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RESEARCH ARTICLE

Tool-use reshapes the boundaries of body and peripersonal space representations

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Abstract Interaction with objects in the environment typically requires integrating information concerning the object location with the position and size of body parts. The former information is coded in a multisensory representation of the space around the body, a representation of peripersonal space (PPS), whereas the latter is enabled by an online, constantly updated, action-orientated multisensory representation of the body (BR). Using a tool to act upon relatively distant objects extends PPS representation. This effect has been interpreted as indicating that tools can be incorporated into BR. However, empirical data showing that tool-use simultaneously affects PPS representation and BR are lacking. To study this issue, we assessed the extent of PPS representation by means of an audio-tactile interaction task and BR by means of a tactile distance perception task and a body-landmarks localisation task, before and after using a 1-m-long tool to reach far objects. Tool-use extended the representation of PPS along the tool axis and concurrently shaped BR; after tool-use, subjects perceived their forearm narrower and longer compared to before tool-use, a shape more similar to the one of the tool. Tool-use was necessary to induce these effects, since a pointing task did not affect PPS and BR. These results show that a brief training with a tool induces plastic changes both to the perceived dimensions of the body part acting upon the tool and to the space around it, suggesting a strong overlap between peripersonal space and body representation.

Keywords Peripersonal space · Body representation · Plasticity · Multisensory integration

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Introduction

In order to interact with objects in space, in either reaching an interesting stimulus or avoiding potential harm, the human brain needs to integrate information about the position and shape of body parts and information about the position and movements of objects in relation to the body. This bodily and spatial information is strictly linked, since the brain needs to represent the space around us mainly with reference to the body.

On the one hand, the brain holds an accurate multisensory representation of the body (body representation—BR). Information related to the shape, dimensions and positions of body parts is computed from incoming multisensory signals from the physical body: somatosensory as well as proprioceptive and kinaesthetic inputs coming from skin, joints and muscles, and also visual and auditory information referring to the different body parts are integrated to generate a sensory-motor representation of the body that is critical for action (Head and Holmes 1911; Gallagher 2005; Medina and Coslett 2010; Longo et al. 2010; Serino and Haggard 2010; de Vignemont 2010).

On the other hand, the notion of peripersonal space (PPS) captures the idea of a portion of space immediately surrounding the body (near space), where external objects are located with respect to body parts, as compared to the far space. In monkeys, neurophysiological studies described bimodal and trimodal neurons—located particularly in the ventral premotor cortex and in the posterior parietal cortex—with a tactile receptive field centred on a specific body part (head, face neck, trunk or shoulders) and a visual (Duhamel et al. 1998; Graziano et al. 1994, 1997; Rizzolatti et al. 1981) and/or an auditory (Graziano et al. 1999; Schlack et al. 2005) receptive field overlapping the tactile RF and extending in depth for about 30 cm. Tactile and visual RFs are in spatial register: if the body part where the tactile RF is anchored moves, the visual RF shifts congruently. This multisensory space is enabled by integration of tactile and proprioceptive information concerning specific body parts and visual (Rizzolatti et al. 1981; Graziano et al. 1994; Làdavas et al. 1998) and/or acoustic (Graziano et al. 1999; Farnè and Làdavas 2002) inputs related to objects presented in a limited portion of space surrounding the same body parts. PPS representation is particularly sensitive to stimuli approaching towards or receding from the body (Colby et al. 1993; Graziano et al. 1997; Fogassi et al. 1996). Moreover, PPS representation has a clear sensory-to-motor function: coding the spatial position and dynamics of an external stimulus with respect to a part of the body potentially interacting with it is fundamental in order to approach towards an interesting object (Rizzolatti et al. 1997) or evade a potential threat (Graziano and Cooke 2006).

A critical property of PPS representation is that it is dynamically modified through experience: using a tool to reach objects in far space extends the limits of PPS representation. In monkeys, Iriki et al. (1996) showed that hand-centred visual RFs of neurons located in the intraparietal sulcus elongated after a training period of using a rake to retrieve pieces of food placed at a distance. Further neuropsychological studies on extinction patients demonstrated that after using a tool to reach distant objects, crossmodal extinction for a tactile stimulus presented on the contralesional hand increased when a visual stimulus was presented at the tip of the tool, as compared to before tool-use (Farnè et al. 2005; Farnè and Làdavas 2000; see also Maravita et al. 2001). In healthy subjects, tool-use may increase the impact of far visual distracters on tactile discrimination (Holmes et al. 2004; Maravita et al. 2002). An extension of the limits of multisensory integration from the PPS to the tool's action space has been shown also in healthy subjects after short- (Serino et al. 2007) and long-term (Serino et al. 2007; Bassolino et al. 2010) tool-use experiences. Taken together, these studies show that the extent of PPS representation is dynamically shaped as a function of where subjects act upon external objects, that is, their action space (Gallese and Sinigaglia 2010; but see Holmes et al. 2007, and Holmes 2012, for a different interpretation of these effects).

Some authors (i.e. Iriki et al. 1996; Maravita and Iriki 2004) have proposed that the extension of PPS after tool-use reflects a plastic modification in BR, such that the tool is incorporated as a part of the body (Berlucchi and Aglioti 1997; Critchley 1979; Head and Holmes 1911; Holmes and Spence 2006; Maravita 2006). BR indeed should be plastic enough to update accordingly to slow and fast changes the body undergoes with time. However, the majority of these previous studies testing the effects of tool-use showed a modification in the effect of visual and/or auditory stimuli presented near or far from the body (at the tip of the tool) on processing of simultaneously presented tactile stimuli; they did not directly show a change in the representation of the body itself after tool-use. Instead, in these studies, tool incorporation has been only indirectly demonstrated through perceptual changes in PPS representations. Three recent papers demonstrated a specific change in BR following tool-use. Cardinali et al. (2009a) showed that kinematics of arm movements during hand grasping changed after pincers were used to grasp objects. This effect was also associated with a change in the localisation of tactile stimuli on the arm. In a recent study, the same group (Cardinali et al. 2011) tested whether the effects of tool-use on body representation were specific for tasks requiring a motor response (pointing to a body part) or a perceptual judgement (localising a body part on a ruler), in order to investigate whether plasticity after tool-use occurred on a representation of the body used for action (i.e. the so-called Body Schema) or for perception (i.e. the so-called Body Image; see Dijkerman and de Haan 2007; de Vignemont 2010; Gallagher 1986). They found that perception of forearm length increased after tool-use for both tasks, but only when the input for the task (which body part was to localise) was given tactilely (by touching the target body part) and not verbally (by naming the target body part). Finally, Sposito et al. (2012) demonstrated a change in the internal representation of body part size (i.e. the forearm) following a training with a functional tool. Interestingly, the length of the tool and the extent to which action capability was influenced affected the occurrence of plastic changes in body representation, resulting in an increase in the perceived forearm's length after tool-use.

These motor and somatosensory effects of tool-use suggested that tool-use could influence the perceived representation of the internal size of body parts. However, these findings cannot demonstrate a direct link between the effects of tool-use on PPS representation and the modification in BR, because in the cited literature these tasks have been specifically designed to investigate changes in body metrics only. The aim of the present study is to directly test whether using a functional tool to act upon objects at a distance concurrently affects both space and body representation in the same sample of subjects, using different tasks that specifically tap into PPS representation and BR, by considering features that mainly define these representations. In order to assess the extension of the multisensory PPS representation in a functionally and ecologically valid condition, we used a new *audio-tactile interaction task* recently developed by our group (Canzoneri et al. 2012). In order to measure the extension of BR, we assessed the perceived dimensions of the forearm by using two different tasks. In a *tactile distance perception task*, participants received two pairs of tactile stimuli, one on the forehead (as a reference body part) and one on the forearm (target body part), and they were asked to judge whether the distance between the two stimuli was larger on the forehead or on the forearm. This task allowed assessing implicitly the perceived representation of body part size. In a *body-landmarks localisation task,* instead, participants were asked to localise two anatomical landmarks, specifically the wrist and the elbow, by verbally indicating when a moving marker overlapped with the felt position of these occluded body parts. This task explicitly assesses a representation of the arm metric properties without involving any tactile signals or a comparison between two different body parts (see also Longo and Haggard 2010; Cardinali et al. 2011; Lopez et al. 2012). In Experiment 1A, participants performed the audio-tactile interaction task and the tactile distance perception task, before and after a training session with a tool. In Experiment 1B, in order to provide evidence that a context-dependent bias applies in the case of the tactile distance perception task used here to assess the perceived dimension of the forearm, we run two further control experiments, a *visual analogue* and a *tactile analogue* of the current tactile distance perception task.

In Experiment 2, in order to provide further evidence for a change in the representation of the arm size, participants performed the tactile distance perception task and the body-landmarks localisation task after the same training with a tool as the one used in Experiment 1A. Finally, in order to demonstrate that any change in PPS and BR was actually due to tool-use, and not to a generic effect of movement, attention, or simply repetition of the tasks, in Experiment 3 we evaluated both PPS representation and BR with the same tasks used in Experiment 1A before and after a control training, consisting in pointing to objects placed in different positions in far space.

Experiment 1

In this experiment, we measured PPS representation by means of the audio-tactile interaction task, and BR, by means of the tactile distance perception task, before and after a training session, consisting in using a tool with the right arm to retrieve objects placed in different positions in far space for 20 min (tool-use training, Experiment 1A). In order to demonstrate that a context-dependent bias applies in the case of distance perception, we conducted a visual analogue and a tactile analogue of the present tactile distance perception task (Experiment 1B).

Experiment 1A

Methods

Participants

Twelve healthy subjects (11 females, mean age 25 years) participated in the study. All subjects were right-handed and had normal hearing and touch. All subjects, students at the University of Bologna, gave their informed consent to participate in the study, which was approved by the local Ethical Committee of the Department of Psychology, University of Bologna, and was performed in accordance with the Declaration of Helsinki.

Materials and procedures

Audio-tactile interaction task Procedures for this task were similar to those of Canzoneri et al. (2012). During the task, subjects were blindfolded and sat down with their right arm resting in a prone position on a table beside them. During each trial, a sound (pink noise) was presented for 3,000 ms. Two types of sound were used: *IN* sound, which gave the impression of approaching towards the subject, and *OUT* sound, which instead gave the impression of receding from the subject. The sounds were generated by two loudspeakers, one placed on the table in the proximity of the forearm and the other one placed on the floor, at a distance of ~100 cm from the near loudspeaker, thus far from the forearm.

Along with the auditory stimulation, in the 60 % of trials, subjects were also presented with a tactile stimulus placed on the hairy surface of the forearm. The remaining trials (40 % out of total) were catch trials with auditory stimulation only. Subjects were asked to respond vocally to the tactile target, when present, saying “TAH” as soon as possible, trying to ignore the auditory stimulus. Tactile RTs were recorded by means of a voice-activated relay. For each trial, the sound was preceded and followed by 1,000 ms of silence. The critical manipulation was that the tactile stimulus was delivered at different temporal delays (from T1 to T5) from the onset of the stimulus, both for IN and OUT sounds. Temporal delays for the tactile stimulus were set as follows: *T1*, tactile stimulation administered at 300 ms after the sound onset (corresponding to 1,300 ms from the beginning of the trial); *T2*, at 800 ms from sound onset (at 1,800 ms from trial beginning); *T3*, at 1,500 ms from sound onset (at 2,500 ms from trial beginning); *T4*, at 2,200 ms from sound onset (at 3,200 ms from trial beginning); and *T5*, at 2,700 ms from sound onset (at 3,700 ms from trial beginning; see Fig. 1A).

In this way, tactile stimulation occurred when the sound source was perceived at different locations with respect to the body: that is, close to the body, at high temporal delays for the IN sound and at low temporal delays for the OUT sound; and far from the body, at low temporal delays for the IN sound and at high temporal delays for the OUT sound.

The rationale of the task is that stimuli from different sensory modalities interact more effectively with one another when presented within the same spatial representation (Stein and Meredith 1993). In line with this principle of multisensory integration, we have recently showed that RTs to tactile stimuli progressively decrease as much as the sound is perceived as approaching the body, and conversely increase as much as the sound is perceived as receding from the body (Canzoneri et al. 2012). Thus, the function describing the relationship between tactile RTs and the perceived position of sounds in space at the occurrence of the tactile stimulation can be used to measure the boundaries of PPS representation along a continuum between near and far space.

Tactile distance perception task Blindfolded subjects were laid down with their right arm resting in a prone position. In order to set the spatial distance between stimuli administered on the forehead and on the forearm, we initially measured the two-point discrimination threshold (2pdt) on the forearm, both for transversal and longitudinal orientations by using a staircase method. Subjects were tactilely stimulated with needles (diameter 5 mm) mounted on a calliper. Either double (67 %) or single posts (33 %) were administered at random. Only double posts were used to compute the staircase. The starting double posts separation was 40 mm, clearly above the 2pdt. The separation was then reduced progressively by 50 % after each set of three successive correct responses. When subjects made an error,

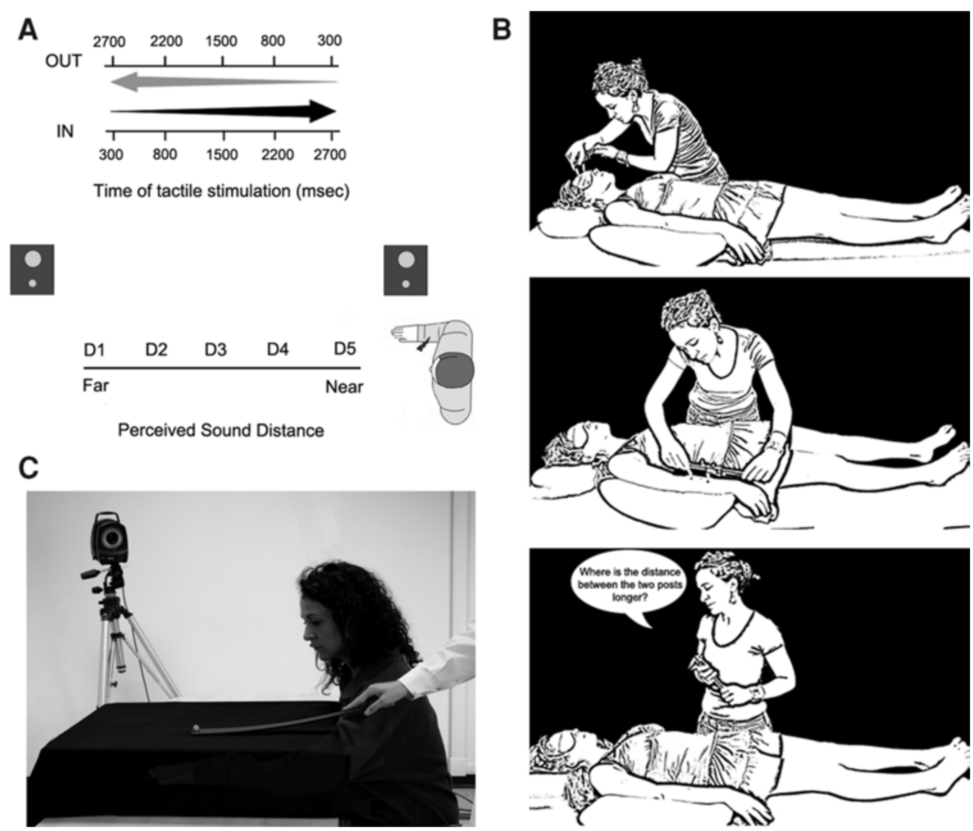

Fig. 1 **A** Experimental set-up for the audio-tactile interaction task. **B** Experimental set-up for the tactile distance perception task. **C** Experimental set-up for the localisation task

the separation was subsequently increased to midpoint of the current (erroneous) trial and the immediately preceding (correct) trial. This procedure was terminated at the shortest separation at which subject clearly perceived two posts. We then confirmed this 2pdt estimate by delivering five double posts at this separation randomly intermixed with five single posts. If subjects scored between 7/10 and 9/10 correct, the threshold estimate was accepted for experimental testing. Otherwise, the procedure was repeated. For each subject, 2pdts were measured both for transversal and longitudinal orientation on the forearm, and the corresponding individual 2pdt was used to set the distance between the pairs of posts used during the tactile distance task. Three different inter-point distances were used: at the 2pdt, 1.5 the 2pdt and twice the 2pdt.

On each trial of the tactile distance perception task, subjects were touched with a pair of posts on the forehead and immediately later with a pair of posts on the forearm. Subjects made un-timed two-alternative forced-choice judgments of whether the two posts felt farther apart on the forehead or on the forearm, responding verbally. The task comprised a total of 36 trials: for 12 trials, the inter-point distance for the pair of posts on the forehead and on the forearm was the same (i.e. at the 2pdt, 1.5 the 2pdt or twice the 2pdt); for 12 trials, the inter-point distance was longer for the pair of posts on the forearm; vice versa for the remaining 12 trials (i.e. the difference between the two distances could be half the forearm threshold or equal to the threshold). An experimenter administered stimuli manually for approximately one second, with an inter-stimulus interval of one second between taps on the forehead and the forearm (see Fig. 1B). Subjects were blindfolded throughout the procedure. In order to assess both the perceived width and the perceived length of the forearm, tactile stimuli were applied in two different orientations, transversally and longitudinally to the forearm axis. Subjects performed the task for transversal and longitudinal orientations, before and after tool-use, in blocked sessions, run in counterbalanced order.

Tool-use training The tool-use training was adapted from Serino et al. (2007). The used tool was a 1-mt wooden stick with a diameter of 2.5 cm and a 10-cm handle. A 21 × 10 × 1 cm plastic plate was fixed on the distal part of the tool. The tool's weight was around 1 k. The training consisted in using the tool to find and retrieve 10 × 3 × 3 cm plastic-made parallelepiped targets randomly placed in each trial in one out of 30 different locations on the floor. Possible locations were chosen on two 3-by-5 matrices, one for each side of space: there were 3 possible longitudinal distances from the body (at 50 cm, at 80 cm and at 110 cm), and 5 transversal positions on the left and 5 on the right of the participants, covering a space ranging from 50 to 110 cm in

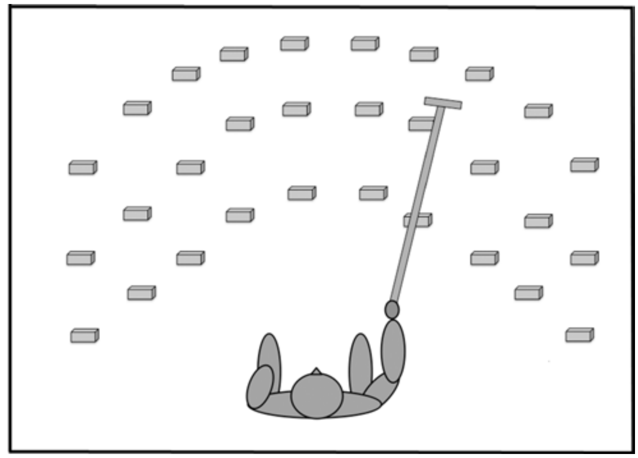

Fig. 2 Tool-use training. Schematic view of tool-use task

front of the subject and up to 140 cm to the right and to the left of the subject's feet (see Fig. 2). Participants performed the task blindfolded. They comfortably sit on a chair in the middle of the experimental room. They hold the tool with the right hand, and they were asked to place the left arm on the leg during the training. On each trial, participants hold the tool in a starting position, with the tip of the tool placed on the floor close to their feet. At the beginning of the trial, the experimenter placed one of the target objects on the floor, avoiding making any sound that could cue the subjects towards the object location. Participants were instructed to explore the space around them, making a continuous fluid movement starting from the left to the right space until they found the object. Once they found it, they drag it until their foot. Then, the experimenter removed the target object and positioned another one. Participants were instructed to place the arm back on the initial position at the end of each trial, until the following trial started. The experimenter monitored the correct execution of tool-use training. On average, during the each session of 20-min training, subjects retrieved 60 target objects, meaning that each exploration lasted for approximately 20 s.

Design We measured PPS representation and BR before and after a block of 20 min of tool training.

The PPS assessment was intermingled with BR assessment. The order of task administration was as follows. Before tool-use, half subjects performed the audio-tactile interaction task first and then the tactile distance perception task, and vice versa for the remaining subjects. Then, each subject performed two sessions of 20-min training, in which they recruited a variable number of objects.

Each training session was intermingled with an assessment session. In the assessment performed after the first training session, half subjects were tested with the audio-tactile interaction task and the other half with the tactile distance perception task. In the assessment performed after the second training session, subjects previously tested with the audio-tactile interaction task were tested with the tactile distance perception task; vice versa for the second half of subjects. In this way, each after tool-use assessment with the PPS representation and the BR task was immediately preceded by the same amount of tool-use (i.e. 20 min), and the order of PPS or BR assessment after tool-use was counterbalanced between subjects. Subjects were blindfolded during both the experiment and the training.

Results and discussion

Audio-tactile interaction task

In order to study the relationship between RTs and the different perceived positions of sound in space as a proxy of PPS extension, we calculated tactile RTs both for IN and for OUT sounds at the different temporal delays at which tactile stimulation was administered. RTs exceeding more than 2 standard deviations from the mean RT were considered outliers and trimmed from the analyses (1.5 % of trials). Since tactile stimuli were administered well above threshold, subjects were extremely accurate in performing the task, as rate of false alarms and omissions was very low, that is, 0.06 and 2.88 %, respectively. Thus, the performance was analysed in terms of reaction time only. Given the symmetric shape of the two sounds (Canzoneri et al. 2012), there was a spatial correspondence between the perceived position of IN and OUT sounds at T1 IN and T5 OUT (both corresponding to the farthest distance from the body = D1), T2 IN and T4 OUT (far distance = D2), T3 IN and T3 OUT (intermediate distance = D3), T4 IN and T2 OUT (close distance = D4), T5 IN and T1 OUT (closest distance = D5). We then analysed tactile RTs as a function of the five possible perceived distances, from D1, the farthest distance, to D5, the closest distance, both for IN and for OUT sounds.

We entered tactile RTs in repeated-measures ANOVA with Sound (IN, OUT), Condition (before and after tool-use) and Distance (D1, D2, D3, D4, D5) as within-subject factors. The ANOVA conducted on RTs with Condition (before tool-use, after tool-use), Sound (IN, OUT) and Distance (from D1 to D5) as within-subjects factors showed a significant main effect of Distance [$F(4,44) = 11.01$, $p < .001$]. Tactile RTs speeded up as soon as the sound was perceived approaching the body (see Canzoneri et al. 2012). The main effect of Condition was not significant [$F(1,11) = 0.06$, $p = .82$], meaning that the training did not induce any general effect on tactile RTs, Critically, the two-way Distance × Condition interaction [$F(4,44) = 3.15$, $p < .05$] was significant. As Fig. 3A shows, before tool-use, the function describing the relationship between tactile RTs and the position of sound in space shows that tactile RTs progressively sped up as the perceived sounds' distance from the body decreased. In particular, RTs at D1 (mean RTs ± S.E.M, 477 ms ± 30) and D2 (481 ms ± 28)—when sounds were perceived far from the body—were significantly longer compared to RTs at D3 (450 ms ± 29), D4 (444 ms ± 27) and D5 (444 ms ± 30; all $p_s < .02$, Newman–Keuls corrected)—when sounds were perceived close to the body. This spatial modulation of tactile perception due to sound position captures the boundaries of PPS representation before tool-use (see Canzoneri et al. 2012 for similar results). Those boundaries were extended after tool-use, as shown by a change in the shape of the function describing the relationship between sound position and tactile RTs. After tool-use, RTs at D2 were no more significantly different than RT at D3, D4 and D5 (all $p_s > .72$). Thus, the critical spatial range where sounds became effective in modulating tactile RTs shifted to include positions more distant from the forearm, that is, around D2, whereas it was located around D3 before tool-use. Indeed, RTs at D2, and not at any other distance, were significantly faster after tool-use compared to before tool-use ($p < .05$). Neither the main effect of Sound nor the interaction of Sound with the other factors was significant (all $p_s > .10$). This rules out the possibility that the direction of sound (approaching to—IN—or receding from—OUT—the body) differentially affected tactile RTs in the different experimental conditions.

Results from the present experiment are in line with several pieces of evidence in the literature, showing that using a tool affected PPS representation. Previous studies in monkeys (Iriki et al. 1996), healthy human subjects (Maravita et al. 2002; Serino et al. 2007; Bassolino et al. 2010) and neuropsychological patients (Farnè and Làdavas 2000; Farnè et al. 2005; Maravita et al. 2002) have shown that after tool-use, visual or auditory stimuli presented in the far space, at the tip of the tool, interact with somatosensory stimuli on the hand holding the tool (see Farnè and Làdavas 2000; Làdavas and Serino 2008; Maravita 2006; Maravita and Iriki 2004). These effects have been interpreted by the majority of the authors as evidence of extension of PPS representation to envelop the space in which the tool is used (see Maravita et al. 2003). Alternatively, some authors interpret similar effects as a consequence of a shift of crossmodal spatial attention (maybe due to motor preparation, see Holmes et al. 2007; Yau et al. 2009; see also Holmes 2012), from the space around the body to that around the tip of the tool, rather than as a change in PPS representation. In order to exclude that the present results were due *only* to a generic shift of attention towards the far space, we conducted Experiment 3 (see below).

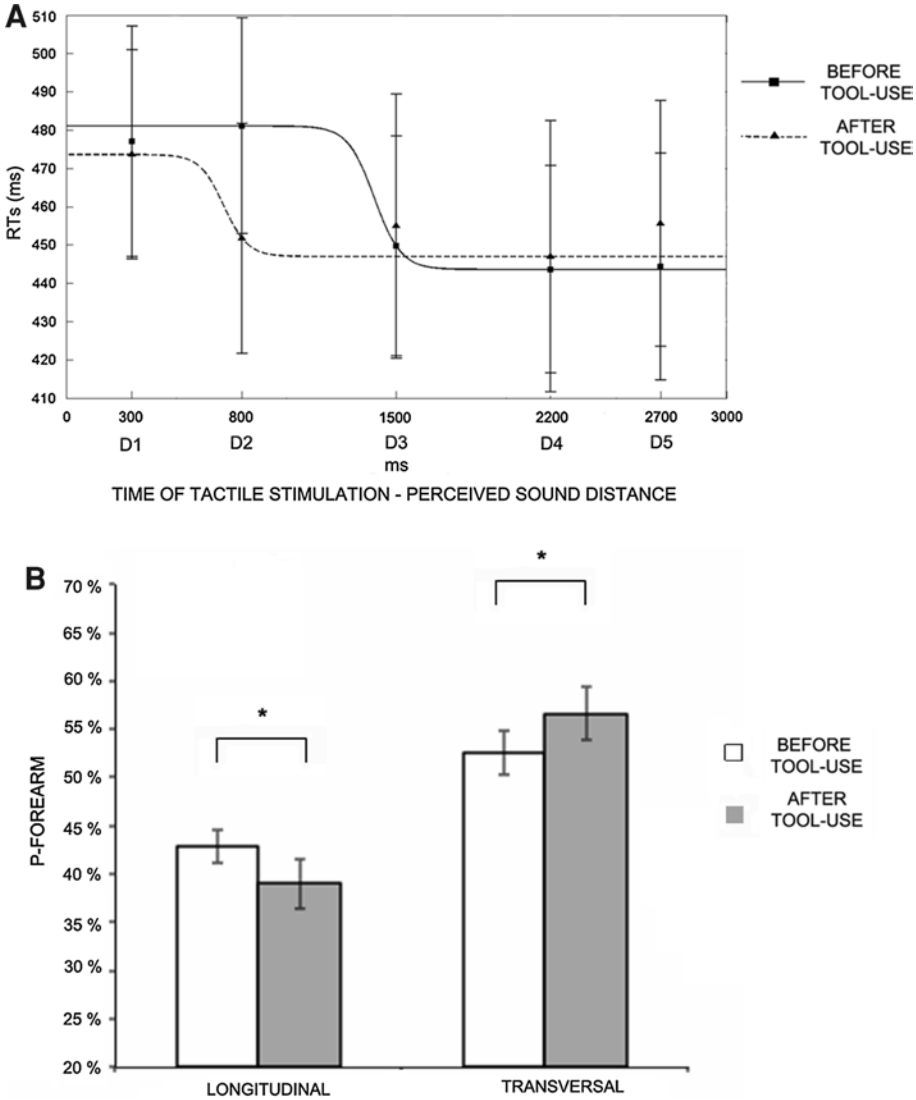

Fig. 3 Experiment 1A results. **A** Tool-use extends PPS representation. Audio-tactile interaction task results. Mean (and S.E.M.) RTs at different perceived sound distances from D1-farthest-to D5-closest-(corresponding to different times of tactile stimulus delivery), and best-fitting sigmoidal functions describing the relationship between RTs and sound distance, before tool-use (*filled line*) and after tool-use (*dotted line*). Tactile RTS are collapsed between IN and OUT sound, since results showed that any effect of Sound direction (IN, OUT) was found. Individual data were averaged, and the mean RTs were fitted with a sigmoidal function with least squares regression; the parameters estimated in the best-fitting procedure were the central point of the sigmoid and the slope of the sigmoid at the central point. The central point of the sigmoidal function shifted towards the far space (715 ms) after tool-use as compared to before tool-use (1,399 ms), showing that, after tool-use, auditory signals affected tactile processing at earlier temporal delays, that is, at farther distances from the subject's body. The figure reports the sigmoidal function fitted after averaging RTs at each distance from individual subjects. **B** Tool-use affects the representation of the perceived dimension of the forearm. Tactile distance perception task results. The graph shows mean P-Forearm (and S.E.M.) both for longitudinal and transversal orientations, before tool-use (*white columns*) and after tool-use (*grey columns*)

Tactile distance perception task

For each subject, we calculated the mean probability of reporting the distance on the forearm as longer for all the combinations of inter-point distances (P-Forearm). All these probabilities were compared before and after tool-use, for longitudinal and transversal orientations, in order to assess the respective perceived length and width of the forearm. Since an equal number of stimuli on the forearm and on the forehead had greater relative inter-stimulus distance, a priori P-Forearm of an unbiased perceiver was expected to equal 50 %. We predicted, instead, that P-Forearm would vary depending on the perceived size of the stimulated forearm.

The ANOVA conducted on the mean P-Forearm with Condition (before tool-use and after tool-use) and

Orientation (Longitudinal and Transversal) as within-subjects factors showed a significant main effect of Orientation [$F(1,11) = 24.06$, $p < .01$]. Subjects systematically perceived greater distance between the two stimuli on the forearm in the Transversal (P-Forearm mean ± S.E.M, 55 % ± 2) than in the Longitudinal orientation (41 % ± 2), showing that subjects normally underestimate tactile distance along the longitudinal axis of the forearm. This effect is already known, and it is probably due to the organisation and shapes of tactile receptive fields along the forearm surface (Longo and Haggard 2011). More importantly, for the aim of the present experiment, the pattern of responses changed when P-Forearm was compared before and after tool-use, as revealed by the significant two-way interaction [$F(1,11) = 11.79$, $p < .01$]. In the Longitudinal orientation, P-forearm decreased after tool-use (38 % ± 2) as compared to before tool-use (44 % ± 2, $p < .05$). Conversely, in the Transversal Orientation, P-Forearm significantly increased after tool-use (57 % ± 3) as compared to before tool-use (53 % ± 2, $p < .05$) (see Fig. 3B). Since the effect of tool-use training was opposite for transversal and longitudinal orientation, the main effect of Condition was not significant [$F(1,11) = 0.3$, $p = .59$].

In summary, the present results show that after tool-use subjects perceived the distance between the two stimuli as shorter in the longitudinal orientation and longer in the transversal orientation. It is currently accepted that tactile signals are processed with reference to an implicit representation of the body (see Longo et al. 2010; Medina and Coslett 2010). Some authors also showed that such representation can be modified by manipulating visual (Taylor-Clarke et al. 2004), proprioceptive (de Vignemont et al. 2005) or acoustic (Tajadura-Jiménez et al. 2012) body-related inputs. Accordingly to these studies, an increase in perceived tactile distances is interpreted as an increase in the represented size of the body part tactilely stimulated. A different body of literature in the field of haptic perception, however, offered an opposite interpretation of similar effects. Other authors have indeed shown that the size of graspable objects is scaled relative to the size of the hand used to grasp them, such that the hand is used as a "perceptual ruler" to measure object's size: the larger the hand is perceived as being, the smaller the object placed in the hand is judged, a "complementary" effect, so to speak (action specific perception perspective; Linkenauger et al. 2010, 2011). This kind of effect is reminiscent of experiences reported by individuals with a neurological condition, called "Alice in Wonderland" syndrome, in which patients experience, for instance, growth of their body followed by shrinkage of the world around them (Todd 1955; Linkenauger et al. 2010). Effects of re-scaling distance perception as a function of the perceived body size have been also recently shown after illusions of ownership of virtual bodies: when participants experienced a tiny body as their own, they perceived objects to be larger and farther away, and conversely, when they experienced a large-body illusion, they perceived objects to be smaller and nearer (van der Hoort et al. 2011).

We are inclined to interpret the results from the present experiment more in line with this last account, proposing that perception of the distance between two tactile stimuli is rescaled on the basis of the context in which they are presented, accordingly to a context-dependent bias: the same distance is perceived as wider when presented in a smaller context as compared to when presented in a wider context. This context-dependent effect is well documented in the field of visual perception, such as, for instance, in the Ebbinghaus illusion (1987), where the same central circle is perceived as smaller or bigger when presented against a background of bigger or smaller surrounding circles, respectively. In order to demonstrate such a context-dependent bias in the case of distance perception, we conducted a visual analogue and a tactile analogue of the present tactile distance perception task.

Experiment 1B

Methods

Participants

Twenty-five healthy subjects participated in Experiment 1B. Nine subjects (2 males, mean age = 24 years) participated in the visual analogue of the tactile distance perception task (Experiment 1), while sixteen subjects (5 males, mean age = 23 years) participated in the tactile analogue task. All subjects were right-handed and had normal vision and touch. All subjects, students at the University of Bologna, gave their informed consent to participate in the study, which was approved by the local Ethical Committee of the Department of Psychology, University of Bologna, and was performed in accordance with the Declaration of Helsinki.

Materials and procedures

Visual analogue task Participants underwent a computerised visual task. During the experimental sessions subjects sat in a dimly lit and sound-attenuated room in front of a 17″ PC monitor (refresh rate 60 Hz) at a distance of 57 cm. Stimulus presentation and response recording were controlled by a PC running C.I.R.O software (http://www.cnc.unibo.psice.unibo/ciro). Participants were presented with two red dots on a white background rectangle projected on the computer screen for 300 ms, followed by a black screen lasting for 500 ms. Then, a second pair of red dots on a white rectangle appeared for 300 ms (see Fig. 4A). Subjects were asked to judge whether the distance between the two red dots was longer in the first or in the second visual stimulus, ignoring the background rectangle and responding verbally. The distance between the two dots was systematically manipulated so as to mimic the tactile distance perception task. The length of the background rectangle was also manipulated so as to mimic the perceived dimensions of the forearm. A 3-by-3 combination of inter-point distances (4, 5.5 and 7 cm) and rectangle length (16, 17 and 18 cm) was used. In 36 trials, the size of the background rectangle was different between the first and the second visual stimulus (case a)—being longer for the first visual stimulus in half trials and longer for the second visual stimulus in the remaining trials—while keeping constant the inter-point distance. In 36 trials, the distance between the two points was different between the first and the second visual stimulus (case b)—being longer for the first visual stimulus in half trials and longer for the second visual stimulus in the remaining trials—while keeping constant the background rectangle. In the remaining 8 trials, the background rectangle and the inter-point distance were the same for the first and the second visual stimulus. Each participant performed two blocks of 80 trials each. In this way, in different trials, subjects were asked to compare two dots whose distance was actually different, or two dots whose distance was equal, but which were placed on a different context. If the context-dependent bias applies as we predicted, subjects' responses should be influenced by the dimension of the background rectangle so that the inter-point distance between a pair of dots presented on a shorter rectangle should be perceived longer than the same inter-point distance between a pair of dots presented on a longer rectangle.

Tactile analogue task Blindfolded subjects were laid down with both their right and left arm resting in a prone position. Participants were tactilely stimulated by two posts, longitudinally applied on their left forearm (reference body part) and, 2 s later, by two posts longitudinally applied on their right forearm (target body part). In two-thirds of trials, target stimuli on the right arm were preceded by a "context stimulation" in which the borders of a rectangular box were applied on the right arm for 1 s and then removed, just before administration of the target stimuli. Target posts were administered in the middle of the skin surface previously framed by the rectangular box (see Fig. 4B). The experiment was conducted in 3 randomised conditions of context stimulation, that is, by using a short (12 cm long × 5 cm wide) rectangular box, a long one (18 cm long × 5 cm wide) or no box. For 12 trials, the inter-point distance for the pair of posts on the reference and on the target arm was the same (i.e. at 4 cm); for 8 trials, the inter-point distance was longer for the pair of posts on the reference (5 cm) than for those on the target arm (3 cm); vice versa for the remaining trials (i.e. 3 cm on the reference and 5 cm on the target arm). A total of 84 trials (3 difference distances by 3 context stimulations) were administered in random order, within a single experimental block.

The short and the long rectangular boxes were used to differently prime the space on the forearm where tactile posts were referenced. Participants made un-timed two-alternative forced-choice judgments of whether the two points felt farther apart on the reference or on the target forearm, responding verbally, while being asked to ignore the context stimulation. An experimenter administered the stimuli manually and recorded the response. Participants were blindfolded throughout the procedure.

Results and discussion

Visual analogue task

For each subject, we calculated the probability of reporting a longer distance between the two dots in the second stimulus (P-Second) when: (a) the inter-point distance was kept constant, and the length of background rectangle was manipulated (being longer in the first visual stimulus, longer in the second visual stimulus or equivalent in the two visual stimuli); (b) the size of the background rectangle (background size) was kept constant, and the inter-point distance was manipulated (being longer in the first visual stimulus, longer in the second visual stimulus, or equivalent in the two visual stimuli). The ANOVA with Inter-point distance and Background size as within-subjects factors showed a significant two-way interaction [$F(1,8) = 397.72$, $p < .01$]. Even when the inter-point distance was equal for the two visual stimuli, P-Second was lower when the background rectangle of the second visual stimulus was longer (P-Second mean ± S.E.M, 58 % ± 6), than when the background rectangle of the second visual stimulus was shorter (75 % ± 7, $p < .01$). Instead, when the inter-point distance was actually manipulated, and the size of the background rectangle was constant, P-Second was correctly higher when the inter-point distance was longer in the second visual stimulus (97 % ± 1) than in the first visual stimulus (3 % ± 1, $p < .01$), confirming that subjects were correctly performing the task (see Fig. 4C). Thus, the dimension of the background rectangle clearly affects distance perception, as predicted by the context-dependent bias, replicating the results obtained by Taylor-Clarke et al. (2004) in a visual analogue of the tactile distance perception task.

Tactile analogue task

For each subject, we calculated the probability of reporting a longer distance between the two posts in the second

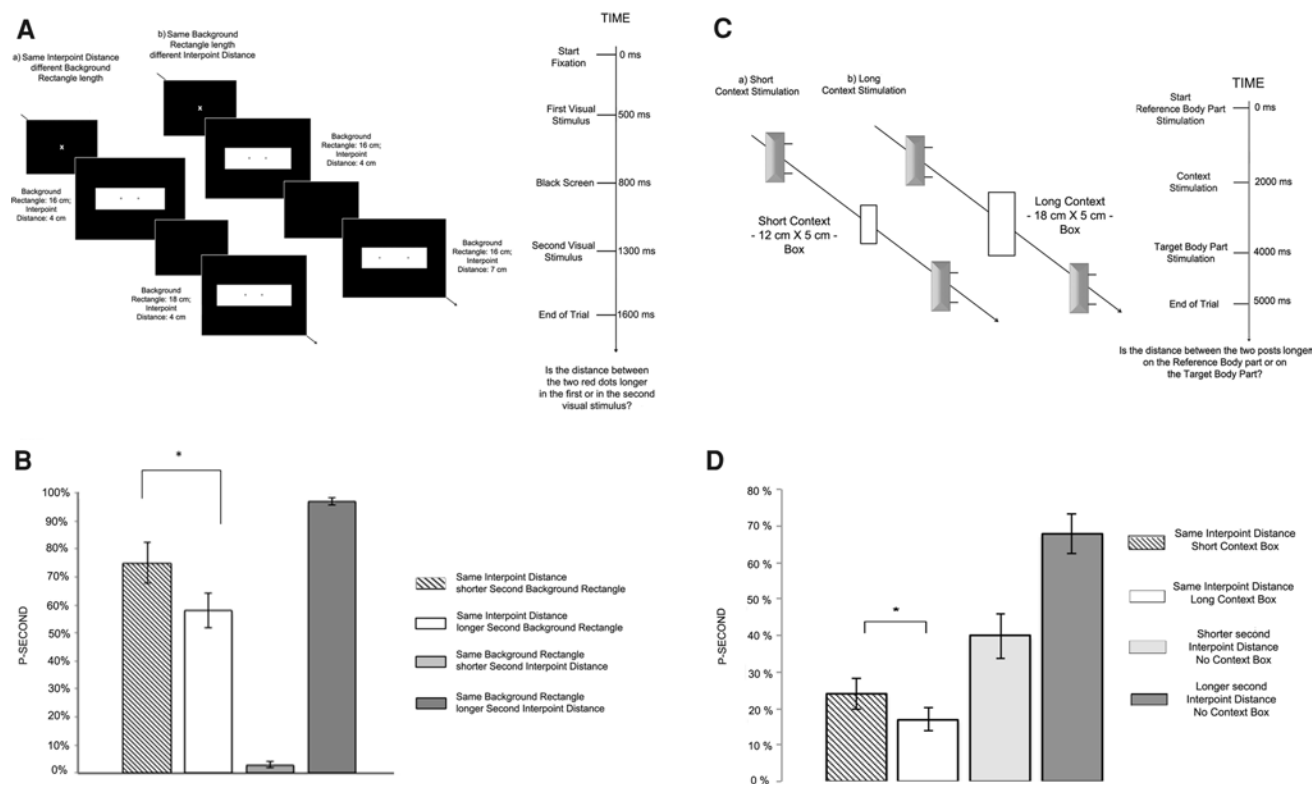

Fig. 4 Experiment 1B results. Visual analogue and tactile analogue of the tactile distance perception task. **A** Schematic representation of stimuli (on the *left*) and trial structure (on the *right*) in the visual analogue of the tactile distance perception task. (a) Example of a trial with same inter-point distance and different background rectangle length between the first and the second visual stimulus. (b) Example of a trial with same background rectangle length and different inter-point distance between the first and the second visual stimulus. **C** Results of the visual analogue of the tactile distance perception task. The *graph* shows the probability of reporting longer the distance between the two dots in the second stimulus (P-Second; *error bars* denote S.E.M.), when the size of the background rectangle (on the *left*) or the inter-point distance (on the *right*) was manipulated. **B** Schematic representation of stimuli (on the *left*) and trial structure (on the *right*) in the control tactile distance perception task. (a) Examples of a trial with short context stimulation on the target arm. (b) Example of a trial with long context stimulation on the target arm. **D** Results of the control tactile distance perception task. The *graph* shows the probability of reporting longer the distance between two posts on the target arm (P-Second, *error bars* denote S.E.M), when the size of the *background rectangle* (on the *left*) or the inter-point distance (on the *right*) was manipulated

stimulus of the target forearm (P-Second). An ANOVA on P-Second with the factors context stimulation (short, long or no rectangle) and inter-point distance showed a significant two-way interaction [$F(4,60) = 4.13$, $p < .01$]. In line with the context-dependent bias hypothesis and with the results of the visual analogue task, we found that in case of uncertainty about the inter-point difference between stimuli applied on the two arms (in conditions of no inter-point difference), the administration of the rectangular box biased subjects' perception so that distance between posts applied on the target arm was underestimated (P-Second mean ± S.E.M, 18 % ± 3.3), when the stimuli were preceded by the long rectangular box, priming a longer arm surface, and over-estimated (24 % ± 4, $p < .05$), when the stimuli were preceded by the short rectangular box, priming a shorter arm surface. As for the visual distance experiment, subjects' perception was accurate, when inter-point distance was actually manipulated: P-Second was correctly higher when the inter-point distance was longer on the target (68 % ± 6) than on the reference (40 % ± 6, $p < .01$) arm (see Fig. 4D).

The results of the present control experiments on visual and tactile distance perception support the context-dependent bias hypothesis. If we translate these effects to the results of the tactile distance perception task run before and after tool-use (Experiment 1A), these findings support the view that after tool-use, subjects more frequently perceived the distance between two points longitudinally applied on their forearm as shorter because they perceived their forearm as longer than compared to before tool-use. A reversed effect was found for the distance between stimuli applied transversally: subjects more frequently perceived the distance between the two points on the forearm as wider after tool-use, because the forearm was perceived as narrower in comparison with before tool-use.

In summary, results from the first experiment demonstrated that tool-use induces plastic change in not only in PPS representation, but also in the BR, compatibly with a representation of a longer arm after tool-use. Finally, in order to verify whether the two measures obtained from Experiment 1A correlated, we calculated an index of change both for BR and PPS representations. For the PPS task, we calculated the difference between RTs at D2 before and after tool-use (by subtracting the before tool-use data to the after tool-use data), that is, the perceived sound distance from the body where audio-tactile interaction changed after tool-use. For the BR, we calculated an index by subtracting the before tool-use data to the after tool-use data for each orientation. We then transformed these indices in z-point, and we performed a correlation analysis. No significant correlation was found (all $p_s > .34$).

Experiment 2

In order to give further support to data from the tactile distance perception task and actually demonstrate that tool-use resulted in an increase of the perceived length of the forearm, in Experiment 2 we evaluated the perceived dimension of the forearm before and after a training with a tool by using both the *tactile distance perception task* and a *body-landmarks localisation task*, explicitly assessing the perceived location of the forearm extremities, the wrist and the elbow. The distance between the two locations was computed to quantify the perceived length of the forearm.

Methods

Participants

Nine healthy subjects (4 females, mean age 28 years) participated in the study. All subjects were right-handed and had normal vision and touch. All subjects gave their informed consent to participate in the study, which was approved by the local Ethical Committee of the Department of Psychology, University of Bologna, and was performed in accordance with the Declaration of Helsinki.

Materials and procedures

Tactile distance perception task The task was the same as for Experiment 1, except that participants performed the task only for longitudinal orientation, in order to assess the perceived arm length.

Body-landmarks localisation task Subjects were instructed to verbally indicate when a moving marker reached the felt position of two occluded body parts, that is, the wrist (specifically, the ulnar styloid) and the tip of the elbow joint (i.e. the olecranon). Before the task, the experimenter explicitly showed these anatomical landmarks on her body. Subjects sat down with their right arm passively placed by the experimenter on a table in a prone position. The forearm was aligned with the shoulder joint. In order to avoid movement, for all the task duration, the arm was fixated on the table with tape. To prevent participants from viewing the forearm during the task, a rectangular black box (90 cm long × 50 cm wide) was placed over the arm. The box covered the entire width of the table. On each trial, the experimenter verbally cued the participant as to which landmark to judge. Then, the experimenter manually moved a retro-reflective marker over the surface of the box, along the longitudinal axis of the forearm. The retro-reflective marker (1.5 cm in diameter) was stuck on the tip of a black cane 50 cm long (see Fig. 1C). On different trials, run in randomised order, the marker was moved in two different directions, either approaching to (distal to proximal direction) or receding (proximal to distal direction) from subjects' body. Participants were instructed to say "Stop" when the retro-reflective marker was perceived just above the felt position of the target anatomical landmark. At that verbal signal, the experimenter ended the movement leaving the marker where indicated by the participant. The participant was allowed to further adjust the final position of the marker, by verbally asking the experimenter to move it backward or forward. When the participant confirmed the final position, the marker's location was recorded through an optical motion capture system (Vicon).

After the last trial, to record the actual positions of the elbow and the wrist, the box was removed, participants were blindfolded, and two retro-reflective markers (1 cm in diameter) were placed on the anatomical landmarks. The task comprised 20 trials, 10 for each body landmark, with an equal number of trials moving in the distal to proximal and proximal to distal directions.

The distance between the mean estimated positions of the wrist and the elbow was considered a measure of the perceived forearm length. Additionally, we checked the position error between the mean estimated location of each target landmark and its actual position. A custom MATLAB (Mathworks, Natick, MA) script was employed to analyse data.

Design The *tactile distance perception task* and the *body-landmarks localisation task* were run before and after a training session, consisting in using a tool with the right arm to retrieve objects placed in different positions in far space for 20 min.

The structure of the Experiment was the same as for Experiment 1A.

Results and discussion

Tactile distance perception task

In order to test whether the implicitly perceived arm length changed before and after tool-use, mean P-Forearm from the two sessions was compared with a paired sample *t* test. P-forearm significantly decreased after tool-use (49 % ± 3) as compared to before tool-use (53 % ± 2; $t(8) = 2.47$, $p < .05$), in line with results from Experiment 1. According to a context-dependent bias, these results confirm that after tool-use the distance between points of contact on the forearm surface is systematically underestimated, suggesting an increase in the perceived length of the forearm.

Body-landmarks localisation task

To compare the perceived arm length before and after tool-use, we calculated the perceived arm length as the distance between the perceived position of the elbow and the wrist (E–W distance). A repeated-measure ANOVA was performed on E–W distance, with Condition (before tool-use, after tool-use) and Marker Movement Direction (distal to proximal, proximal to distal) as within-subjects factors. The main effect of Condition was significant [$F(1,8) = 5.80$, $p < .05$], showing that E–W distance significantly increased after the training with the tool (before tool-use = 23.57 ± 1.8 cm; after tool-use = 24.70 ± 1.7 cm). This effect was independent from movement direction as both the two-way interaction Condition × Marker Movements Direction and the main effect of Marker Movement Direction were not significant (all $p_s > .06$). These results suggest that after tool-use, the forearm was perceived as longer than before tool-use.

A repeated-measure ANOVA was also run on wrist and elbow position error (i.e. the difference between the mean estimated location of each landmark and its actual position) with Condition (before tool-use, after tool-use), Marker Movements Direction (distal to proximal, proximal to distal) and Landmarks (elbow, wrist) as within-subjects factors. Results showed a significant Condition × Landmarks interaction [$F(1,8) = 5.53$, $p < .05$]. This effect was due to a change in the perceived location of the wrist, rather than of the elbow. Indeed, after tool-use, the wrist was perceived farther from the body than before (before tool-use = −2.25 ± 1.5, after tool-use = −.72 ± 1.5), while the elbow position did not significantly change (before tool-use = −1.39 ± 0.9, after tool-use = −1.05 ± 1; $p = .38$, Newman–Keuls corrected). This effect was again independent from the direction of the marker movement, as the three-way interaction was not significant ($p = .69$). Since results showed a change in the perceived location of the wrist only, the main effect of Condition was not significant ($p = .17$) (Fig. 5).

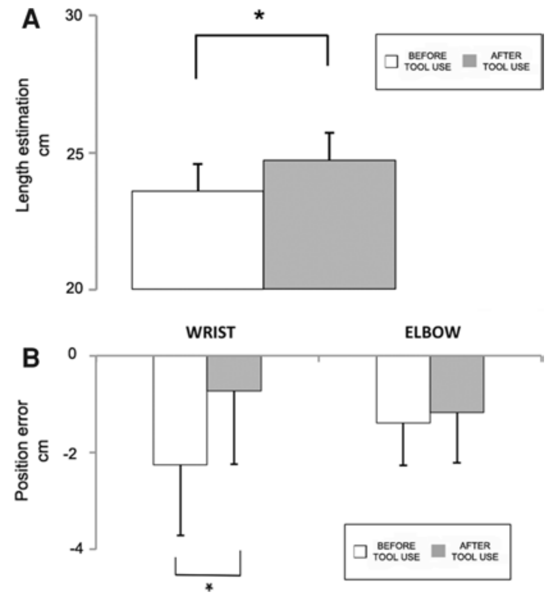

Fig. 5 Experiment 2 results, body-landmarks localisation task. Tool-use affects the perceived length of the forearm. **A** The *graph* shows mean length estimation before tool-use (*white columns*) and after tool-use (*grey columns*) **B** The *graph* shows mean wrist (on the *left*) and elbow (on the *right*) position errors before tool-use (*white columns*) and after tool-use (*grey columns*)

In order to verify whether and to what extent the measures obtained from this experiment are related, we calculated an index of change for both the tactile distance perception task and the body-landmarks localisation task, by normalising the scores from the two tasks and subtracting the before tool-use data from the after tool-use data for each participant, in order to allow a more direct comparison between the two Experiments. We then performed a correlation analysis between these two indices. Results did not indicate any significant correlation ($r = 0.33$, $p = .38$).

Results from the tactile distance perception in Experiment 2 were in line with results from the same task in Experiment 1A, showing that after tool-use participants underestimated the tactile distance between two taps administered on the trained forearm. At the same time, results from the localisation task showed an increase in the distance between the perceived location of the wrist and the elbow after tool-use, compatible with an increase in the perceived forearm length after the training. Numerically, the increase was around 1.1 cm. Considering that subjects used a 100-cm tool during the training, one might suggest that 1 % of the tool length was "embodied" into the arm representation after tool-use. However, at the moment we cannot establish whether that value has a perceptual valence, or it simply depends on the sensitivity of the task used to measure the effect of tool-use. One way to answer this question would be testing the effects of using tools of different lengths: for instance, using a 200-cm tools should lead to a ~2 cm of elongation. To the best of our knowledge, nobody tested whether plastic effects of tool-use on BR actually depend on the physical size of the tool. Only Sposito et al. (2012) compared the effect of using a long versus a short (20 cm), functionally useless, stick and found that only the former, but not the latter, tool did affected perceived length of the forearm. But, no data are available on whether a longer tool, which would allow acting on further portions of space, would actually make the subjects feeling their arm even longer.

The present findings are in line with results of Cardinali et al. after a training with a long mechanical grabber (Cardinali et al. 2009a; but see also Cardinali et al. 2011). Moreover, findings from the present experiment demonstrated that the change in the perceived length of the forearm was not due to a subjective proprioceptive shift of the whole arm towards the far space, since only the wrist, but not the elbow, was perceived farther from the body (see also Sposito et al. 2012). In summary, these findings confirmed the results from the Experiment 1 and provided strong evidence for an actual extension of the perceived length of the arm after tool-use.

As the body continuously changes in position and dimensions throughout life, its brain representations need to be updated in order to correctly interact with the external world. The concept of body representations nowadays encompasses different concepts, with rather specific plastic properties. In line with a "dyadic view" of body representations, most authors usually make a distinction between Body Image and Body Schema (see de Vignemont 2010; Dijkerman and de Haan 2007; Gallagher 2005; Cardinali et al. 2011). Body Schema is an implicit, online adapted representation of body parts size and position for action, whereas Body Image is a more explicit, offline updated, representation of body appearance for perception (see Dijkerman and de Haan 2007; De Vignemont 2010; Carruthers 2008; Gallagher 1986). Accordingly, it has been proposed that these two representations can also be updated selectively depending on different types of experiences (de Vignemont and Farnè 2010; Kammers et al. 2009). For instance, recent works on the effect of tool-use tried to disentangle the effects of tool-use on the body schema and the body image (see Cardinali et al. 2011; Sposito et al. 2012). Some authors proposed instead a triadic taxonomy of body representations, whereby, maintaining the classic concept of Body Schema, the concept of Body Image is further divided into a Body Structural Description, more related to perception, and Body Semantics, interfacing with Language (see e.g. Schwoebel and Coslett 2005; Sirigu et al. 1991). Reminiscing of the concept of Body Structural Description, Longo and Haggard (2010, 2011) recently proposed that there is a specific model of the body in the brain (which they call "body-model"), containing information about the size and shape of body parts. But the same group also proposed further fragmentations between a number of body representations devoted to perception (which they refer to with the generic term of somatoperception) and others devoted to cognitive processing of body-related information (which they call somatorepresentation) (Longo et al. 2010). Thus, at the moment, the exact number and functions of different body representations are a matter of debate (see Kammers et al. 2010). For this reason, in the present paper, we deliberately decided to not enter into this debate, but to adopt the more neutral and generic term of body representations (BR), being well aware of potentially including in this way rather different levels of body-related information processing in the brain. Having said that, we used both the tactile distance perception task (Experiment 1, 2 and 3) and the body-landmarks localisation task (Experiment 2) to assess a multisensory, high-level, mental representation of the body, processing several sensory cues to represent the size and shape of different parts of the body. We believe that the modification of BR after tool-use is strictly dependent on the sensory consequences of action: because, thanks to tool-use, we act on a portion of space exceeding the normal limits of our physical body, our brain starts processing multisensory inputs related to one's own body, but arising from a distal portion of space. For instance, tactile and proprioceptive cues processed at the upper limb via the tool handle refer to objects contacting the tip of the tool. Such contacts also generate sensory feedback in other modalities, for example auditory feedback, as in the present experiments, when subjects were blindfolded, but also visual feedback in everyday life tool-use activities. We believe that this action-dependent extension of the space where body-related sensory information arises from is the trigger for the changes in body representation and PPS representation documented by the present experiments. This proposal has been recently introduced by our group in the context of a neural network model designed to account for plasticity in PPS representation (Magosso et al. 2010). In the following experiments, we controlled that these effects were strictly related to tool-use mediated interactions with far objects and were not the consequence of movement per-se, shifting of spatial attention or just tasks repetition.

Experiment 3

In order to demonstrate that any change in PPS representation and BR was actually due to tool-use, and not to a generic effect of movement, attention or simply repetition of the tasks, in Experiment 3 we evaluated both PPS representation with the *audio-tactile interaction task* and BR with the *tactile distance perception task* before and after a control training, consisting in pointing to objects placed in different positions in far space (pointing task). Subjects were asked to point with their right hand towards objects placed in the same location, just as in the tool-use experiments; however, no tool was used. We predicted that the pointing task, that drives subjects' attention towards the far space during the training, but does not involve any tool-mediated interaction between the subject's body and objects in far space, affects neither PPS representation nor BR.

Methods

Participants

Twelve healthy subjects (all females, mean age 25 years) participated in the study. All subjects were right-handed and had normal hearing and touch. All subjects, students at the University of Bologna, gave their informed consent to participate in the study, which was approved by the local Ethical Committee of the Department of Psychology, University of Bologna, and was performed in accordance with the Declaration of Helsinki.

Materials and procedures

The audio-tactile interaction task and the tactile distance task were the same as used for Experiment 1A.

Design The structure of the experiment was the same as for Experiment 1A, except for the training session, which consisted in a 20-min pointing task: blindfolded subjects sit on chair with their left arm relaxed, while they held in the right hand a 15-cm-long wooden handle, of the same weight as the tool. In this way, fatigue effects due to holding the handle or the tool were similar between Experiment 3 and Experiment 1. During the training session, in each trial the experimenter touched an object placed on the floor, at a random location in far space, with the tip of the stick used for the previous experiments. In this way, a sound was generated, comparable to that made by the subjects in Experiment 1A when they touched the object with the tool. Subjects were asked to point the handle towards the perceived location of the sound.

Results and discussion

First of all, we compared results from Experiment 1A and Experiment 3 with a mixed-design ANOVA with the within-subjects factors of Sound, Distance and Condition and the between-subjects factor of Experiment (Experiments 1A and 3) both for the audio-tactile interaction task and the tactile distance perception task. For the audio-tactile interaction task, we found a three-way Condition × Distance × Experiment interaction [$F(4,88) = 4.27$, $p < .01$], suggesting that the function describing the relationship between tactile RTs and the position of sound in space is differentially modulated by the tool-use training as compared to the pointing training. This significant interaction allows conducting two separate ANOVAs for each experiment. Similarly, for the tactile distance perception task, we found a trend in the three-way interaction [$F(1,22) = 3.31$, $p = .08$]. We then analysed the two Experiments separately.

Audio-tactile interaction task

False alarm and omission rates were extremely low, that is, 0.76 and 1.57 %, respectively. We analysed mean RTs to tactile targets (after outliers removal, see Experiment 1 for procedure) administered when sounds were perceived at different distances from the body. The ANOVA conducted on tactile RTs with Condition (before pointing, after pointing), Sound (IN, OUT) and Distance (from D1 to D5) showed a significant main effect of Distance [$F(4,44) = 25.79$, $p < .01$]. The pattern of results, shown in Fig. 6A, mirrors the same effect found in Experiment 1A before tool-use: as sound distance from the body decreased, RTs progressively shortened. Newman–Keuls post hoc comparisons confirmed this effect, since RTs at D1 (Mean RTs ± S.E.M, 429 ms ± 26) and D2 (414 ms ± 27), when the sound was perceived far from the body, were slower compared to RTs at D3 (397 ms ± 25), D4 (398 ms ± 26) and D5 (390 ms ± 25, all $p_s < .01$), when the sound was perceived close to the body. Importantly, the space dependent modulation of RTs due to sound position was not different before and after the training session, as the two-way interaction was not significant [$F(4,44) = 1.87$, $p = .13$], as well as the main effect of Condition [$F(1,11) = 0.99$, $p = .34$]. Thus, no extension effect of the boundaries of PPS representation was found after the pointing training session. The main effect of Sound as well as the Sound × Condition interaction and the three-way interaction were not significant (all $p_s > .36$), revealing that the direction of sound did not affect tactile RTs in a different way.

Tactile distance perception task

A repeated-measure ANOVA was conducted on the mean P-Forearm with Condition (before pointing and after pointing) and Orientation (transversal and longitudinal) as within-subjects factors. The main effect of Orientation was significant [$F(1,11) = 29.58$, $p < .01$], mirroring the same trend found in Experiment 1 (P-forearm for transversal orientation = 57 % ± 1; P-forearm for longitudinal

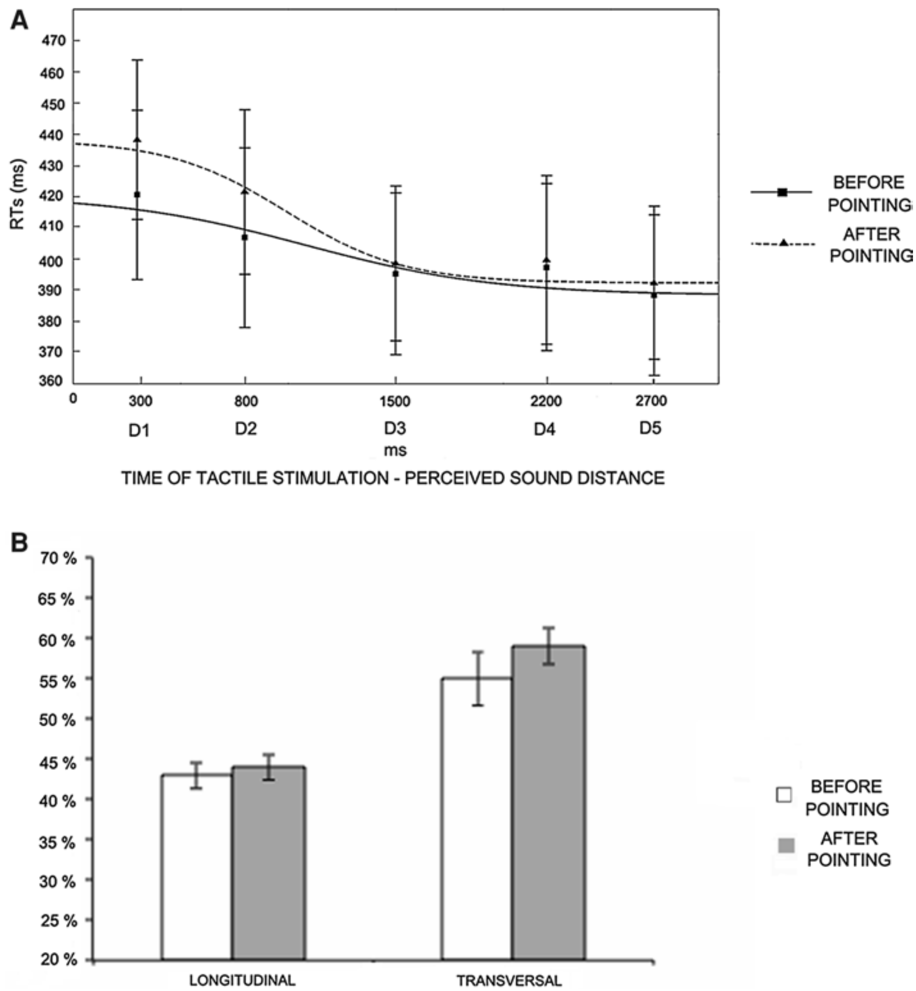

Fig. 6 Experiment 3 results. **A** Pointing task does not affect PPS representation. Audio-tactile interaction task results. Mean (and S.E.M.) RTs at different perceived sound distances (from D1-farthest-to D5-closest), corresponding to different time of tactile stimulus delivery and best-fitting sigmoidal functions describing the relationship between RTs and sound distance, before pointing (*filled line*) and after pointing (*dotted line*). Tactile RTS are collapsed between IN and OUT sound, since results showed that any effect of Sound direction (IN, OUT) was found. The central point of the sigmoidal function can be taken as a measure of the critical distance where sounds affect tactile RTs on the forearm and therefore can be considered an index of the boundary of PPS. As shown in the figure, there is no shift of the central point of the sigmoidal function after pointing (989 ms) as compared to before pointing (1,082 ms). **B** Pointing task does not affect the perceived dimension of the forearm. Tactile distance perception task results. The *graph* shows mean (and S.E.M.) P-Forearm both for longitudinal and transversal orientations, before pointing (*white columns*) and after pointing (*grey columns*)

orientation = 44 % ± 1; see Fig. 6B) and again in line with the results obtained by Longo and Haggard (2011). Importantly, the interaction Condition × Orientation was not significant [$F(1,11) = 0.91$, $p = .36$], suggesting that the pointing task did not affect subjects' performance in the tactile distance perception task and therefore subjects' perception of length or width of their arm.

General discussion

In the present study, we investigated whether PPS and BR changed in parallel after using a tool, extending action space from the space immediately surrounding the body to the far space. In order to dynamically assess PPS representation, we used a new audio-tactile interaction task developed by our group (Canzoneri et al. 2012): we have recently shown that tactile RTs coupled to moving sounds progressively speeded up to the extent that the sound source was perceived close to the body. The function describing the relationship between tactile RTs and the position of sounds in space can be used to localise the boundaries of PPS representation (Canzoneri et al. 2012) and in this study has been used to measure plasticity of PPS representation after a short-term tool-use experience. Results from Experiment 1 show that after tool-use, the boundaries of PPS representation shifted to include farther locations, so that an auditory stimulus presented in a far position, where the tool has been used, was recoded as it were closer to the body and therefore interacted with a tactile stimulus delivered on the arm. This effect was associated with a change in the representation of the arm shape: after tool-use, subjects perceived the distance between the two stimuli delivered on the forearm longitudinally to the arm axis as significantly shorter and perceived the distance between two stimuli delivered transversally on the forearm as significantly longer. Moreover, when asked to localise the position of their wrist and elbow, they localised those body landmarks farther apart between each other after tool-use. Taken together, these findings are compatible with an extension of perceived arm length after tool-use, assessed by means of two independent tasks.

In sum, the present study demonstrates a plastic modification of both body and space representations, suggesting that a tool, extending the action space of the body (Gallese and Sinigaglia 2010), is incorporated into BR and affects both the spatial perception of the body itself and of objects presented in space.

A control experiment confirmed that these effects were actually due to tool-use and were not due to the simple repetitions of the tasks or to a generic shift of spatial attention towards the far space. Subjects performed a pointing training task, involving a shift of attention towards far space as in the tool-use training task, but not involving any interaction between the body and far space. No changes in the audio-tactile interaction tasks and in the tactile distance perception task were found after the pointing task, indicating that both PPS representation and the BR were unaffected.

The correspondence between the extension effect for PPS and the perceived arm length suggests that body and PPS representations strongly overlap. This is not surprising considering that the receptive fields of bimodal neurons representing PPS around different body parts are anchored to specific body parts (Graziano and Cooke 2006). Moreover, brain systems involved in PPS representation and BR are localised within the same fronto-parietal areas, encompassing the ventral premotor cortex and the posterior parietal cortex, both in monkeys (Duhamel et al. 1998; Graziano et al. 1997, 2000) and in humans (Bremmer et al. 2001; Filimon et al. 2009; Makin et al. 2007; Sereno and Huang 2006; Serino et al. 2011; Blanke 2012). Thus, a similar fronto-parietal network might represent both the body surface and the visual and/or auditory space surrounding the body. PPS and BR also have a closely related role in action execution (Brozzoli et al. 2009; Gallese and Sinigaglia 2010; Graziano and Cooke 2006): in order to reach and manipulate an object, or in order to avoid contact with a harm, the brain needs to compute information about the position, shape and movement of the object in space and concurrently about the position, shape and dimensions of the body part potentially interacting with it. Moreover, it has been demonstrated that the physical dimensions of the body (the arm length, in this case) determine the location of the boundary between near and far space (Longo and Lourenco 2007). Our study provides experimental evidence of a further level of overlap between PPS and BR, that is, their plastic properties.

Such overlap can be interpreted in three ways. First, it might be the case that the extension of PPS representation directly depends on the plastic change of BR, such that the elongation of the perceived size of the forearm extends the representation of the space around it (see Maravita 2006; Maravita and Iriki 2004). In other words, a "longer" arm would imply a more extended PPS around it. Conversely, an opposite relationship between the two effects, that is the arm is perceived as longer, because the PPS around it has extended, appears logically less likely. Second, the two plastic phenomena might be simply associated, without any causal relationship between them. A third interpretation is possible, that is, that the representation of the size and position of body parts devoted to action, that is, BR, and that of the space immediately surrounding the same body parts actually consist in a unique representation of the body in space (for comments, see Cardinali et al. 2009b; Gallese and Sinigaglia 2010). The present results, by providing evidence for similar plastic effects of tool-use on PPS and BR, support this third view, in favour of a unified body and space representation. However, this evidence is not sufficient to definitively conclude that PPS and BR consist, as showing an association does not necessarily imply any causal relationship. Future studies are needed to theoretically and experimentally investigate possible consistency or dissociation between body and space representation.

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