition (*Frontal View*) participants were asked to imagine themselves standing with their back against the wall. In the second condition (*Dorsal View*) participants were asked to imagine their own silhouette from behind (i.e. as if they

were looking at their back). Each participant performed both conditions, which were counterbalanced across participants.

Four small black dots (150 mm of diameter) were placed on the wall in order to provide references for the four corners (frame reference points) of a rectangular frame (100x200cm) located at 9 cm from the floor. Participants, who were not aware of the actual distance between the dots, were asked to imagine their own silhouette within the frame and to indicate, by means of a laser pointer, a total of 17 body parts: 3 midline points, 8 landmarks for the arms and 6 landmarks for legs (see Table 1). Body parts were read aloud one each a time by the examiner. The three body midline points were read first then the others in pseudorandom order. The experimenter stood behind the participant's chair throughout the experiment to record each response taking pictures with a digital camera mounted on a tripod (see Figure 1).

--- Insert Figure 1 about here---

The first location requested was always the navel. To avoid possible 'shift' of the imagined silhouette during testing, the perceived position of the navel was marked (with a small dot) on the wall and was used as visible landmark during the entire task. While the examiner marked the subjective position of the navel, participants were asked to close their eyes to avoid any reference (i.e. seeing the examiner close to the wall). Once the examiner was again standing behind the camera, participants were asked to open their eyes and indicate the other two midline landmarks (i.e., top of the forehead and the nose; their order was counterbalanced across participants) followed by the remaining body parts. These were <u>not</u> marked on the wall but the examiner recorded each response by taking a picture with a Nikon Reflex D3100 mounted on a tripod located behind the participants. Both conditions (Frontal and Dorsal views) were repeated three times. Therefore, each of the 17 landmark locations was recorded 6 times (3 in Frontal and 3 in Dorsal view) for a total of 102 responses across both conditions.

Before leaving the experimental setting, a picture of each participant standing against the wall was taken and actual location of the navel was noted for later analyses.

Visuo-spatial estimation task

To assess general ability to perform spatial estimation, at the end of the modified BIT, each participant was asked to imagine a well-known object (i.e. a A4 sheet on landscape view) on the wall and to indicate its size by pointing to the four corners by means of the laser pointer. Finally, participants were asked to estimate a vertical line of 1 meter by indicating the two extremities.

--- Insert Table 1 about here ---

Data acquisition of BIT

To calculate actual and subjective sizes of body parts and to compare real and subjective participants' body measures, a software was developed in the MatLab environment. In order to produce a consistent output, the pictures (including the final photo of the participant) were cropped according to the specific four frame's reference points and scaled to a standard dimension of 1262×2668 pixels. The software automatically detected the four frame reference points and transformed pixels into actual distances expressed in centimetres. It also recorded the position of each subjective landmark that referred to specific body parts (i.e. the points indicated by the participants). This procedure was conducted for each set of pictures obtained from each of the three trials. Finally, the 'real' image of the participant was considered, and the experimenter manually marked all 17 body parts to obtain the real body map. The software computed the distances (expressed in centimetres) between different points and produced two sets of outputs for both real and subjective body maps: i) actual/subjective distance between landmarks and ii) graphic analogical representation of all landmarks. Width and length of body parts were calculated by measuring distances, expressed in

centimetres, between pairs of points as described in Table 2. Two width measures were considered, one for upper body (shoulders) and one for lower body (hips); two length measures were considered for each limb (arms and legs) and one length measurement was considered for the central part of the body (i.e. torso).

--- Insert Table 2 about here ---

Two overall measures were then considered: the *Real Body Measure* (RBM) and the *Subjective Body Measure* (SBM). Similar to previous studies (i.e., Fuentes et al., 2013a), real and subjective body measurements (RBM and SBM, respectively) were compared and analyzed in *percentage body part estimation error* (%BPE), which is expressed as the percentage difference between the perceived length/width and the participant's real body part length/width:

$$\%BPE = \frac{SBM - RBM}{RBM} \times 100$$

According to this formula, negative BPE values indicate underestimation, while positive values indicate overestimation; zero indicates perfect estimation.

Results

BIT

Body parts - Lengths

The most evident result was that participants tended to underestimate the upper part of the arms (overall BPE mean -19.07%) but overestimated the lower parts of the legs (+34.24%) (see Figure 2a and b). This pattern of results was similar for both views (Frontal and Dorsal) and sides (Right and Left).

In order to assess whether there was a significant distortion of individual body parts, we ran a series of two-tailed t-tests, one for each body part, to compare BPE with zero (i.e., no distortion). Bonferroni correction for multiple comparisons was applied (i.e., 12 comparisons; significant p values < 0.004). Results showed that the length of 6 out of 10 body parts were significantly distorted from real size in the *Frontal* and 7 out of 10 in the *Dorsal* view (see Table 3 – Lengths). In detail, the forearms and the torso were consistently underestimated in both sides (Left and Right) and views (Frontal and *Dorsal*), whereas the lower legs were consistently overestimated in both sides and views. Upper arms and upper legs tended to be underestimated in all conditions, but the distortion was significant only for the left upper leg in Dorsal view.

--- Insert Table 3 about here---

A repeated measure ANOVA 5 (Body Part) \times 2 (View) \times 2 (Side) was performed to consider possible differences among body parts, side and view. Results yielded main effect of Body Part [F(2.6, 70.24) = 74.85, p < .001; $\eta_{partial}^2$ = .74] whilst there was no effect of View [F(1,27) = .73, p = .40; $\eta_{partial}^2$ = .026], Side [F(1,27) = .52, p = .27; $\eta_{partial}^2$ = .010] nor interactions. Post-hoc analysis of

the single body parts (corrected for 12 multiple comparisons, p < .005) showed that the BPE for forearms and lower legs significantly differed from BPE of all the other body parts (p < .001).

Finally, we evaluated whether participants' mental representation of their own body (i.e., SBM) reflected their real measures (i.e., RBM). Since previous analyses showed no differences between the two views (Frontal and Dorsal) and the body sides (Left and Right), these factors were collapsed. We then ran a bivariate Pearson correlation to assess whether there was a correlation between the SBM and the RBM of each body parts (i.e. total length of the arms, legs, and torso expressed in centimetres).

Results showed a positive correlation for all the body parts considered (arms: r = .59, p = .001; legs: r = .51, p = .005; torso: r = .51, p = .006), suggesting that, even if participants hold a distorted representation of some of their own body parts, this representation is still reflecting participants' real sizes. In addition, the SBM of the torso correlated positively with the SBM of the arms (r = .68, p < .001) but not with legs (r = .28, p = .14).

Body parts - Widths

Overall, participants showed a trend in underestimating the width of shoulders and hips (i.e., -13.67% and -4.86%, respectively; See Figure 2a & b). Analyses on distortions by means of t-test comparisons between BPE and zero (i.e., no distortion) showed that only shoulder width was significantly underestimated but only in the Dorsal view (See Table 3 – Widths).

A repeated ANOVA 2 (Body Part) × 2 (View) to consider possible difference between different body parts and views, showed no significant main effect of Body Part [F(1,27) = .87, p = .36; $\eta_{partial}^2$ = .031], View [F(1,27) = 3.15, p = .087; $\eta_{partial}^2$ = .11] nor Body Part × View [F(1,27) = 1.43, p = .24; $\eta_{partial}^2$ = .05].

As for the lengths, we ran a Pearson correlation between the SBM and the RBM widths for shoulders and hips (width expressed in centimetres). Results showed a positive correlation for shoulder width (r = .67, p < .001) but not for hip width (r = 0.34, p = .07).

Visuo-spatial estimation task

To investigate whether the distortion observed on the body parts' length could be related, at least in part, to participants' general visuo-spatial estimation skills, we considered individual estimation accuracy when asked to estimate 1 meter vertical segment and the size (height and width) of A4 sheet in landscape view. The percentage of the estimation measurement error (%ME) for the Subjective Mean (SM) and Real Mean (RM) of both measures was calculated using a formula similar to the one adopted for %BPE, that is:

$$\%ME = \frac{SM - RM}{RM} \times 100$$

On average, for the 1 meter segment, participants ME was -10.57% (SD = 9.5); whereas for the A4 sheet size was -15.01% (SD = 14.01) for height and -6.61% (SD = 7.53) for width. We ran Pearson correlations between individual averaged BPE values and averaged ME values for each of the visuo-spatial tasks. Results showed no significant correlation for any BPE and ME (highest value: r = 0.35, p = 0.07), suggesting that estimation errors for body parts' measures was not easily tracked back to a more general visuo-spatial bias.

Preliminary discussion

Unlike recent studies showing dissociation between different view representations, such as dorsal and palmar views of the hand (e.g., Mancini, Longo, Iannetti & Haggard, 2011; Longo & Haggard, 2011), our participants showed a systematic pattern of distortion of their body representation regardless the prospective (frontal or dorsal views), and a symmetrical representation with no difference between sides (left or right). We exclude that participants have maintained a preferred view point (e.g., frontal view) during both conditions otherwise they would have incorrectly reported landmarks referring to the right or left side. It seems more likely that, in this task, participants managed to maintain a reliable perspective of their silhouette under different conditions. Under these circumstances, participants showed a similar and systematic distortion of body parts in all conditions. In detail, the upper body parts, in particular forearms, were considerably underestimated (almost 20%) whereas the lower parts, in particular lower legs, were overestimated by more than one third. Therefore, the upper and lower parts of the body appear to be asymmetrically represented with the first being shrunk and the second being more elongated than real lengths. Despite the emergence of such stereotyped pattern of distortion, the represented measures positively correlated with the true body size. Nonetheless, it is possible that the seated position may have been, at least in part, responsible for the distorted representation. In fact, to avoid that participants' responses reflected a mere 'translation' on the wall of the current body landmark positions, they were asked to perform the task while seated in order to induce a mismatched between the landmarks of the actual position and those of the imagined silhouette on the wall. If the seated position had any significant effect on the representation of the silhouette on the wall, we would have observed a considerable underestimation of the upper legs, and a very accurate estimation of the lower legs since the position of knees and ankles were those matching their position on the wall. On the contrary, our results showed a greater systematic distortion, in terms of overestimation, of the lower legs and only a marginal underestimation of the upper legs, the latter only significant for the left leg under dorsal view.

Therefore, it seems unlikely that the seated position can explain the specific different distortion between representation of upper and lower parts of the body.

A further possible reason for the subjective overestimation of the legs may be due to participants' expectation induced by the instructions. Since participants were asked to imagine themselves standing, the instructions implied that their feet should have touched the floor. As showed in Figure 2b, the perceived position of the navel, indicated at the beginning of the task, was slightly higher than the real one. As such, it is possible that this initial 'misjudgement' may have determined an "artefact" stretch of the lower legs 'to touch' the floor. Therefore, while the findings related to the upper body parts seem to reflect a genuine underestimation, that will be discussed later, we cannot exclude that the overestimation of the lower legs, may be due to a possible conceptual issue. To address this potential alternative explanation for leg overestimation, we ran a follow-up experiment (Experiment 1b) where participants were asked to imagine their silhouette in elevated positions.

Experiment 1b. Localization of body landmark on elevated positions (metric task)

Method and Procedure

Participants

Based on the Experiment 1 results, we ran a new power analysis for one sample t-test with an effect size of d = 1.4, $\alpha = .05$, and power = .95 and for analysis of variance set for an $\eta_{partial}^2 = .7$, $\alpha = .05$ and power of .95. The analysis showed that a sample of 10 participants was sufficient to find an effect.

Ten participants (5 females and 5 males) took part in the second experiment. None of them entered Experiment 1a. Age ranged from 19 to 26 years, with a mean of 23 years (SD = 2.1). All participants were right-handed (Edinburgh Inventory mean score = 0.95; SD = 0.07). The study was

approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

BIT – Elevated position

The main procedure and data acquisition were similar to the Experiment 1a. Since no differences in View were found in the previous experiment, participants were asked to perform the task only in the Frontal view, that is imagining themselves standing with their back against the wall. There were two conditions: in one condition, the top of the forehead was given before initiating the task as fixed anchor point (Head condition) and in the second condition the navel (Navel condition) was given as fixed anchor point by the examiner. In both conditions, the anchor points were located in an elevated (i.e. higher than normal) position. In the *Head* condition the anchor point was located at the top edge of the frame at 198 cm from the floor; whereas in the Navel condition the anchor point was located at 115cm from the floor (See Figure 3). Each participant performed both conditions which were counterbalanced across participants. The procedure adopted was similar to Experiment 1a; however, the participants were asked to imagine themselves as if their forehead or navel, depending on the condition, were actually located at the fixed and visible anchor point. They were also told that, their feet may not touch the floor. Participants sat on a chair and, following the initial instructions about the anchor point, they were asked to indicate using the laser pointer, each of the remaining 16 landmarks (See Table 1). As in Experiment 1a, landmarks were read aloud one at the time in pseudorandom order and each of the 16 landmarks was asked 6 times (3 for the Head and 3 for the Navel conditions) for a total of 96 trials across both conditions. The examiner recorded each response by taking a picture with a Nikon Reflex D3100 as in the previous experiment.

Before leaving the experimental setting, a picture of each participant standing against the wall was taken and actual location of the navel was noted for later analyses.

Visuo-spatial estimation task

We assessed the participants' ability to estimate the length and size of a vertical line of 1 meter and a A4 sheet on landscape view. Participants were asked to make their judgment by pointing on the wall the extremities of the 1 metre line and the four corners of the A4 sheet by means of the laser pointer.

--- Insert Figure 3 about here ---

Results

BIT – Elevated position

Body parts - Lengths

As in Experiment 1, participants showed a general tendency to underestimate the length of their upper body parts (BPE -15.52%) and overestimate the lower legs (BPE +22.54%) (see Figure 4a and b).

A series of t-tests, corrected for multiple comparisons (significant p values < 0.004) showed that the length of 4 out of 12 body parts were significantly distorted in the Head condition, and 3 out of 12 in the Navel condition (see Table 4). Overall, participants displayed a similar trend to the one observed in Experiment 1a, that is the left and right forearms were significantly underestimated for both *Head* and *Navel* conditions, whereas the upper legs showed an overestimation only for in the *Head* condition. The left side of the torso was significantly distorted in the *Navel* condition, only.

Results from a three-way factor ANOVA 5 (Body Part) × 2 (Condition) × 2 (Side) confirmed the original finding of a significant main effect of Body Part [F(2.66, 23.95) = 23.81, p < .001; $\eta_{partial}^2$ = .72]; whilst no main effect of Condition [F(1,9) = 1.51, p = .25; $\eta_{partial}^2$ = .14] nor Side [F(1,9) = .18, p = .68; $\eta_{partial}^2$ = .020] was found. None of the interactions resulted significant.

The Pearson correlation between the SBM and RBM of body parts (arms, legs, torso) showed a positive correlation for the arms (r = .65, p = .04) and legs (r = 0.79, p = 0.006) whilst torso did not show a significant correlation (r = 42, p = .22). Yet, as in the previous experiment, the SBM length of torso showed a significant correlation with SBM length of the arms (r = 0.69, p = .03) but not with legs (r = 0.59, p = .73).

Body parts - Width

Participants showed a trend in overestimating the width of shoulders and hips (i.e., +10.79% and +4.12%, respectively; See Figure 4a and b) yet, t-test comparisons between BPE and zero (no distortion) did not show significant distortions in both conditions.

A 2 (Body Part) × 2 (Condition) ANOVA showed no significant effects of Body Part [F(1, 89 = 1.34, p = .28; $\eta_{partial}^2$ = .129] nor Condition [F(1, 9) = .561, p = .47; $\eta_{partial}^2$ = .059] . Interaction was also not significant.

The Pearson correlation between the SBM and RBM of shoulder and hip width resulted not significant for both body parts (r = .47, p = .16; r = .49, p = .15 respectively).

Visuospatial performance

We evaluated whether participants' BPE correlated with estimation accuracy of 1 metre (mean = -7.54%, SD = 8.99) and A4 sheet size (length: mean = -5.07, SD = 6.53; width: mean = 10.6, SD = 12.96). Results showed a significant positive correlation between the BPE of the upper arm and estimation errors of 1 metre segment (r = 0.67, p = 0.034). No other significant correlations were reported.

Preliminary Discussion

Results from the Experiment 1b, with elevated positions, replicated the same pattern of findings observed in the previous experiment, whereby a systematic distortion of specific body parts occurred. In particular, the forearms were again considerably underestimated and the lower legs were significantly overestimated. Changing the location of the anchor points had little impact on the metric representation of the lower legs.

It should be noted that our systematic pattern of results of short arms and long legs is not, at first glance, in line with findings by Fuentes and collaborators (2013a). Their participants were asked to indicate body landmarks on a PC screen and they tended to delineate silhouettes with overall longer arms and shorter legs. Inspecting Fuentes and collaborators' figure (Fig. 2, p. 346) the tip of the hands were aligned with the waist line, which represents the semantic lower landmark of the upper half of the body (Reed, McGoldrick, Shackelford, & Fidopiastis, 2004; de Vignemont, Majid, Jola & Haggard, 2009). In other words, it seems that also in Fuentes and coll.'s study, arms tend to be represented within the upper section of the body delimited by the hips. Interestingly, the closer relationship between arms and torso is confirmed in our study as the length of torso was positively correlated with arms but not with legs. Therefore, the represented length of body parts seems to be defined by the relationship with other body parts rather than an intrinsic distortion of each part. Recent studies (Romano et al., 2018; Ferretti, 2016; D'Angelo et al., 2018) showed a close relationship between function (i.e. motor training) and perceived length of the arms. In line with these findings, the asymmetrical representation for upper and lower parts of the body found in our study could be better interpreted considering the functional link between specific body parts and the actions we perform with them. In this respect the arms (and hands) are mainly used to bring objects toward the upper side of the body whilst the legs are mainly used to walk "away" or hit objects (e.g. kicking a ball; Ferretti, 2016). This may result in an implicit modulation of the represented upper limbs as shorter, or above the waist line (as in Fuentes et al., 2013a), and lower limbs as longer.

The fact that arms and torso were highly correlated and they were both underestimated seems to support the idea of a close relationship between these two body areas. It would then be interesting to explore the extent of this relationship by keeping the size of the torso 'fixed' while the size of the limbs is manipulated. Furthermore, since the general motor functions of upper and lower limbs are common to all human beings, we would expect to observe similar findings regardless the method (metric or depictive) adopted and ownership of the silhouette considered. In other words, we would expect to find a qualitatively similar pattern of results for *body image* and for own or other people's body. To this aim, we ran a last experiment where the metrics of the body image were explicitly assessed by means of a depictive task where the limbs of own or an avatar's silhouette were distorted while the torso's size remained unchanged.

Experiment 2. Depictive task for own and prototypical body

In this experiment two types of stimuli were used: a "prototypical" body (Avatar) and a participants' image (Own) taken before the start of the study.

Method and Procedure

Participants

Experiments 1a and 1b showed quite large effect sizes for both differences between real and represented body measures as well as among represented body parts. Therefore, we carried out two a priori power analysis assuming large effect sizes. For one sample t-test we set the parameters of d = 1, $\alpha = .05$, and power = .95 and the calculation indicated a sample size of 16. For a repeated measures ANOVA with 2 conditions and 2 body parts estimations, we calculated the sample size for $\eta_{partial}^2 = 0$

.2, α = .05, and power = .95. The analysis showed that a sample of 16 participants would be appropriate to find an effect.

Twenty participants (10 females) took part the Experiment 2. None of them participated in the previous experiments. Age ranged 20 to 28 years, mean 23.9 years (SD = 2.9). All participants were right handed (Edinburgh Inventory mean score = 0.96; SD = 0.06; range: 1 - 0.89).

The study was approved by the Goldsmiths Ethics Committee and it was carried out in accordance with the Declaration of Helsinki (BMJ 1991; 302: 1194). All participants gave informed written consent.

Stimuli

Two types of stimuli were used: i) *Own* - a digital photograph of each participant taken in advance; and ii) *Avatar* - a standard avatar of a prototypical male or female body. Both types of stimuli were in black and white on a monotonous, white-coloured background in a frontal standardized pose (i.e. standing with arms aligned with the body and the feet aligned approximately to the shoulder width). The pictures showed the participants' and avatar's whole body; however, following a pilot study, it was decided to blur the face area to reduce attentional drift toward the face. A customized computer program was used to stretch or shrink the arms or the legs of the pictures (the rest of the body was not modified). Based on previous pilot studies, the distortion ranged from +20% to -20% of the body part increasing or decreasing by 2% (See Figure 5). Therefore, we obtained 20 images with distorted arms (10 shorter and 10 longer), 20 images for legs (10 shorter and 10 longer) and 2 images with non-distorted arms and legs for *Own* and for *Avatar* conditions. To maintain a realistic appearance of the body part's shape, hands and feet were not distorted. While stimuli for the *Own* condition changed with every participant, the stimuli for the *Avatar* condition remained the same for all participants and only changed to match the participant's gender.

Depictive body parts estimation task

Images were displayed on a computer screen (resolution 1280×1024 pixels) using E-prime 2.0. Participants were seated on a chair in front of the computer screen at approximately 60 cm distance. They were instructed to fixate on the central cross that was displayed 300 msec before each stimulus was presented. Stimuli remained visible until response or for 1000 msec, then a blank screen followed. Participants provided a response by pressing two buttons on a standard keyboard. Feedback was not provided. Each Own and Avatar condition consisted of two blocks: Arms (where only arms were distorted) and Legs (where only legs were distorted). The stimuli were presented according to the method of limits, from shortest to longest length and reverse. Each block consisted of seven ascending and seven descending trials. Participants were informed that the pictures were distorted and that specific body parts (i.e. arms or legs) were longer or shorter than the original picture. After each stimulus, participants were asked to decide whether the target body part (arms or legs, depending on the series of stimuli presented) was veridical (for own images) or proportionate to the rest of the body (for avatar stimuli). The pilot study indicated that a distortion of 20% was well above the subjective threshold of distortion detection and easily identified, therefore each block of stimuli started from +/- 20% distortion as we expected that participants had no difficulty to correctly identify the first images as distorted (i.e. too short or too long, depending if ascending or descending order, respectively). Presentation series continued until participants' responses changed (e.g., switched from 'not veridical' to 'veridical'). Then the next series in the opposite direction begun. To avoid adaptation effect and participants switching response after a set number of trials, four series out of seven had different starting points; two series started at +/-18% distortion level and two started at +/-16%. The presentation order of the series was random. Also, presentation order of conditions (own or avatar), ascending/descending series and body part distorted (arm and leg) were counterbalanced across participants.

Data analysis

For each series (both ascending and descending) we calculated the *Transition point*, which corresponds to the average point where the participants' response changed (i.e., the last "not veridical" response and the first "veridical" response). For example, on a descending series, if the last "not veridical" was at a distortion level of +6%, and the "veridical" response at +4%, the transition point was +5%. Transition points for each trial were then averaged across ascending and descending conditions. These values represented the discrepancy between the actual midpoint of the ascending and descending series (the non-distorted image at 0% distortion level) and the "perceived" midpoint of the series (point of subjective equality).

Results

Figure 6a shows a general tendency to underestimate the arms (*Own*: -3.3%, *Avatar*: -3.7%) and overestimate the legs (*Own*: +1.8%, *Avatar*: +0.7%). Two-tailed t-tests, comparing transition points with zero, showed that the under- and over-estimation of the body parts in both conditions were statistically significant (see Table 5).

---- Insert Table 5 about here ----

A two-way factor ANOVA 2 (Condition) \times 2 (Body part) showed significant main effects of Body Part [F(1,19) = 515.39, p < .001; $\eta_{partial}^2$ = .96] and Condition [F(1,19) = 11.19, p = .003; $\eta_{partial}^2$ = .37] as well as a two-way interaction [F(1,19) = 7.26, p = .014; $\eta_{partial}^2$ = .27]. Post-hoc analyses with Bonferroni correction (p < .025) were conducted comparing the same body part between conditions. Results revealed that leg length was perceived as significantly different between the

Avatar and Own conditions (p < .002), while the difference between the two conditions for the arms was not significant (p = .24).

Further analyses were conducted to assess if the presentation order of the stimuli affected participants' responses between conditions (See Figure 6 b and c). We run two separate ANOVA, one for each body part. A two-way factor ANOVA 2 (Order) × 2 (Condition) for the Arm blocks showed significant main effects of Order [F(1,19) = 163.91, p < .001; $\eta_{partial}^2$ = .89] and a trend for the interaction Order × Condition [F(1,19) = 4.31, p < .052; $\eta_{partial}^2$ = .19] while Condition did not show any significant effect [F(1,19) = 1.47, p = .24; = .07]. Regardless of the condition, arms were significantly underestimated in the ascending series more (-6.2%) than the descending series (-1.04%). For the leg blocks, a two-way factor ANOVA 2 (Order) × 2 (Condition) showed significant main effects of Condition [F(1,19) = 175.56, p < .001; $\eta_{partial}^2$ = .91] and Order [F(1,19) = 15.61, p < .001; $\eta_{partial}^2$ = .45] but no interaction [F(1,19) = 1.98, p = .18; = .09]. Participants underestimated the legs in the ascending series (-1.21%) and overestimated them in the descending series (+3.71%). As previously reported, the overestimation was more marked in the *Own* condition compared to the *Avatar* one.

Findings indicate that participants considered images with arms shorter and legs longer than the original own picture and standard avatar as proportional.

--- Insert Figure 6 about here ---

Discussion and Conclusion

Overall, the pattern of distortions found in this experiment was qualitatively similar to our previous findings with the metric task. In detail, the legs were overestimated and the arms were underestimated. In line with previous studies (e.g., Longo & Haggard, 2010) participants were more accurate when performing the depictive than the localization task. This is not surprising as in the

depictive task the torso size remained constant across the trials, allowing less margin of errors for the other body parts.

The pattern of findings reported in the present study may be linked to the particular structural components of the body representation (i.e. *body image*) modulated by the function that specific body parts fulfill when performing actions (*body schema*; Ferretti, 2016; Brozzoli, Makin, Cardinali, Holmes & Farnè, 2012; Costantini, Ambrosini, Scorolli & Borghi, 2011; Cardinali, Brozzoli & Farnè, 2009b; Holmes & Spence, 2004; Mora et al., 2018; Cocchini et al., 2018).

Crucially, to fully understand the nature of these distortions, we need to consider not only the usual action linked to each body part but also 'where' this action usually occurs. In fact, in everyday life we use our arms (and hands) mainly in the upper personal and peri-personal space (for example, using objects, writing, eating, gesturing when we talk); therefore, the movements that we perform on a daily basis may affect the content of the *body image* in relation to the function and the feeling of these body parts operating mainly in the upper personal space.

Bearing in mind the operational cogency of the triadic taxonomy of body representation (Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler & Sunderland, 1991), we argue that the coherence of the body representation is the result of a dynamic interaction between sub-components of the *body image* and the *body schema*. Despite the structural representation of the body being mainly based on visual information, it also feeds on semantic information that describes and conceptually identifies the functional purpose of body parts. Ultimately, the type of actions and where these occur in space may modulate the represented physical features of body parts (e.g. limbs; D'Angelo et al., 2018).

The positive correlation between represented arms and torso lengths seems in line with this interpretation and strongly supports the involvement of configural processing in body representation (Reed, Stone, Grubb & McGoldrick, 2006). From visual inspection of the analogic illustrations in Figures 2 and 4, the perceived location of the tips of the hands does not go much below the hip, suggesting a close relationship between arms/hands and the waist, which may represent the lower

border of the upper body. A similar pattern of distortion was observed for own and avatar's silhouettes in Experiment 2. This point is crucial as it may reconcile findings from recent studies investigating whole body representation in healthy adults. Indeed, also in Fuentes et al. (2013a) the arms terminated just above the hip. In other words, the nature of the distortion depends on the relationship between body parts rather than merely its intrinsic size properties. Arms and torso were showing a similar profile as, we claim, they are functionally part of the upper body.

The overestimation of the lower legs also appears to be a consistent finding within our study. In Experiment 1b we dismissed a possible methodological bias by providing the participants with a fixed and elevated landmark to be used as anchor points to build the representation of their own body. The amplitude of the error was slightly reduced compared to Experiment 1a; nonetheless, the distortion was still significant. The overestimation of the lower leg seems to fit within the hypothesis mentioned above. The actions we actively perform with legs on a daily basis mainly involve extension movements of the lower section of the leg (e.g., walking, running, kicking; Ferretti, 2016). This interpretation is in line with the data reported and may also explain the different trend of distortions between upper and lower legs.

Data reported in previous studies (i.e. Linkenauger et al., 2015; Sadibolova et al., 2019) showed that individuals tend to generally overestimate their body size. According to these authors, the perceived size of their own body parts depends on tactile sensitivity and physical size (*reversed distortion hypothesis*), so that bodily areas with lower numbers of tactile receptive fields are overrepresented in a cortical body map in order to compensate for this lack of resolution (Linkenauger et al., 2015). According to the authors, this implies that arms and legs, which have similar degree of tactile sensitivity, tend to be more distorted compared to other more sensitive body parts. However, because legs are physically larger than arms, they should be overestimated less. This explanation accounts for Sadibolova et al.'s (2019) study but does not fully explain our findings and why Fuentes et al. (2013a) reported overestimation of arms and underestimation of legs. We argue that the subjective over- or under-estimation of a body part, is not just an intrinsic feature of that segment, but

that various factors can interact and modulate the subjective map. Following this line of thought, differences between previous research and our results are not necessarily in contrast and can be considered within the frame of the co-construction model (Pitron et al., 2018; Pitron & de Vignemont, 2017). Task demand characteristics may modulate and influence the direction of the outcome. According to this model, body schema and body image interact and, we argue, the direction of such interaction is modulated by whether or not the body is considered (and represented) as an object in space. By definition, body schema consists in sensorimotor representations of the body that guide actions, these actions necessarily occur in space therefore the spatial component is pivotal in the building up of a coherent representation. In this circumstance, body schema information may be predominant regardless to whether the task is depictive or metric because body parts need to be represented in space and in relation to one another and this has a direct effect in the representation of body parts size and their spatial relationships. Instead, when the task requires to imagine a body segment length relative to another metric standard, as in Linkenauger et al.'s (2015) and Sadibolova et al.'s (2019) studies, such body parts are represented in more "abstract" terms, where the spatial context is less relevant. In these cases, more "weight" is given to somatosensory information in the construction of a body representation and, as a consequence, a different pattern can be observed.

We would therefore expect that loss of sensorimotor information would result in body representation alteration for the affected body part. Fuentes et al. (2013b) tested this hypothesis in a study conducted on patients affected by spinal cord injury. Crucially, patients presented a global alteration of the body configuration and metrics that the authors interpreted as a secondary consequence of prolonged changes in body posture, possibly reflecting an inability to stand or walk (Fuentes et al., 2013b; Arnhoff & Mehl, 1963). Therefore, according to the *co-construction model*, different body representations result from different interaction between *body schema* and *body image* and the weight that each component has in a specific context and task.

However, this model has only been recently developed and, as such, more systematic investigation is needed to support it with empirical evidence. The primary aim of the present study

was to establish how *body image* and *body schema* can normally interact with each other in a "steady state". Our results, far from being conclusive, can partially answer two critical aspects considered by Pitron and colleagues (2018): i) a systematic interaction between the *body image* and the *body schema* with ii) the process of co-construction being serial rather than parallel. The authors argued that the *body schema*, built on multisensory signals and motor expertise, works as a trace for the construction of the *body image*. However, in the process of the *body image* being "constructed", other factors come into play (e.g. visual information, semantic knowledge, social and affective factors, etc.). It follows that the *body image* increases its complexity but loses details and accuracy, becoming more susceptible to distortions (Pitron et al., 2018).

In line with previous studies, we observed a pattern of distortions that could be explained as the result of a possible influence of typical motor functions even when action is absent. Critically, information concerning the physical aspects of one's own body are integrated with the peripersonal space and the motor perspective as well as to the motor capabilities of the individual performing an action (Ferretti, 2016; Brozzoli et al., 2012; Costantini et al., 2011). Therefore, the representation of our body and the surrounding space may be influenced by actions that can be potentially/usually performed within such space with specific body parts, even in the absence of a concomitant motor performance. Such a remark is also supported by Cocchini et al. (2018) who showed that motor expertise can modulate and have profound and long-lasting effect on body metric representation.

In conclusion, as for other parts of the body, such as hands (e.g, Longo & Haggard, 2012a, 2012b) and face (Mora et al., 2018), the representation of the body as a whole is distorted and representation of its parts seem to be modulated, at least in part, by their motor functions. These findings imply that the *body image* is not necessarily based on "pictorial" information only, but there is a crucial influence of the *body schema* information that, indirectly, shapes the mental image of our body. We would argue that the *co-construction model* fit to our findings and helps to explain the similar pattern of distortions observed within the different tasks, such as metric and pictorial.

In our study we did not control for possible eating disorders. This may represent a limitation of our study as eating disorders can significantly impact on body image (Irvine et al., 2019; Skrzypek, Wehmeier, Remschmidt, 2001). Further studies should take into account not only the specific functions of body representations (*body image* vs *body schema*) but also their role in multimodal integration of sensory information, the context and dynamics in which this information is computed.

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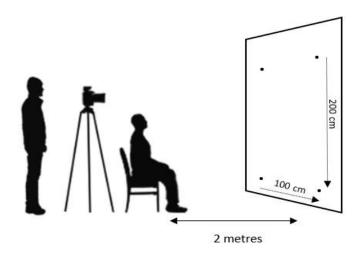
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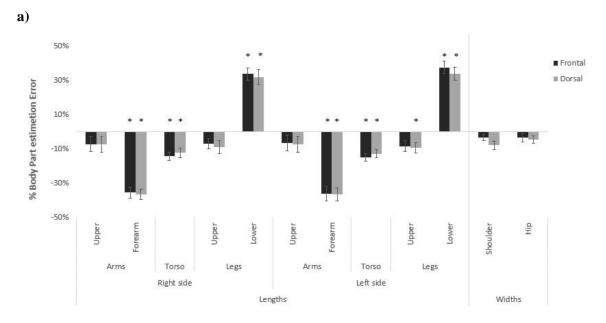
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Figure 1. Schematic sketch of the experimental setting.

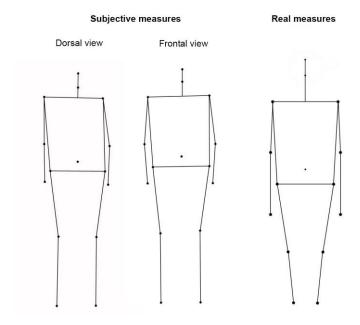


The camera was positioned on a tripod behind the participant and aligned with the center of the wall frame.

Figure 2. Under/overestimation of perceived body parts' lengths.



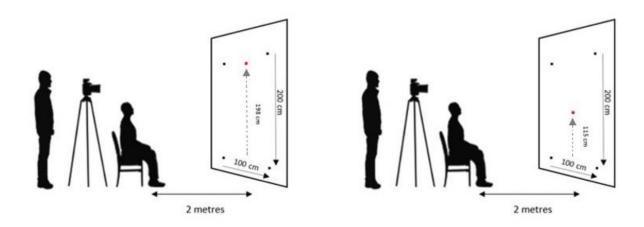
b)



- a) %BPE averaged across 28 individuals. * indicates significant (p<.004) difference from 0 (no distortion).
 b) Graphic output of averaged subjective responses and real body dimensions for 28 participants. Note that in
- both Frontal and Real images, the egocentric right side is on the left of the drawing and viceversa.

Figure 3. Schematic sketch of the experimental setting

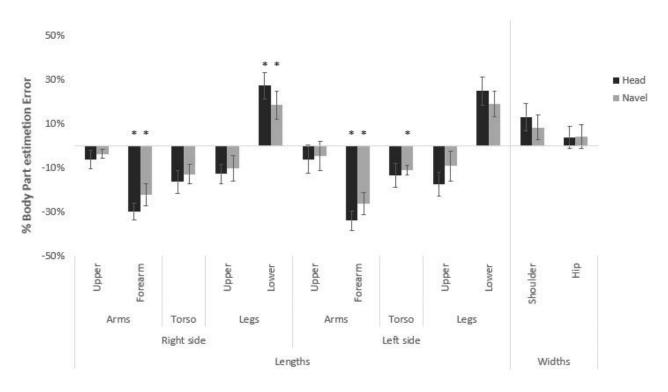




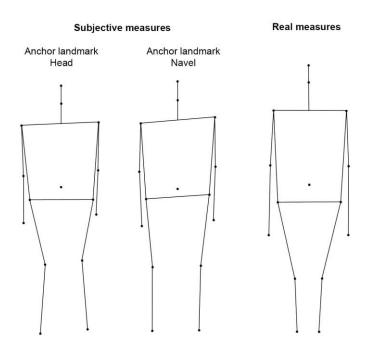
a) *Head* condition: the landmark was located at the top edge of the frame (198 cm from the lower edge); **b)** *Navel* condition: the landmark was located 15 cm above the middle of the frame (115 cm from the lower edge of the frame).

Figure 4. Under/overestimation in perceived body parts' length

a)

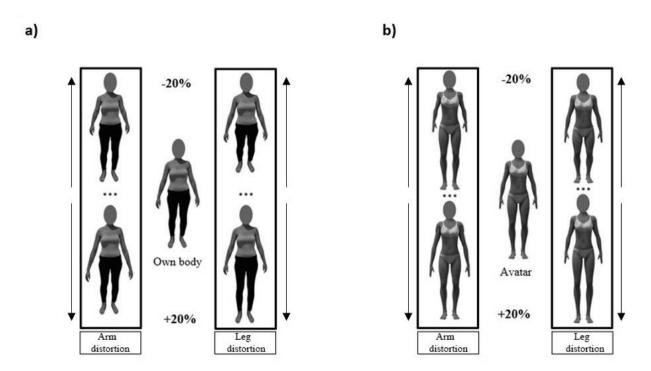


b)



a) %BPE averaged across 28 individuals. * indicates significant (p<.004) difference from 0 (no distortion). **b)** Graphic output of averaged subjective responses and real body dimensions for 10 participants in both conditions. Note that in all

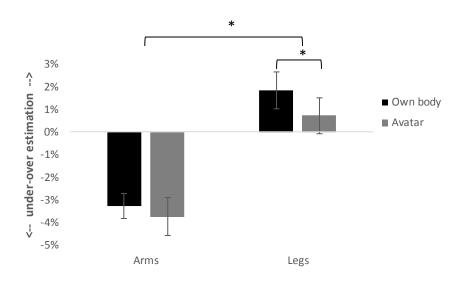
Figure 5. Types of stimuli adopted in the Experiment 2

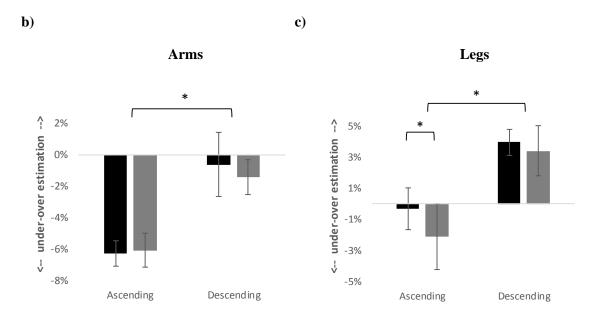


For both conditions, two sets of images were created (arms and legs). Each set ranged from maximum overestimation of +20% to a maximum underestimation of -20% from the original picture. Consecutive distorted images differed of +/-2% and each set consisted of 21 pictures (10 stretched, 10 shortened and 1 non-distorted). An example of 'female' avatar is reported here. Avatar gender was matched with the participant one.

Figure 6. Under/overestimation in perceived body parts' length

a)





a) Point of subjective equality averaged across participants for both arms and legs. * indicates significant difference between conditions and series direction.
 b) Percentage of distortion of arms perceived as "veridical" or "proportional" according to presentation order.
 c) Percentage of distortion of legs perceived as "veridical" or "proportional" according to presentation order.

Table 1. Body parts that participants were asked to locate.

BODY PARTS ASKED

ANATOMICAL POINT

MIDLINE LANDMARKS *

Navel Umbilicus

Top of the forehead Middle point of frontal eminence

Nose Tip of the nose

ARM LANDMARKS

Corner of the right/left shoulder Acromion

Right/Left elbow Olecranon

Right/Left wrist Ulnar styloid process

LEG LANDMARKS

Right/left hip Most lateral part of the iliac crest

Right/left knee Patella

Right/left ankle Anterior and distal point of the tibia

^{*} The midline landmarks were asked first to facilitate participants' representation of their own body and to allow them to familiarize with the frame size. Only the navel was marked on the wall and used as visible fixed landmark.

Table 2. Length and width of body segments

	BODY SEGMENTS	POINTS CONSIDERED		
LENGHT	Right/Left Upper Arms	Right/Left Shoulder-Elbow		
	Right/Left Forearms	Right/Left Elbow-Hand tip		
	Right/Left Torso	Right/Left Shoulder-Hip		
	Right/Left Upper Legs	Right/Left Hip-Knee		
	Right/Left Lower Legs	Right/Left Knee-Ankle		
WIDTH	Shoulder	Right-Left Shoulders		
	Hip width	Right-Left Hips		
\geqslant				

Table 3. Two-tailed t-tests results comparing %BPE with 0.

Body parts		Frontal (n = 28)			Dorsal (n = 28)		
		t-critical	p	d	t-critical	p	d
		L					
T.T	right	-1.67	.101	.31	-1.64	.113	.31
Upper Arm	left	-1.44	.162	.27	-1.69	.105	.32
	right	-11.35	<.004	2.15	-12.36	<.004	2.34
Forearm	left	-8.63	<.004	1.63	-9.23	<.004	1.74
Т	right	-5.73	<.004	1.08	-4.47	<.004	.84
Torso	left	-6.49	<.004	1.22	-5.24	<.004	.99
II	right	-2.28	.031	.43	-2.32	.028	.44
Upper Leg	left	-2.72	.011	.51	-3.10	<.004	.59
	right	9.10	<.004	1.71	7.04	<.004	1.33
Lower Leg	left	10.79	<.004	2.03	8.63	<.004	1.63
		V	VIDTHS				
Shoulder		-1.88	.070	.36	-3.28	<.004	.62
Hip	<u> </u>	-1.44	.161	.27	-1.98	.058	.37

[%]BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

Table 4. Results of two-tailed t-tests comparing %BPE with 0.

Body part		Head (n = 10	Navel (n = 10)			
		t-critical	p	d	t-critical	p	d
		L]	ENGTHS	S			
TT A	right	-1.41	.119	.45	-1.83	.100	.57
Upper Arm	left	772	.035	.24	69	.505	.21
	right	-7.56	<.004	2.39	-4.41	.002	1.39
Forearm	left	-7.62	<.004	2.41	-5.41	<.004	1.71
	right	-3.08	.013	.97	-2.92	<.017	.92
Torso	left	-2.47	.035	.78	-5.07	<.001	1.60
IImmon I on	right	-2.84	.019	.89	-1.72	.119	.54
Upper Leg	left	-3.25	.010	1.02	-1.34	<.212	.42
	right	4.61	.001	1.45	2.92	<.017	.92
Lower Leg	left	3.87	.004	1.22	3.25	<.010	1.02
		V	VIDTHS				
Shoulder		2.13	.061	.67	-1.47	.175	.46
Hip		.771	.461	.24	81	.435	.25

[%]BPE indicates the percentage difference between the perceived length/width and the participant's real body part length/width. AnP; Anchor point. Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

Table 5. Results of two-tailed t-tests comparing transition points with 0 for Own body and Avatar.

	Own	body	Avatar				
	t-critical	p-value	Cohen's d	t-critical	p-value	Cohen's d	
Arms	-30.13	<.001	6.74	-17.24	<.001	3.85	
Legs	4.08	.001	0.91	10.34	<.001	2.31	

Transition points indicates the percentage difference between the perceived length/width and the avatar or the participant's real body part length/width. Negative t-values indicate underestimations. In bold significant differences following correction for multiple comparisons.