*In press Experimental Brain Research*

**Title Page:**

Different tool training induces specific effects on body metric representation

**Authorship:** Daniele Romano[1,2], Elena Uberti[1,3], Pietro Caggiano[3], Gianna Cocchini[3,*], Angelo Maravita[1,2*]

**Affiliation:**

[1] University of Milano Bicocca, Department of Psychology; piazza Ateneo Nuovo 1; 20126 Milan - Italy

[2] NeuroMi – Milan Center for Neuroscience; Milan - Italy

[3] Goldsmiths University of London, Department of Psychology; New Cross SE14 6NW, London – United Kingdom

[*] Authors for correspondence

e-mail address: angelo.maravita@unimib.it

Fax: +39 0264483768

Telephone Number: +39 0264483788

e-mail address: g.cocchini@gold.ac.uk

Telephone Number: +44 (0)20 7919 5024

Other authors e-mail addresses:

Daniele Romano: daniele.romano@unimib.it

Elena Uberti: e.uberti1@campus.unimib.it

Pietro Caggiano: psp01pc@gold.ac.uk

**Word Count**: 5126 words

## ABSTRACT

Morphology and functional aspects of the tool have been proposed to be critical factors modulating tool-use induced plasticity. However how these aspects contribute in changing body representation is underinvestigated.

In the arm bisection task participants have to estimate the length of their own arm by indicating its midpoint, a paradigm used to investigate the representation of metric properties of the body. We employed this paradigm to investigate the impact of different actions onto tool embodiment.

Our findings suggest that a training requiring actions mostly with proximal (shoulder) or distal (wrist) parts induces a different shift in the perceived arm midpoint. This effect is independent from, but enhanced by, the use of the tool during the training and it is in part influenced by specific demands of the task. These results suggest that specific motor patterns required by the training can induce different changes of body representation, calling for rethinking the concept of tool embodiment, which would be characterized not simply by the morphology of the tools, but also by the actions required for their specific use.



**Keywords:**

Embodiment, tool-use, body representation, body schema, arm bisection task


**Public Significance Statements**

This study shows that embodiment of tools is modulated by the specific motor pattern required by the training. These findings are particular relevant because they challenge the concept of tool embodiment, which would be characterized not simply by the morphology of the different tools (i.e., length, shape), but also by the actions required for their specific use.

## 1. Introduction

Each tool holds intrinsic physical and dynamic properties (i.e., shape, length, and weight) that make it ideal to fulfil a given task. Therefore, planning a movement requires a careful perceptual analysis of the kind of tool we are going to use and the environment on which we are going to operate. This information is then integrated with the representation of our own body, in order to reach the desired goal (de Vignemont, 2010; Gallagher, 2005; Head & Holmes, 1911; Longo & Haggard, 2010).

Humans use tools with such a level of expertise that it has been conceptualized that actively used tools may become incorporated in the representation of our body as functional body extensions for action (Iriki, Tanaka, & Iwamura, 1996; Maravita & Iriki, 2004). This idea has been originally assessed experimentally in the macaque, considering changes in neural responses of bimodal parietal neurons holding both somatosensory and visual responses to stimuli presented close to the body. Following tool use, these neurons showed an expansion of peripersonal visual space (Iriki et al., 1996). In a similar way, in humans, the use of long tools to reach for objects beyond hand's reach has shown to expand visuo-tactile integration of stimuli at the tool tip (Farné, Serino, & Ladavas 2007; Maravita, Spence, Kennett, & Driver, 2002; Maravita & Iriki 2004). Further studies in animals and humans have characterized this seminal discovery using a number of different tasks, assessing how the use of tools impinges on different and specific aspects of body representation (Canzoneri et al., 2013; Cardinali et al., 2009; Higuchi, Imamizu, & Kawato, 2007; Miller, Cawley-Bennett, Longo, & Saygin, 2017; Rossetti, Romano, Bolognini, & Maravita, 2015).

From a conceptual point of view, a central aspect of body representation, which may be crucial to interpret the effect of tool use, is that of *body schema* defined as an unconscious, dynamic representation of the body, mainly relying on proprioceptive information (de Vignemont, 2010). Starting from Head and Holmes (1911) it has been suggested that the nature of body schema is not only sensory-motor but also, crucially, “action-oriented”. In particular, action can modulate, by itself, our representation of the spatial extension of the body with respect to the external world (Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015; Gallese & Sinigaglia, 2010). Tools may further mediate the representation of the body schema, as they can physically modify (e.g. extend) our action space. This can be achieved through the activation of specific motor programs that are tailored on the mechanical features and purpose of each particular tool. For example, Cardinali and colleagues (2009) have shown that using a mechanical grabber to reach for objects affects the reaching component of action kinematics when the action is performed after tool training. Together with this change of kinematic patterns, they observed a distal shift of the perceived position of a tactile stimulus on the arm. Those findings are compatible with the implicit representation of a longer arm when holding a tool (Cardinali et al., 2009; Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Cardinali et al., 2012). Congruently, changes in tactile processing on the arm following tool training have been shown in a tactile distance task (Miller, Longo, & Saygin, 2014, 2017). On a similar line, it has been shown recently that tool use can induce subjective changes on the metric representation of own body. In an arm bisection paradigm, in which participants were asked to point to the subjective midpoint of their arm (Bolognini, Casanova, Maravita, & Vallar, 2012; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010; Tosi, Romano, & Maravita, 2018), the perceived midpoint shifted distally - i.e. towards the hand - following a motor training with a tool (Garbarini et al., 2015; Sposito, Bolognini, Vallar, & Maravita, 2012).

The present work aimed at investigating the role of user-specific factors in affecting the body metric representation. By means of the aforementioned arm bisection task, we tested whether training sessions involving predominantly different motor patterns (i.e., requiring more proximal vs. more distal motor control) can differently modulate body metrics. This result would imply a crucial role of motor programming in the dynamic modulation of body representation following tool use. To explore for the first time this potential effect, we maximised the use of proximal or distal part of the arm during the entire duration of an action.

## 2. EXPERIMENT 1

### 2.1 METHODS AND PROCEDURE

#### *2.1.1 Participants*

A group of naïve participants was composed by a sample of 21 healthy volunteers (mean age= 23.26; SD= 4.61; 11 females; 20 right-handed) with no neurological or psychiatric history.

The Goldsmiths Departmental Ethics Committee approved the study and all volunteers gave written informed consent before taking part to the experimental procedure, which was in accordance with the standards of the 1964 Declaration of Helsinki (BMJ 1991; 302: 1194).

None of the participants was familiar with activities that require a high level of manual skills with specific instruments (i.e. sports such as tennis, baseball or playing musical instruments) and they were all naïve to the experimental procedure.

#### *2.1.2 Forearm bisection task*

Participants were assessed using the arm bisection task adopted in previous studies (Garbarini et al., 2015; Sposito et al., 2012, 2010; Tosi, et al., 2018). According to this method, participants were asked to indicate the perceived midpoint between the elbow (Olecranon) and the tip of the middle finger of their arms (See Figure 1). During the task, participants comfortably sat at a table in a floodlit and sound-attenuated room. The bisection was measured for both the dominant and non-dominant arms, using the contralateral index finger. Bisections were performed using the index finger of the other hand with ballistic movements and no corrections allowed, participants were blindfolded during the arm bisection task. The arm to be bisected rested on the table extended in front, palm down. In order to avoid any tactile feedback from the bisection task, a custom-made plastic ruler was placed few millimetres above the to-be-bisected arm. Each bisection trial started with the index finger of the pointing hand placed at 30-cm distance from the midsagittal plane. The finger touched the ruler and remained in place for a few seconds, allowing the experimenter to record the position, then it returned to the starting position, ready for the next trial. There were 10 trials for each condition. Bisections were performed in blocks so that a participant do bisection 10 times for the dominant arm and then 10 times for the non-dominant arm. Which arm has to be bisected for first was counterbalanced across participants. Participants were asked to perform the forearm bisection task before and after two different *training sessions* (described below). Each participant attended to both types of training, scheduled in different days and spaced at least 24 hours from each other. The order of training session was counterbalanced across participants.

Zero was set at the most distal landmark (i.e., middle finger tip). Individual arms lengths (i.e., distance from the middle finger tip to the olecranon) were measured at the end of the session to calculate the objective arm midpoint.

The perceived midpoint was then calculated by dividing each pointing position for the total length of the arm and multiplying this value by 100 to obtain percentage deviation scores (indicated midpoint/arm length*100). With this procedure, a value above 50% indicates a proximal deviation (i.e. a perceived midline shift toward the elbow), a value less than 50% indicates a distal deviation (i.e. a perceived midline shift toward the wrist) and a value equal to 50% indicates no deviation.

[Insert Figure 1 about here]

*2.1.3 Training Sessions*

Two training sessions were designed to target different sections of the arm selectively: the Proximal (Hit task) and the Distal (Grasp task) training. In both sessions, participants used the same tool with their dominant arm for an identical amount of time, 15 minutes, and performed actions at a comparable distance from the body (see Figure 1). The non-dominant arm was kept stationary along the side. The tool consisted of a 70-cm long stick with an ergonomic handle at one extremity and a grabber at the other extremity. Each participant performed the arm bisection task immediately before and after each training session.

*2.1.3.1 Proximal training (hit task)*

Participants were asked to use the tool like a bat, a task that required mostly movements of the proximal part of the dominant upper limb (i.e., the arm and the shoulder).

Participants stood up, with both feet on a starting position placed 1m from the wall, on their dominant side. A foam rubber ball of 7 cm of diameter was hung up on the ceiling (by a rope 155 cm length) at one meter distance in front of the participants. Participants were asked to hit the ball with the stick in order to strike specific targets on the wall (numbered from 1 to 20 for increasing difficulty) with different size (i.e. big or small), colour (i.e. blue, purple, red) and shape (i.e. circle, square). Numbers from 1 to 20 were written on each target, according to their size (higher number for smaller size) and served as score during the task. During the training, participants were instructed to practice the task using the entire arm, avoiding as much as possible movements limited to the wrist. Participants were then asked to hit the ball to touch as many targets as possible placed on the wall, trying to reach the highest possible score by targeting the most difficult ones (see Figure 1). The participants' performance was scored by the investigator who also checked that the training was done as requested. In order to monitor the efficacy of the training we compared the scoring achieved during the first and last minute of training.

*2.1.3.2 Distal training (grasp task)*

Participants were asked to use the tool like a grabber, in order to grab the highest number of balls placed in a box (all different by size, colour, material, weight) and put them into a basket (see Figure 1). The participant's position and distance from the target balls were similar to the training described above; however in this task the position of the basket was calculated in order to make it reachable by wrist movements. Indeed this task was selected in order to shift the pattern of motor programming towards the distal segment of the dominant upper limb (i.e., the hand and the wrist), thus mimicking what was previously done by different works (Cardinali et al., 2012; Sposito et al., 2012; Garbarini et al., 2015). Participants were explicitly instructed to avoid the use of the proximal part of the arm also during the carrying phase, so that the training maximised the use of the distal end of the arm during the entire duration of the training.

In order to monitor the efficacy of the training, we compared the scoring (i.e. number of balls placed in the basket) achieved during the first and last minute of the training.

*2.1.4 Statistical analysis*

Inferential statistics were performed through linear mixed models (LMM) as implemented in SPSS 22.0 (Chicago, Illinois).

Subjective shift was used as dependent variable, including subjects as random intercept variable. A 2X (Time: pre/post-training) 2X (Hand: dominant/non-dominant) 2X (Training: proximal/distal) fixed factor model was then tested.

The sample size of our experiments was not based on a priori power because a priori power analysis for LMM has not a standard method yet, despite promising tools are on the verge to be developed (Green & Macleod, 2016; Westfall, Kenny, & Judd, 2014). On the other hand, observed (also known as: achieved, or post-hoc) power is not considered a reliable measure to reduce Type2 error anymore (Hoenig & Heisey, 2001). Thus, in order to produce a transparent research assessing the reliability of our results, we employed a sensitivity analysis which is concerned with understanding how changes in the model inputs influence the outputs (Oakley & O'Hagan, 2004). Specifically, in the method we used, we maintained fix all the parameters and the model and we systematically varied the effect size of the critical effect in order to identify the smallest significant effect detectable given our experimental conditions, thus answering to the question "What effect size was our study able to detect given the experimental conditions?" In other words, what is the minimum effect size to which the test was sufficiently sensitive?

(Faul, Erdfelder, Lang, & Buchner, 2007). The sensitivity analysis we used followed these three steps: a) measure the effect of our predictor or interaction of interest (the “b” parameter) under the model we designed with the random effect structure and the sample size that we actually collected; b) execute a simulation analysis using the model and the parameters estimated at point (a), decreasing artificially only the size of the critical effect. We decreased the effect size until the p-value associated surpassed two different limits, the canonical .05 and .1, a more conservative limit to sustain that an effect is non-significant. Effect sizes and p-values were rounded at the forth decimal at this stage; c) calculate the percentage of effect decrease from the observed effect, thus finding how much smaller an effect could be to remain significant under the current situation. Therefore, for example we may find that an effect 25% smaller would still have a p-value $\leq .05$ and 30% smaller would result as a non-significant effect with a p-value $\geq .1$. We did sensitivity analysis using the packages lme4 and Simr implemented in the statistical software R (R Core Team 2016).

For significant effects and interactions, we reported mean values and 95% Confidence Intervals (CI) (Cohen, 1990, 1994; Masson & Loftus, 2003).

We also tested the efficacy of the training by comparing the first and the last minute of participant’s performance with paired sample t-tests.

## 2.2 RESULTS

First the efficacy of the training was confirmed, indeed participants improved following both trainings (Hit training: $t(21)= 21.24$, $p< .001$; first minute= 19.9 ±1.4(SEM), last minute= 45.4 ±1.6; Grasp training: $t(21)= 19.3$, $p< .001$; first minute= 9.8 ±.6, last minute= 19.4 ±.8).

LMM analysis revealed a significant main effect of Training [$F(1,1652)= 9.40$, $p< .01$] and of Hand [$F(1,1652)= 6.45$, $p =.01$]. The main factor Time was not significant [$F(1,1652)= 0.839$, $p= .359$].

We also found significant the interaction between Time and Training [F(1,1652)=30.98, p<.001] and the three way interaction: Time*Hand*Training [F(1,1652)= 26.23, p <.001].

The three-way interaction showed that the dominant hand had a proximal shift of the midpoint after the hit training (pre-training: 54.8% [52.7, 56.8]; post-training: 64.3% [62.2, 66.3]), and a distal shift after the grasp training (pre-training: 59.8% [57.8, 61.8]; post-training: 52.1% [50.1, 54.1]). Crucially, no differences were found in the bisection performance for the non-dominant hand following both trainings (hit pre-training: 55.9% [53.9, 57.9]; hit post-training: 56.8% [54.8, 58.9]; grasp pre-training: 54.9% [52.9, 56.9]; grasp post-training: 55.1% [53.1, 57.1]) (Figure 2).

[Insert Figure 2 about here]

Sensitivity analysis performed on the three-way interaction effect highlighted that the effect reduced of 63.29% would remain significant with an associated p≤.05 and it would cross the .1 limit when it is reduced of 67.87%, suggesting that results are strongly reliable.

**2.4 EXPERIMENT 1 SHORT DISCUSSION**

Results showed that different training types produce different effects on body metric representation. Specifically a training impinging more upon distal motor programming would produce a distal shift, in agreement with previous studies results (Sposito, et al., 2012; Garbarini, et al., 2015). By contrast, a training with a tool requiring a more proximal motor control, would bias bisection towards the shoulder, the proximal end of the trained limb.

As suggested by the anonymous reviewers, however, our results may also indicate that mere motor activation may modulate arm bisection *per se*. In addition, the different result from the two trainings may be due not only by the different motor pattern required, but also by the scope of the tasks and thus the functional use of the tool. We therefore controlled for these potential effects in a second experiment. In this experiment, using a factorial design, participants were required to perform 4 tasks requiring either proximal or distal movements, and a tool vs. the participant's own hand, in order to control for the effect of the type of movement and the effect of tool use *per se* over forearm bisection.

## 3. EXPERIMENT 2

### 3.1 METHODS AND PROCEDURE

*3.1.1 Participants*

Nineteen new right-handed participants (11 females and 8 males) took part in the Experiment 2. They were naïve to the scope of the experiment and anybody participated to Experiment 1. Their age ranged from 19 to 35 years, with a mean of 29.4 years (SD = 3.8). The Goldsmiths Ethics Committee approved the study. All participants gave informed consent.

*3.1.2 Training Sessions*

Participants were asked to carry out four training sessions, which required specific movements to be performed with discrete sections of the arm. Three out of four trainings involved the same task (i.e. hitting a ball; *Hit tasks*), the remaining one consisted in a sorting task whereby participants had to move a number of balls (according to their colour) into two different boxes (i.e., similar to the *Grasp task* of Experiment 1). We had to adopt a different training for the fourth session since, following a pilot, it became evident that it was almost impossible to have a hit training similar to the previous conditions performed by wrist movements only, without a tool. In two of the *hit tasks,* participants used the same tool as in Experiment 1 with their dominant arm. The remaining hit task and the grasp task did not require the use of any tool and participants had to use their own dominant hand to perform both tasks. Finally, the four tasks were classified according to the type of action required (i.e., distal or proximal) and the use of the tool (tool/ no-tool). Participants had to carry out all the four trainings, which lasted 15 minutes each. Each participant performed the forearm bisection task as described in the Experiment 1 before and after each training session. A single testing block comprises the pre and post arm bisection task and the training session. The training order was balanced across participants and a break of 20 minutes was given between each testing block.

*Hit task*

The three hit tasks followed a similar procedure described in the Experiment 1 and the same material was used (i.e. scoring board, tool and ball). Few methodological adjustments were made (described below) in order to control for possible undesired movements of the participants' arm.

*Proximal hit with tool*

Participants were asked to use the tool like a racket and they were instructed to perform the task using the entire arm focusing on the movement of the shoulder (i.e., "like a tennis player"). They were also reminded to avoid as much as possible movements of the wrist. To limit wrist movements, participants had to wear a wristband reinforced with two small wood splints positioned on the ventral and dorsal sides of the wrist-forearm section.

*Proximal hit without tool*

Participants were asked to hit the ball with the palm of their dominant hand performing the same arm movement as described in the section above, avoiding as much as possible movements of the wrist. Again, in order to reduce wrist movements, participants had to wear a wristband reinforced with two small wood splints positioned on the ventral and dorsal sides of the wrist-forearm section. In this version of the task, the distance from the ball was adjusted according to the participants' arm length to allow an easy reach of the ball.

*Distal hit with tool*

In this version of the task, participants were instructed to hit the ball moving only the wrist, avoiding as much as possible movements of both shoulder and elbow. To reduce the risk of possible subtle movements of the upper part of the arm, the experimenter banded the participants with two velcro bands. One velcro band surrounded participants chest, from underneath the non-dominant armpit and covered the dominant arm section just below the deltoid muscle; the second band surrounded the participants' waist and covered the arm section just above the elbow blocking the upper part of the arm to participants' torso. The forearm was almost parallel to the floor and the angle formed by the upper arm and forearm was approximately 90°. Also in this case, some adjustment of the ball position was necessary to allow easy reach of the ball.

Participants were instructed to complete the task by focusing on wrist movements; however, it was not possible to completely avoid minimal lateral movements of the forearm and the torso.

*Distal grasp without tool*

Two flat boxes were placed in front of the participants on a 110 cm height table. The boxes were attached together and had a block of 3 cm height at the bottom so that the surface of the boxes was slightly inclined toward the participants. This allowed the balls contained into the boxes to roll toward the lower side of the boxes and be always at hand reach distance for the participants. At the lower side, the boxes had a communication passage so that the balls could be easily moved from one box to another.

Participants were asked to grab and move the highest number of balls from one box to another according to their colour. The participant's position and distance from the target balls was adjusted to make it reachable by wrist movements. As in the *distal hit task*, the participants were banded with two velcro bands to block movements of the upper parts of the arm. Although participants were instructed to accomplish the task by focusing on wrist movement, it was impossible to eliminate minimal lateral movement of the forearm during the sorting task.

### *3.1.3 Statistical analysis*

Inferential statistics were performed through linear mixed models (LMM) as implemented in lme4 (version 1.1-18-1) package of R software (R Core Team 2016). Analysis of variance is estimated with Satterthwaite's method. Subjective shift was used as dependent variable, including subjects as random intercept variable. A 2X (Time: pre/post-training) 2X (Hand: dominant/non-dominant) 2X (Training: proximal/distal) 2X (Tool: tool/no-tool) fixed factor model was then tested.

Sensitivity analysis was done on critical interaction as described in Experiment 1.

**3.2 RESULTS**

LMM analysis revealed a significant main effect of Training [F(1,3006)=7.69, p<.01], Hand [F(1,3006)=572.17, p<.001], Time [F(1,3006)=52.28, p<.001]; the main factor Tool was not significant [F(1,3006)=.01, p=.93].

Crucially to the purpose of the study the four-way interaction was not significant [F(1,3006)=.94, p=.33]. Interestingly the three-way interaction Time*Hand*Training [F(1,3006)=13.01, p<.001] was statistically significant, replicating results of Experiment 1. Additionally also the three-way interaction Time*Hand*Tool was significant [F(1,3006)=3.95, p=.046], as well as the Hand*Training*Tool [F(1,3006)=11.71, p<.001]. The latter was not investigated further as it does not depend on the pre-post timing effect and thus falls outside the scopes of this study.

The crucial Time*Hand*Training interaction showed that the dominant hand had a strong proximal shift of the midpoint after the proximal training (pre-training: 61.4% [58.3, 64.4]; post-training: 66.5% [63.8, 69.2]), and a no-shift after the distal training (pre-training: 63.1% [60.1, 66.1]; post-training: 64.7% [60.8, 68.6]). Crucially, any change was found in the bisection performance for the non-dominant hand following both trainings (distal pre-training non-dominant: 59.8% [56.3, 63.3]; distal post-training non-dominant: 59.2% [56.2, 62.2]; proximal pre-training non-dominant: 58.4% [55.6, 61.2]; proximal post-training non-dominant: 58.2% [55.3, 61.1]).

Sensitivity analysis performed on the Time*Hand*Training interaction effect highlighted that if the effect is reduced by 41.84%, it would still remain significant with an associated p≤.05 and it would cross the .1 limit if reduced by 49.15%.

We also examined the significant interaction Time*Hand*Tool for its potential interest with the scope of the present study. The interaction showed that the dominant hand had a stronger proximal shift following the training sessions with the tool (pre-training: 61.6% [58.9, 64.3]; post-training: 66.7% [63.8, 69.6]), than following the training sessions without the tool (pre-training: 62.8% [59.5, 66.1]; post-training: 64.5% [60.8, 68.2]). The non-dominant (untrained) hand did not show any interesting shift with (pre-training: 58.4% [55.4, 61.4]; post-training: 58.9% [55.9, 61.9]) or without (pre-training: 59.8% [56.5, 63.1]; post-training: 58.5% [55.6, 61.4]) the tool.

Sensitivity analysis performed on the Time*Hand*Tool interaction effect showed that the effect reduced by 10.02% still remains significant ($p \leq .05$) and it would cross the upper threshold ($p > .1$) if reduced of 21.33%.

[Insert Figure 3 about here]

### 3.3 EXPERIMENT 2 SHORT DISCUSSION.

Results replicated the interaction between the three crucial factors time, hand and training. The lack of four-ways interaction suggests that the presence of the tool is not necessary to induce a bisection shift related to body parts movements. Nonetheless, the tool plays a role in the bisection modification enhancing the effects, as suggested by the three-ways interaction with hand and time.

Even if the main pattern of results of the Experiment 1 has been replicated in Experiment 2, some aspects of the new conditions are specific to this experiment. Indeed, we have not been able to replicate the distal shift following a distal training. This may suggest that the scope of the task of Experiment 1, and thus the functional use of the tool, had a role in biasing the bisection shift. An anonymous reviewer suggested that the hit task might generally induces a proximal shift. If so, in Experiment 2, when the hit task was performed with distal movements, the general proximal shift induced by the hit task could have been contrasted by the distal shift induced by the wrist movements, resulting in a null effect. When the hit training was done with a proximal action the proximal shift strongly emerged also in Experiment 2.

Overall, these results suggest that actions can drive a potential modification of body metric representation *per se*, possibly because of the agency experienced during the training (D'Angelo, et al., 2018), that integrates with the morphological and functional features of the tool.

## 4. Discussion

We investigated how different actions with a tool can impact on subjective metric representation of the body. We hypothesized that any specific modulation effects of the subjective metric of the upper limb is critically determined by the pattern of motor programs required by the use of the specific tool. Participants were asked to indicate the perceived midpoint of their forearm before and after two different types of training that selectively maximised either proximal or distal movements of one arm, while the other hand was kept stationary.

We observed that the perceived midline did not change for the non-dominant stationary arm, while we found a proximal shift when the training involved more movements of the shoulder, and a distal shift when the training asked for a larger use of the wrist and fingers.

This finding is in line with quick sensory effects modulated by tool manipulation (Berti & Frassinetti, 2000; Maravita, Husain, Clarke, & Driver, 2001; Pegna et al., 2001) suggesting that modulation of subjective metric body representation is rather malleable and it can occur in response to fairly general and short practice, as also observed in other studies (Cardinali et al., 2009; Sposito et al., 2012; Garbarini et al., 2015). While previous studies reported a shift towards the tool tip (i.e., distally) and this has been interpreted as due to a subjective increment of reaching space or as physical embodiment of the tool (Garbarini et al., 2015; Sposito et al., 2012), our results suggest that the effect is influenced by the specific actions involved in the training possibly being related not only to the morphological features of the tool, but more on the way it is specifically used.

The additional four control conditions of Experiment 2 were run in order to control for the role of task demand (i.e., hit and grasp require different movements, but also have different scopes), and thus the functional use of the tool as well as the direct effect that  motor pattern activation may have in inducing the bisection shift.

We addressed the first point by asking participants to perform the same task (i.e. *Hit task*) with the same tool but with different motor styles (distal and proximal). For the second point, we asked participants to carry out both  proximal and distal training without the tool, so that the tasks goal and motor movements were similar to the Experiment 1, but without the physical manipulation of the tool.

Experiment 2 results confirmed the idea that different type of motor training induce different effects on body representation. These results also pictured a more complex scenario where motor pattern is crucial to determine the direction of the perceived changes in body metric representation. The morphological and functional aspects of the tool and the task goals further affect such changes.

What could explain such variable modulation of body representation following motor training and tool-use?

Increasing research on the behavioural and neural effects of tool use have put the focus on the complex picture. On one side, certainly the use of tools extending action space can change our response to environmental stimuli, due to the fact that those stimuli can be now reached by the tool (Canzoneri et al., 2013; Farné, et al., 2007; Iriki et al., 1996). Such changes are likely determined by a number of reasons that include the physical properties of the tool in terms of the size, length, or shape (Miller, et al., 2014, 2017; Sposito et al., 2012), as well as premotor, attentional, perceptual and affective mechanisms focused on the body district that is actively used during the tool actions (Cardinali et al., 2016; Holmes, Calvert, & Charles, 2008; Holmes, Sanabria, Calvert, & Spence, 2007; Rossetti et al., 2014).

Our results open a new window into another potential contributor to the body schema malleability such as the specific actions required for tool use. This effect is potentially related to the sense of agency modulated during the training. Indeed, it was recently shown that agency is involved in body schema and peripersonal space modulation (D'Angelo, et al., 2018).

Also the neural substrate of tool-use is known to involve several components, from the perceptual integration of somatosensory and visual input during tool-use, to the semantic aspects of tool recognition and the selection of appropriate motor patterns for the use of a particular tool (Maravita and Iriki, 2004; Johnson-Frey, Newman-Norlund, & Grafton, 2005).

No matter the kind of tool that can induce an operational advantage for the user (Arbib, Bonaiuto, Jacobs, & Frey, 2009), either physical or more indirect, such in the case of robotic surgery (Sengül et al., 2012) or virtual settings (Bassolino, Serino, Ubaldi, & Làdavas, 2010), any kind of tool requires the selection of an appropriate motor program in order to be used. Consistently, learning the use of novel tools has strong effects on brain plasticity, which has been linked to the selection of appropriate internal models for tool control (e.g. Imamizu et al., 2000).

The above considerations and the present results suggest that any changes of body representation that follow the use of tools is shaped by the specific motor pattern required by the tool, which should be viewed as a core determinant of any effect of embodiment, together with the morphological and functional features of the tool.

## Reference List

Arbib, M. A., Bonaiuto, J. B., Jacobs, S., & Frey, S. H. (2009). Tool use and the distalization of the end-effector. *Psychological Research Psychologische Forschung*, 73(4), 441–462.

Bassolino, M., Finisguerra, A., Canzoneri, E., Serino, A., & Pozzo, T. (2015). Dissociating effect of upper limb non-use and overuse on space and body representations. *Neuropsychologia*, 70, 385-392.

Bassolino, M., Serino, A., Ubaldi, S., & Làdavas, E. (2010). Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia*, 48(3), 803-811.

Berti, A., & Frassinetti, F. (2000). When far becomes near: re-mapping of space by tool use. *Journal of Cognitive Neuroscience*, 12(3), 415–420.

Bolognini, N., Casanova, D., Maravita, A., & Vallar, G. (2012). Bisecting real and fake body parts: effects of prism adaptation after right brain damage. *Frontiers in Human Neuroscience*, 6, 154.

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, 228(1), 25-42.

Cardinali, L., Brozzoli, C., Finos, L., Roy, A. C., & Farnè, A. (2016). The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition*, 149, 1–5.

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farne, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology*, 19(12), R478-9.

Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A. C., & Farnè, A. (2012). Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Experimental Brain Research*, 218(2), 259–271.

Cohen, J. (1990). Things I Have Learned (So Far). *American Psychologist*, 45(12), 1304–1312.

Cohen, J. (1994). The Earth Is Round (p < .05). *American Psychologist*, 49(12), 997–1003.

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*, 8:13847.

de Vignemont, F. (2010). Body schema and body image--pros and cons. *Neuropsychologia*, 48(3), 669–680.

Farné, A., Serino, A., & Ladavas, E. (2007). Dynamic size-change of peri-hand space following tool-use: Determinants and spatial characteristics revealed through cross-modal extinction. *Cortex*, 43(3), 436–443.

Faul, F., Erdfelder, E., Lang, A.G., & Buchner, A. (2007). G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavioral Research Methods*, 39(2), 175–91.

Gallagher, S. (2005). *How the Body Shapes the Mind*. Oxford: Claredon Press.

Gallese, V., & Sinigaglia, C. (2010). The bodily self as power for action. *Neuropsychologia*, 48(3), 746–755.

Garbarini, F., Fossataro, C., Berti, A., Gindri, P., Romano, D., Pia, L., … Neppi-Modona, M. (2015). When your arm becomes mine: Pathological embodiment of alien limbs using tools modulates own body representation. *Neuropsychologia*, 70, 402–413.

Green, P., & Macleod, C. J. (2016). SIMR: An R package for power analysis of generalized linear mixed models by simulation. *Methods in Ecology and Evolution*, 7(4), 493–498.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34(2–3), 102–254.

Higuchi, S., Imamizu, H., & Kawato, M. (2007). Cerebellar activity evoked by common tool-use execution and imagery tasks: An fMRI study. *Cortex*, 43(3), 350–358.

Hoenig, J. M., & Heisey, D. M. (2001). The abuse of power: The pervasive fallacy of power calculations for data analysis. *American Statistician*, 55(1), 19–24.

Holmes, N. P., Calvert, G. A., & Charles, S. (2008). Tool use changes multisensory interactions in seconds: evidence from the crossmodal congruency task. *Brain, Behavior, and Immunity*, 22(5), 629–629.

Holmes, N. P., Sanabria, D., Calvert, G. A., & Spence, C. (2007). Tool-use: Capturing multisensory spatial attention or extending multisensory peripersonal space? *Cortex*, 43(3), 469–489.

Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., PuÈtz, B., ... & Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, *403*(6766), 192-195

Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, 7(14), 2325—2330.

Johnson-Frey. (2003). What’s so special about human tool use? *Neuron*, 39(17), 201–204.

Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, 15(6), 681–695.

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *PNAS*, 2010(17), 1–6.

Maravita, A., Husain, M., Clarke, K., & Driver, J. (2001). Reaching with a tool extends visual–tactile interactions into far space: evidence from cross-modal extinction. *Neuropsychologia*, 39(6), 580–585.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8(2), 79–86.

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), B25-34.

Masson, M. E. J., & Loftus, G. R. (2003). Using confidence intervals for graphically based data interpretation. *Canadian Journal of Experimental Psychology,* 57(3), 203–220.

Miller, L. E., Cawley-Bennett, A., Longo, M. R., & Saygin, A. P. (2017). The recalibration of tactile perception during tool-use is body-part specific. *Experimental Brain Research,* 235(10), 2917-26.

Miller, L. E., Longo, M. R., & Saygin, A. P. (2014). Tool Morphology Constrains the Effects of Tool Use on Body Representations *Journal of Experimental Psychology: Human Perception and Performance*, 40(6), 2143.

Miller, L. E., Longo, M. R., & Saygin, A. P. (2017). Visual illusion of tool use recalibrates tactile perception. *Cognition*, 162, 32–40.

Oakley, J. E., & O'Hagan, A. (2004). Probabilistic sensitivity analysis of complex models: A Bayesian approach. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, 66(3), 751–769.

Pegna, A. J., Petit, L., Caldara-Schnetzer, A.-S., Khateb, A., Annoni, J.-M., Sztajzel, R., & Landis, T. (2001). So Near Yet So Far: Neglect in Far or Near Space Depends on Tool Use. *Annals of Neurology*, 50, 820–822.

Rossetti, A., Romano, D., Bolognini, N., & Maravita, A. (2014). Dynamic expansion of alert responses to incoming painful stimuli following tool use. *Neuropsychologia*, 70, 486-494.

Sengül, A., van Elk, M., Rognini, G., Aspell, J. E., Bleuler, H., & Blanke, O. (2012). Extending the body to virtual tools using a robotic surgical interface: evidence from the crossmodal congruency task. *PloS One*, 7(12), e49473.

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, A. V, 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.

Tosi, G., Romano, D., & Maravita, A. (2017). Mirror Box training in hemiplegic stroke patients affects body representation. *Frontiers in Human Neuroscience*, 11, 617.

Westfall, J., Kenny, D. A., & Judd, C. M. (2014). Statistical power and optimal design in experiments in which samples of participants respond to samples of stimuli. *Journal of Experimental Psychology: General*, 143(5), 2020.

**Picture Captions**

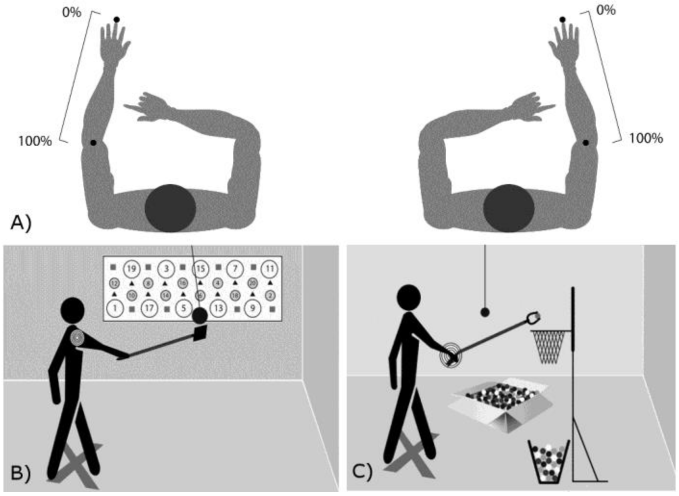


**Fig.1 Experimental Procedures.** Upper panels (A) show arm bisection task. Landmarks for the task were the olecranon (elbow) and tip of the middle finger for both arms.

Lower panels show a schematic representation of: hit training involving proximal movements (B), and grasping training involving distal movements (C).

Both trainings used the same tool, a 70-cm long grabber that was modified in order to offer a flat surface during the hit task. Each training session lasted 15 minutes and every participant take part to both trainings in different days.

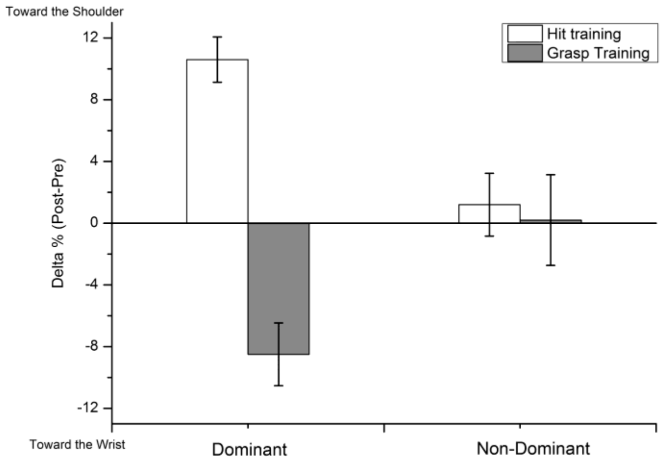


**Fig.2 Experiment 1 Results.** The three way interaction time (pre/post) *hand (dominant/non-dominant) *training (hit/grasp) is represented as a difference in the performance between pre and post training in the two hands, following the two different trainings. A value of 0% indicate that there was no change in performance after the training, positive values indicate for a proximal shift (toward the shoulder), negative values indicate for a distal shift (toward the wrist).

Thin dark lines indicate 95% Confidence Interval.

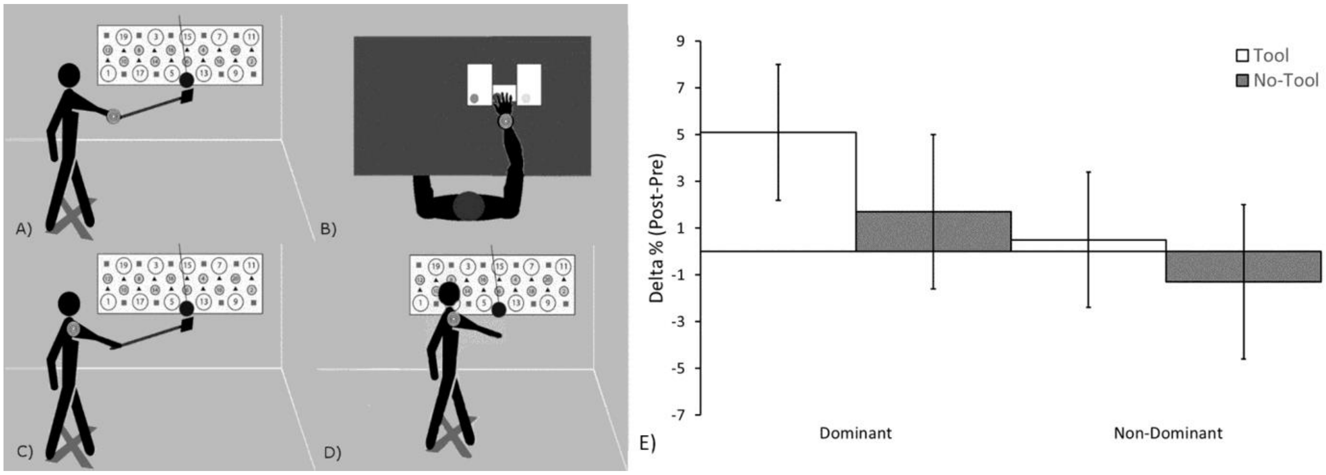


**Fig.3 Experiment 2.** Panels show a schematic representation of the training involving distal movements (A), or proximal movements (C) done by means of the tool, or the proximal movements done without the tool (D). Panel (B) shows a schematic representation of the distal training done without the tool.

In panel (E) the three way interaction time (pre/post) *hand (dominant/non-dominant) *tool (tool/no-tool) is represented as a difference in the performance between pre and post training in the two hands (dominant/non-dominant), in the conditions involving the use of the tool (white bars), or not (grey bars). A value of 0% indicates that there was no change in performance after the training, positive values indicate for a proximal shift (toward the shoulder), negative values indicate for a distal shift (toward the wrist). Thin dark lines indicate 95% Confidence Interval. The graph shows that the training with the tool induces a larger shift than the training using only the arm.