Same action in different spatial locations induces selective modulation of body metric representation

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Abstract

Recent studies have hypothesised that the stereotypical representation of the body may reflect some functional aspects of routine actions that are performed in specific peripersonal domains. For example, the lower and upper limbs tend to 'act' in different peripersonal spaces and perform different functions. The present study aims to directly investigate the relationship between body representation and the spatial context where actions are performed. By means of a modified version of the Body Image Task we investigated body representation before and after a sorting task training in two groups of participants who were asked to carry out the same task/actions in two different spaces: on a table or on the floor, while sitting on a chair. Findings showed that a significant recalibration of the perceived upper arms' length occurred when participants were asked to perform a motor task on the floor. These results seem to suggest that the modulation of the body representation reflects an increase action capabilities driven by the contribution of motor training modulates and, importantly, the location in which the action occurs. Furthermore, the modulation was not limited to the body part actively involved in the action (the arms), it extended to other upper body parts (the torso) to maintain, we propose, a functionally coherent representation of the upper body.

Keywords: Body metric representation \cdot Body image \cdot Body schema \cdot Action \cdot Spatial location \cdot Posture

Introduction

We constantly move and perform actions to interact with the external environment and, as clearly pointed out by Gallese and Sinigaglia (2010), the nature of the *body schema* does not consist only of sensory attributes, but also of motor action-oriented qualities, which then define body representation components. Therefore actions modulate the perceived localization and length of body segments and ultimately, shape how the body is represented (Gallese and Sinigaglia 2010). Recent studies have shown that represented body metrics and configurations (i.e. relationship between specific body parts) are systematically distorted (e.g., Caggiano and Cocchini 2020; Fuentes et al. 2013) and that the direction of these distortions may reflect the functional characteristics of specific body parts defined as the type of motor actions that can be potentially performed in space (Brozzoli et al. 2012; Caggiano and Cocchini 2020; Costantini et al. 2011; Cardinali et al. 2009; Ferretti 2016; Holmes and Spence 2004; Mora et al. 2018; Cocchini et al. 2018).

In support of this claim, recent findings on the effect of tool-use strongly suggest that tools can shape one's own *body schema* even extending the usual reaching space. Studies on non-human primates have shown that five minutes of tool-use are enough to modify the visual receptive fields of bimodal visuo-tactile neurons in parietal regions, as if the tool used was incorporated into the paw. Crucially, when the macaques stopped using the tool, the visual receptive fields returned to their previous extension indicating that tools can temporarily shape one's own *body schema* by extending the reaching space (Iriki et al. 1996; Ishibashi et al. 2000). Similar results have been reported also in humans. Consistent with the hypothesis of a 'malleable' body schema, Maravita and colleagues (2002) showed that prolonged active tool-use modulates visuo-tactile spatial integration, so that visual stimuli located at the end of a 75 cm long tool interacted with tactile stimuli delivered on the tool's handle (Maravita et al. 2002). More recently, it has been shown that tool-use not only alters the kinematic profile of arm movements in a reach-to-grasp task but also the subjective perception of the arms' length (Cardinali, et al. 2009; see also Sposito et al. 2010). Notably, the majority of studies on tool-use have investigated the effect of tools in modulating body representation without explicitly addressing the active motor component required to operate the tool and perform the appropriate action. A recent study by Bruno et al. (2019) addressed this point by evaluating the effect of active and passive use of tools on body metrics. To do so, the authors developed a paradigm in which participants carried out two different training sessions. In one session, participants had to actively use a tool; in a second one, participants were asked to maintain a relaxed posture during the tool-use while, by means of robotic assistance, the action was passively performed. Interestingly, compared to the baseline, participants exhibited a significant increase in the perceived arm length after the active training session, while no modulation was observed after the passive one. These results clearly suggest that the simple and passive reproduction of tool action is not enough to impacts on subjective body metrics; the effect occurs insofar as the action is actively enforced by the agent (Bruno et al. 2019). Romano et al. (2019) also showed that a training requiring different goal-oriented actions using the same tool induces a proximal shift of the perceived midpoint of the arm when the training mostly involved proximal movements (i.e. movements of the shoulder), and a distal shift when participants were asked to perform distal movements (i.e. with the wrist). These findings indicated that, following a motor training with tools, the body representation is modulated by the type of action rather than by the morphological aspects of the tool (Miller et al. 2017; Sposito et al. 2012).

Two studies from Longo and Lourenco (2009, 2007) have shown that the perceived length of the arms and its motor action-oriented qualities can systematically modulate the 'extent' of peripersonal space. These findings provide interesting insight on the role of action in shaping body representation and, because actions occur *in* space, set the ground to address the representation of body parts in different portions of space. In fact, while consistent evidence has been reported on the effect of motor training in reshaping one's own body representation (e.g. extending peripersonal space and modulating the subjective length of related body parts), the effect of motor trainings in different sectors of the space has not been systematically explored.

In a previous study, we observed a consistent pattern of distortions whereby the length of the upper limbs was systematically underestimated and the length of the lower limbs was systematically overestimated. We argued that the typical body distortions observed by means of Body Image Task (BIT; Fuentes et al. 2013) could be explained by the specific functions of the body parts and the locations in which the related actions usually occur (Caggiano and Cocchini 2020). In fact, the actions that we usually perform with the legs tend to involve extension movements while walking, running, kicking (Ferretti 2016) and these recurrent actions may reflect the overestimation of these body parts. On the other hand, the arms tend to perform actions in the peripersonal space above the hips and this aspect may have had an impact on the underestimation of their length (Caggiano and Cocchini 2020). Similarly, Fuentes et al. (2013) observed that participants tend to align the most distal point of the arms/hands with the hips, confirming a subjective boundary that may reflect the aforementioned function-space role of the arms.

The main purpose of the present study was to further investigate this *functional hypothesis* and evaluate the relevance of the acting space in the context of body representation. By means of a modified version of the BIT (Caggiano and Cocchini 2020), the participants' subjective size of the body was compared before and after motor training. Two separate groups of participants were asked to perform an identical sorting task in two different spatial locations: in one condition participants were asked to carry out a sorting task in the upper sector of space (i.e. on a table) while in a second condition the task was carried out on the floor (lower sector of space), well below the hips. Our hypothesis was that if the metric representation is associated with where actions usually occur, then

simply changing the location of this action can modulate the represented size of the body part involved in the motor execution. Furthermore, and perhaps even more interesting, we question whether such modulation may not be restricted to the arms but it may reshape the overall relationship and proportions of the configuration of different body parts.

Methods and procedures

Participants

Sample size was determined by an a priori power analysis run with G* Power (Faul et al. 2009), for a repeated measures, within-between interaction design with two groups and 10 body parts to estimate with medium size $\eta_{partial}^2 = .04$, $\alpha = .05$ and power of .95 (parameters were selected according to similar studies such as Caggiano & Cocchini, 2020; Sadibolova et al., 2019). The analysis suggested a sample of 32 participants.

Thirty participants (20 females) took part in the experiment; their age ranged from 20 to 30 years, with a mean of 24.2 years (SD = 2.8). 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.

Procedure

The experiment consisted of a modified version of the Body Image Task (BIT; Fuentes et al. 2013; Caggiano and Cocchini 2020). Participants were asked to imagine their silhouette with their arm aligned with the body, as if they were standing.

Participants were seated on a chair located 2 meters away from a white wall. Participants were informed that during the task they would see a gray oval (14×7.8 cm) with a black dot at the center resembling the outline of a head projected at the top of the illuminated area on the wall. The projecting area was 140×192 cm at 150cm from the floor. Participants, who were not aware of the projecting

area size, were instructed to imagine their silhouette with their arm aligned with the body, as if they were standing in front of a mirror. Because the pointing did not occur in real scale, the head was used as landmark to provide a reference to scale the body: participants were asked to scale the imagined picture of themselves such that the size of their head (i.e. face outline) matched the size of the oval displayed on the wall. The name of the body part to be located during the task was displayed, in random order, at the bottom left of the projecting area. Participants used a laser pointer to indicate where they thought the body parts would be and were asked to hold the position until the experimenter recorded the response with a cursor by clicking the corresponding location on a computer connected to the projector. The task was carried out three times. To avoid possible 'shift' of the imagined silhouette during testing, the gray oval was used as landmark and remained visible throughout the task. A total of 13 body parts: 1 midline point (navel), 6 landmarks for the arms and 6 landmarks for legs.

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

The task was repeated two times: before and after a motor training.

Training sessions

After locating the body parts on the wall, participants were asked to run a 10-minute training and then they were re-tested on the BIT. During the training, participants were engaged in a sorting task in which they had to sort cubes and balls from a container into separate containers: cubes in the container to the left, balls in the container to the right. Half of the participants had to sort cubes and balls from a container located on the floor (*Down-training*), the other half from a container located on a table (*Top-training*). In both conditions, participants were blindfolded and asked to execute the task with their arms outstretched (Figure 1). To ensure that participants were able to correctly reach the boxes after being blindfolded, the experimenter guided participants hand onto the correct location. The aim was to maximize the use of afferent somatosensory information to carry out the sorting and,

maintain an outstretched position of the arms across the two conditions. Therefore, in both trainings the task's goal and procedure as well as the arms configuration, remained outstretched while the location of the action execution changed (*Top* vs *Down*). To encourage participants to perform the task as best they could, the experimenter took a live count of how many cubes and balls were divided correctly until the end of the training.

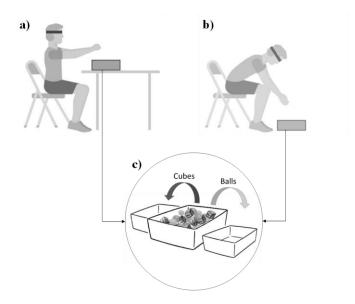


Figure 1. Schematic representation of training sessions.

a) 'Top' training, b) 'Down' training, c) sorting task.

Data acquisition of BIT

Two measures were considered: the *Real Body Measure* (RBM) and the *Subjective Body Measure* (SBM). Similar to previous studies (i.e., Fuentes et al. 2013; Caggiano and Cocchini 2020), real and subjective body measurements (RBM and SBM, respectively) were compared and analyzed in *percentage body part estimation error* (%BPE). Negative BPE values indicate underestimation, while positive values indicate overestimation; zero indicates perfect estimation. For the purpose of the present experiment, subjective body widths (shoulder and hip) were not considered for statistical analysis.

In a second set analysis, we compared body part ratios to test whether the motor training would modulate the overall represented body proportions. We calculated the following three ratios for each participant: leg/torso, arm/torso and arm/leg.

Results

Body parts - Length

Overall, participants from both groups showed a tendency to underestimate most of their body parts, in particular the lower arms (-44%) and overestimate the torso (+10%) and lower legs (+7%).

In order to assess whether the distortion of individual body parts was significant, a series of twotailed t-tests were performed, one for each body part, to compare %BPEs with zero (i.e., no distortion). Bonferroni correction for multiple comparisons was applied (i.e., 10 comparisons; significant p values < .005). Results showed that the length of 3 out of 10 body parts was significantly distorted from real size in the *Down-training* and 4 out of 10 in the *Top-training* groups (see Table1). In detail, the lower arms were consistently underestimated in both sides (left and right) and training groups, whereas the upper right arm was significantly underestimated only in the *Down-training* group. The upper right leg and left torso were underestimated and overestimated respectively in the *Top-training* group only (see Figure 2).

Four main factors were considered: Body Part (upper and lower arm, upper and lower leg and torso), Side (left and right), Group (Top-training and Down-training) and Time (pre/post-training).

A mixed factor ANOVA 5 (Body Part) \times 2 (Side) \times 2 (Group) \times 2 (Time) was performed to consider possible differences among body parts, side and groups. Greenhouse–Geisser correction was used where applicable, and post-hoc paired t tests were systematically adjusted using the Bonferroni correction for multiple comparisons (significant-p \leq .05).

Results yielded main effect of Body Part [F(2.4, 65.92) = 42.51, p < .001; $\eta_{partial}^2$ = .61], Side [F(1,28) = 5.99, p = .021; $\eta_{partial}^2$ = .18] and Time [F(1, 28) = 7.02, p = .013; $\eta_{partial}^2$ = .21] while Group

[F(1,28) = .203, p = .65; $\eta_{partial}^2$ = .01] was not significant. Crucially to the purpose of the study, the three-way interaction Body Part × Group × Time was significant [F(2.61, 73.15) = 3.46, p = .026; $\eta_{partial}^2$ = .11].

To investigate the Body Part × Group × Time interaction, we run a post-hoc analysis, which showed that, in the post-training task, participants in the Down-training group, significantly overestimated the upper arms [pre: -16.5%; post: +4.5%; t (14) = 6.18, p < .001, d = 1.59] and torso [pre: +4.8%; post: +18.3%; t (14) = 3.76, p = .001, d = .97] compared to baseline. On the other hand, the Top-training group showed a reduced underestimation of the upper legs [pre: -19.4%; post: -12.5%; t (14) = 3.22, p = .044, d = .83]. Furthermore, while in the pre-training task %BPEs for all body parts did not significantly differ between groups, in the post-training a significant difference was observed for the upper arms [Dow-training: +4.5%; Top-training: +0.5%; t(28) = 2.26, p = .03, d = .82].

Body parts	Down-Training group $(n = 15)$					<i>Top-Training</i> group (n = 15)		
		t-critical	р	d	t-critical	р	d	
Upper Arm	right	-3.82	.002*	2.04	-1.76	.101	.94	
	left	-2.11	.054	1.13	-1.75	.103	.93	
Lower Arm	right	-17.43	<.005*	9.31	-11.41	<.005*	6.10	
	left	-12.56	<.005*	6.71	-8.26	<.005*	4.42	
Torso	right	.937	.364	.50	2.57	.022	1.37	
	left	.927	.371	.50	3.27	.006	1.75	
Upper Leg	right	-2.51	.025	1.34	-3.29	.005*	1.76	
	left	-1.91	.078	1.02	-2.29	.038	1.22	
Lower Leg	right	.862	.403	.46	1.92	.076	1.03	
	left	.621	.545	.33	1.51	.153	.81	

 Table 1. Two-tailed t-tests results comparing %BPE with 0.

%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.

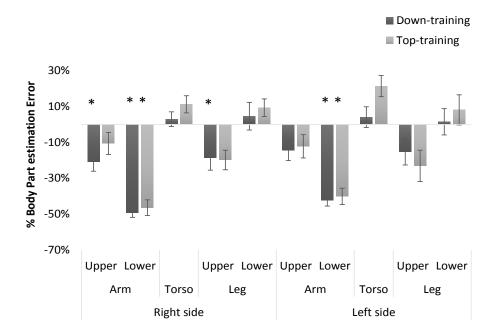


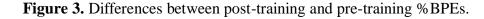
Figure 2. Under/overestimation in perceived body parts' length.

Positive values indicate overestimation. Negative values indicate underestimation. * indicates significant ($p \le .005$) difference from 0 (no distortion). Error bars indicate standard error.

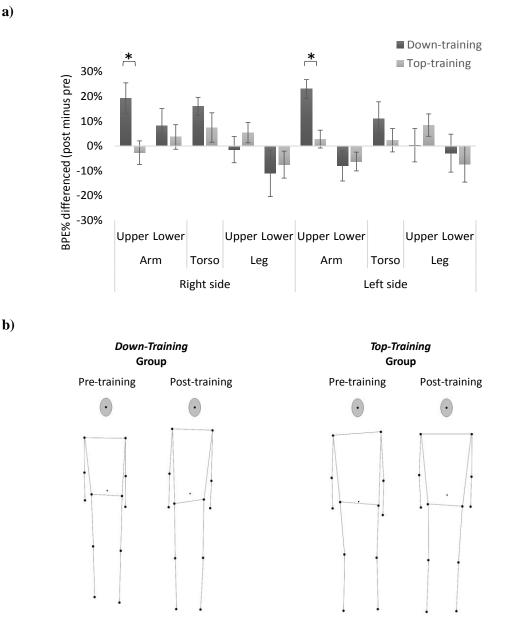
Differences between pre- and post-training (Delta)

To have a clearer measure of the amplitude of the training effect, *delta* BPEs (i.e., post-*minus* pre-training) were calculated for each participant (see Figure 3). A mixed factor ANOVA 5 (Body Part) \times 2 (Side) \times 2 (Group) was then carried out to test significant discrepancies for body parts between the two groups. Greenhouse–Geisser correction was used where applicable, and post-hoc paired t tests were systematically adjusted using the Bonferroni correction for multiple comparisons (significant-p \leq .05).

A significant main effect for Body Part [F(2.6, 72.98) = 6.26, p = .001; $\eta_{partial}^2$ = .18] was observed as well as Body Part × Group interaction effect [F(2.6, 72.98) = 3.39, p = .028; $\eta_{partial}^2$ = .11]. Side [F(1,28) = .325, p = .57; $\eta_{partial}^2$ = .01] and Group [F(1,28) = 4.32, p = .47; $\eta_{partial}^2$ = .13] were not significant. Post-hoc analysis revealed that in the *Down-Training* group, the differences (*delta* BPEs) for the upper arms were significantly larger than those for the lower arms [t (14) = 3.57, p = .002, d = .92], upper [t (14) = 4.08, p = .001, d = 1.05] and lower legs [t (14) = 3.04, p = .01, d = .01.79]. No significant differences were found in the Top-training group. Furthermore, the Down-Training group showed larger delta BPEs for the upper arms compared to the Top-Training group [t (28) = 5.08, p < .001, d = 1.85]. No significant differences were observed for any other body part.



a)



a) Positive values indicate an increase in perceived length in the post-training phase compared to baseline. Negative values indicate a decrease in perceived length in the post-training phase compared to baseline. * Highlight the significant difference between delta BPEs for the Down and Top-training groups. Error bars indicate standard error. b) Graphic output of averaged subjective responses (pre- and post-training). Note that the egocentric right side is on the left of the drawing and viceversa.

Body parts - Ratios

A further investigation of distortions in body metrics across groups was conducted by comparing body aspect ratios as we may expect that body parts are perceived in a wider context of the whole body, and perception of each body part is modulated by those of other body parts (Figure 4). Specifically, three body part ratios were calculated for each participant: leg/torso, arm/torso and leg/arm. As for to BPEs, ratios were expressed as the difference between the perceived ratio and the participant's true ratio, as a proportion of the true ratio.

Two-tailed t-tests were conducted for each body-ratio compared with zero (i.e. no error). Bonferroni correction for multiple comparisons was applied (i.e., 3 comparisons; significant p values < 0.016). Results showed that, with the exception of leg/torso in the *Down-training* group, participants perceived body ratios were significantly different from the real ones (see Table 2).

A 2 (Group) × 3 (Ratio) × 2 (Time) ANOVA was carried out. Greenhouse–Geisser correction was used where applicable, and post-hoc paired t tests were systematically adjusted using the Bonferroni correction for multiple comparisons (significant- $p \le .05$). The main factors Ratio [F(1.11, 31.02) = 108.33, p < .001; $\eta_{partial}^2 = .79$] and Time [F(1, 28) = 8.12, p = .008; $\eta_{partial}^2 = .23$] were significant. The two-way interaction Group × Time [F(1, 28) = 6.16, p = .019; $\eta_{partial}^2 = .18$] and threeway interaction Group × Ratio × Time [F(1.11, 31.09) = 4.11, p = .047; $\eta_{partial}^2 = .13$] were also significant.

Analysis of the three-way interaction showed that the difference of body parts ratios between pre- and pot-training was present only in Down-training group; in particular for the leg/torso [t (14) = 3.25, p = .006, d = .84] and leg/arm [t (14) = 2.43, p = .029, d = .63]. Interestingly, post-training arm/torso ratio was not significantly different from the pre-training condition.

Ratios		Down-Train group (n =	0	<i>Top-Training</i> group (n = 15)			
	t-critical	р	d	t-critical	р	d	
Leg/Torso	-1.64	.122	.43	-3.26	006*	.84	
Arm/Torso	-12.83	<.001*	3.31	-15.31	<.001*	3.85	
Leg/Arm	3.88	.002*	1	3.19	.006*	.82	

Table 2. Two-tailed t-tests results comparing % ratio aspects with 0.

Negative t-values indicate underestimation. In bold significant differences following correction for multiple comparisons.

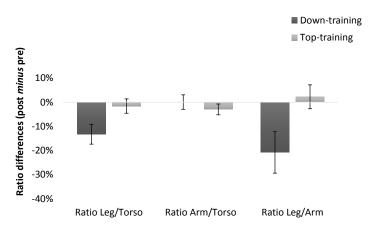


Figure 4. Differences between post- and pre-training body part ratios.

Positive values indicate that ratios considered were larger in the pre-training compared to the posttraining condition. Negative values indicate that ratios were smaller in the pre-training compared to the post-training condition. Error bars indicate standard deviation.

Discussion and conclusions

We investigated whether the same action performed in two different spatial locations can impact on subjective metric representation of the body. Participants were divided in two groups and asked to carry out the BIT before and after a sorting task. One group had to sort cubes and balls placed on the floor (*Down-training*), the other group performed the same task/action from containers located on a table (*Top-training*).

Firstly, the present study showed a systematic distortion of specific body parts, confirming the findings from previous studies (e.g. Fuentes et al. 2003; Caggiano and Cocchini 2020). In the pretraining phase of both training groups, bodily distortions were statistically significant for 4 out of 10 body parts. The most striking effect was the consistent underestimation of the lower arms for both groups, though the right upper arm and the right upper leg were significantly distorted only in one group (*Down-training* and *Top-training*, respectively). In addition, following the training session, results showed that a significant modulation of the perceived upper body parts' length occurred for the group that performed the sorting task on the floor (*Down-training*), while participants of the *Top-training* group showed a reduced overestimation on the upper legs in the post-training task. Crucially, while the body parts representation did not differ between the two groups before the training, a significant difference emerged in the post-training for the upper arm.

Altogether, these findings are particularly interesting as they seem to suggest that, although the motor training is relevant to modify the perceived length of body segments, the location in which the action occurs also plays a pivotal role in re-modulating the body parts representations and their relationship.

In literature, the peripersonal space is described as a particular region surrounding the body that acts as an interface between the body and the environment, functionally defined according to the distance at which an object can be reached (Cardinali, Brozzoli, & Farne', 2009). This definition crucially involves the 'action' as an important component in the definition of what the peripersonal space is. The *body schema* also plays a critical role in action execution (Gallagher, 2005) and for this reason both the peripersonal space and *body schema* are tightly linked (Holmes & Spence, 2004). On the other hand, the personal space is the space occupied by the body itself. The body, by nature, is spatially organized with clear anatomical landmarks that define its structure. In fact, when asked to locate body parts, participants maintained a reasonable configuration of the body, without committing gross errors, in regard to the overall relationship between body parts. Notably, as reported in previous studies using the same methods (i.e. Caggiano and Cocchini 2020; Fuentes et al. 2013), the emergent

body configuration manifests a similarity in the way left and right sides are represented. On the other hand, upper and lower limb distortions are not fully symmetrical and appear to follow different trends, suggesting that the upper and lower body space are represented differently (Fuentes et al. 2013). Ultimately the body is a means *for* action. Therefore, performing an action in a spatial location with body segments that are not naturally (or frequently) represented in that portion of space may extend the subjective action range and impact on represented body parts *for* action. In this sense, the type of actions and where these occur in space may modulate both spatial and bodily representations.

One of the main source of information the body schema relies on its proprioception, which allows us to be aware of the position of the body (and body parts) (Gallagher, 1986; Gallagher & Cole, 1995; Paillard, 1999). Within the context of the present study, an important distinction to consider is the one between reflexive proprioception and instrumental proprioception (O'Shaughnessy, 1995). The former refers to a deliberate act of reflection about the state and posture of the body. However, when we move, we do not constantly focus our attention on the state of the body and most of the time proprioceptive information is used in an instrumental fashion. Theories of motor control suggest that sensorimotor behaviour is the product of interacting feedforward and sensory feedback processes. Feedforward control is guided by internal action representations that plan initial motor output and estimate the sensory consequence of the action (Wolpert et al., 1995; Wolpert & Flanagan, 2001; Maeda et al., 2018). Features of the body and the environment are then mapped and compared with the actual sensory feedback of the action and task-relevant information (Wolpert et al., 2011). This process allows the system to minimize prediction errors and translate sensory feedback into corrective adjustments (Ghez et al., 1991). Because proprioception is closely tied to the control of movement, it must combine with other senses to locate external objects relative to the body and, as such, contributes to body image (Taylor, 2009). Therefore, it could be argued that the difference between Down-training and Top-training groups stems from different prediction errors resulting from intentional body movements in different spatial positions to carry out the task. In other words, the perceived elongation of the upper arms (and torso) occurred in the Down-training group

and not in the Top-training group because in the latter case there was no need for the system to make any corrective adjustment as there was no functional benefit in doing so (i.e. the action occurred in a sector of space presumably linked with the natural function of the body parts involved). Indeed, studies on tool-use have shown that the extension of perceived reachable space occurs only when individuals use a tool that functionally increases action capabilities (Bourgeois et al., 2014; Patané et al., 2016; Patané et al., 2017). Similarly, a significant modulation of the perceived arm length-occurs when individuals control a 3D virtual hand located in the far extrapersonal space (D'Angelo et al., 2018) and when they actively engage with the tool rather than passively use it (Anelli et al., 2015; Witt et al., 2005). The effect manifests only if there is congruency between the intention to perform the action, the motor output and the corresponding virtual hand movement; in other terms, when the participants experience a sense of agency over their actions.

Crucially, an action requires a more integrated representation of body parts. This consideration leads to the second main point of the current discussion. Results showed that the modulation of arms' length is coupled with a modulation of torso's length. At first glance, this should not come entirely as a surprise as changes in torso's length may be easily linked to the postural component associated with sorting objects on the floor while seated. However, since performing the *Down training* requires the torso to be bent down in order to reach the floor, based on such posture, one would expect to observe an underestimation in the post-training testing phase. Yet, perceived torso's length was overestimated and, more interestingly, the arm/torso ratios remained constant in the post-training compared to the pre-training phase. It seems therefore that such modulation may rely on instrumental proprioceptive information, that is, the torso's length was implicitly adjusted to reflect arms elongation, reflecting an integrated representation of these two body parts functional to the purpose of action execution. Thus, although the represented body is indeed distorted, a coherence between body parts must be maintained. This reasoning is in line with findings coming from studies on the sense of ownership. For example, Tsakiris, Prabhu and Haggard (2006) showed that in a RHI paradigm the illusory ownership was confined to the stimulated finger. However, when the stimulated

finger was actively moved, the illusion included other fingers because, arguably, the movement triggered a re-modulation of the relationship between the finger and the hand as a whole. In other words, it seems that actions require a unified and integrated representation of the body that put individual body parts 'back together' (de Vignemont et al., 2009).

A possible complementary interpretation for the results observed might take into account the cortical representation and anatomical organization of the motor cortex (M1). It is well known that, similarly to the somatosensory cortex, M1 presents a motor 'homunculus' onto which the motor representations of the different body parts are mapped. However, the cortical representation of body parts in M1 is not discrete and neatly segmented and, as in the somatosensory cortex, the cortical areas of adjacent body parts show some degree of overlap and local connections (Rathelot and Strick, 2006). Critically, M1 seems to be organized for representing muscle groups and patterns of movements rather than individual muscles (Lemon, 1988). In fact, it has been shown that stimulation of the M1 rather than eliciting the contractions of individual muscles, it elicits complex movement responses, which often involved several groups of muscles functionally related (Graziano, 2009). Recent studies have shown that upper limb movements, even for a short period of time, alter cortical excitability of the motor regions dedicated to limb control (Avanzino et al., 2011; Facchini et al., 2002; Huber et al., 2006). From these observations, it could be argued that, because of the contiguity of the torso and upper limb areas in M1, the modulation of the represented length of these body parts is the result of local connections.

A central idea of the *functional hypothesis* is that the body is functional because specific actions need to be performed with specific body parts in order to appropriately interact with the environment. As indicated by neurophysiological studies, within M1, muscles are grouped together to form functionally coherent units (Hluštík et al., 2001). Furthermore, a number of studies (e.g. Colby, 1998; Rizzolatti et al., 1998; Jeannerod et al., 1995) have shown that information coming from the body surface and external space is integrated in a way that is functionally relevant to specific actions performed by different body parts. From a cognitive point of view, these studies suggest that both representations of the surrounding space and the body are, at least to some extent, action-oriented (Maravita and Iriki, 2004). Indeed, the conscious perceptual judgements about any bodily feature or actions that are programmed on the basis of information about the position and the size of the limbs are influenced by the activation of these functionally related body parts (de Vignemont et al., 2009).

In conclusion, the present work provides evidence on the link between body representation and action performance. Previous studies have shown the effect of motor training in reshaping one's own body representation (e.g. extending peripersonal space and modulating the subjective length of related body parts). The present work expands on these observations by showing that, although motor training is relevant to modify the perceived length of body segments, the location in which the action occurs is also crucial. Furthermore, by means of the BIT, which looks at the overall body configuration, we observed that the modulation of body metrics was not restricted to the body part actively involved in the action execution (the arms) but, in this specific case, affected other segments of the upper body (i.e., the torso).

It should be acknowledged that one potential limitation of the study is that the task did not occurred in real scale. Participants had to image matching the oval of the silhouette to their own face, and then congruently scaling all the remaining parts. This could have affected participants' own body representation. However, it has been shown that the BIT (even when carried out on a computer screen) can be sensitive enough to catch the modulation of perceived body parts' length following experimental manipulation. For example, Perez-Marcos and collegues (2018) reported a significant recalibration of the upper/lower arm lengths on the BIT following asynchronous visuo-tactile stimulation in a Rubber Hand Illusion paradigm. These results, and the ones reported in the present study, provide additional support on how the internal representation of the *body image* is a highly dynamic process influenced by the way the body is used (*body schema*).

It should be noted that the majority of the literature on body representation (including the present one) has mainly focused on the distortions and modulation of hands and/or upper limbs body

metrics. Future studies may want to further look at the possible link between action, space and conscious representation of other body parts such as legs.

This implicit adjustment of body proportion seems to reflect a functionally coherent representation of the upper body. Indeed, the visual perception (and representation) of our body cannot be reduced to the *mere* visual discrimination given by visual inputs (i.e. physical characteristics of the body). The experience of seeing and perceiving our own bodies is conditioned by our attitudes toward it, our physical posture, motor control as well as pragmatic intentions and responses to environmental stimuli (Gallagher, 2005).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Compliance with ethical standards

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethical approval

All participants completed an informed consent form before performing the experiments. 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).

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References

- Anelli F, Candini M, Cappelletti M, Oliveri M, Frassinetti F (2015) The Remapping of Time by Active Tool-Use. *PLoS ONE* 10(12): e0146175.
- Avanzino L, Bassolino M, Pozzo T, Bove M. (2011). Use-dependent hemispheric balance. The Journal of Neuroscience 31(9): 3423–3428.
- Brozzoli C, Makin TR, Cardinali L, Holmes NP, Farnè A (2012). Peripersonal Space: A Multisensory Interface for Body–Object Interactions. In: Murray MM, Wallace MT, editors. The Neural Bases of Multisensory Processes. Boca Raton (FL): CRC Press/Taylor & Francis; 2012. Chapter 23.
- Bruno V, Carpinella I, Rabuffetti M, De Giuli L, Sinigaglia C, Garbarini F, Ferrarin M (2019). How Tool-Use Shapes Body Metric Representation: Evidence From Motor Training With and Without Robotic Assistance. *Frontiers in Human Neuroscience* 13: 299.
- Bourgeois J, Farnè A, Coello Y. (2014). Costs and benefits of tool-use on the perception of reachable space. *Acta Psychol. (Amst.)* 148, 91–95 10.1016/j.actpsy.2014.01.008.
- Caggiano P, Cocchini G (2020). The functional body: does body representation reflect functional properties? *Experimental Brain Research* 238(1): 153-169.
- Cardinali L, Brozzoli C, Farnè A (2009). Peripersonal space and body schema: two labels for the same concept? *Brain Topography*, 21, 252–260.
- Cardinali L, Frassinetti F, Brozzoli C, Urquizar C, Roy AC, Farnè A (2009). Tool-use induces morphological updating of the body schema. *Current Biology* 19(12): R478–R479.
- Cocchini G, Galligan T, Mora L, Kuhn G (2018). The magic hand: Effect of expertise on representation of own hand. *Quarterly Journal of Experimental Psychology* 71(11): 2314-2324.
- Costantini M, Ambrosini E, Scorolli C, Borghi AM (2011). When objects are close to me: Affordances in the peripersonal space. *Psychonomic Bulletin & Review* 18: 302–308. http://dx.doi.org/10.3758/s13423-011-0054-4.
- Colby CL (1998) Action-Oriented spatial reference frames in cortex. Neuron 20(1): 15-24.
- D'Angelo M, di Pellegrino G, Seriani S, Gallina P, Frassinetti F (2018) The sense of agency shapes body schema and peripersonal space. *Scientific Reports*, 8(1), 13847.

- de Vignemont F, Majid A, Jola C, Haggard P (2009). Segmenting the body into parts: evidence from biases in tactile perception. *The Quarterly Journal of Experimental Psychology* 62(3): 500-12. doi: 10.1080/17470210802000802.
- Facchini S, Muellbacher W, Battaglia F, Boroojerdi B, Hallett M (2002) Focal enhancement of motor cortex excitability during motor imagery: a transcranial magnetic stimulation study. *Acta Neurol Scand* 105(3): 146-51. doi: 10.1034/j.1600-0404.2002.10004.x.PMID: 11886355
- Faul F, Erdfelder E, Buchner A, Lang A-G (2009). Statistical power analyses using G*Power 31: Tests for correlation and regression analyses. *Behavioural Research Methods* 41(4): 1149–1160.

Ferretti G (2016). Through the forest of motor representations. Consciousness and Cognition 43: 177–196.

Fuentes CT, Longo MR., Haggard P (2013). Body image distortions in healthy adults. *Acta Psychologica 144:* 344-351.

Gallagher S (2005). How the body shapes the mind. New York: Oxford University Press.

- Gallagher, S (1986). Body image and body schema: A conceptual clarification. *Journal of Mind and Behavior*, 7, 541–554.
- Gallagher, S, & Cole, J (1995). Body schema and body image in a deafferented subject. *Journal of Mind and Behavior*, 16, 369-390.
- Gallese V, Sinigaglia C (2010). The bodily self as power for action. Neuropsychologia 48(3): 746–755.

Ghez C, Hening W, Gordon J (1991) Organization of voluntary movement. Curr Opin Neurobiol. 1:664-671.

- Graziano MSA (2009). The intelligent movement machine: An ethological perspective on the primate motor system. New York, NY: Oxford University Press.
- Hluštík P, Solodkin A, Gullapalli RP, Noll DC, Small SL (2001). Somatopy in human primary motor and somatosensory hand representations revisited. *Cerebral Cortex* 11: 312-321.
- Holmes NP, Spence C (2004). The body schema and multisensory representation(s) of peripersonal space. *Cognitive Processing* 5: 94–105.
- Huber R, Ghilardi MF, Massimini M, Ferrarelli F, Riedner BA, Peterson MJ, Tononi G. (2006). Arm immobilization causes cortical plastic changes and locally decreases sleep slow wave activity. *Nature Neuroscience* 9(9): 1169–1176.
- Iriki A, Tanaka M, Iwamura Y (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7(14): 2325–2330.

- Jeannerod M, Decety J (1995). Mental motor imagery: A window into the representational stages of action. *Current Opinion in Neurobiology* 5(6): 727–732.
- Ishibashi H, Hihara S, Iriki A (2000). Acquisition and development of monkey tool-use: behavioral and kinematic analyses. *Canadian Journal of Physiology and Pharmacology* 78(11): 958-66.

Lemon R (1988). The output map of the primate motor cortex. Trends in Neurosciences 11(11): 501-6.

- Longo MR, Lourenco SF (2007). Space perception and body morphology: extent of near space scales with arm length. *Experimental Brain Research* 177(2): 285-90. doi: 10.1007/s00221-007-0855-x.
- Lourenco SF, Longo MR. (2009). The plasticity of near space: Evidence for contraction. Cognition, 112(3), 451–456.
- Maravita A, Iriki A (2004). Tools for the body (schema). Trends in Cognitive Science 8: 79-86.
- Maeda RS, Cluff T, Gribble PL, Pruszynski JA (2018) Feedforward and Feedback Control Share an Internal Model of the Arm's Dynamics. *Journal of Neuroscience* 38 (49) 10505-10514.
- Maravita A, Spence C, Kennett S, Driver J (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83(2): B25–B34.
- Miller LE, Longo MR, Saygin AP (2017). Visual illusion of tool use recalibrates tactile perception. *Cognition* 162: 32-40.
- Mora L, Cowie D, Banissy MJ, Cocchini G (2018). My true face: Unmasking one's own face representation. *Acta Psychologica* 191: 63-68.
- O'Shaughnessy, B (1995) "Proprioception and the Body Image", in Bermúdez, Marcel, and Eilan 1995: 175– 204.
- Paillard, J (1999) Body schema and body image: A double dissociation in deafferented patients. In: *Motor control, today and tomorrow*, ed. Gantchev, G. N., Mori, S., & Massion, J., pp. 197–214. Academic Publishing House.
- Patané I, Iachini T, Farnè A, Frassinetti F (2016) Disentangling Action from Social Space: Tool-Use Differently Shapes the Space around Us. *PLoS ONE* 11(5): e0154247.
- Patané I, Farnè A, Frassinetti F (2017) Cooperative tool-use reveals peripersonal and interpersonal spaces are dissociable. *Cognition* 166:13-22.
- Perez-Marcos D, Martini M, Fuentes CT, Bellido Rivas AI, Haggard P, Sanchez-Vives MV (2018) Selective distortion of body image by asynchronous visuotactile stimulation. *Body Image* 24:55-61.

- Rathelot J-A, Strick PL (2006) Muscle representation in the macaque motor cortex: An anatomical perspective. *PANS* 103(21): 8257–8262. doi: 10.1073/pnas.0602933103
- Rizzolatti G, Luppino G, Matelli M. (1998). The organization of the cortical motor system: new concepts. *Electroencephalography and Clinical Neurophysiology* 106(4): 283-96. doi: 10.1016/s0013-4694(98)00022-4.
- Romano D, Uberti E, Caggiano P, Cocchini G, Maravita A (2019). Different tool training induces specific effects on body metric representation. *Experimental Brain Research* 237(2): 493-501.
- Sadibolova R, Ferrè ER, Linkenauger SA, Longo MR (2019) Distortions of perceived volume and length of body parts. *Cortex* 111:74–86.
- Sposito A, Bolognini N, Vallar G, Maravita A (2012). Extension of perceived arm length following tool-use: clues to plasticity of body metrics. *Neuropsychologia*, 50(9): 2187–2194.
- Sposito AV, Bolognini N, Vallar G, Posteraro L, Maravita A (2010). The spatial encoding of body parts in patients with neglect and neurologically unimpaired participants. *Neuropsychologia* 48(1): 334–340.
- Taylor JL (2009) Proprioception. Encyclopedia of Neuroscience. Ed Squire LR Academic Press, 1143-1149
- Tsakiris M, Prabhu G, Haggard P (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition* 15(2): 423-32.
- Witt JK, Proffitt DR, Epstein W (2005) Tool use affects perceived distance but only when you intend to use it. *J Exp Psychol Human*. 31, 880–888.
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880-1882.
- Wolpert DM, Flanagan JR (2001) Motor prediction. Current Biology 11(18):R729-32.
- Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. *Nat Rev Neurosci* 12:739 -751.