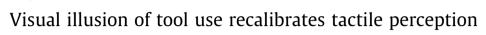
Cognition 162 (2017) 32-40

Contents lists available at ScienceDirect

# Cognition

journal homepage: www.elsevier.com/locate/COGNIT



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#### ARTICLE INFO

Article history: Received 27 June 2016 Revised 27 January 2017 Accepted 31 January 2017 Available online 11 February 2017

Keywords: Body representation Somatosensory Embodiment Plasticity Multisensory Psychophysics

1. Introduction

#### ABSTRACT

Brief use of a tool recalibrates multisensory representations of the user's body, a phenomenon called tool embodiment. Despite two decades of research, little is known about its boundary conditions. It has been widely argued that embodiment requires active tool use, suggesting a critical role for somatosensory and motor feedback. The present study used a visual illusion to cast doubt on this view. We used a mirrorbased setup to induce a visual experience of tool use with an arm that was in fact stationary. Following illusory tool use, tactile perception was recalibrated on this stationary arm, and with equal magnitude as physical use. Recalibration was not found following illusory passive tool holding, and could not be accounted for by sensory conflict or general interhemispheric plasticity. These results suggest visual tool-use signals play a critical role in driving tool embodiment.

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# Tool use is a hallmark of the human species and a ubiquitous part of daily life (Vaesen, 2012). From everyday items, like cutlery, to physical augmentation equipment, such as prosthetics, tool use is often accompanied by a sense of "feeling" the world through the tool (Marasco, Kim, Colgate, Peshkin, & Kuiken, 2011; Yamamoto & Kitazawa, 2001). Indeed, the body and tool fuse into a single functional system during tool use (Maravita & Iriki, 2004). This process, known as tool embodiment, aids in seamless and successful interaction with the environment, and involves rapid recalibration of multisensory representations of the user's body (Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Cardinali et al., 2012; Farnè, Iriki, & Làdavas, 2005; Iriki, Tanaka, & Iwamura, 1996; Maravita, Spence, & Driver, 2002; Sposito, Bolognini, Vallar, & Maravita, 2012). For example, brief tool use modulates a multisensory representation of the arm that structures tactile perception (Canzoneri et al., 2013; Cardinali et al., 2009, 2011; Miller, Longo, & Saygin, 2014).

While tool embodiment has been studied extensively over the past two decades (Maravita & Iriki, 2004), little is known about its *boundary conditions*. The idea that embodiment would be

primarily driven by somato-motor feedback during tool use is intuitive and compelling. Indeed, studies have reported that active use of the tool, as opposed to mere passive holding, is necessary for embodiment (Garbarini et al., 2015; Maravita et al., 2002; Witt, Proffitt, & Epstein, 2005; though, see Baccarini et al., 2014). This suggests that a range of specific motor and kinesthetic factors (Wolpert & Ghahramani, 2000)—such as efference copies and somatosensory feedback—may be critical for the process (Brown, Doole, & Malfait, 2011; Rademaker, Wu, Bloem, & Sack, 2014). Indeed, a recent study failed to find evidence for tool-modulated reaching kinematics in a deafferented patient (Cardinali, Brozzoli, Luauté, Roy, & Farnè, 2016). Here, in contrast, we provide evidence that tool embodiment can be purely driven by the visual experience of tool use.

There is a long tradition in the perceptual sciences of using illusions to illuminate the fundamental machinery of perception (Eagleman, 2001); illusory contours (Murray & Herrmann, 2013) and the rubber hand illusion (Botvinick & Cohen, 1998) are classic examples. We take this approach in the present study to explore the boundary conditions of tool embodiment, as well as its underlying multisensory mechanisms. We explored tool use with a variation of the *mirror visual illusion* (Ramachandran, Rogers-Ramachandran, & Cobb, 1995), which isolates visual feedback of a body part from concomitant proprioceptive and kinesthetic signals. Several studies have found that this illusion has profound effects on body perception (Romano, Bottini, & Maravita, 2013),



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such as modulating the conscious awareness of phantom limbs (Hunter, Katz, & Davis, 2003; Ramachandran & Rogers-Ramachandran, 1996; Ramachandran et al., 1995), biasing the felt position of the unseen hand (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005; Snijders, Holmes, & Spence, 2007), and altering the perception of action space (Creem-Regehr, Payne, Rand, & Hansen, 2014). To foreshadow our results, we found that a visual illusion of tool use recalibrated tactile perception on a *stationary* arm that appeared to be using the tool during the illusion. This finding has significant implications for our understanding of the multisensory machinery that constructs body perception and its relation to objects in the external world.

#### 2. Experiment 1: Visual illusion of tool use

In Experiment 1, we used the mirror visual illusion to investigate whether participants could embody visual feedback of a limb using a tool, as measured by a recalibration in tactile perception on a stationary arm that did not use the tool. Further, the stationary arm was placed either behind the mirror (Experiment 1a) or down by the hip (Experiment 1b), allowing us to address whether the magnitude of visual-proprioceptive conflict influences the effect.

#### 2.1. Methods and materials

#### 2.1.1. Participants

Twenty-two participants in total took part in Experiment 1; twelve participants took part in Experiment 1a (10 females; 11 right-handed by self-report; Mean age: 22.34, SD: 2.80) and ten participants took part in Experiment 1b (7 females; all righthanded; Mean age: 21.83 SD: 2.71). All participants had normal or corrected-to-normal vision. The experiment was run under the ethical guidelines of the University of California, San Diego, and all participants gave informed consent before participating in the experiment.

### 2.1.2. Mirror illusion setup

The setup of the mirror illusion occurred following the first (pre-tool use) block of the tactile task (see *Tactile Paradigm* and Fig. 1a, below). A long mirror (119 cm in length and 41 cm in height) was placed slightly to the left of the mid-sagittal plane of the participant. In Experiment 1a, the participant's left arm was placed out-of-sight and palm-down behind the mirror, with the

elbow resting 10 cm distally from the start of the mirror's body. The right elbow was initially placed at the location directly opposite the left elbow so that the mirror image accurately reflected the true location of the left arm during rest. In Experiment 1b, participants instead rested their left arm down by the left hip throughout the course of the illusion. This produced a complete dissociation between the mirror image and the proprioceptively specified location of the left arm.

#### 2.1.3. Mechanical grabber

The tool used in the experiment was a mechanical grabber that extended the user's reach by a maximum of 40 cm (Fig. 1a). The grabber's pincers had a maximal width of approximately 18 cm apart. When an object was grasped within the pincers it was approximately 34 cm from the user's hand.

## 2.1.4. Object interaction task and mirror illusion

After the initial mirror box setup (performed immediately after the first block of the tactile task, described below), a tool was placed in the participant's right hand as it rested on the table. They were instructed to wrap their fingers around the handle of the tool, but not to move it. The location of the tip of the tool was marked with tape on the table and a foam cube  $(5 \times 5 \times 5 \text{ cm})$  was placed 8 cm distal to the midpoint of the tape. Participants used the tool to pick up the foam cube. They were explicitly instructed to only focus on the contents of the mirror image and never look directly at their actual right hand as it used the tool. Their head orientation and gaze was monitored throughout the course of the task by the experimenter. During tool use, they initially started with the grabber's pincers at the most proximal location of the tape. They then used the tool to pick the cube straight up and place it back down in approximately the same location it was in prior to lifting. They then returned the pincers back to the tape before initiating the next action. This produced visual feedback that the participant's left arm was using a tool when it was in fact completely stationary (Fig. 1a). The object-interaction task was self-paced, and lasted for a total duration of 8 min.

The mirror illusion procedure produced two forms of sensory conflict: visual-proprioceptive conflict, where there was a mismatch between the seen and felt location of the left arm, and visual-kinesthetic conflict, where there was a mismatch between the seen and felt movements of the left arm. The visualkinesthetic conflict was likely very similar between Exp. 1a and

a b Arm distance is larger view of the truth of the truth

**Fig. 1.** Visual illusion and tactile paradigm. (a) Mirror Visual Illusion: A long mirror was placed slightly to the left of the mid-sagittal plane of the participant. The participant's left arm was placed out-of-sight and hand palm-down behind the mirror (Exp. 1a) or resting next to the participant's left hip (Exp. 1b). The illusion produced the experience that the left arm was using the tool, despite remaining completely stationary. (b) Tactile distance judgment task: Two tactile points separated by various distances (blue dots) were applied manually to the arm (target surface) and forehead (reference surface). Participants judged which of the two body parts was touched with the farthest distance between the two tactile points. Each participant's responses, before and after tool use, were fit with a logistic curve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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