Original Articles

Standard body-space relationships: Fingers hold spatial information

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ABSTRACT

The representation of the body in the brain is constantly updated to allow optimal sensorimotor interactions with the external world. In addition to dynamic features, body representation holds stable features that are still largely unknown. In the present work we explored the hypothesis that body parts have preferential associations with relative spatial locations. Specifically, in three experiments, we found consistent preferential associations between the index finger and the *top* position, and between the thumb and the *bottom* position. This association was found in a tactile sensory discrimination task, which was conducted both with and without vision, as well as at the implicit conceptual association level. These findings show that body parts and spatial locations are stably associated. Therefore, not only are body segments dynamically mapped in space for perception and action, but they also hold intrinsic spatial information that contributes to somatosensory spatial processing.

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1. Introduction

The idea that everyone has a mental representation of his/her own body has received wide support in the multidisciplinary field of research at the intersection of philosophy, experimental psychology, and cognitive neuroscience that focuses on how mind and body interact. This representation is thought to help localizing the bodily self and interacting with the external world (Blanke & Metzinger, 2009; de Vignemont, 2010). Different sub-components of body representations (BR) have been distinguished since its first description (e.g. Head & Holmes, 1911). On the one hand, a dynamic representation of the body oriented to action, namely the body schema (Cardinali, Frassinetti et al., 2009; Coslett, 1998; Kammers, Kootker, Hogendoorn, & Dijkerman, 2009; Maravita, Spence, & Driver, 2003), allows processing of information necessary to plan actions in space (Cardinali, Brozzoli, & Farnè, 2009; de Vignemont, 2010; Holmes & Spence, 2004; Kammers, van der Ham, & Dijkerman, 2006; Tsakiris & Fotopoulou, 2008). On the other hand, BR also includes more stable aspects about semantic and structural aspects of one's own body, whose nature is still debated (de Vignemont, 2010; Dijkerman & de Haan, 2007; Gallagher, 2005; Gandevia & Phegan, 1999; Ionta, Perruchoud, Draganski, & Blanke, 2012; Kammers, Mulder, de Vignemont, & Dijkerman, 2009; Longo, Azañón, & Haggard, 2010; Melzack & Bromage, 1973; Moseley, 2005; Tsakiris & Fotopoulou, 2008).

The characterization of different components of BR is of paramount importance because both dynamic and stable features of BR continuously affect our everyday interactions with the external world. Considering a critical aspect of behavior, i.e. the interaction between the body and external objects, there is evidence that body posture may affect the spatial processing of sensory stimuli (Azañón & Soto-Faraco, 2008; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1987a, 1987b; Reed & Farah, 1995). Even in a simple tactile temporal order judgment task, the relative position of limbs in space can affect performance by automatically referring skin stimulations to the egocentric spatial coordinates (Yamamoto & Kitazawa, 2001a, 2001b), although the early stage of the processing is coded in a somatotopic frame of reference (Azañón & Soto-Faraco, 2008). This suggests the existence of a continuous comparison process between visual, somatosensory, and proprioceptive information, in which contingent bodily and visuospatial representations influence each other. Alternatively, spatial information might be deeply embedded in BR and invariantly modulate performance independent of ongoing postural changes. This intriguing possibility implies the existence of a standard representation of the relationship between body and space that potentially modulates all body-space interactions regardless of any potential postural change.

We sought out the existence of standard associations between spatial locations and body parts focusing on the fingers because

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their relative spatial positions are highly flexible and not affected by strong postural or gravitational constraints about spatial elevations. Specifically, we tested the hypothesis that preferential associations existed between the thumb and the index finger and the relative spatial positions of "top" and "bottom", respectively. Those are relative spatial positions that are often experienced with the fingers and are neutral with respect to the left/right aspect, which is known to be associated with more specific egocentric representations and cerebral dominance processes (Yamamoto & Kitazawa, 2001a, 2001b).

Across three experiments, we investigated the putative intrinsic associations between fingers and space using perceptual discrimination and cognitive tasks. In Experiments 1 and 2, we used a localization discrimination task seeking whether tactile stimuli are detected faster and more accurately when the target fingers occupy a specific relative spatial location. The rationale was that if bodily segments hold spatial information then stimuli delivered to a given body part should be processed more efficiently when that body part holds its preferred ("standard") position. Furthermore, in Experiment 2 the task was performed by blind-folded participants under the hypothesis that the contribution of stable internal spatial representations should be maximal in the absence of visual information (although task-irrelevant) about one's own body. In Experiment 3, we used the Implicit Association Test (IAT) (Greenwald, McGhee, & Schwartz, 1998; Greenwald, Nosek, & Banaji, 2003), which measures the strength of implicit associations between a stimulus category (here, fingers) and a class of attributes (here, spatial labels), in order to test the existence of conceptual associations between body parts and spatial concepts.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Experiment 1 was comprised of twenty-one (age = 26 ± 15 (sd) range = 21–43) participants, with normal or corrected-to-normal vision who were naïve to the purpose of the experiment. We originally set the sample size at twenty, however one participant was replaced before data inspection because he did not execute the task as requested, resulting in twenty-one participants tested. Participants were recruited among the students of the University of Milano-Bicocca and gave their written informed consent before the experiment.

The study was approved by the ethical committee of the University of Milano-Bicocca and was conducted in accordance with the Declaration of Helsinki (World Medical Organization, 1996).

2.1.2. Stimuli

The experimental apparatus consisted of a black panel (70 cm × 70 cm) with a fixation point at the center. Computerized stimuli were delivered through four tactile stimulators (custom-made electromagnetic solenoids, Heijo Electronics, Beckenham, UK; www.heijo.com), controlled by a custom-made I/O box and E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA, psychotoolbox.org). Each stimulus consisted of three 30 ms on-phases (single pulses) with two interleaved 30 ms off-phases, resulting in a 150 ms vibration

2.1.3. Task

A unimodal tactile position discrimination task was used, inspired by the one previously used to investigate cross-modal effects (Maravita, Spence, Sergent, & Driver, 2002; Marini, Chelazzi, & Maravita, 2013; Marini, Romano, & Maravita, 2016; Spence, Pavani, & Driver, 2004)

Participants sat at a table, 50 cm away from the previously mentioned black panel standing in front of them. Tactile stimulators were applied directly to the fingertips of each index finger and thumb with medical tape. Both hands were placed about 2 cm in front of the black panel and at fixed distance of about 6 cm from the fixation point, without touching each other, in such a way that the four stimulators corresponded to the vertexes of an imaginary square around the fixation point (Fig.1a). With this configuration, the distance between all adjacent stimulators was 8 cm. Moreover, one hand was placed at the "top" position and the other hand was placed at the "bottom" position (see Marini et al., 2016 for further details on this experimental manipulation). The position of each hand (right hand at the top and left at the bottom, or vice versa) was fixed for each participant and counterbalanced across participants (right hand at the top for 10 participants and left hand at top for the remaining 10 participants). On each trial, participants received a tactile stimulation at one of the four possible locations on their fingertips - finger (index/thumb), side (left/right), or hand (left/right). They were asked to discriminate as quickly as possible the elevation of the tactile stimulus (top or bottom) regardless of the stimulated finger.

Responses were delivered through two foot-pedals, one below the toe and one below the heel of the right foot. Participants raised the toe to respond "top" or the heel to respond "bottom". A total of 120 trials (30 for each position) were delivered in a randomized sequence. Error rate and reaction time (RT) were collected.

2.1.4. Analysis

RTs were first trimmed to eliminate outliers, which were defined as trials faster than 200 ms (anticipatory responses) as well as trials exceeding 3 standard deviations above the mean (late responses), and then converted to log-values to overcome the typical asymmetry of the RT distribution (Ratcliff, 1993). Error rate scores were converted to the arcsine of the root square, a mathematical transformation that aims at aligning the distribution of the error rate data (and its residuals) with the assumptions of ANOVA (Zubin, 1935). Participants with mean Error rate exceeding 3 standard deviations above the group average were excluded from the analysis. This criterion led to the exclusion of 3 additional participants, thus the ANOVAs on RT and error rate were run on a sample of 17 participants

Statistical analyses used repeated-measure analysis of variance (ANOVA) with two factors: relative Position (top/bottom) and Finger (thumb/index) receiving the tactile stimulation. RTs and error rate were tested separately as dependent variables. We reported the effect size of significant effects calculating the partial eta-squared (η_p^2). In ANOVAs, post hoc comparisons were conducted with the HSD-Tukey test. Statistical analyses were performed using Statistica 6.0 for Windows (StatSoft Italia SRL) and SPSS 22 (IBM® SPSS® Chicago, Illinois).

We predicted faster and more accurate discrimination of tactile stimuli when fingers occupy whichever is their preferential spatial location between the upper (top) and the lower position (bottom), as reflected by an interaction of the Position and Finger factors. We did not formulate any specific prediction about which posture would be "preferential" among the two possible associations (i.e., thumb-top and index-bottom, or vice versa) because both postures can be naturally experienced in daily life and therefore both associations seemed equally plausible.

2.2. Results

2.2.1. Reaction Times (RT)

The ANOVA showed significant effects both for the main factor Position [$F(1,16) = 5.08$, $p = 0.04$, $\eta_p^2 = 0.241$; top = 634 ms (mean) ±18 (Standard Error), bottom = 602 ms ± 15] and for the interaction
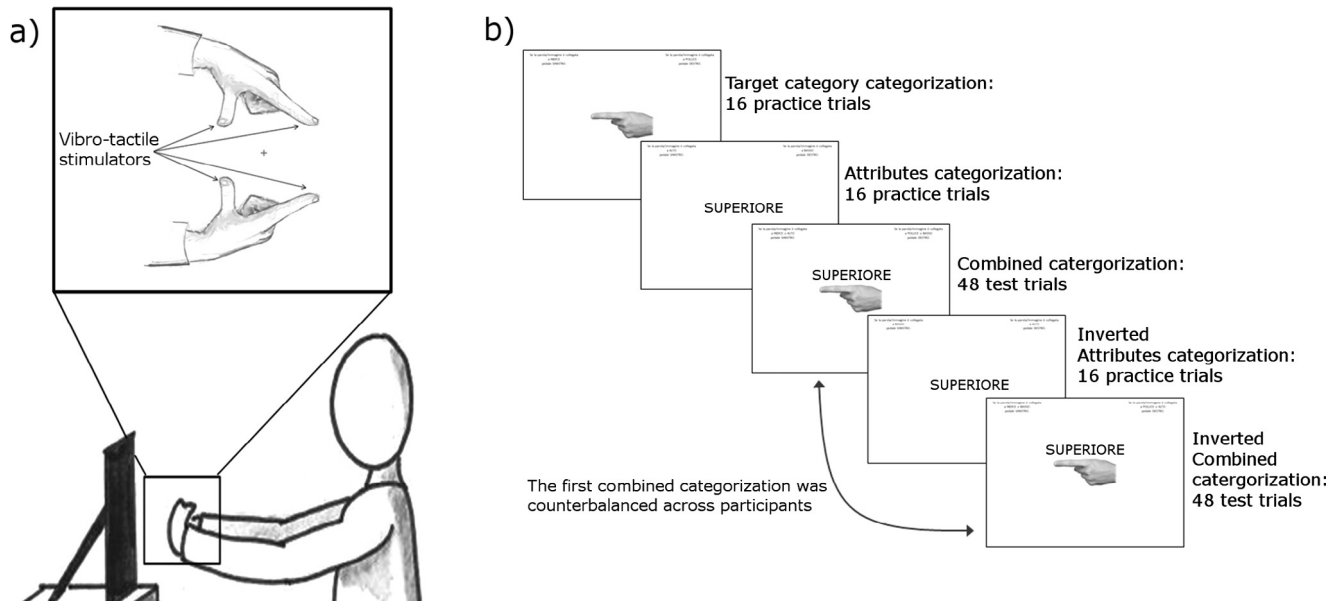
Fig. 1. (a) Experimental setup for Experiment 1 and for Experiment 2. Hand posture is magnified in the upper part of the figure. (b) Schematic representation of the IAT procedure in Experiment 3. Critical blocks are the combined categorization blocks, represented here in the third and fifth small panels ("superiore" is the Italian for superior). The order of presentation of the combined categorization blocks was counterbalanced across participants.

between the two factors Position and Finger [$F(1,16) = 64.08$, $p < 0.001$, $\eta_p^2 = 0.800$], while the main factor Finger was not significant [$F(1,16) = 1.18$, $p = 0.29$].

Post-hoc comparisons for the interaction revealed that the thumb-bottom (558 ms ± 14) and the index-top (581 ms ± 16) associations had faster responses (all $p < 0.01$) than the thumb-top (687 ms ± 23) and the index-bottom (647 ms ± 20) associations (Fig.2).

2.2.2. Error rate

The ANOVA showed an interaction between Finger and Position [$F(1,16) = 77.25$, $p < 0.001$ $\eta_p^2 = 0.828$], while the two main factors were not significant [Finger: $F(1,16) = 0.86$, $p = 0.37$; Position: $F(1,16) = 1.2$, $p = 0.29$].

The post hoc comparisons showed that responses for the thumb-bottom (1.8 % (error rate) ±0.6) and index-top (3.4% ± 0.8) associations were more accurate (all p$s < 0.001$) than those for the thumb-top (13.1% ± 1.7) and index-bottom (12.7 % ± 1.8) (Fig.2) associations.

2.2.3. Short discussion of Experiment 1

Our results showed faster and more accurate responses to tactile stimuli delivered to the index finger in the top position and to the thumb in the bottom position, in line with the hypothesis of preferred relative spatial locations for these fingers. We propose that the slower and less accurate responses observed for index-bottom and thumb-top associations may be due to a mismatch between different representations of the spatial position of body parts, i.e., the proprioceptive representation, the visual representation and the internal standard representation. Visual and proprioceptive feedbacks were always congruent in Experiment 1 and therefore possible mismatches (if any) would be between sensory feedbacks and the internal standard representation of the reciprocal finger positions. If so, we reasoned that the relative contribution of the internal representation should increase if visual feedback is removed. This should result in increased RT and/or accuracy costs in presence of mismatches between proprioceptive feedback and the internal standard representation. Experiment 2 investigated this hypothesis.
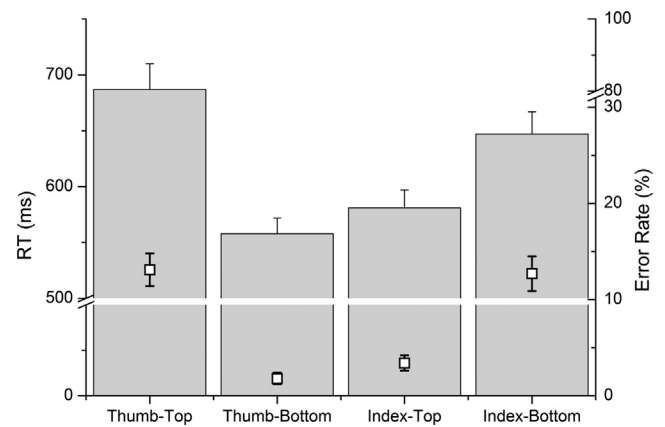

Fig. 2. Results of Experiment 1. Columns represent average RTs (left y axis). Squares indicate percentage of errors (right y axes). Thin bars represent standard errors of the mean.

3. Experiment 2

3.1. Materials and methods

3.1.1. Participants

Twenty (age = 24 ± 2.22 (sd), range = 19–29) new naïve students took part in Experiment 2, after giving their informed consent. All participants were recruited at the University of Milano-Bicocca and had normal or corrected-to-normal vision.

3.1.2. Procedure

Materials and experimental procedure were the same of Experiment 1, except that Experiment 2 consisted of two blocks of 120 trials each. In one block, which was identical to Experiment 1, participants performed the same task of Experiment 1 (see paragraph 2.1.3) while looking at the fixation cross, while in the other block participants executed the same task without vision (i.e. they were blindfolded). This prevented any visual sensory information, including that about body posture (which was, however, task-

irrelevant). The order of blocks was counterbalanced across participants

3.1.3. Analysis

The design was similar as Experiment 1, with the addition of the factor Vision (vision/no-vision), in addition to the factors Position (top/bottom) and Finger (thumb/index), hence resulting in a $2*2*2$ repeated-measure ANOVA design. Two ANOVAs were conducted (for RT and error rate, respectively).

We predicted that incongruent positions would affect performance in the same direction and with stronger magnitudes when visual feedback is removed, due to a stronger weighting of the internal representations. This should emerge as a three-way interaction, showing larger differences in RTs and error rate between preferred and non-preferred postures on trials with closed eyes.

3.2. RESULTS

3.2.1. Reaction Times (RT)

The ANOVA showed significant results for the main factors Finger [$F(1,19) = 9.289$; $p < 0.01$; $\eta_p^2 = 0.328$], Position [$F(1,19) = 8.075$; $p = 0.01$; $\eta_p^2 = 0.298$], and Vision [$F(1,19) = 9.657$; $p < 0.01$; $\eta_p^2 = 0.337$]. Moreover, and crucial to our prediction, the interactions Finger∗Position [$F(1,19) = 98.932$; $p < 0.001$; $\eta_p^2 = 0.839$] and Vision ∗Finger∗Position [$F(1,19) = 8.423$; $p < 0.01$; $\eta_p^2 = 0.307$] were significant.

Post-hoc comparisons for the three-way interaction showed that the thumb-bottom (vision: 590 ms ± 15; no-vision: 612 ms ± 17) and the index-top (vision: 545 ms ± 14; no-vision: 563 ms ± 18) conditions had faster responses than the thumb-top (vision: 658 ms ± 21; no-vision: 703 ms ± 20) and the index-bottom (vision: 636 ms ± 18; no-vision: 701 ms ± 22) conditions both in vision and in no-vision conditions (all ps < 0.01). Notably, the differences were larger in the no-vision than in the vision block (Fig.3).

3.2.2. Error rate

The ANOVA showed non-significant effects for the main factors Finger [$F(1,19) = 2.220$; $p = 0.153$], Position [$F(1,19) = 0.744$; $p = 0.399$], and Vision [$F(1,19) = 0.842$; $p = 0.37$]. However, the interactions Finger∗Position [$F(1,19) = 73.122$; $p < 0.001$; $\eta_p^2 = 0.794$] and Vision∗Finger∗Position [$F(1,19) = 5.791$; $p = 0.03$; $\eta_p^2 = 0.234$] were significant.

Post-hoc comparisons for the three-way interaction showed that the thumb-bottom (vision: 2.8% ± 3.7; no-vision: 2.6% ± 3.9) and the index-top (vision: 1.9% ± 2.2; no-vision: 2.0% ± 3.1) conditions had more accurate responses than the thumb-top (vision: 12.3% ± 8; no-vision: 15.4% ± 10.3) and the index-bottom (vision: 9.4% ± 9.4; no-vision: 12.6% ± 13.2) conditions both in vision and in no-vision conditions (all ps < 0.01). Similar to RT results, these differences were larger in the no-vision block (Fig.3).

3.2.3. Short discussion of Experiment 2

Experiment 2 replicated Experiment 1 results by showing a preferential relative spatial location when responding to tactile stimulation in the absence of visual perception, confirming the preferred spatial associations index-top and thumb-bottom. Importantly, effects were strongest in the no-vision condition of Experiment 2, as predicted by our hypothesis of an increased role of the internal representation when vision is absent. Next, Experiment 3 used the Implicit Association Test (IAT) (Greenwald et al., 1998, 2003) to investigate whether preferential body-space associations extend to the level of abstract associations between body parts and spatial concepts.

4. Experiment 3

4.1. Materials and methods

4.1.1. Participants

40 (age = 27 ± 3 (sd), range = 20–35) naïve participants took part in Experiment 3. All participants were recruited at the University of Milano-Bicocca and gave informed consent before the experiment. All participants had normal or corrected-to-normal vision. Sample size included twice as many participants as Experiments 1 and 2 in order to match the size of each group of the critical between-subject comparison with the sample-size of previous experiments.

4.1.2. Stimuli

Stimuli were photographs of right and left hands closed to a fist except for one finger, which was extended; the extended finger could be either the index finger or the thumb. The extended thumb or index finger pointed either to the right or to the left side. Images were presented on a 20-inch computer screen (resolution 1280×1024 pixels, refresh rate 60 Hz). Attributes related to the concepts of "top" and "bottom" were constituted by the following verbal stimuli (in Italian): *alto, superiore, su, sopra* (high, superior,[1] up, above) for the "top" concept; *basso, inferiore, giù, sotto* (low, inferior, down, below) for the "bottom" concept. Words appeared on the screen with the font 'Courier new' with a size of 24pt. All stimuli were presented at the center of the screen and stayed onscreen until a response occurred (with a 10,000 ms timeout). Trials were presented in a random sequence and were separated by a random inter stimulus interval (range: 250–750 ms) through E-Prime software. Responses were given through the 'a' and 'l' keys of a computer keyboard (with Italian layout) to categorize the target stimulus. The correspondence between buttons and categories was specified at the beginning of each part of the IAT procedure and stayed visible on the upper part of the screen throughout each trial

4.1.3. Procedure: The Implicit Association Test (IAT)

The IAT is a computerized task designed to measure the strength of association between the association of two contrasted target categories (here, index vs. thumb) with two contrasted attribute categories (here, high position vs. low position) (Greenwald et al., 1998, 2003).

If an implicit association were to exist between a target and an attribute (e.g., the index finger and "top" position) responses should be faster on trials in which the relevant target (e.g., the image of an index finger) and attribute (e.g. the word "up") require the same response (e.g., to press the same button 'a' for either stimulus) relative to trials in which they require different responses (e.g. to press the button 'l' for the image of an index finger and the button 'a' for the word "up") (Greenwald et al., 1998, 2003). After having categorized stimuli from the two target categories (finger pictures) and stimuli from the two attribute categories (top/bottom position words) in separate blocks of a first training phase, participants categorized stimuli in a combined task where fingers pictures and spatial terms were associated to the same response key and their presentation onscreen was mixed in such a way that either finger pictures or position words could appear as trial probes. We compared RTs between the two combined categorization blocks (i.e., index-top/thumb-bottom vs.

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[1] As suggested by an anonymous reviewer, it is useful to specify that the Italian word "superiore" was used here, given that in Italian this word may be used with spatial ('above') and comparative ('better') meanings interchangeably and with the same frequency. On the other hand, the primary meaning of the English word 'superior' is 'better', and its usage for 'top' is much less common (i.e., limited to the technical-anatomical usage).
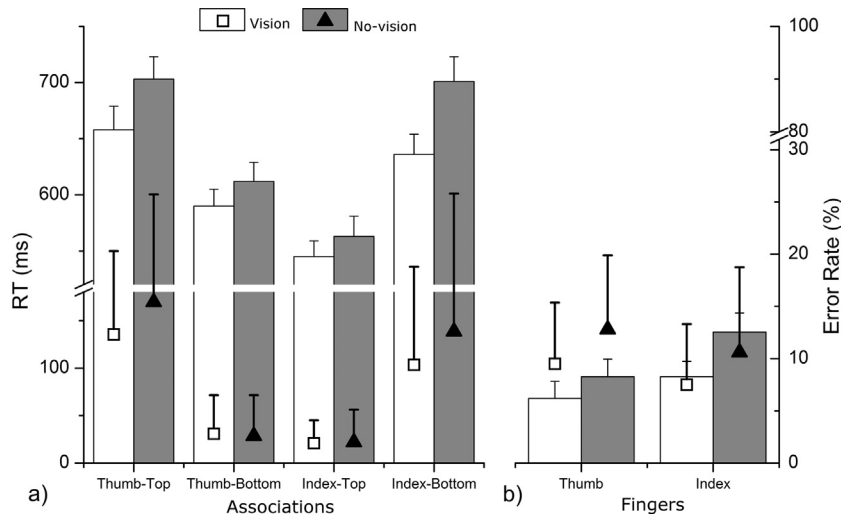
Fig. 3. Results of Experiment 2. In panel (a) each condition is represented. In panel (b) the differences between the predicted preferred and non-preferred positions (i.e., "thumb top" minus "thumb bottom", and "index bottom" minus "index top") are represented. Columns represent the average RTs (left y axis). Symbols indicate percentage of errors (right y axis). Dark columns and triangles represent no-vision conditions, while light columns and squares represent vision conditions. Thin bars represent standard errors of the mean.

index-bottom/thumb-top). Twenty participants performed the task with the "*strong association*" first (i.e., the putative standard association of index-top/thumb-bottom, as found in the previous experiments) while the remaining twenty performed the task with the "*weak association*" first (index-bottom/thumb-top).

The entire IAT procedure included 144 trials. Each practice block had 16 trials and critical blocks where composed of 48 trials each (Fig.1b).

4.1.4. Analysis

The IAT scores were determined using an algorithm (Greenwald et al., 2003) that balances RTs and accuracy within each condition by substituting RTs on error trials with the average RT-value of the same condition plus a fixed penalty of 600 ms.

The Greenwald algorithm typically combines data from the two critical blocks into a single index, calculating a standardized difference of the two (e.g., Greenwald d). Because we were interested in comparing the two possible association combinations separately, we kept the two blocks separated and counterbalanced the order of associations between participants in order to present each combination as first or second for the same number of times. The IAT scores (expressed in ms) were analysed with an ANOVA with factors: Strength of the association (weak/strong, within-subject) and the Order of the association (weak first/strong first, between-subject).

We expected to observe faster RTs when categorizing together (i.e., using the same response key) stimuli that are strongly associated (index-top/thumb-bottom) compared to stimuli with a weaker association (index-bottom/thumb-top), corresponding to a main effect of the factor Strength of the association.

4.2. Results

4.2.1. Reaction Times (RT)

The ANOVA showed a main effect for the factor Strength of the association [$F(1,38) = 8.614$, $p < 0.01$; $\eta_p^2 = 0.185$; strong = 718 ms ± 18, weak = 801 ms ± 25] (Fig.4). The main factor Order of the association [$F(1, 38) = 1.305$, $p = 0.26$] and the interaction [$F(1,38) = 1.918$, $p = 0.174$] were not significant
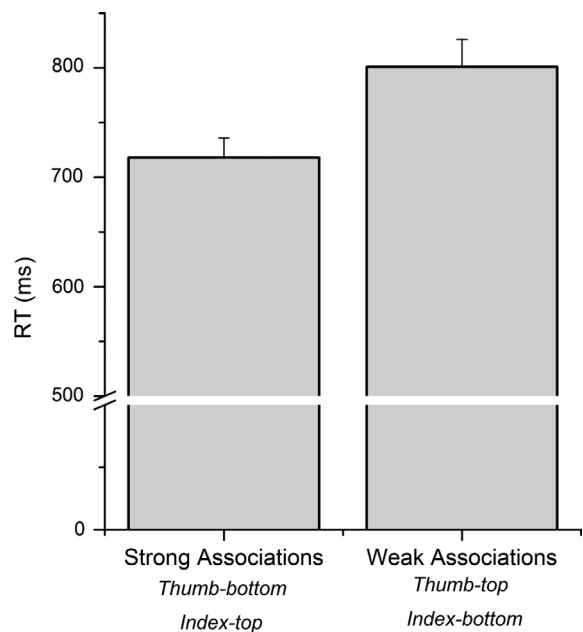

Fig. 4. Results of Experiment 3. Columns represent average RTs for the strong (left side) and weak (right side) associations (i.e., strong associations are "thumb bottom" and "index top"; weak associations are "thumb top" and "index bottom"). Thin bars show standard errors of the mean.

4.2.2. Short discussion of Experiment 3

Experiment 3 showed that images of the index finger and thumb are categorized faster when they are respectively associated with the spatial attributes of top and bottom than vice versa. These results are fully consistent with, and extend, those of Experiments 1 and 2 and support the existence of generalized preferential associations between body parts and spatial concepts that also manifests at the level of implicit conceptual associations.

5. General discussion

This study explored the existence of a standard representation of body-space relationships seeking for preferential associations

between body parts and spatial information. Results showed that different fingers hold preferential relative spatial locations. Specifically, Experiment 1 showed that the localization of tactile stimuli was more efficient when stimuli were delivered to index fingers in a relative top position or to thumbs in a relative bottom position. This suggests that proprioceptive and visual information about current body posture is automatically integrated with information about a preferential (standard) internal spatial representation of the body. Furthermore, in absence of visual perception (Experiment 2) RT-differences between preferred and non-preferred postures increased, thus suggesting an increase in the contribution of the standard internal representation. These findings are reminiscent of the classic hand laterality task (Parsons, 1987b), in which participants discriminated whether a screen-displayed picture showed a left or right hand. In that task RTs typically increase proportionally to the distance between the orientation of one's own hand and that of the screen-displayed hand (Ionta et al., 2007; Parsons, 1987b). In the hand laterality task, RT costs are ascribed to the time-consuming operation of mental rotation, which is necessary to match hand-related visual information (i.e., the hand seen on the screen) with the proprioceptive localization of one's own hand. Our novel finding is that contingent postural changes, together with visual input from the body, modulate spatial judgments of simple tactile stimuli, as if the body parts to which these stimuli are delivered were automatically matched to an invariant internal spatial representation. According to our findings, this internal representation seems to map "*a priori*" index fingers into a relative top position and thumbs into a relative bottom position. During common tasks, ongoing visual and proprioceptive feedbacks may interact with this representation depending on the actual location of the fingers. When the spatial aspects of the internal representation match the sensory feedback stimuli are detected faster and more accurately relative to when internal and sensory-driven spatial information does not match.

Noteworthy, this body/space association differs from other well-characterized body/space couplings that regard the position of hands in space relative to the body midline. Known effects of such couplings include faster responses when the stimulus and the responding hand are on the same (versus opposite) side and are observed even when the stimulus side is task-irrelevant as in the Simon effect (Simon & Acosta, 1982). These faster responses are possibly due to shorter intra- (versus inter-) hemispherical brain processing time (Marzi, 1999) and/or to stimulus-response compatibility effects (Berlucchi, Crea, di Stefano, & Tassinari, 1977). Furthermore, in temporal order judgments of stimuli delivered to both hands, RTs increase when the hands are crossed (Yamamoto & Kitazawa, 2001a, 2001b) indicating that the spatial localization of somatosensory stimuli is automatically referred to the location of the stimulated limb in the external egocentric space. Similarly, Azañón and Soto-Faraco (2008) used a crossmodal cueing paradigm (Kennett, Spence, & Driver, 2002) to show that, when hands are crossed, tactile stimuli are initially unconsciously processed in a somatotopic frame of reference, and only at a second stage they are remapped and consciously reported in an egocentric spatial frame of reference. These results support the idea of a canonical representation of the body in space that is constantly updated due to incoming sensory information. Such body-space interdependencies rely on a fronto-parietal brain network that continuously monitors limb position in external space and allows to maintain efficient hand/object interactions during movements (Bolognini & Maravita, 2007) for optimal manipulation, for multisensory spatial integration (Maravita et al., 2003), and for the localization of touches on the body surface and their remapping into external space (Azañón, Longo, Soto-Faraco, & Haggard, 2010). Further research will help clarifying whether or not the representation of standard body-space association relies on the same brain network.

It is worth noting that the idea of a canonical (standard) representation of the body is not new. First, Melzack in his seminal studies using spinal anesthesia observed that during the induced phantom sensation participants reported the position of the phantom limb as to appear consistently in one out of a few recurrent positions (e.g. on the side or above the abdomen/lower chest) (Bromage & Melzack, 1974; Gross & Melzack, 1978; Melzack & Bromage, 1973). Although it was thought that phantom sensations were completely independent from the actual position of the arm, further evidence has shown that some aspects of the induced phantom sensation are dynamic and change according to the posture held by the arm at the time of anesthesia (Inui, Walsh, Taylor, & Gandevia, 2011). These studies altogether suggested that the standard body representation has a postural configuration and our results seem to extend such findings, suggesting that not only body parts (or at least the fingers) have a preferential position in space, but also that this preference can be generalized to the conceptual domain.

Why the thumb is associated specifically with bottom and the index finger with top, and how these associations would appear in a canonical posture, remain compelling, open questions. Indeed, no physical or bodily constraints typically exist that make either of these two fingers to be more frequently experienced in a given location, as compared to the other. It may be speculated that action habits play a role in the observed effect. 'Grasping' actions are frequently (yet not always) performed with the index finger in a relatively higher location than the thumb, although the opposite is true for 'holding' gestures, therefore the role of the potential for action cannot be unambiguously determined insofar. Based on the present results, one can only speculate that, for the seated body posture, i.e. the posture held by participants in the present paradigm, a putative standard representation may exist with one's hands extended in front, palms down. If so, the thumbs would occupy a relatively lower position compared to the index fingers. However, our data also show the existence of abstract conceptual associations between spatial information and fingers, which suggests that such associations may not be strictly contingent on hand (or body) posture.

Our findings further suggest the existence of preferential associations between spatial information and bodily segments. These associations seem to be intrinsically embedded (or embodied) as stable features of individual body parts independent of any left/right distinction. Such body-space associations reach the level of conceptual representations, as shown by the implicit associations between fingers and spatial concepts that were found in Experiment 3 in absence of any direct motor or postural effect. Similarly, van Elk and Blanke (2011) showed that spatial relationships between body parts modulated the speed of response to body-part names displayed onscreen in compatible or incompatible spatial positions (e.g., faster responses to the word pair "eyes/feet" when the word "eyes" was displayed above the word "feet" than vice versa). These results support the idea of abstract associations between space and words related to body parts, indicating the existence of a link between the semantic knowledge of the body and the relative spatial location of body-relevant stimuli and thus hinting at a putative standard representation of space in BR. However, it is crucial to observe that the body parts studied by van Elk and Blanke (2011) were characterized by strong and fixed spatial constraints that may have promoted the formation of such a link (i.e., feet are typically experienced below eyes). Our study overcame this potential limitation by probing two body parts that do not have any strong spatial constraint in terms of reciprocal spatial elevation and that are typically experienced in a relative upper or lower position interchangeably across different daily life situations. Furthermore, our task did not provide any 'affordance clue' to specific preferential postures (Jakobson & Goodale, 1991; Jeannerod, 1988) given that no object had to be grasped. Our
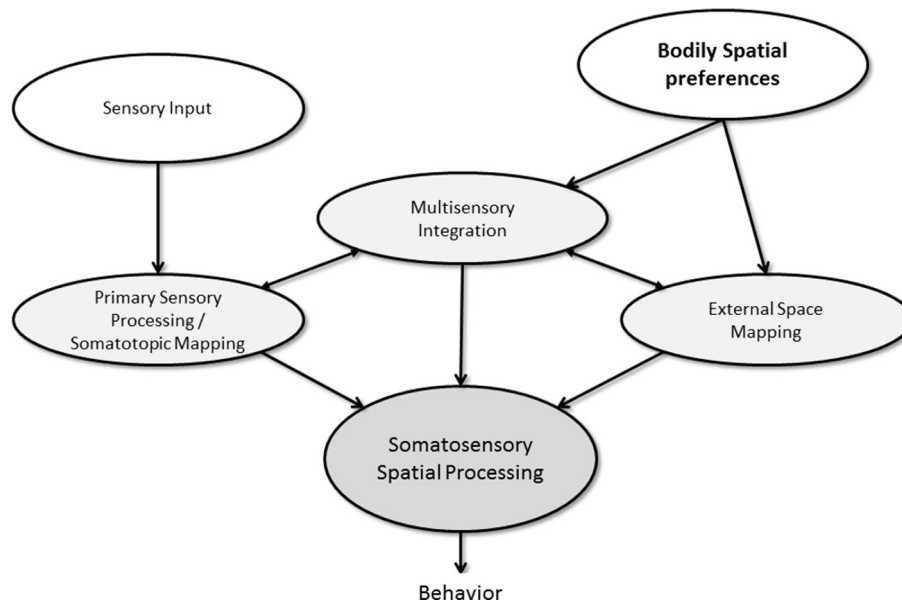
Fig. 5. Contribution of the bodily spatial preferences to spatial somatosensory processing. We propose that standard preferences contribute to the processing of spatial somatosensory information, adding to multisensory integration and egocentric space mapping mechanisms, by means of spatial information held by body parts.

results seem to suggest the existence of an inner "standard spatial preference" that guides perception (and possibly motor acts). Because of their novelty, these findings introduced a number of additional experimental questions. Why do humans have these preferential associations, how do they emerge, and do these associations reflect a preferential location relative to the vertical body or to the absolute gravitational vertical dimension, are only a few of the many questions that this study has opened.

Overall, a new concept seems to emerge from the present study: space is mapped in the human body. This mapping appears to be fine graded, in the sense that it is not limited to gross left/right (Yamamoto & Kitazawa, 2001a) or top/down (van Elk & Blanke, 2011) distinctions based on rigid anatomical or gravitational constraints. Rather, the mapping of space in the body seems to point to the existence of stable finger-space preferences that could potentially extend to other body parts and districts. In a tentative theoretical framework, standard bodily spatial preferences would add to other known levels of somatosensory analysis – i.e., the somatotopic cortical mapping and the spatial localization relative to the egocentric space (de Vignemont, 2010; Longo et al., 2010) – that are known to increase the efficiency of haptic analysis and to promote optimal object manipulation and recognition (see Fig.5).

In this framework, the relationship between body and space appears to be more bi-directional than previously thought: not only the body would be constantly mapped in space, but also the space would be mapped on the body in a hard-wired, *a priori* fashion. The inherent relationship between body and space may represent an interface to encode and integrate sensory information from the environment in a fast and reliable way in order to shape the representation of the world relative to the self.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2017.05.014.

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