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When action is not enough: Tool-use reveals tactile-dependent access to Body Schema

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ABSTRACT

Proper motor control of our own body implies a reliable representation of body parts. This information is supposed to be stored in the Body Schema (BS), a body representation that appears separate from a more perceptual body representation, the Body Image (BI). The dissociation between BS for action and BI for perception, originally based on neuropsychological evidence, has recently become the focus of behavioural studies in physiological conditions. By inducing the rubber hand illusion in healthy participants, Kammers et al. (2009) showed perceptual changes attributable to the BI to which the BS, as indexed via motor tasks, was immune. To more definitively support the existence of dissociable body representations in physiological conditions, here we tested for the opposite dissociation, namely, whether a tool-use paradigm would induce a functional update of the BS (via a motor localization task) without affecting the BI (via a perceptual localization task). Healthy subjects were required to localize three anatomical landmarks on their right arm, before and after using the same arm to control a tool. In addition to this classical task-dependency approach, we assessed whether preferential access to the BS could also depend upon the way positional information about forearm targets is provided, to subsequently execute the same task. To this aim, participants performed either verbally or tactually driven versions of the motor and perceptual localization tasks. Results showed that both the motor and perceptual tasks were sensitive to the update of the forearm representation, but only when the localization task (perceptual or motor) was driven by a tactile input. This pattern reveals that the motor output is not sufficient per se, but has to be coupled with tactually mediated information to guarantee access to the BS. These findings shade a new light on the action–perception models of body representations and underlie how functional plasticity may be a useful tool to clarify their operational definition.

1. Introduction

A peculiar relationship exists between the body and the brain, the latter being physically inside the former, but at the same time being the master. The brain receives information from and sends commands to the entire body. This dialectic relationship suggests that body and brain shape each other in a continuous exchange of information (Gallagher, 2005) with the essential goals of successfully interacting with the environment and preserving life. To succeed in these tasks, the brain needs to represent the body in a way that is useful for the specific activity it performs at a given time, which implies, for example, to represent the body differentially for perception and action (Cardinali, Brozzoli, & Farnè, 2009; Dijkerman & De Haan, 2007). This functional feature underpins dyadic as well as triadic models of body representation proposed in the literature since the seminal neuropsychological work by Head and Holmes (1911–1912). They suggested the existence of (at least) two representations: The Postural Schemata (later termed Body Schema, BS), hypothesized to serve the guidance of actions and being mainly constructed on proprioceptive and tactile information, and the Superficial Schemata (later termed Body Image, BI), which would instead serve perception and be formed mainly by visual, but also other sensory inputs.

Neuropsychological work from Paillard, Michel, and Stelmach (1983) established the action–perception distinction in the somatosensory domain by reporting a patient who, after a left

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parietal lesion, was unable to detect touches on the contralesional deafferented hand, but could accurately point to them in 40% of the trials, thus revealing a blind-sight phenomenon in the tactile modality (see also Rossetti, Rode, & Boisson, 1995). Anema et al. (2009) recently extended this dissociation at higher levels of somatosensory processing, when tactile detection abilities are spared by the brain lesion. They asked two stroke patients to localize a tactile stimulus by either pointing directly to their tactually stimulated hand (hand task), or to a visual map of the hand (map task). The first task involved the body representation for action (i.e., the BS), as it relies mainly on unconscious "online processing and integration of proprioceptive and tactile input" (p. 1620), whereas in the second task the felt touch had to be consciously integrated with a stored representation of the hand's visual features (i.e., the BI). The authors reported a double dissociation, as one patient was impaired in the map task, but not in the hand task while the other patient displayed the opposite pattern. Overall, these findings strengthen the functional principle of division of labour between body representations, akin to the perception–action distinction proposed for vision and touch (Dijkerman & De Haan, 2007; Milner & Goodale, 1995) and support the existence of multiple representations of the body (see, for review, de Vignemont, 2010; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). In particular, relative consensus exists on the definition of BS, which has been closely associated to its unconscious, action-devoted nature, whereas vagueness still persists in the description of the BI, frequently associated with the conscious, perceptual scrutiny of body features (de Vignemont, 2010).

A crucial feature of body representations is their plasticity, which arises from the need for the brain to update body representations according to both the slow and fast changes the body undergoes with time. Owing to the notion that different body representations are built and accessed to for different purposes, it has been proposed that they can also be updated selectively (deVignemont & Farnè, 2010). Kammers, de Vignemont, Verhagen, and Dijkerman (2009) provided evidence for a selective modification of the BI, to which the BS was immune, in physiological conditions. They proceeded by first inducing in healthy subjects the phenomenon of the Rubber Hand Illusion (RHI), in which synchronous visual-tactile stroking of the participant's real hand (unseen) and a plausibly oriented (visible) rubber hand evokes the feeling of ownership of the rubber hand and, of particular interest here, also induces a proprioceptive bias such that participants localize their hand as being closer to the rubber hand (Botvinick & Cohen, 1998; Ehrsson, Holmes, & Passingham, 2005; Folegatti, de Vignemont, Pavani, Rossetti, & Farnè, 2009; Tsakiris & Haggard, 2005). Kammers and colleagues then assessed the proprioceptive bias by requiring either perceptual tasks (i.e., recruiting the BI), or motor tasks (i.e., recruiting the BS). A perceptual task consisted in a visually based task in which subjects watched the experimenter's right and left fingers moving along a line perpendicular to their sagittal axis. In order to judge the proprioceptively perceived position of their index fingers, they had to (verbally) stop the experimenter when they thought the moving fingers were just in front of each of them. Another perceptual task consisted of choosing, among differently sized wooden sticks, the one whose length matched the perceived distance between their right and left index fingers. One of the two motor tasks consisted in a ballistic pointing, performed using either the right (stimulated) or the left (unstimulated) hand to localize, respectively the (unseen) left or right hand. In the other motor task, participants were required to use both index fingertips to reach the extremities of a stick horizontally arranged in front of them. The authors reported that, after induction of the RHI, healthy subjects were biased in localizing their own hand when the task was perceptually based, but not when it was action-based, thus providing a simple dissociation supporting the hypothesis that body representations can be selectively updated (Kammers et al., 2009; Kammers, Kootker, Hogendoorn, & Dijkerman, 2010).

The present study aimed at further assessing the selectivity of the plastic updating of body representations. As a first aim, we tested the case for the opposite dissociation to that reported by Kammers and colleagues. To this aim, we took advantage of a novel sensorimotor paradigm we recently introduced for assessing the changes in metrical aspect of the forearm representation after the use of a tool (Cardinali, Frassinetti et al., 2009). By comparing the kinematics of free-hand movements performed before and after the use of a mechanical grabber that increased subjects' armlength, we showed that movement execution was modified after tool-use. Both grasping and pointing movements were characterized by different kinematic profiles after grasping objects with a 40 cm-long tool. Noteworthy, this difference was compatible with an increase of the represented length of the arm. The temporary increase of the internally represented arm-length, compatible with the idea that tool-use can update the BS, was supported by the fact that, when asked to point to the tactile stimuli that were delivered to their tool-trained forearm, participants pointed to locations that were farther apart. Building onto well-established task-dependent access to either the BS or the BI, here we used motor and perceptual tasks to assess whether the metric of body representations can be updated selectively, namely whether tool-use may affect the BS without altering the BI. Pointing to tactile stimuli delivered on anatomical landmarks of the forearm operating the tool, as in Cardinali, Frassinetti et al.'s work (2009), was used to assess for changes in the BS, whereas visual localization of the same anatomical landmarks was used to probe changes in the BI.

As a second aim, we assessed whether the way subjects are informed about the to-be-localized targets may play a discriminating role in determining which body representation is used. To date, the hallmark of the dissociation between body representations is the outcome: different results emerge when participants perform different tasks (perceptual vs. motor) on the very same incoming information. Neuropsychological work by Rossetti et al. (1995), however, already pointed out that the same tactile localization task may bring to opposite findings as a function of whether motor (BS) or verbal (BI) modalities are used by the patient. Here we hypothesized that using somatosensory or verbal indication as different entries for the same task of pointing to, or visually localizing the anatomical landmarks on the participants' forearm, may bring to a different pattern of results. As suggested by Kammers, Mulder, de Vignemont, and Dijkerman (2010), a better understanding of the level of dissociation among body representations should pass through a more complete approach which uses not only an output-type of criterion, but also considers the input used to trigger the same task.

To jointly address these aims, we ran a series of four experiments in which we asked healthy participants to localize three landmarks on their forearm either through a motor task (Experiments 1 and 2), or a perceptual task (Experiments 3 and 4), to indirectly estimate the represented length of their arm, before and after the use of a tool. Crucially, the two types of tasks could be triggered by the experimenter either touching (Experiments 1 and 3), or naming (Experiments 2 and 4) each target body-part. As the BS is motor in nature, and essentially fed by somatosensory inputs, we predicted to observe a modification of arm-length representation after tool-use in the motor, but not in the perceptual task, and when subjects were asked to localize touched, but not named, body-parts. If the BI is immune to the tool-use-dependent plasticity, the perceptual task should be unaffected, particularly when subjects were asked to localize named body-parts