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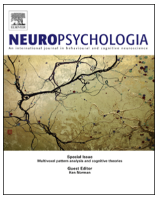

Intensive tool-practice and skillfulness facilitate the extension of body representations in humans

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ABSTRACT

The brain's representation of the body can be extended to include objects that are not originally part of the body. Various studies have found both extremely rapid extensions that occur as soon as an object is held, as well as extremely slow extensions that require weeks of training. Due to species and methodological differences, it is unclear whether the studies were probing different representations, or revealing multiple aspects of the same representation. Here, we present evidence that objects (cotton balls) held by a tool (chopsticks) are rapidly integrated into the body representation, as indexed by fading of the cotton balls (or 'second-order extensions') from a positive afterimage. Skillfulness with chopsticks was predictive of more rapid integration of the second-order cotton balls held by this tool. We also found that extensive training over a period of weeks augmented the level of integration. Together, our findings demonstrate integration of second-order objects held by tools, and reveal that the body representation probed by positive afterimages is subject to both rapid and slow processes of adaptive change.

1. Introduction

Imagine a skillful tennis player immersed in a heated match requiring his upmost capacity and focus. For an external observer, the tennis player is typically considered an independent actor and cause of the events he initiates within his surrounding environment. But in the tennis-player's mental experience, his body, the racket and even the ball can be felt as part of his sensory and intentional self. As the ball approaches, his thoughts are less likely to be on the desired trajectory of his arm, than on the trajectory of the racket head. When the racket makes contact with the ball, the feeling of impact is perceived not at the tactile sensors in his hand, but in the racket head itself. At high levels of skill and concentration, even the racket may become secondary in his experience, all thoughts becoming based on the ball and its desired trajectory. This ability for conscious awareness to be focused on the ball requires that the intermediate effectors (muscles, joints, racket) be integrated into a subconscious, automatically processed model. This model must be capable of tracking the current states of the effectors, and of back-calculating conscious goals into basic motor commands.

The original positing of a model representing the body came from studies of neurological patients by Head and Holmes (1911). Based on observed deficits in postural awareness and tactile localization, they proposed that the normally functioning brain has two types of bodily representations. First there is the *body image*, a conscious representation that is the subject of our thoughts and perceptual judgments. Second, there is the *body schema*, an unconscious framework that automatically integrates posture, proprioceptive input and action goals into a common spatial frame.

The *body image* is believed to be a multisensory representation of the body that integrates stored knowledge, and by subserving mainly perceptual purposes it is subject to bodily illusions (Kammers, Kootker, Hogendoorn, & Dijkerman, 2010). For example, vibrations applied to a tendon causing the sensation of that tendon stretching will result in the perceptual experience of the corresponding limb being moved (Goodwin, McCloskey, & Matthews, 1972). Another manipulation of the body image is demonstrated by the 'rubber hand illusion'. Here, sensory conflict is induced by simultaneous stroking of the own (unseen) hand and

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a visible rubber hand, resulting in an experience of tactile sensations occurring at the rubber hand (Botvinick & Cohen, 1998).

The *body schema*, on the other hand, is described as an unconscious representation that subserves action rather than perception. Head and Holmes proposed that this schema does not exclusively code for the physical body, but is capable of extending to objects that are needed to support skilled actions or smooth movement through the environment. Thus, the body schema would need to include tools, or even a large feather in one's hat, in order to support one's actions or avoid collisions. Though generally believed to be highly robust, also this motoric body representation is not entirely immune to bodily illusions. For example, after inducing the rubber hand illusion, the grip aperture of a real hand was found to mimic that of a rubber hand (Kammers et al., 2010).

Since the early work of Head and Holmes, people largely agree on the existence of multiple body representations, though their exact number and definition is still a matter of debate (Cardinali et al., 2009, 2012; de Vignemont, 2010; Kammers, et al., 2010).

Evidence that tools become integrated into these body representations has come via various experimental routes. Changes in the *body schema* are most directly observed by monitoring the kinematics of action execution. In a study by Cardinali et al. (2009), participants who used a mechanical grabber subsequently changed the kinematics of their empty-handed movements, pointing and grasping as if their arms had lengthened. Simple motor learning was an unlikely account for these changes, as the kinematics of tool-use itself did not change throughout the period in which the mechanical grabber was used. Given that tool-use induced changes in empty-handed actions, the results suggested that a change had occurred in a generalized model of action generation. These findings therefore imply a highly plastic representation of the body schema, similar to what had been suggested by Head and Holmes almost a century prior.

The other major class of tool-use experiments uses measures of multimodal integration to investigate body representations (Maravita & Iriki, 2004). Certain sensory processes are selective for stimuli originating from within "peripersonal space", which corresponds to the reachable or "actionable" space immediately surrounding the body. Bodily representations both define the extent of this space, and also form a basis for the spatial mapping of sensory stimuli within it. Thus, monitoring changes in the extent and organization of this sensory space allows one to infer changes in body representations.

A lot of what is known about body representations in peripersonal space comes from neurophysiological studies in primates. Fronto-parietal networks have been identified that continuously update spatial representations of body shape and posture. These networks integrate multimodal sensory information (primarily proprioceptive, somatosensory and visual information) such that it is functionally relevant to specific actions, and serves the ability to localize the body in space (Colby, 1998; Maravita, Spence, & Driver, 2003; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Notably, there are neurons in ventral-premotor cortex that have both somatosensory and visual receptive fields, coding for the space surrounding the same body part. These bimodal neurons integrate information such that even if a body part (for example a hand) is moved through space, the visual receptive field remains anchored to the body part it belongs to Graziano, Yap, and Gross (1994).

Intriguingly, these fronto-parietal networks can represent external objects in a similar fashion. After weeks of practice with a simple tool, bimodal neurons in intraparietal cortex of macaques were found to expand their visual receptive fields to include the space surrounding the tool whenever the monkey was engaged in deliberate tool interaction (Iriki, Tanaka, & Iwamura, 1996). This finding suggests that peripersonal space can be expanded via the use of a tool (but see also Holmes (2012)). Similarly, a study investigating structural brain changes in macaques exposed to tool-use training for the first time, showed an increase in grey matter volume in fronto-parietal areas including intraparietal cortex (Quallo et al., 2009). In a study of a human patient with right-hemisphere lesions, tool-use altered the domain in which visual neglect was experienced. Whereas the patient's visual neglect was typically restricted to judgments regarding stimuli in peripersonal space, the neglect spread to more distant areas if the task was performed using a long pointing tool, again suggestive of the expansion of peripersonal space (Berti & Frassinetti, 2000). Increased multisensory weights assigned to the processing of visual stimuli around the *functional* part of a tool are likely responsible for the remapping of peripersonal space to include this new region of space after tool-use (Holmes, 2012). Note that none of these studies probed motor output as a dependent measure, so it is unclear whether these body representations subserve action planning as a body schema, or if they subserve only perceptual processing.

The present study utilizes another method of probing bodily representations, which has recently been extended to investigate tool use. The paradigm involves a cross-modal effect whereby proprioceptive inputs profoundly disrupt visual representations of the body (Bross, 2000; Davies, 1973a; Gregory, Wallace, & Campbell, 1959). In these experiments, participants in a completely darkened room are exposed to a brief flash of light, which creates a crisp, long-lasting afterimage of the entire field of view. When the afterimage includes a body part, such as the participant's arm, moving the arm from its imaged position causes the afterimage of the arm to 'fade' or 'crumble' while the rest of the afterimage scene remains intact. The mismatch between proprioceptive and visual representations of the same body part leads to a Gestalt-like disruption of the visual percept. Versions of this experiment done with mirrors confirm that this fading effect occurs in accordance with proprioceptive and visual representations organized on the basis of one's own body (Ritchie & Carlson, 2010).

Such afterimage-based experiments have also demonstrated the rapid modulation of body representations to include held objects. Carlson, Alvarez, Wu and Verstraten (2010) showed that objects grasped by the observer (referred to as *'first-order' objects*) faded upon being dropped. Similarly, when the observer removed a first-order object from the area of peripersonal space being viewed in the afterimage, the object would also fade. This indicates that somatosensory and proprioceptive information is integrated with visual information in much the same way for both held objects and body parts.

Afterimage studies do not investigate motor output, and thus the body representations that were probed may or may not function as body schema. The representations seem more clearly akin to the ones probed in the studies of peripersonal space. Both involve multisensory integration and measurements based on perceptual outcomes. Using the afterimage paradigm, we aim to address several related issues raised by the preceding studies. What kinds of external objects are assimilated? What factors govern whether or not an object is assimilated? How quickly does assimilation occur?

Although the monkey physiology studies found that tool integration developed after weeks of use (Iriki et al., 1996), the human behavioral studies found tool integration as soon as the tools were grasped (Cardinali et al., 2009; Carlson et al., 2010). The behavioral findings closely match our daily functioning and the feeling that we can rapidly assimilate objects (like picking up a pen and beginning to write). There are many functional advantages to a body system capable of rapidly incorporating, as well as disincorporating, an object or tool. The ability to readily expand