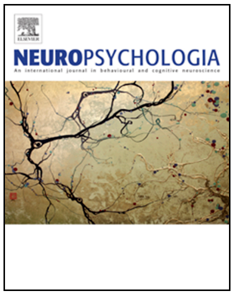


Effect of tool-use observation on metric body representation and peripersonal space

M. Galigani, N. Castellani, B. Donno, M. Franza, C. Zuber, L. Allet, F. Garbarini, M. Bassolino

PII: S0028-3932(20)30294-3

DOI: https://doi.org/10.1016/j.neuropsychologia.2020.107622

Reference: NSY 107622

To appear in: *Neuropsychologia*

Received Date: 23 April 2020

Revised Date: 13 August 2020

Accepted Date: 4 September 2020

Please cite this article as: Galigani, M., Castellani, N., Donno, B., Franza, M., Zuber, C., Allet, L., Garbarini, F., Bassolino, M., Effect of tool-use observation on metric body representation and peripersonal space, *Neuropsychologia* (2020), doi: https://doi.org/10.1016/j.neuropsychologia.2020.107622.

Author contributions

MG, MB and FG designed the study; MG, NC, CZ and MF performed the experiments; MG, BD, MF, CZ and MB analyzed the data; BD, MG and MB prepared the figures; MG, MB and FG wrote the manuscript; BD, MF, NC, CZ and LA reviewed the manuscript.

- **Title**: Effect of tool-use observation on metric body representation and peripersonal space

- **Author names and affiliations:**

Galigani M. [1], Castellani N. [1], Donno B. [2], Franza M. [3], Zuber C. [4], Allet L. [2,5], Garbarini F. [1], Bassolino M. [2,3]

[1] MANIBUS Laboratory, Psychology Department, University of Turin, Turin, Italy

[2] School of Health Sciences, HES-SO Valais-Wallis, Sion, Switzerland

[3] Center for Neuroprosthetics, Laboratory of Cognitive Neuroscience, Brain Mind Institute, School of Life Science Swiss Federal Institute of Technology (Ecole Polytechnique Fédérale de Lausanne), Campus Biotech, Geneva, and Campus SUVA, Sion, Switzerland

[4] Master of Science, University of Applied Sciences of Western Switzerland

[5] Department of Community Medicine, University Hospitals and University of Geneva, Geneva, Switzerland

- **Corresponding author: Michela Bassolino**
  School of Health Sciences, HES-SO Valais-Wallis, Chemin de l’Agasse 5, 1950 Sion, Switzerland.
  E-mail address: michela.bassolino@hevs.ch

Abstract

In everyday life we constantly act and interact with objects and with others' people through our body. To properly perform actions, the representations of the dimension of body-parts (metric body representation, BR) and of the space surrounding the body (peripersonal space, PPS) need to be constantly updated. Previous evidence has shown that BR and PPS representation are highly flexible, being modulated by sensorimotor experiences, such as the active use of tools to reach objects in the far space. In this study, we investigate whether the observation of another person using a tool to interact with objects located in the far space is sufficient to influence the plasticity of BR and PPS representation in a similar way to active tool-use. With this aim, two groups of young healthy participants were asked to perform twenty minutes trainings based on the active use of a tool to retrieve far cubes (active tool-use) and on the first-person observation of an experimenter doing the same tool-use training (observational tool-use). Behavioural tasks adapted from literature were used to evaluate the effects of the active and observational tool-use on BR (body-landmarks localization task- group 1), and PPS (audio-tactile interaction task – group 2). Results show that after active tool-use, participants perceived the length of their arm as longer than at baseline, while no significant differences appear after observation. Similarly, significant modifications in PPS representation, with comparable multisensory facilitation on tactile responses due to near and far sounds, were seen only after active tool-use, while this did not occur after observation. Together these results suggest that a mere observational training could not be sufficient to significantly modulate BR or PPS. The dissociation found in the active and observational tool-use points out differences between action execution and action observation, by suggesting a fundamental role of the motor planning, the motor intention and the related sensorimotor feedback in driving BR and PPS plasticity.

Keywords (5): body representation, peripersonal space, tool-use, action observation, motor intention

1. Introduction

To efficiently interact with the environment, as to plan and execute properly the action of reaching for an object positioned in front of the body, the brain needs updated representations related to the shape and the dimension of the involved body parts (i.e. metric body representations, BR) (de Vignemont, 2010; Longo et al., 2010; Schwoebel and Coslett, 2005), and of the space closely surrounding the body in which the interactions with the environment take place (i.e peripersonal space, PPS) (Rizzolatti et al., 1997; Serino, 2019). During the last years, many studies have been dedicated to investigating these representations, that contribute, in different ways, to the conscious experience of the self as an acting body (Garbarini et al., 2015).

As far as concerns BR, since no unique sensory signal directly conveys to the brain information about the size and the shape of the different body parts, authors have hypothesized that an implicit representation of the body metric is stored in the brain (Longo and Haggard, 2012, 2010; Tamè et al., 2019). This representation is constantly updated through on-line peripheral signals related to body parts, such as somatosensory, proprioceptive and kinaesthetic inputs coming from the skin, the muscles and the joints, as well as through visual bodily information, during the interactions with the environment (de Vignemont, 2010; Longo et al., 2010; Medina and Coslett, 2011; Riva, 2018; Serino and Haggard, 2010).

On the other hand, PPS representation has been originally studied in primates, where specific populations of multisensory neurons integrating visual and/or auditory stimuli near the body with tactile information on the body surface (Duhamel et al., 1997; Fogassi, 1996; Graziano et al., 1997; Graziano and Cooke, 2006) have been identified within a fronto-parietal network. Evidence for this has been corroborated by results also obtained in humans through neuropsychological (Di Pellegrino et al., 1997; Ladavas, 1998; Làdavas et al., 1998), neuroimaging (Grivaz et al., 2017; Makin et al., 2008) and behavioural (Bassolino et al., 2010; Canzoneri et al., 2012; Teneggi et al., 2013) studies. These works demonstrated a speed-up effect in responding to tactile stimuli when these were associated to visual or auditory stimuli presented close (i.e. within PPS), but not far from the body (Cléry and Ben Hamed, 2018; de Vignemont and Iannetti, 2015; di Pellegrino and Làdavas, 2015). This form of multisensory facilitation within PPS allows the brain to detect and anticipate potential interactions between the body and external objects and to trigger appropriate motor responses both in terms of defensive behavior (e.g. prevents a potential threat) or approaching (reaching/grasping) actions (Bufacchi and Iannetti, 2018; Serino, 2019).

Taking together, previous studies indicate that both BR and PPS have a multisensory nature, being built and constantly updated thanks to the integration of signals from different sensory modalities (Dijkerman and Lenggenhager, 2018; Kandula et al., 2017; Maravita et al., 2003; Salomon et al., 2017). This implies that BR and PPS are not fixed, but could be plastically modified through actions, and specifically through changes in the in- and out- flows of sensorimotor information arising from the interactions with the environment (e.g. reaching for an object). From this perspective, the nature of those representations is not only multisensory but also sensorimotor in the sense that the action execution can modulate both PPS and BR (Gallese and Sinigaglia, 2010).

A classic example of the plasticity of BR and PPS after action execution is the use of the tools allowing to reach objects located in the far space (Canzoneri et al., 2013; Cardinali et al., 2009; Maravita and Iriki, 2004; Martel et al., 2016). Using a tool to reach far objects allows to act outside PPS making outside-reach objects ready-to-hand (Iriki et al., 1996), and modifies the functional dimension of the effector holding the tool (e.g. the arm) (Martel et al., 2016). More specifically, it has been shown that tool-use re-shapes BR, by extending the estimated length of the body part (arm/hand) using the tool or by altering the subsequent hand free movement kinematic profile (Bassolino et al., 2014; Canzoneri et al., 2013; Cardinali et al., 2009; Garbarini et al., 2015; Romano et al., 2018; Sposito et al., 2012). Analogously, previous research has shown that, after tool-use, PPS representation is modified. In primates, PPS neurons normally coding tactile stimuli on the hand and associated external visual or auditory stimuli presented close to the hand started also to respond to associated visual/auditory stimuli located in the more distant space of the tool’s reach (Iriki et al., 1996; Maravita and Iriki, 2004; Radman, 2013). Similarly, studies with both healthy participants and patients have found that after tool-use, it is possible to extend the representation of the PPS, by increasing the multisensory interaction between tactile stimuli on the body and visual or auditory cues presented in the far space, in particular at the functional location where the tool was used (Farnè and Làdavas, 2000; Galli et al., 2015; Holmes and Spence, 2004; Maravita et al., 2001). This effect was reported after a short experience with a tool (around 15 minutes) as well as after persistent use of specific tools in different populations, such as blind people using the cane (Serino et al., 2007), computer mouse users (Bassolino et al., 2010) or professional tennis players (Biggio et al., 2017). In line with this, it has been argued that the space is accurately represented in relation to action capabilities by allowing the brain to determine whether a certain spatial sector is accessible and to select the most appropriate motor actions in the accessible space (Bufacchi and Iannetti, 2018; Serino, 2019).

The evidence of BR and PPS modifications after tool-use would drive the question if mere observation of someone else acting with a tool in far space may impact on bodily and spatial representations as execution. Previous works in monkeys and humans suggest that visual perception of an action performed by others is mapped onto the motor representation of the same action in the observer, by activating a shared representation between the observer and the agent (e.g. Buccino, 2014; Rizzolatti et al., 2001). The cortical activation induced by action observation in the observer partially overlapped with that activated by movement execution (Filimon et al., 2007; Jeannerod, 2001; Rizzolatti and Craighero, 2004) and maintains some specific proprieties of the observed action, such as the temporal structure and the muscular organization (Borroni et al., 2005; Finisguerra et al., 2015). Importantly, action observation may also induce plastic effects. For instance, trainings based on action observation can significantly change the preferential direction of thumb motion evoked by transcranial magnetic stimulation (Stefan et al., 2005), prevent cortical modifications observed after immobilization in healthy participants (Bassolino et al., 2014a) and seem to have positive effects in motor rehabilitation (e.g. Bassolino et al., 2015; Buccino, 2014). Considering this evidence, it is possible to hypothesize that observing an action performed by another person would be sufficient to drive plastic effects on PPS and BR similar to action execution. Coherently, the only study on space representation after observational tool-use so far (Costantini et al., 2011), reported an extension of the explicit perceived reaching space of the observer in a visual distance judgment task, in which participants had to judge the distance of a graspable object with respect to their body. Importantly, these authors found that observing tool actions can extend the representation of reaching space only when observers shared the same action potentialities with the agent, namely holding a tool compatible with the goal and the spatial range of the observed action. However, Garbarini and colleagues (2015) did not find any modification in the perceived length of the arm (BR) evaluated with a “body bisection task” (Sposito et al., 2012) after observational tool-use. These contrasting results would lead to the hypothesis of a possible dissociation in the effects of tool-use observation on BR and PPS. Nevertheless, the different results previously reported on reaching space and BR modifications after observational tool-use could be related to participants’ age. Indeed the study by Costantini and colleagues was performed in young adults, while the one by Garbarini and collaborators was done in healthy elderly controls, who could potentially show reduced plasticity after tool-use because of age (Costello et al., 2015).

To solve this issue, the present study aims to investigate the effects of active and observational tool-use on BR and PPS representations in young healthy adults. Although previous studies have demonstrated similar effects of the extension of both BR and PPS representations after active tool-use (Canzoneri et al., 2013), one can hypothesise dissociable effects after observational tool-use. Indeed, if BR modifications could be mainly mediated by multisensory and sensorimotor information related to *one's own* body (Bassolino et al., 2014b), the mere visual observation of *another person* using the tool could be not enough to induce alterations of BR in the observer. In contrast, if plastic changes in PPS are mostly dependent on the motor representation of the space in which the body potentially acts, the activation of a shared motor representation between the person using the tool and an observer holding the same tool (Costantini et al., 2011) through action observation (Rizzolatti and Craighero, 2004b) could be sufficient to affect PPS. However, alternative hypotheses could be considered; first, given that PPS is strictly anchored to one's own body and related somatosensory information (Serino, 2019), the mere observation of someone else acting in the same space could be not sufficient to modify the representation of the observer's PPS, as in the case of BR. Second, we can anticipate that the mere visual observation of *another person* using the tool could be enough to drive a plastic change of both PPS and BR, suggesting that the lack of modification of the BR after observational tool-use found by Garbarini and colleagues (2015) was mainly due to the age of their sample.

2. Materials and methods

2.1 Participants

Two groups of twenty-one healthy, right-handed participants were included in the study. According to a prior power analysis (GPower version 3.1) conducted on previous data from Canzoneri (Canzoneri et al., 2013), a sample of 14 subjects would be sufficient to detect possible forearm BR modifications due to active tool-use in healthy young participants (Cohen's dz = 0.843, with significance level = 0.05 and power = 0.8). Concerning PPS, the prior power analysis (GPower version 3.1) conducted on unpublished data (Ronga et al., *under review*) indicates that a sample of 20 subjects would be sufficient to detect possible modifications in PPS representation (i.e. in the difference between RTs to audio-tactile stimuli in near and far condition, see below) due to active tool-use in healthy young participants (Cohen's dz = 0.672, with significance level = 0.05 and power = 0.8).We decided to recruit more participants (i.e. n=21) to prevent any reduction in statistical power due to potential technical problems during data acquisition (e.g. missing data) or a posteriori data exclusion (outliers). This sample size is also in line with previous studies on observational tool-use (Costantini et al., 2011; Garbarini et al., 2015).

Participants in group 1 (age: 24.50 ± 3.02, range: 19-31, gender: 57% of female) underwent a task previously reported to assess the implicit perceived length of their arm, the body-landmarks localization task (BL) (e.g. Bassolino et al., 2014b; Longo, 2017), while subjects in group 2 (age: 23.71 ± 1.49, range: 20-26 gender: 67% of female) performed a task previously described to capture multisensory characteristics of PPS representation around their right hand. i.e. audio-tactile interaction task (e.g. Bassolino et al., 2010; Ronga et al., *under review*.; Serino et al., 2007). The subjects' handedness was evaluated with the Flinders Handedness survey (FLANDERS) (Nicholls et al., 2013). The following exclusion criteria were considered: the presence of neurological or psychiatric diseases or any other deficits impairing their capacities to perform the tasks (e.g. visual deficits, acoustic deficits, the presence of chronic pain in the upper limbs, sensorimotor deficits or recent fractures < 1 year). All the participants were naive to the experimental procedures and the purpose of the study and participated after having signed the informed consent. The study was conducted with the approval of the local ethics committee (group 1: Commission Cantonale Valaisanne d'Ethique Medicale, CCVEM 107/14, group 2: Ethics Committee of the University of Torino, prot. n. 125055, 12/07/16).

2.2 Procedure

2.2.1 Active tool-use training

During the training session, participants were comfortably seated on a chair in the experiment room and they were asked to place their left hand on their left leg and the right one in a prone position on a table by holding a standardized tool (aluminium rake, length: 100 cm, width: 8 mm diameter, with at the end a 15 x 10 cm plastic plate with two rectangular 6 x 10 cm sides at 90°, total weight of the tool: around 1kg) in the starting position (i.e. on the right side) (see Fig.1.A). They had to then perform a tool-use training session, inspired by similar works (Canzoneri et al., 2013; Costantini et al., 2011; Garbarini et al., 2015; Sposito et al., 2012). The training consisted in using the tool to retrieve 30 wooden coloured (red or blue) cubes (5.5 cm^3) that had to be placed into the coherent coloured squares (blue or red depending on the colour of the cube. The use of the tool produced auditory effects due to the tool sliding on the table and dragging the target wooden cubes. This choice was motivated by the fact that the post-training task used to assess the PPS representation involved auditory stimuli. During the training, participants were not blindfolded and could freely decide which objects to reach. They were asked to retrieve an object every time they heard a "bip" sound coming from an audio track, made to emit a "bip" every 5 seconds. This procedure was chosen to standardize the duration of the training among participants. Before the training, participants were familiarized with the tool to ensure that they could perform the task easily (few minutes). Overall, participants retrieved all the objects in 150 seconds and had a 60 second break while the experimenter recomposed the initial objects' composition on the table. During the break, participants were asked to hold the rake in their hand in the starting position. The task was performed in 6 blocks lasting 20 minutes in total.

2.2.2 Observational tool-use training

The observational procedure was the same as for the active condition, but in this case, the experimenter actively retrieved the objects at each "bip" by using the tool, while the participant observed the experimenter's actions while holding an identical tool with his/her right hand in the starting position (i.e. on the right side). Participants also perceived the auditory effects of the observed action due to the tool sliding on the table and dragging the wooden cubes. As for the active tool-use training, this was designed because the task used to assess the PPS representation involved auditory stimuli. The experimenter stood behind and slightly to the side of the participant during this condition, with the back anteriorly flexed at around 45°, so that the participant could see the arm and the trunk of the experimenter in first-person perspective (Garbarini et al., 2015; Costantini et al., 2011) (see Fig.1.B). We opted to place the experimenter in this position in order to design an observational tool-use training by keeping the visual aspects more similar as possible to the active training (i.e., exploiting a first-person perspective) and by manipulating only the agent of the tool-use. To maintain participants' attention during the training, the subjects were specifically asked to carefully observe the action performed by the examiner and orient their gaze to the left or to the right, according to the location of the target, as already described elsewhere (Garbarini et al., 2015). Experimenters checked that participants complied with these instructions by visual inspection.

INSERT FIGURE 1 AROUND HERE

Figure 1. Experimental task: (A) Active tool-use training: schematic aerial view of the experimental setting depicting the participant holding the tool in the starting position (black circle); (B) Observational tool-use training: schematic aerial view of the experimental setting depicting the participant holding the tool in the starting position and the experimenter actively using the tool. The experiment was standing behind and slightly to the side of the participant with the back anteriorly flexed at around 45°, so that the participant could see the arm and the trunk of the experimenter in first-

person perspective.

2.2.3 Group 1: Body-landmarks Localisation task (BL)

In group 1, the implicit perceived dimension of the upper limb (arm length) was measured before (pre) and after (post) the training (active and observational) with the body-landmarks localisation task (BL), already described in previous works (Bassolino et al., 2014; Canzoneri et al., 2013). The order of the sessions was balanced between participants, with half of the participants doing the observational training as first, and the other half beginning with active tool-use training.

The BL task can be considered an implicit measure of BR because participants had to indicate only the locations of some anatomical landmark, without explicit judgements about the perceived length of the body parts (Fuentes et al., 2013). To evaluate the perceived arm length, we considered two anatomical landmarks: the external part of the wrist (ulnar styloid) and the elbow joint (olecranon). The perceived arm length was then reconstructed a posteriori during the data analysis and compared with the individual real arm length captured at the beginning of the experiment, while participants were blindfolded.

During the task, participants were seated on a chair with the right forearm resting palm-down on a table in front of them. The forearm and hand positions were standardized. Participants' right forearm was aligned with the shoulder, positioned 20 cm away from the body midline without any contact between the elbow and the edge of the table and it was fixed to the table. In addition, the hand was resting on a not-working computer mouse. The left forearm was relaxed on the left leg.

After having acquired the actual position of the 2 landmarks, the experimenter positioned a wooden table (80 cm x 80 cm) above their arm and put an additional cloth to occlude the shoulders, in order to prevent participants from viewing their own arm during the task. Afterwards, subjects removed the eyeshades, and, in every trial, the experimenter showed to the participant the location of the target landmark on her body. Participants were instructed to verbally indicate, by saying "stop", when a retro-reflective marker (see below) attached to a wooden stick and moved by the experimenter along the table's longitudinal axis, reached the felt position of the target non-visible anatomical landmarks (wrist or elbow depending on the trial). Before recording the marker position, subjects were allowed to adjust their judgement, by verbally asking the experimenter to move it backward or forward, to the left or to the right. Ten randomized trials were repeated for each landmark. This exact procedure was reproduced after the training (post), taking care of placing the participants' upper limb in the same position of the pre-training session.

Retro-reflective markers (1 cm of diameter) captured by means of an optical motion capture system (Optitrack V120: TRIO; Motive 1.7.5 Final 64-bit, 2015) and a custom-made script written in Matlab (R2018a) were used for the recording. The positions of the markers on the limb and of the limb on the table were also marked to be used for the post training session.

INSERT FIGURE 2 AROUND HERE

Figure 2. (A) The anatomical landmarks recorded during the body landmark (BL) task: the external part of the wrist (ulnar styloid, cross) and the elbow joint (olecranon, circle). (B) The reconstruction of the anatomical landmarks, recorded at the beginning of the experiment (black) as well as the reconstruction of the perceived position recorded for each landmark on every single trial (ten repetitions for each landmark, light grey) and averaged among repetitions (dark grey) in one representative subject (the horizontal displacement is depicted on the x, mm, while the vertical ones on the y, mm). The data of the subject displayed in the figure are representative of the group and show overall general biases similar to those previously reported in literature, with an horizontal shift towards the body midline (see for instance Fuch et al., 2016; Ghilardi et al., 1995; Wann & Ibrahim, 1992) and an underestimation of the location of the wrist and the elbow (e.g. Canzoneri et al., 2013).

2.2.4 Group 2: Audio-tactile interaction task

In group 2, to investigate performed the task after the tool-use training, they had ceiling RTs likely due to a learning effect because of the repetition of the task, with a relevant speeding up of RTs in response to unimodal tactile stimulation. This would reduce the effect of sound in speeding up the RTs to tactile stimuli and thus decrease any difference between near and far bimodal conditions. Based on those data, in group 2, we adopted an only-post design to compare the effect of the three different trainings on the audio-tactile interaction task. The baseline is represented by the unimodal tactile condition, that is expected to be comparable among the three experimental sessions, thus ensuring that any differences in the audio-tactile interaction task is due to the different trainings (i.e. active, observational, and cognitive). In the cognitive training participants underwent a task in the far space without performing any motor action. They performed a visual task, in which they were asked to judge whether two sequentially presented (50 ms of duration; 1 s of interstimulus interval) configurations were identical or different. Visual stimuli consisted of four configurations of three dots, forming triangles pointing upwards, downwards, rightwards or leftwards, and were presented on a computer screen placed at a 100 cm of distance from the hand (a distance corresponding to the length of tool-use). In this way, the cognitive training allows also to control for possible unspecific attentional shifts, merely driven by operating in a more distant portion of space (Holmes, 2012).

In the audio-tactile interaction task, participants were seated on a chair with their right hand placed on the table while holding the tool, and tactile and auditory stimuli were administered by an Arduino system (https://www.arduino.cc) – E-Prime system.

Tactile stimuli consisted of non-painful transcutaneous electrical, constant current square-wave pulses (duration: 200 μs, delivered by DS7A, Digitimer) applied to the right-hand dorsum, using surface bipolar electrodes (1 cm between electrodes). The stimulus intensity, adjusted according to participants' sensitivity, corresponded to the individual threshold * 2. The individual sensory threshold was estimated before each experimental session, using the methods of limits (Gescheider, 1997). The mean stimulus intensity was 3.14 ± 0.97 mA (Active session: 3.55 ± 1.24 mA; Observational Session: 3.1 ± 0.88; Cognitive session: 3.18 ± 0.71 mA). To prevent habituation, three electrodes were placed at a constant distance between each other (i.e. about 1 cm) and connected to the electrical stimulator, so that the one with the negative polarity was kept always active, whereas the other two electrodes with positive polarity were activated on at a time. In this way, participants might perceive the stimulation coming from two distinct sites of the hand dorsum as if the stimulation was randomly shifted by displacing the electrodes' position of about 1 cm.

Auditory stimuli consisted of 784 Hz tones (intensity ≅ 65 dB; 50 ms duration) delivered by two different loudspeakers: the first loudspeaker was placed near (< 5 cm) to participants' right (stimulated) hand (henceforth *near position*), the second loudspeaker was positioned 100 cm (i.e. a distance corresponding to length of tool-use) from subjects' right hand (henceforth *far position*).

To explore multisensory integration effects within PPS, tactile and auditory stimulations could occur either in isolation (i.e. *unimodal conditions*: Touch, henceforth *T*; Auditory stimulus, catch trials, coming from near position, henceforth *ANear*; Auditory stimulus coming from far position, henceforth *AFar*) or combined (i.e, *bimodal conditions*: Touch+Auditory stimulus coming from near position, henceforth *TANear*; Touch+Auditory stimulus coming from far position, henceforth *TAFar*). Between each stimulation, the inter-trial interval was randomly jittered between 7 and 9 s, in a way that participants could not anticipate stimulus occurrence.

Participants were asked to respond as fast as possible to tactile stimuli, ignoring auditory ones, by pressing a button on the response box with their right index finger. The audio-tactile interaction task consisted of a 16 minutes experimental block and 24 trials per condition were delivered. Stimulus delivering and RTs were controlled and recorded by Eprime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

During the piloting phase we ensured that subjects perceived synchronously the tactile and the auditory stimuli and we calculated that our Arduino-E-Prime system administered the two stimuli with a maximum delay of 40 ms, with the auditory stimulus occurring later.

INSERT FIGURE 3 AROUND HERE

Figure 3. Audio-tactile interaction task, setup: tactile stimulation was administered alone (T condition) or simultaneously with an auditory stimulation coming from near position (TANear condition) or coming from far position (TAFar condition). During the stimulation, participants always hold the tool.

Please see Figure 4, for a schematic representation of the experimental procedures used in group1 and 2.

INSERT FIGURE 4 AROUND HERE

Figure 4. Schematic representation of the experimental procedures applied in group 1 and group 2. (A) Participants in group 1 performed the body-landmarks localization task before (PRE) and after (POST) a training based on the active tool-use or observational tool-use. (B) Participants in group 2 underwent the audio-tactile interaction task (POST) after three different trainings (active tool-use, observational tool-use and cognitive session). In both groups, the order of the trainings has been counterbalanced among participants.

2.2.5. Data analysis

Body-landmarks localization task. For each participant, the mean estimated location of the elbow and wrist among trials was computed and the distance between the two landmarks was considered as an indirect measure of the perceived arm length. We then calculated an index of the bias in the perceived dimension with respect to the actual one (estimated dimension, e.g. Peviani and Bottini, 2018), as the ratio between the perceived and the real length of the arm. In this way, we obtained an index of *estimated arm length* with respect to the real length of the arm, with values > 1 indicating an overestimation of the perceived arm length with regard to the real one and values < 1 referring to an underestimation (see Fig. 4). One subject was excluded from the final analysis because his index of *estimated arm length* at baseline (A_pre and O_pre) was greater than 2 standard deviations from the group mean. In addition, another subject was excluded because of a technical error during the acquisition of the real position of the landmarks. To compare the *estimated arm length* of the remaining 19 participants before and after the active and observational tool-use, we ran a 2x2 RM- ANOVA (Statistica Software 7.0 – StatSoft Inc.) with the within-in subject factors “Session” (pre or post) and “Training” (active or observational). Planned comparisons, Bonferroni corrected (with significance level set at 0.05/4 comparisons) were used to explore significant interactions. Moreover, one sample t-tests against the value of 1, where 1 indicates the equivalence between the perceived and the real dimension, have been performed on each condition: active_pre, active_post, observational_pre, observational_post (significance level set at 0.05/4 comparisons, Bonferroni corrected).

Audio-tactile interaction task. First, the accuracy of each participant was calculated to ensure that they detected correctly at least the 97% of the trials (bimodal and unimodal) (e.g. Bassolino et al., 2010; Serino et al., 2015, 2007). Second, outliers were discarded if participants’ RTs exceeded two standard deviations from the average of RTs collected within all the repetitions of any specific distance (Ronga et al., 2018; Sarasso et al., 2019). This procedure was applied for both bimodal and unimodal trials. The average number of discarded responses among all the types of stimulation in all conditions (active, cognitive and observational) was around 5%. Then, subjects’ RTs in response to T, TANear and TAFar conditions were averaged.

To investigate the multisensory integration effect (i.e. significant differences between unimodal and bimodal stimulation) and to explore the presence/absence of a space-dependent effect (i.e. significant differences between near and far positions), we ran a 3x3 RM- ANOVA (Statistica Software 7.0 – StatSoft Inc.) with RTs as dependent variable, and “Condition” (three levels: T, TANear and TAFar) and “Training” (three levels: cognitive, active, observational) as within-subject factors. Planned comparisons were performed to investigate a possible significant interaction effect (significance was set at =0.05/18 comparisons, Bonferroni corrected).

3. Results

3.1.**Differentials effects on active and observational tool-use on BR and PPS representation**

Body-landmarks localization task. Results to the body-landmarks localization task are represented in Figure 5.

The repeated measures ANOVA performed on the estimated arm length, with “Training” (active or observational) and “Session” (pre and post training session) as within subjects factors, revealed a significant interaction between “Training and Session” (F(1,18) =7.11; p =0.016; η_p^2 =0.283) (main significant effects: training [F(1,18) =8.27; p =0.010; η_p^2 =0.314], session [F(1,18) =15.4; p <0.001; η^2 =0.462]). Planned comparisons, Bonferroni corrected (with significance level set at 0.05/4=0.0125) revealed that the arm length before (pre) the active tool-use training and after (post) were significantly different (*active_pre* vs *active_post*: p= 0.001; mean±SD: *active_pre*: 0.89±0.12 mm; *active_post*: 1.03±0.18 mm), with the arm length perceived significant longer after active tool-use than at baseline. In contrast, the perceived arm length before and after (post) the observational tool-use training was not significantly different (*observational_pre* vs *observational_post*: p= 0.91; mean±SD: *observational_pre*: 0.86±0.16 mm; *observational_post*: 0.86±0.21 mm). This finding indicates that the observational tool-use training does not induce a significant change in the perception of the arm length. Accordingly, further planned comparisons show that even if the perceived arm length at the baselines was not significantly different (*active_pre* vs *observational_pre*: p= 0.35), the perceived arm length after the active training was significantly larger than after the observational tool-use (*active_post* vs *observational_post*: p= 0.003, see Fig.4).

We noted also that the perceived arm length was statistically different from 1-value (where 1 indicates the equivalence between the perceived and the real length of the arm, see Fig.4) at baseline (active_pre, p value<0.0125, significance level set at 0.05/4 comparisons, Bonferroni corrected), while this was not the case after the active tool-use (p=0.47). This indicates that the significant underestimation observed at the baseline was no more significant after active tool-use. This effect was not found after observational tool-use, where the perceived arm length remained statistically different from 1-value both before and after the training (all p values<0.0125, significance level set at 0.05/4 comparisons, Bonferroni corrected).

INSERT FIGURE 5 AROUND HERE

Figure 5. The figure shows the results of the body-landmarks localization task (BL), expressed as the ratio between the perceived and the real arm length (mean ± SD). Values below 1 (dashed line) indicate an underestimation of the perceived dimension with respect to the real one, while values above 1 indicate an overestimation. After (post) active tool-use (dark red) the arm length was perceived significantly longer than before (pre), while no significant changes emerged after observational tool-use (green). The perceived arm length was statistically smaller than 1 (i.e. underestimation) at the baselines and after observational tool-use, but not after the active training. Error bars represents SD; asterisks indicate significant differences ($p<0.0125$, significance level set at 0.05/4 comparisons, Bonferroni corrected).

Audio-tactile interaction task with corrected RTs

Results to the audio-tactile interaction task are represented in Figure 6.

The repeated measures ANOVA on RTs revealed a main effect of Condition ($F=(40;2)=26.609$; $p<0.001$; $\eta_p^2=0.571$), with overall faster RTs in TANear (mean±SD: 353.63±113.12 ms) and TAFar (mean±SD: 367.96±113.00 ms) as compared to T (mean±SD: 390.63±104.91 ms) (TANear vs T: $p<0.001$; TAFar vs T: $p=0.001$). Crucially, RTs in TANear were faster than those in than TAFar (TANear vs TAFar: $p<0.001$). The main effect of Training was not significant ($F=(40;2)=0.648$; $p=0.529$; $\eta_p^2=0.031$). Crucially, we found a significant interaction between “Condition and Training”, ($F=(80;2)=3.192$; $p=0.017$; $\eta_p^2=0.138$). Planned comparisons corrected with Bonferroni ($p<0.003$, significance level set at 0.05/18 comparisons) showed that after the cognitive training RTs were faster in TANear (mean±SD: 350.29±126.90 ms) as compared to TAFar (mean±SD: 373.31±134.96 ms) and T (mean±SD: 401.08±128.91 ms), whereas RTs in TAFar and T did not significantly differ (TANear vs T: $p<0.001$; TANear vs TAFar: $p<0.001$; TANear vs TAFar: $p=0.011$). After the active training we found significantly differences comparing bimodal conditions with unimodal tactile condition, with smaller RTs in TANear (mean±SD: 367.31±123.48 ms) and TAFar (mean±SD: 370.09±118.64 ms) than in T (mean±SD: 392.05±114.52 ms), while RTs in TANear and TAFar were not significantly different (TANear vs T: $p<0.001$; TAFar vs T: $p<0.001$; TANear vs TAFar: $p=0.347$). Moreover, after the observational training, RTs were faster in TANear (mean±SD: 343.55±107.64 ms) as compared to TAFar (mean±SD: 359.69±107.75 ms) and T (mean±SD: 378.73±97.40 ms), whereas RTs in TAFar and T did not significantly differ (TANear vs T: $p<0.001$; TANear vs TAFar: $p<0.001$; TANear vs

TAFar: p=0.019). Finally, as expected, no significant differences emerged on RTs in T (unimodal tactile condition) among the different trainings (i.e. active, observational, and cognitive) (all p values>0.272).

Overall, these results suggest that, after all the three trainings, a greater RT facilitation occurred when the tactile stimulation was coupled with a sound originating from near position, in line with the spatial congruency law and according to multisensory facilitation within PPS (e.g. Serino, 2019). Importantly, we found this RT facilitation also when the sound originated from the far position only after the active training, pointing out that the active tool-use, but not the observational tool-use and the cognitive task, induced a PPS remapping, eliminating the space-dependent effect of multisensory integration.

INSERT FIGURE 6 AROUND HERE

Figure 6. (A) Mean of reaction times (RTs) in the three conditions: after cognitive training (on the left), after active-tool use training (on the middle); after observational tool-use training (on the right). Only after active tool-use training, the two bimodal conditions (TA, tactile+auditory stimuli) did not significantly differ, suggesting that the PPS remapping occurs only when the subject actively use the tool. Error bars represents SEM; asterisks indicate significant differences ($p<0.003$, significance level set at 0.05/18 comparisons, Bonferroni corrected).

4. Discussion

The present study aimed at investigating whether the mere observation of someone else acting with a tool in far space impacts on bodily and spatial representations as execution. To answer this question, BR and PPS were assessed with a body-landmarks localization task and an audio-tactile interaction task. Our results show that, as expected, active tool-use induced a modulation of BR and PPS, respectively highlighted by an increased perceived length of the arm, and comparable multisensory facilitation on tactile responses due to near and far sounds after active training. On the contrary, such modulations were not found after observational tool-use, pointing out that a mere observational training is not sufficient to affect BR and PPS.

Body-landmarks localization task. The findings from the BL task, aiming to capture the implicit metric representations of the upper limb, suggest that participants underestimated the arm length (i.e. perceived length smaller than real length) at baseline (before the training) similarly in both conditions in agreement with earlier studies (e.g. Longo, 2017).

As expected, after the active condition, a significantly longer perception of the arm length after the training compared to the baseline was found. This is in line with an extension of the arm length after tool-use demonstrated in previous studies using the same task as in the present work (Canzoneri et al., 2013), an arm bisection task (Garbarini et al., 2015; Sposito et al., 2012), or by analysing free hand movements kinematics (Cardinali et al., 2009). In the present work, the increased perceived length of the used arm in the active condition could be also interpreted as a bias reduction (see Fig. 5), considering the fact that the post session was not statistically different from the 1 ratio representing the correct estimation of the perceived arm length. Importantly, the bias reduction in the arm length perception after active tool-use (Bassolino et al., 2014; Canzoneri et al., 2013; Cardinali et al., 2009; Sposito et al., 2012), could be interpreted as driven by the flow of sensorimotor information, as well the motor planning and intention, related to the active movement performed during the training, which contribute to update the representation and to correct the underestimation found at the baseline.

In contrast, after the observational condition, the arm length was not statistically different from baseline: both pre and post assessment demonstrated an underestimation of the arm length (values significantly different from 1). This result is also line with a previous study demonstrating no change in BR after observational tool-use in older adults (Garbarini et al., 2015). Considering together the two studies, it is possible to suggest that observing an actor using a tool while holding the same tool could be sufficient to modify BR neither in young nor in elderly participants. It has been demonstrated that action observation could activate motor areas (Jeannerod, 2001), but here these results suggest that a central brain activation of motor region through observation is not enough to shape BR. If BR modifications could be mainly mediated by multisensory and sensorimotor information related to *one's own* body, it is possible that the mere visual observation of *someone else* using the tool could not be sufficient to induce alterations of one's own BR (Bassolino et al., 2014b), because of a lack of updated afferent information from ones' own body. In line with this assumption, a previous study on a patient with proprioception impairment demonstrated that only visual information of the movement in absence of the perception of one's own arm in motion is not sufficient to induce an incorporation of the tool, pointing out the role of afferent information in shaping BR (Cardinali et al., 2016). However, recently Bruno and colleagues (Bruno et al., 2019) showed that the mere sensorimotor feedback of the arm movement action is not sufficient either to induce plastic changes of BR. Indeed, authors found no plastic changes in BR when participants performed a passive tool-use. In that study, the active session consisted of the execution of “enfold-and-push” movements with a tool in order to place cubes in a target area; instead, in the passive session, participants were asked to be completely relaxed, and the movements towards the target area were performed with robotic assistance. Results displayed a significant increase of the perceived arm length only after active training, suggesting that the passive execution of tool action is not enough to shape the BR. Together, these two studies in line with the present results seem to suggest that sensorimotor feedback are necessary to induce plasticity of BR (Cardinali et al., 2016), although not sufficient (Bruno et al., 2019). This may indicate that the congruency between sensorimotor feedback, and motor planning and intention are crucial to induce a plastic modulation of BR.

Audio-tactile interaction task. The audio-tactile interaction task aimed at investigating the effect of active and observational tool-use on the PPS plasticity exploiting the multisensory integration phenomenon, i.e. speeding up in RTs to tactile stimuli due to simultaneous auditory stimuli appearing near the hand, within PPS (e.g. Bassolino et al., 2010; Sambo and Forster, 2009; Serino et al., 2007). As expected, after the active tool-use condition, we found comparable RTs in near and in far position (see Fig 5A), pointing out that following tool-use the auditory stimulus delivered in the far space induced similar multisensory facilitation as in the near space. The present results are fully in agreement with previous studies (Bassolino et al., 2010; Biggio et al., 2017; Iriki et al., 1996; Neppi-Mòdona et al., 2007; Ronga et al., *under review*; Serino et al., 2007), showing that tool-use results in a modification of PPS by extending the typical multisensory integration of the space surrounding the body to the farther spatial sector where the tool is used. In contrast, after cognitive training (i.e. a visual discrimination task performed at a distance from participants’ chest corresponding to the length of tool radius action), we found a greater multisensory facilitation effect in the near space as compared to the far space (see Fig. 6A), revealed by significantly faster RTs when the auditory stimulus occurred close to the stimulated hand as compared to when it occurred in far positions. This finding excludes that an attentional shift towards the far space is the only determinant of PPS remapping after tool-use (Holmes, 2012). Similarly to cognitive training, also following observational tool-use we found a differential behavioural performance between bimodal near and bimodal far conditions (see Fig. 6A). These results suggest that the observation of another individual performing a tool-use does not modify the PPS representation. However, some effects of tool-use observation on space representation were found in previous works. In particular, Costantini and colleagues (2011) showed that observing an alien arm performing actions extends the reaching space of the observers if they hold a similar tool in the hand. It could be then possible that during the observation of goal-oriented actions in the extrapersonal space, a mirror mechanism is activated (Rizzolatti et al., 2001) that is robust enough to remap a spatial representation of the observer in an explicit reachability task such as that employed in the Costantini's et al. (2011) study, but not sufficient to significantly modify the implicit multisensory representation of the observers' PPS as evaluated with the present paradigm. Accordingly, in the Costantini and colleagues' work, the mirrored movement experienced during the training (i.e. grasping with a rake) reflects the same movement involved during the reachability judgment task (i.e. grasping); thus, it is reasonable to hypothesize that the effect may be due to the fact that the "grasping network" is recruited both in the training and in the task phase. Furthermore, we can also speculate that, in Costantini and colleagues' work, the visuo-motor similarity between observational tool-use training, based on visual perception, and the post-training task, again based on vision, may have induced a direct transfer from tool-use training to the post-training task. On the contrary, in our present work we exploited a post-training task based on audio-tactile interaction, where vision was not involved, thus possibly leading to the lack of significant effects after observational tool-use. However, the observational tool-use training in the present experiment was not simply based on visual perception, but also on the auditory effects of the action (i.e. the noise of the tool sliding on the table and the noise of the contact between the tool and the target wooden cubes), thus making unlikely an explanation of our results based on the absence of the visual component during the PPS task. In this regard, it is interesting to note that the effectiveness of active tool-use in modulating PPS has been previously tested with multimodal tasks always involving the same sensory modalities, which were pivotal in the realization of the tool-use training (i.e., a visuo-tactile tool-use training matched with a visuo-tactile multimodal task in (Forsberg et al., 2019); and an audio-tactile tool-use training matched with an audio-tactile multimodal task in (e.g. Canzoneri et al., 2013)). Interestingly, in the present study, the audio-tactile interaction task was preceded by a visuo-auditory-tactile tool-use training, thus providing evidence that tool-use dependent plasticity arises even when the post-training assessment task does not include all the sensory modalities involved in the training.

A third explanation refers to the kind of PPS assessed; Costantini and colleagues tested the reaching-related spatial representation, whereas our task specifically focused on PPS representation as the preferential space for multisensory integration, thus directly contributing to the emergence and maintenance of a coherent multimodal bodily self-representation (i.e., self-consciousness purpose – for a recent review see e.g., (Noel et al., 2018)). Hence, we can suppose a dissociation between a reaching-related spatial representation, assessed by Costantini and co-authors' task, and a multisensory PPS representation, assessed by the task in the present study, assuming a different effect of observation of another agent performing the tool-use in modifying such representations. The lack of remapping of multisensory PPS after observational tool-use may indicate that PPS plasticity could rely on the feedback related to the effects of the action in the far space, coupled with the sensory feedback arising from one's own hand during this movement. In line with this, Serino and colleagues (Serino et al., 2015) proposed that the plasticity of multisensory PPS is triggered by the association between synchronous tactile stimulation at the hand, due to holding the tool, and multisensory -auditory or visual stimulation - from the far space, where the tool is operated.

Similar dissociable effects of active and observational tool-use in BR and PPS representation

To sum up, the present findings suggest different effects both on the BR and PPS representation during the active and observational tool-use. In line with previous studies (Bassolino et al., 2014; Berti and Frassinetti, 2000; Biggio et al., 2017; Canzoneri et al., 2013; Cardinali et al., 2009; Sposito et al., 2012), after active tool-use, BR and PPS were modified. In particular, after active tool-use participants reported a longer perceived length of the arm than at baseline (group 1) and equally facilitated RTs to tactile stimuli when combined with near and far sounds (group 2). Crucially, no significant plastic effects in BR or PPS occur after a training of the same duration based on observational tool-use. More precisely, after observational tool-use, no significant modification of the perceived length of the arm occurred (group 1), and higher facilitation in RTs to tactile stimuli associated with near sounds as compared to far sounds occurred as in the control condition (cognitive) (group 2). The absence of effects on BR and PPS in the observational condition suggests that, at least in our sample, active tool-use is necessary to induce plastic changes of these representations, whereas tool-use observation is not sufficient. In line with this assumption, previous studies demonstrated that sensorimotor feedback is necessary, but not sufficient, to drive BR plasticity (Bassolino et al., 2010; Bruno et al., 2019; Cardinali et al., 2016). This evidence seems to highlight a fundamental role of motor intention and planning in reshaping own BR and PPS, as pointed out by previous studies that pinpointed the role of motor intention and motor planning in inducing tool-use related effects (Osiurak and Badets, 2014; Patané et al., 2019; Witt et al., 2005). This is also supported by evidence provided by Garbarini and coauthors (2015). They showed that brain-damaged hemiplegic patients, manifesting a pathological embodiment of someone else's arm, exhibited an increase of the perceived length of their forearm after a training phase in which an experimenter was aligned to them and performed movements with a tool in the far space. The crucial aspect of this study is that these patients, while observing the experimenter's arm performing the tool-action, were firmly convinced to perform it with their own (paralyzed) arm. It has been proposed that the pathological embodiment of the experimenter's arm movement automatically triggers intentional motor processes of the own arm that, in turn, induces a forearm length remapping comparable to that found in healthy subjects actually performing the tool-use training. Thus, these findings point out that having real motor intentions to move the tool, even in absence of actual movement execution, induces a modulation of BR. Coherently, BR and the reaching space (evaluated with a reaching distance estimation task) have been shown to be affected by the sense of agency (D'Angelo et al., 2018); in this study, BR and the reaching space were assessed after a training phase, in which participants virtually grasped objects by controlling the virtual hand in a 3D environment. In the training phase, the sense of agency was modulated introducing a synchronous condition, wherein participants were shown virtual hands movements responding in real-time to their own movements, and an asynchronous condition, wherein a 3-second delay was interposed between the participant's actual hand and the virtual hand movements. Crucially, only when subjects sensed agency for the virtual hand, induced by the synchronicity between motor and visual feedbacks, BR and the reaching space enlarged. Therefore, the modulation of BR seems strictly dependent to the sense of congruency between the intention to perform an action and the resulting sensorimotor feedback. Overall, this would suggest that motor planning and intention related to performing tool-actions and consequent sensorimotor feedback may play a crucial role in driving BR, and probably also PPS plasticity. Alternatively, two further explanations could account for the lack of BR and PPS modifications after observational tool-use. First, in the observational training the experimenter stood beside the participants, by keeping the arm in a posture anatomically compatible with that assumed by the participants during the action execution. This could evoke a "feeling of embodiment" towards the experimenter's arm in the participants. However, this feeling would be inconsistent with the observation of their own non-moving arm, thus creating a sort of conflict that, in turn, might have reduced the effects of the tool-use training. Second, previous studies showed that in order to evoke plastic changes in motor cortex activity and motor learning, action observation (as well as motor imagery) should be coupled with peripheral stimulations (Bisio et al., 2019, 2017b, 2017a, 2015a, 2015b; Bonassi et al., 2017), which were not present in our observational tool-use training. While the absence of a peripheral stimulation coupled with action observation could represent an explanation of our present results on BR and PPS, however, it worth noting that other researches pointed out effects on motor processes after action observation and motor imagery also in absence of afferent feedbacks (Bruno et al., 2020; Garbarini et al., 2014; Piedimonte et al., 2014).

In view of the foregoing, further studies would be addressed to investigate whether the mere motor intention and planning are sufficient to induce plastic changes of BR and PPS, or whether the congruency between the intention to perform an action and the resulting sensorimotor feedback are necessary to cause these modulations. Motor imagery could help to disentangle between the role of motor intention and sensorimotor consequences, allowing to isolate the contribution of motor planning. Motor imagery can be considered as a promising tool, also in light of previous results showing that kinematics of free-hand movements was affected after tool-use imagery, in a similar way to that previously documented after active tool-use (Baccarini et al., 2014). Then, if motor intention and motor planning are sufficient to induce a tool-related BR and PPS broadening, we should expect a modulation of these representations following tool-use imagery. Alternatively, if PPS, and also BR plasticity is triggered by the congruency between the intention to perform an action and the resulting actual sensorimotor feedback, we should expect any change on these representations after motor imagery-based tool-use, as found here after observational tool-use.

5. Conclusion

In conclusion, ~~the present findings seem to provide evidence that the observation of another person using a tool to interact with objects located in the far space is not sufficient to influence the plasticity of PPS and BR. Thus,~~ the dissociation found in the active and observational tool-use highlights differences between action execution and action observation, pointing out a crucial role of motor intention and planning and the related sensorimotor feedback in driving BR and PPS plasticity.

Acknowledgements

We thank Laura Taverna (Italian Institute of Technology) for her help in preparing Figure 1. This work was supported by the Swiss National Science Foundation, Ambizione Grant to MB (PZ00P1_161210), by “Fondation Mercier pour la Science” grant to MB, and by Bando Talenti della Società Civile 2019 (Goria Foundation, CRT foundation) to MG.

References

Baccarini, M., Martel, M., Cardinali, L., Sillan, O., Farnè, A., Roy, A.C., 2014. Tool use imagery triggers tool incorporation in the body schema. Front. Psychol. 5, 1–8. https://doi.org/10.3389/fpsyg.2014.00492

Bassolino, M., Campanella, M., Bove, M., Pozzo, T., Fadiga, L., 2014a. Training the motor cortex by observing the actions of others during immobilization. Cereb. Cortex 24, 3268–3276.

https://doi.org/10.1093/cercor/bht190

Bassolino, M., Finisguerra, A., Canzoneri, E., Serino, A., Pozzo, T., 2014b. Dissociating effect of upper limb non-use and overuse on space and body representations. Neuropsychologia 70, 385–392. https://doi.org/10.1016/j.neuropsychologia.2014.11.028

Bassolino, M., Sandini, G., Pozzo, T., 2015. Activating the motor system through action observation: Is this an efficient approach in adults and children? Dev. Med. Child Neurol. 57, 42–45. https://doi.org/10.1111/dmcn.12686

Bassolino, M., Serino, A., Ubaldi, S., Làdavas, E., 2010. Everyday use of the computer mouse extends peripersonal space representation. Neuropsychologia 48, 803–811. https://doi.org/10.1016/j.neuropsychologia.2009.11.009

Berti, A., Frassinetti, F., 2000. When Far Becomes Near : Remapping of Space. J. Cogn. Neurosci. 12, 415–420.

Biggio, M., Bisio, A., Avanzino, L., Ruggeri, P., Bove, M., 2017. This racket is not mine: The influence of the tool-use on peripersonal space. Neuropsychologia 103, 54–58. https://doi.org/10.1016/j.neuropsychologia.2017.07.018

Bisio, A., Avanzino, L., Biggio, M., Ruggeri, P., Bove, M., 2017a. Motor training and the combination of action observation and peripheral nerve stimulation reciprocally interfere with the plastic changes induced in primary motor cortex excitability. Neuroscience 348, 33–40. https://doi.org/10.1016/j.neuroscience.2017.02.018

Bisio, A., Avanzino, L., Gueugneau, N., Pozzo, T., Ruggeri, P., Bove, M., 2015a. Observing and perceiving: A combined approach to induce plasticity in human motor cortex. Clin. Neurophysiol. 126, 1212–1220. https://doi.org/10.1016/j.clinph.2014.08.024

Bisio, A., Avanzino, L., Lagravinese, G., Biggio, M., Ruggeri, P., Bove, M., 2015b. Spontaneous movement tempo can be influenced by combining action observation and somatosensory stimulation. Front. Behav. Neurosci. 9, 1–7. https://doi.org/10.3389/fnbeh.2015.00228

Bisio, A., Biggio, M., Avanzino, L., Ruggeri, P., Bove, M., 2019. Kinaesthetic illusion shapes the cortical plasticity evoked by action observation. J. Physiol. 597, 3233–3245.

https://doi.org/10.1113/JP277799

Bisio, A., Garbarini, F., Biggio, M., Fossataro, C., Ruggeri, P., Bove, M., 2017b. Dynamic shaping of the defensive peripersonal space through predictive motor mechanisms: When the “near” becomes “far.” J. Neurosci. 37, 2415–2424. https://doi.org/10.1523/JNEUROSCI.0371-16.2016

Bonassi, G., Biggio, M., Bisio, A., Ruggeri, P., Bove, M., Avanzino, L., 2017. Provision of somatosensory inputs during motor imagery enhances learning-induced plasticity in human motor cortex. Sci. Rep. 7, 1–10. https://doi.org/10.1038/s41598-017-09597-0

Borroni, P., Montagna, M., Cerri, G., Baldissera, F., 2005. Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. Brain Res. 1065, 115–124. https://doi.org/10.1016/j.brainres.2005.10.034

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. Front. Hum. Neurosci. 13, 1–9. https://doi.org/10.3389/fnhum.2019.00299

Bruno, V., Ronga, I., Fossataro, C., Galigani, M., Sacco, K., Garbarini, F., 2020. Long-term limb immobilization modulates inhibition-related electrophysiological brain activity. Neuroimage 116911. https://doi.org/10.1016/j.neuroimage.2020.116911

Buccino, G. , 2014. Action observation treatment: a novel tool in neurorehabilitation. Phil. Trans. R. Soc. B. 5; 369(1644): 20130185. https://doi: 10.1098/rstb.2013.0185

Bufacchi, R.J., Iannetti, G.D., 2018. An Action Field Theory of Peripersonal Space. Trends Cogn. Sci. 22, 1076–1090. https://doi.org/10.1016/j.tics.2018.09.004

Canzoneri, E., Magosso, E., Serino, A., 2012. Dynamic Sounds Capture the Boundaries of Peripersonal Space Representation in Humans. PLoS One 7, 3–10. https://doi.org/10.1371/journal.pone.0044306

Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., Serino, A., 2013a. Amputation and prosthesis implantation shape body and peripersonal space representations. Sci. Rep. 3, 1–8. https://doi.org/10.1038/srep02844

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013b. Tool-use reshapes the boundaries of body and peripersonal space representations. Exp. Brain Res. 228, 25–42. https://doi.org/10.1007/s00221-013-3532-2

Cardinali, L., Brozzoli, C., Luauté, J., Roy, A.C., Farnè, A., 2016. Proprioception is necessary for body schema plasticity: Evidence from a deafferented patient. Front. Hum. Neurosci. 10, 1–8. https://doi.org/10.3389/fnhum.2016.00272

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009. Tool-use induces morphological updating of the body schema (DOI:10.1016/j.cub.2009.05.009). Curr. Biol. 19, 1157. https://doi.org/10.1016/j.cub.2009.06.048

Cléry, J., Ben Hamed, S., 2018. Frontier of self and impact prediction. Front. Psychol. 9, 1–17. https://doi.org/10.3389/fpsyg.2018.01073

Costantini, M., Ambrosini, E., Sinigaglia, C., Gallese, V., 2011. Tool-use observation makes far objects ready-to-hand. Neuropsychologia 49, 2658–2663. https://doi.org/10.1016/j.neuropsychologia.2011.05.013

Costello, M.C., Bloesch, E.K., Davoli, C.C., 2015. Spatial Representations in Older Adults are Not Modified by Action: Evidence from Tool Use. Psychol. Aging 30, 656–668. https://doi.org/10.1037/pag0000029.Spatial

D'Angelo, M., di Pellegrino, G., Seriani, S., Gallina, P., Frassinetti, F., 2018. The sense of agency shapes body schema and peripersonal space. Sci. Rep. 8, 1–11. https://doi.org/10.1038/s41598-018-32238-z

de Vignemont, F., 2010. Body schema and body image-Pros and cons. Neuropsychologia 48, 669–680. https://doi.org/10.1016/j.neuropsychologia.2009.09.022

de Vignemont, F., Iannetti, G.D., 2015. How many peripersonal spaces? Neuropsychologia 70, 327–334. https://doi.org/10.1016/j.neuropsychologia.2014.11.018

Dell'Anna, A., Rosso, M., Bruno, V., Garbarini, F., Leman, M., Berti, A., 2020. Does musical interaction in a jazz duet modulate peripersonal space? Psychol. Res. https://doi.org/10.1007/s00426-020-01365-6 di Pellegrino, G., Làdavas, E., 2015. Peripersonal space in the brain. Neuropsychologia 66, 126–133. https://doi.org/10.1016/j.neuropsychologia.2014.11.011

Di Pellegrino, G., Ladavas, E., Farne', A., 1997. Seeing where your hands are [11]. Nature 388, 730. https://doi.org/10.1038/41921

Dijkerman, C., Lenggenhager, B., 2018. The body and cognition: The relation between body representations and higher level cognitive and social processes. Cortex 104, 133–139. https://doi.org/10.1016/j.cortex.2018.06.001

Duhamel, J.R., Bremmer, F., BenHamed, S., Graf, W., 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. Nature 389, 845–848. https://doi.org/10.1038/39865

Farnè, A., Làdavas, E., 2000. Dynamic size-change of hand peripersonal space following tool use. Neuroreport 11, 1645–1649. https://doi.org/10.1097/00001756-200006050-00010

Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I., 2007. Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. Neuroimage 37, 1315–1328. https://doi.org/10.1016/j.neuroimage.2007.06.008

Finisguerra, A., Maffongelli, L., Bassolino, M., Jacono, M., Pozzo, T., D'Ausilio, A., 2015. Generalization of motor resonance during the observation of hand, mouth, and eye movements. J. Neurophysiol. 114, 2295–2304. https://doi.org/10.1152/jn.00433.2015

Fogassi, L., 1996. Fogassi (1996a) Coding of peripersonal space in inferior premotor cortex (area F4).pdf 76.

Forsberg, A., O'Dowd, A., Gherri, E., 2019. Tool use modulates early stages of visuo-tactile integration in far space: Evidence from event-related potentials. Biol. Psychol. 145, 42–54. https://doi.org/10.1016/j.biopsycho.2019.03.020

Fuchs, X., Riemer, M., Diers, M., Flor, H., Trojan, J., 2016. Perceptual drifts of real and artificial limbs in the rubber hand illusion. Sci. Rep. 6. https://doi.org/10.1038/srep24362

Fuentes, C.T., Longo, M.R., Haggard, P., 2013. Body image distortions in healthy adults. Acta Psychol. (Amst). 144, 344–351. https://doi.org/10.1016/j.actpsy.2013.06.012

Gallese, V., Sinigaglia, C., 2010. The bodily self as power for action. Neuropsychologia 48, 746–755.

https://doi.org/10.1016/j.neuropsychologia.2009.09.038

Galli, G., Noel, J.P., Canzoneri, E., Blanke, O., Serino, A., 2015. The wheelchair as a full-body tool extending the peripersonal space. Front. Psychol. 6, 1–11. https://doi.org/10.3389/fpsyg.2015.00639

Gamberini, L., Seraglia, B., Priftis, K., 2008. Processing of peripersonal and extrapersonal space using tools: Evidence from visual line bisection in real and virtual environments. Neuropsychologia 46, 1298–1304. https://doi.org/10.1016/j.neuropsychologia.2007.12.016

Garbarini, F., D'Agata, F., Piedimonte, A., Sacco, K., Rabuffetti, M., Tam, F., Cauda, F., Pia, L., Geminiani, G., Duca, S., Graham, S.J., Berti, A., 2014. Drawing lines while imagining circles: Neural basis of the bimanual coupling effect during motor execution and motor imagery. Neuroimage 88, 100–112. https://doi.org/10.1016/j.neuroimage.2013.10.061

Garbarini, F., Fossataro, C., Berti, A., Gindri, P., Romano, D., Pia, L., della Gatta, F., Maravita, A., Neppi-Modona, M., 2015. When your arm becomes mine: Pathological embodiment of alien limbs using tools modulates own body representation. Neuropsychologia 70, 402–413. https://doi.org/10.1016/j.neuropsychologia.2014.11.008

Gescheider, G., 1997. "Chapter 4: Classical Psychophysical Theory"e, in: Associates, L.E. (Ed.), Psychophysics: The Fundamentals (3rd Ed.).

Ghilardi, M.F., Gordon, J., Ghez, C., 1995. Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. Journal of Neurophysiology 73, 2535-2539. https://doi.org/10.1152/jn.1995.73.6.2535

Graziano, M.S.A., Cooke, D.F., 2006. Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia 44, 845–859. https://doi.org/10.1016/j.neuropsychologia.2005.09.009

Graziano, M.S.A., Hu, X.T., Gross, C.G., 1997. Visuospatial properties of ventral premotor cortex. J. Neurophysiol. 77, 2268–2292. https://doi.org/10.1152/jn.1997.77.5.2268

Grivaz, P., Blanke, O., Serino, A., 2017. Common and distinct brain regions processing multisensory bodily signals for peripersonal space and body ownership. Neuroimage 147, 602–618. https://doi.org/10.1016/j.neuroimage.2016.12.052

Holmes, N.P., 2012. Does tool use extend peripersonal space? A review and re-analysis. Exp. Brain

Res. 218, 273–282. https://doi.org/10.1007/s00221-012-3042-7

Holmes, N.P., Spence, C., 2004. The body schema and the multisensory representation (s) of peripersonal space. Cogn Process 5, 94–105. https://doi.org/10.1007/s10339-004-0013-3.The

Iriki, A., Tanaka, M., Iwamura, Y., 1996. Coding of modified body schema during tool use by macaque postcentral neurones. Neuroreport. https://doi.org/10.1097/00001756-199610020-00010

Jeannerod, M., 2001. Neural simulation of action: A unifying mechanism for motor cognition. Neuroimage 14, 103–109. https://doi.org/10.1006/nimg.2001.0832

Kandula, M., Van der Stoep, N., Hofman, D., Dijkerman, H.C., 2017. On the contribution of overt tactile expectations to visuo-tactile interactions within the peripersonal space. Exp. Brain Res. 235, 2511–2522. https://doi.org/10.1007/s00221-017-4965-9

Ladavas, E., 1998. Visual peripersonal space centred on the face in humans. Brain 121, 2317–2326. https://doi.org/10.1093/brain/121.12.2317

Làdavas, E., Di Pellegrino, G., Farnè, A., Zeloni, G., 1998. Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. J. Cogn. Neurosci. 10, 581–589. https://doi.org/10.1162/089892998562988

Longo, M.R., 2017. Expansion of perceptual body maps near – But not across – The wrist. Front. Hum. Neurosci. 11, 1–9. https://doi.org/10.3389/fnhum.2017.00111

Longo, M.R., Azañón, E., Haggard, P., 2010. More than skin deep: Body representation beyond primary somatosensory cortex. Neuropsychologia 48, 655–668. https://doi.org/10.1016/j.neuropsychologia.2009.08.022

Longo, M.R., Haggard, P., 2012. Implicit body representations and the conscious body image. Acta Psychol. (Amst). 141, 164–168. https://doi.org/10.1016/j.actpsy.2012.07.015

Longo, M.R., Haggard, P., 2010. An implicit body representation underlying human position sense. Proc. Natl. Acad. Sci. U. S. A. 107, 11727–11732. https://doi.org/10.1073/pnas.1003483107

Makin, T.R., Holmes, N.P., Ehrsson, H.H., 2008. On the other hand: Dummy hands and peripersonal space. Behav. Brain Res. 191, 1–10. https://doi.org/10.1016/j.bbr.2008.02.041

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, 580–585. https://doi.org/10.1016/S0028-3932(00)00150-0

Maravita, A., Iriki, A., 2004. Tools for the body (schema). Trends Cogn. Sci. 8, 79–86. https://doi.org/10.1016/j.tics.2003.12.008

Maravita, A., Spence, C., Driver, J., 2003. Multisensory integration and the body schema: Close to hand and within reach. Curr. Biol. 13, 531–539. https://doi.org/10.1016/S0960-9822(03)00449-4

Martel, M., Cardinali, L., Roy, A.C., Farnè, A., 2016. Tool-use: An open window into body representation and its plasticity. Cogn. Neuropsychol. 33, 82–101. https://doi.org/10.1080/02643294.2016.1167678

Medina, J., Coslett, H.B., 2011. From Maps To Form To Space_2010.Pdf 48, 1–19. https://doi.org/10.1016/j.neuropsychologia.2009.08.017.From

Neppi-Mòdona, M., Rabuffetti, M., Folegatti, A., Ricci, R., Spinazzola, L., Schiavone, F., Ferrarin, M., Berti, A., 2007. Bisecting lines with different tools in right brain damaged patients: The role of action programming and sensory feedback in modulating spatial remapping. Cortex 43, 397–410. https://doi.org/10.1016/S0010-9452(08)70465-9

Nicholls, M.E.R., Thomas, N.A., Loetscher, T., Grimshaw, G.M., 2013. The flinders handedness survey (FLANDERS): A brief measure of skilled hand preference. Cortex 49, 2914–2926. https://doi.org/10.1016/j.cortex.2013.02.002

Noel, J.P., Blanke, O., Serino, A., 2018. From multisensory integration in peripersonal space to bodily self-consciousness: From statistical regularities to statistical inference. Ann. N. Y. Acad. Sci. https://doi.org/10.1111/nyas.13867

Osiurak, F., Badets, A., 2014. Pliers, not fingers: Tool-action effect in a motor intention paradigm. Cognition 130, 66–73. https://doi.org/10.1016/j.cognition.2013.09.005

Patané, I., Cardinali, L., Salemme, R., Pavani, F., 2019. Action Planning Modulates Peripersonal Space. J. Cogn. Neurosci. 31. https://doi.org/https://doi.org/10.1162/jocn_a_01349

Peviani, V., Bottini, G., 2018. The distorted hand metric representation serves both perception and action. J. Cogn. Psychol. 30, 880–893. https://doi.org/10.1080/20445911.2018.1538154

Piedimonte, A., Garbarini, F., Rabuffetti, M., Pia, L., Berti, A., 2014. Executed and imagined bimanual movements: A study across different ages. Dev. Psychol. 50, 1073–1080. https://doi.org/10.1037/a0034482

Radman, Z., 2013. The Hand, an Organ of the Mind. What the Manual Tells the Mental. MIT Press.

Riva, G., 2018. The neuroscience of body memory: From the self through the space to the others. Cortex 104, 241–260. https://doi.org/10.1016/j.cortex.2017.07.013

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192. https://doi.org/10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., Fadiga, L., Fogassi, L., Gallese, V., 1997. The space around us. Science (80-.). 277, 190–191. https://doi.org/10.1126/science.277.5323.190

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms and imitation of action 2, 1–10.

Romano, D., Uberti, E., Caggiano, P., Cocchini, G., Maravita, A., 2019. Different tool training induces specific effects on body metric representation. Exp. Brain Res. 237, 493–501. https://doi.org/10.1007/s00221-018-5405-1

Ronga, I., Bruno, V., Galigani, M., Castellani, N., Rossi Sebastiano, A., Valentini, E., Fossataro, C., Neppi-Modona, M., Garbarini, F., n.d. Seeming confines: electrophysiological evidence of peripersonal space remapping following tool-use in humans.

Ronga, I., Sarasso, P., Fossataro, C., Salatino, A., Garbarini, F., Ricci, R., Neppi-Modona, M., 2018. Everything is illuminated: Prismatic adaptation lowers visual detection threshold in normal subjects. J. Exp. Psychol. Hum. Percept. Perform. 44, 1619–1628. https://doi.org/10.1037/xhp0000559

Salomon, R., Noel, J.P., Łukowska, M., Faivre, N., Metzinger, T., Serino, A., Blanke, O., 2017. Unconscious integration of multisensory bodily inputs in the peripersonal space shapes bodily self-consciousness. Cognition 166, 174–183. https://doi.org/10.1016/j.cognition.2017.05.028

Sambo, C.F., Forster, B., 2009. An ERP investigation on visuotactile interactions in peripersonal and extrapersonal space: Evidence for the spatial rule. J. Cogn. Neurosci. 21, 1550–1559. https://doi.org/10.1162/jocn.2009.21109

Sarasso, P., Ninghetto, M., Salatino, A., Ronga, I., Bongiardina, A., Iarrobino, I., Neppi-Modona, M., Ricci, R., 2019. Everything is (still) illuminated: Dual right cathodal-left anodal tDCS of PPC prevents fatigue on a visual detection task. Brain Stimul. 12, 187–189. https://doi.org/10.1016/j.brs.2018.09.017

Schwoebel, J., Coslett, H.B., 2005. Evidence for multiple, distinct representations of the human body. J. Cogn. Neurosci. 17, 543–553. https://doi.org/10.1162/0898929053467587

Serino, A., 2019. Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self. Neurosci. Biobehav. Rev. 99, 138–159. https://doi.org/10.1016/j.neubiorev.2019.01.016

Serino, A., Bassolino, M., Farnè, A., Làdavas, E., 2007. Extended multisensory space in blind cane users. Psychol. Sci. 18, 642–648. https://doi.org/10.1111/j.1467-9280.2007.01952.x

Serino, A., Canzoneri, E., Marzolla, M., di Pellegrino, G., Magosso, E., 2015. Extending peripersonal space representation without tool-use: Evidence from a combined behavioral-computational approach. Front. Behav. Neurosci. 9, 1–14. https://doi.org/10.3389/fnbeh.2015.00004

Serino, A., Haggard, P., 2010. Touch and the body. Neurosci. Biobehav. Rev. 34, 224–236. https://doi.org/10.1016/j.neubiorev.2009.04.004

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, 2187–2194. https://doi.org/10.1016/j.neuropsychologia.2012.05.022

Stefan, K., Cohen, L.G., Duque, J., Mazzocchio, R., Celnik, P., Sawaki, L., Ungerleider, L., Classen, J., 2005. Formation of a motor memory by action observation. J. Neurosci. 25, 9339–9346. https://doi.org/10.1523/JNEUROSCI.2282-05.2005

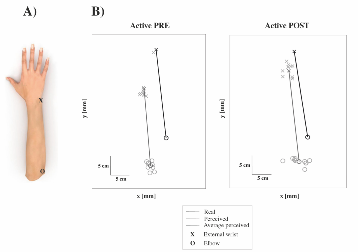
Tamè, L., Azañón, E., Longo, M.R., 2019. A conceptual model of tactile processing across body features of size, shape, side, and spatial location. Front. Psychol. 10.

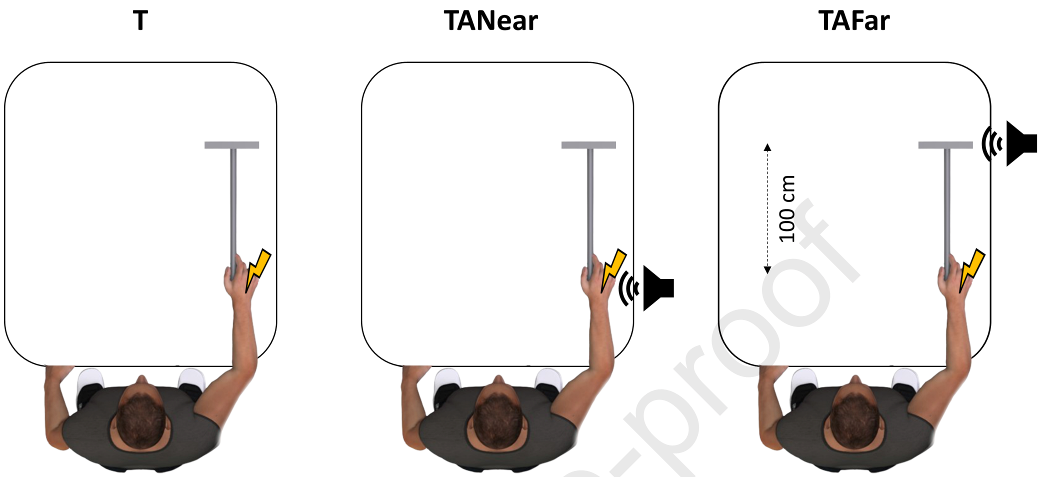
https://doi.org/10.3389/fpsyg.2019.00291

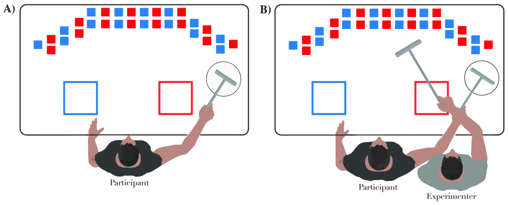
Teneggi, C., Canzoneri, E., Di Pellegrino, G., Serino, A., 2013. Social modulation of peripersonal space boundaries. Curr. Biol. 23, 406–411. https://doi.org/10.1016/j.cub.2013.01.043

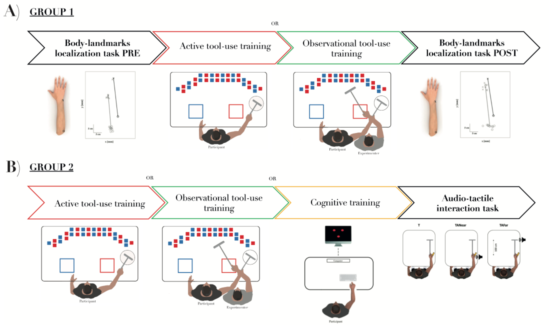
Wann, J.P., Ibrahim, S.F., 1992. Does limb proprioception drift? Exp. Brain Res. 91, 162–166. https://doi.org/10.1007/BF00230024

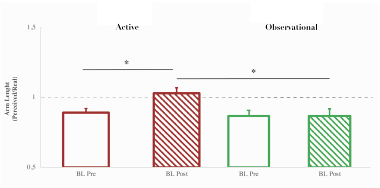
Witt, J.K., Proffitt, D.R., Epstein, W., 2005. Tool use affects perceived distance, but only when you intend to use it. J. Exp. Psychol. Hum. Percept. Perform. 31, 880–888. https://doi.org/10.1037/0096-1523.31.5.880

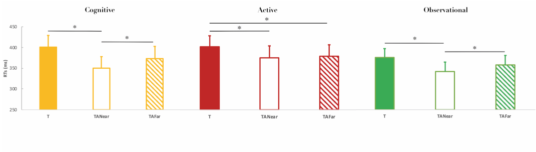

A)
X
O
B)
Active PRE
Active POST
y [mm]
5 cm
5 cm
x [mm]
y [mm]
5 cm
5 cm
x [mm]
Real
Perceived
Average perceived
X External wrist
O Elbow


T
TANear
TAFar
100 cm


A)
B)
Participant
Participant
Experimenter


A)
GROUP 1
OR
Body-landmarks localization task PRE
Active tool-use training
Observational tool-use training
Body-landmarks localization task POST
y [mm]
x [mm]
5 cm
Participant
Participant
Experimenter
B)
GROUP 2
OR
OR
Active tool-use training
Observational tool-use training
Cognitive training
Audio-tactile interaction task
Participant
Participant
Experimenter
Computer
Participant
T
TANear
TAFar
100 cm


Active
Observational
1,5
1
0,5
Arm Lenght
(Perceived/Real)
*
*
BL Pre
BL Post
BL Pre
BL Post


Cognitive
Active
Observational
RTs (ms)
450
400
350
300
250
*
*
*
*
*
*
T
TANear
TAFar
T
TANear
TAFar
T
TANear
TAFar

- **Highlight**

1. Does observational tool-use affect body and peripersonal space representations?
2. A longer perceived arm length is reported after active but not observational tool-use
3. Active, but not observational tool-use induces a peripersonal space remapping
4. Observational tool-use is not sufficient to affect body and space representations
5. Motor intention and sensory feedback seem necessary to alter these representations