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The Body in Flux: Tool Use Modulates Multisensory Body Representations

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The Body in Flux: Tool Use Modulates Multisensory Body Representations

A dissertation submitted in partial satisfaction of the requirements for the degree
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in

Cognitive Science

by

Luke Edward Christian Miller

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The Dissertation of Luke Edward Christian Miller is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

Chair

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LIST OF ABBREVIATIONS

aIPS: anterior intraparietal sulcus

EEG: electroencephalogram

EOG: electrooculogram

ERP: event-related brain potential

JND: just noticeable difference

LRT: likelihood ratio test

LLR: likelihood ratio

PPC: posterior parietal cortex

PSE: point of subjective equality

RHI: rubber hand illusion

RF: receptive field

SEP: somatosensory evoked potential

SI: shape index

SI: primary somatosensory cortex

SII: secondary somatosensory cortex

SMI: shape modulation index

TDJ: tactile distance judgment task

VET: visual enhancement of touch

vPMC: ventral premotor cortex

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Chapter 1, in full, was published in the *Journal of Experimental Psychology: Human Perception and Performance* with Ayse P. Saygin and Matthew R. Longo.

Chapter 2, in full, is in preparation for publication as a manuscript with Ayse P. Saygin and Matthew R. Longo.

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ABSTRACT OF THE DISSERTATION

The Body in Flux: Tool Use Modulates Multisensory Body Representations

by

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Doctor of Philosophy in Cognitive Science

University of California, San Diego, 2015

Professor Ayse P. Saygin, Chair

Tool use is a hallmark of the human species and an essential aspect of daily life. Tools serve to functionally extend the body, allowing the user to overcome physical limitations and interact with the environment in previously impossible ways. Tool-body interactions lead to significant modulation in the user's representations of body size, a phenomenon known as tool embodiment. In the present dissertation, I used psychophysics and event-related brain potentials to investigate several aspects of tool embodiment that are otherwise poorly understood. First, we investigated the sensory boundary conditions of tool embodiment, specifically the role of visual feedback during tool use. In several studies, we demonstrate that visual feedback of tool use is a critical driver of tool embodiment. In one such study, we find that participants can embody a visual illusion of tool use, suggesting that visual feedback may be sufficient for tool-induced plasticity. Second, we investigated the level of representation modulated by tool use. Is embodiment confined to sensorimotor body representations, as several researchers have claimed, or can it extend to levels of self-representation (often called the body image)? Utilizing well-established psychophysical tasks, we found that using a tool modulated the body image in a similar manner as sensorimotor representations. This finding suggesting that similar embodiment mechanisms are involved at multiple levels of body representation. Third, we used event-related brain potentials to investigate the electrophysiological correlates of tool embodiment. Several studies with tool-trained macaques have implicated multisensory stages of somatosensory processing in embodiment. Whether the same is true for humans is unknown. Consistent with what is found in macaques, we found that using a tool modulates an ERP component (the P100) thought to index the multisensory representation of the body. The work presented in this dissertation advances our understanding of tool embodiment, both at the behavioral and neural level, and opens up novel avenues of research.

Introduction to Dissertation

In this dissertation, I report on several studies designed to investigate how tool use modulates the user's body representations. To do so, I used two experimental approaches: psychophysics and event-related brain potentials.

It is intuitive to think of the way the brain represents the body as a bottom-up process, where the processing of incoming somatosensory signals is all that is needed. However, cognitive neuroscience and experimental psychology have demonstrated that this characterization is too simplistic. Creating a coherent yet dynamic representation of our body, with which we can successfully interact with the world, requires the integration of information across distinct sensory modalities (Blanke, 2012). The overall goal of my research is to understand the mechanisms underlying this process.

One common approach to understanding the mechanisms underlying the construction of body representations is by characterizing the conditions that modulate them. One particular phenomenon that has been the focus of my research is called *tool embodiment*, the notion that using a tool modulates the user's perceived arm size. While this idea has been around for at least a century (Head & Holmes, 1911), it wasn't until recently that neuroscientists uncovered empirical evidence for it (Iriki, Tanaka, & Iwamura, 1996). It is now well established that tools modulate several representational aspects of the tool-using limb including its peripersonal space (Farnè, Iriki, & Làdavas, 2005; Farnè, Serino, & Ladavas, 2007; Galli, Noel, Canzoneri, Blanke, & Serino, 2015; Holmes, Calvert, & Spence, 2004; Longo & Lourenco, 2006; Maravita, Spence, & Driver, 2002; Serino, Bassolino, Farnè, & Làdavas, 2007), kinematics (Baccarini, Martel, Cardinali, Sillan, Farnè, & Roy, 2014; Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009; Cardinali, Jacobs, Brozzoli, Frassinetti, Roy, & Farne, 2012), and tactile processing (Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Cardinali et al., 2009; Sposito, Bolognini, Vallar, & Maravita, 2012).

While there has been considerable research on tool embodiment over the past two decades (Maravita & Iriki, 2004), there are still several aspects of tool embodiment that have not been adequately addressed. My research has focused on addressing three unknown aspects of tool embodiment: 1) What are the sensory boundary conditions of tool embodiment? Specifically, what role does visual feedback during tool use play in the embodiment of the tool? 2) What levels of body representation are modulated by tool use? Using a tool modulates representations underlying sensorimotor interaction, but what about representations underlying the bodily sense of self—the *me* in body perception? 3) What are the cortical mechanisms underlying tool embodiment? Whereas a few studies have investigated this in macaques, the neural mechanisms of tool embodiment in humans are currently unknown.

I will next give an introduction to each of these questions separately. Note that these three questions are often addressed in more than one chapter, and any individual chapter can be relevant to more than one question.

a. What role does vision play in tool embodiment?

Vision plays a crucial role in maintaining a coherent sense of the body (de Vignemont, 2014). For example, visually magnifying the hand leads to a "magnification" in tactile perception on the hand (Kennett, Taylor-Clarke, & Haggard, 2001; Taylor-Clarke, Jacobsen, & Haggard, 2004) and changes grip aperture when reaching for a non-magnified object (Bernardi, Marino, Maravita, Castelnuovo, Tebano, & Bricolo, 2013). Visual shape processing is important in determining which objects can "belong" to the body. The rubber hand illusion (RHI), an illusion of body ownership, only occurs if the rubber object is shaped like a hand (Haans, IJsselsteijn, & de Kort, 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005). This shape-specificity has since been extended to several other body phenomena (Kennett et al., 2001; Longo, Betti, Aglioti, & Haggard, 2009a; Mancini, Longo, Kammers, & Haggard, 2011).

In my opinion, the best example of the dominance of vision over the somatosensory modality is the mirror visual illusion (Ramachandran, Rogers-Ramachandran, & Cobb, 1995). In the typical experimental setup, subjects rest one arm behind the body of a mirror (aligned along their mid-sagittal plane) and view the reflection of their other arm. This produces the strikingly vivid experience that they are looking at the arm behind the mirror, producing misattributions of movement to the stationary arm (Holmes, Snijders, & Spence, 2006) and the feeling that the stationary arm is in the location of the reflected arm (Holmes et al., 2006; Longo et al., 2009a; Mancini et al., 2011). This illusion is so powerful subjects can even mislocalize their non-reflected arm by half a meter (Newport & Gilpin, 2011). Further, the mirror visual illusion has been shown to re-animate phantom limbs that were previously “frozen” in place (Ramachandran et al., 1995).

What role does visual feedback during tool use play in embodiment? This question drove the bulk of my dissertation research, as it had not been previously addressed in a published study. In **Chapter 1**, we investigated whether the shape of the tool constrained the body part affected by embodiment. This question was inspired by the RHI findings mentioned above. In our study, participants used either a hand-shaped or an arm-shaped tool and tactile perception was tested on either the arm or the hand. Tool embodiment only occurred on the body part congruently shaped with the tool, suggesting that visual signals of tool shape constrain embodiment.

In **Chapter 2**, we directly investigated the importance of vision. Participants used a tool in one of two sensory contexts: vision-present or vision-absent (they were blindfolded). Embodiment occurred when vision was present during tool use, but not when vision was absent. We went to the opposite extreme in **Chapter 3**, investigating whether embodiment was possible when only visual signals were present. We used the mirror visual illusion to produce the vivid illusion that the arm behind the mirror was using a tool, despite remaining completely stationary on a table. All measurements of tactile perception occurred on the stationary arm. We found evidence that visual illusion modulated the representation of the stationary arm; several controls ruled out alternative explanations. This suggests to us that visual tool use signals might be sufficient for embodiment.

b. What levels of body representation are modulated by tool use?

How many mental body representations are there? This question has been debated in both philosophy and psychology for decades, with little agreement between researchers. However, it is an essential question if we wish to scientifically understand what it is like to be an embodied agent. A proper framework for thinking about body representations should capture the complex experience of having a body (Longo & Haggard, 2012) while simultaneously being parsimonious—not postulating separate representations for every task (Kammers, Mulder, de Vignemont, & Dijkerman, 2010).

Over the past two or three decades several models of body representation have been proposed. Perhaps the most popular, often called the dyadic model, postulates separate representations for *perceiving* your body and *using* your body (S. Gallagher, 1986; Shaun Gallagher & Cole, 1995), often called *body image* and *body schema*, respectively (de Vignemont, 2010). Empirical research with brain-damaged patients (Paillard, 1999; Rossetti, Rode, & Boisson, 1995) as well as neurologically healthy participants (e.g. Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kammers, van der Ham, & Dijkerman, 2006) has offered considerable empirical support for this perception-action distinction (Dijkerman & de Haan, 2007).

There is considerable evidence that body representation in the somatosensory modality is considerably more distorted than the visual modality (Longo, 2014; Longo & Haggard, 2010, 2011)—for example, just imagine how strange you'd feel if your conscious bodily awareness was based upon the somatosensory homunculus (Penfield & Boldrey, 1937). This has led some researchers to postulate the existence of at least two perceptual body representations (Longo, Azanon, & Haggard, 2010; Longo & Haggard, 2010). Under their conception, somatosensory perception is structured by a representation called the *body model*. The *body image*, on the other hand, underlies the perceptual impression of what our own body looks like (called the *bodily self*) in the visual modality, often like looking in the mirror (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009b; Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012). I will stick to the terminology of this triadic model throughout this dissertation.

The level of body representation that is modulated by tool use has recently become an active area of research. Recent work by Farnè and colleagues demonstrates that using a ~40 cm tool modulates the user's reaching kinematics (Baccarini et al., 2014; Cardinali et al., 2009; Cardinali et al., 2012), suggesting that tool use modulates the user's body schema. Studies have also found that using a tool modulates the user's tactile perception (Canzoneri et al., 2013; Cardinali, Brozzoli, Urquizar, Salemme, Roy, & Farnè, 2011; Cardinali et al., 2009) and proprioceptive localization (Garbarini, Fossataro, Berti, Gindri, Romano, Pia, della Gatta, Maravita, & Neppi-Modona, 2015; Sposito et al., 2012), suggesting that tool use also modulates the user's body model. Whether the user's body image is also modulated by tool use is currently unknown. In fact, several researchers have claimed that tool embodiment is specific to the body model and body schema (De Preester & Tsakiris, 2009; de Vignemont & Farnè, 2010). Given that only one study has investigated whether tool embodiment modulates the body image (Cardinali et al., 2011), this strong claim is unwarranted.

In **Chapter 2**, we investigate whether tool use modulates the user's body image. Whereas the study mentioned above used a task that indirectly tapped into the body image (Cardinali et al., 2011), we used a task that is widely considered to be the most direct way to measure the body image (Gandevia & Phegan, 1999; Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Longo & Haggard, 2012b). In this task, subjects match images of different hand shapes to their own remembered hand shape. We found that tool use modulated this judgment, suggesting that tool use affects the user's body image. In **Chapters 1 through 3**, we provide further evidence that tool use modulates the user's body model.

c. Which cortical somatosensory processing stages are modulated by tool use?

The brain contains multiple representations of the body within both classically uni- and multisensory regions of the somatosensory system (Berlucchi & Aglioti, 1997; Blanke, 2012). The somatosensory sub-modalities (e.g., vibration, proprioception) are initially processed in the primary somatosensory cortex (SI), which contains several receptor-based representations (Mountcastle, 2005). The secondary somatosensory cortex (SII) contains representations with more complex receptive fields (RFs) (Fitzgerald, Lane, Thakur, & Hsiao, 2004, 2006; Thakur, Fitzgerald, Lane, & Hsiao, 2006). Further, these representations are likely body-based (Hsiao, 2008; Lin & Forss, 2002), meaning that they reflect properties of the body and not just the receptor sheet (i.e., the skin). While traditionally thought of as unisensory, there is recent evidence for audio-tactile processing in SII (Iguchi, Hoshi, Nemoto, Taira, & Hashimoto, 2007). Multisensory representations—particularly those constructed by integrating vision and touch—exist in the posterior parietal (PPC) and ventral premotor cortices (vPMC) (Brozzoli, Gentile, & Ehrsson, 2012; Graziano, Hu,

& Gross, 1997; Iriki, Tanaka, Obayashi, & Iwamura, 2001; Serino, Canzoneri, & Avenanti, 2011). These representations are unequivocally based on the physical body. Both PPC and vPMC are involved in remapping tactile signals from a skin-centered reference frame to one based on external space (i.e., current limb position) (Azanon, Longo, Soto-Faraco, & Haggard, 2010; Graziano, 1999). Activity throughout this interconnected network underlies the experience of having a body (Tsakiris, 2010).

Tool embodiment is currently not well understood at the neural level. In macaques, tool use learning leads to gray and white matter changes in SII, vPMC, and anterior intraparietal sulcus (aIPS) (Hihara, Notoya, Tanaka, Ichinose, Ojima, Obayashi, Fujii, & Iriki, 2006; Quallo, Price, Ueno, Asamizuya, Cheng, Lemon, & Iriki, 2009). Further, neurophysiology studies have found that active tool use modulates multisensory body representation in the aIPS (Iriki et al., 1996). While no studies to date have directly investigated tool embodiment in the human brain, the close spatial proximity of tool and body representations (Gallivan, McLean, Valyear, & Culham, 2013; Peeters, Simone, Nelissen, Fabbri-Destro, Vanduffel, Rizzolatti, & Orban, 2009) suggests that parietal and premotor regions may be involved. However, the question still remains open as to which brain regions underlie tool embodiment in the human brain.

In **Chapter 4**, we used event-related brain potentials (ERP) to investigate the stage(s) of somatosensory processing modulated by tool use in humans. The benefits for using ERP to investigate this research question are two-fold: 1) ERPs have exquisite temporal resolution, providing a means to measure processing stages over time. 2) The cortical generators of somatosensory evoked potentials (SEPs) in humans have been mapped out with intracranial recordings and magnetoencephalography (Allison, McCarthy, Wood, & Jones, 1991; Hoshiyama & Kakigi, 2001). Short-latency SEPs reflect processing in SI (Allison, McCarthy, & Wood, 1992; Yamada, Kayamori, Kimura, & Beck, 1984) whereas mid-latency SEPs (>60 ms) reflect processing in SII, PPC, and regions of the frontal cortex (Forss, Hari, Salmelin, Ahonen, Hamalainen, Kajola, Knuutila, & Simola, 1994; Mauguiere, Merlet, Forss, Vanni, Jousmaki, Adeleine, & Hari, 1997). We hypothesized that using a tool would modulate the amplitude of mid-latency SEPs that index multisensory body representations. Consistent with this, we found that extended use of a tool (but not the hand alone) increased the amplitude of the P100 component, which is thought to reflect multisensory body representations (Sambo & Forster, 2009) in SII and PPC (Barba, Valeriani, Colicchio, Tonali, & Restuccia, 2004; Forss et al., 1994). This finding is consistent with what is found in tool-trained macaques (Iriki et al., 1996; Quallo et al., 2009).

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Chapter 1

Tool Morphology Constrains the Effects of Tool Use on Body Representations

Abstract

What factors constrain whether tool use modulates the user's body representations? To date, studies on representational plasticity following tool use have primarily focused on the act of using the tool. Here, we investigated whether the tool's morphology also serves to constrain plasticity. In two experiments, we varied whether the tool was morphologically similar to a target body part (Experiment 1: hand; Experiment 2: arm). Participants judged the tactile distance between pairs of points applied to their tool-using target body surface and forehead (control surface), before and after tool use. We applied touch in two orientations, allowing us to quantify how tool use modulates the representation's shape. Significant representational plasticity in hand shape (increase in width, decrease in length) was found when the tool was morphologically similar to a hand (Experiment 1A), but not when the tool was arm-shaped (Experiment 1B). Conversely, significant representational plasticity was found on the arm when the tool was arm-shaped (Experiment 2B), but not when hand-shaped (Experiment 2A). Taken together, our results indicate that morphological similarity between the tool and the effector constrains tool-induced representational plasticity. The embodiment of tools may thus depend on a match-to-template process between tool morphology and representation of the body.

Introduction

Tool use is one of the hallmark features of the human species. Tools are used in almost every facet of our lives, from the most mundane (e.g., knives for slicing food) to the most awe-inspiring (e.g., robotic surgical tools). Tools can help overcome the limitations of our bodies, changing the way we interact with and manipulate the environment. However, the influence of tool use is not limited to the way the body is used; tools can also change the way we *represent* our own body.

The idea that the brain treats a tool as part of the body has been around for over a century (Butler, 1872). More recent empirical support for this claim has come from neuroscience and experimental psychology (Maravita & Iriki, 2004). Using a tool leads to plastic changes the user's body representations (i.e., *representational plasticity*). Studies with macaque monkeys (Iriki, Tanaka, & Iwamura, 1996) and humans (Farnè, Iriki, & Làdavas, 2005; Maravita, Spence, Kennett, & Driver, 2002b) have demonstrated that the neural representation of the space around the hand extends to include a tool after use. Tool use can also modulate representations of the body itself, as evidenced by changes in reaching kinematics (Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009b) , distal shifts in localization of touch on the arm wielding the tool (Cardinali, Brozzoli, Urquizar, Salemme, Roy, & Farnè, 2011), and altered perception of the midpoint of the arm (Sposito, Bolognini, Vallar, & Maravita, 2012). Together, these results indicate that tool use has widespread influences on the representation of not only the peripersonal space surrounding the body, but also of the body itself.

What factors constrain representational plasticity following tool use? One proposal that has received considerable attention is that plasticity is driven by the functional consequences of tool use. Indeed, representational plasticity has been found following active use (Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Farnè et al., 2005; Farnè & Làdavas, 2000; Maravita, Clarke, Husain, & Driver, 2002a; Maravita et al., 2002b; Serino, Bassolino, Farnè, & Làdavas, 2007), and in preparation to use the tool (Costantini, Ambrosini, Sinigaglia, & Gallese, 2011; Holmes, Calvert, & Spence, 2007; Witt, Proffitt, & Epstein, 2005), but not when the tool was passively held (Kao & Goodale, 2009; Maravita et al., 2002b).

Another potential factor constraining plasticity, one that has yet to receive attention from researchers, is the *morphology* of the tool. Tools do not need to be shaped like the body in order to be effective. On the contrary, the efficacy of some tools (e.g., corkscrews or knives) is critically dependent on the very fact that they have morphological features very different from our bodies. Nevertheless, the embodiment of an external object can be contingent upon it having a similar overall form (i.e., size and shape) to one's own body. For example, the experience of illusory body ownership of an object in the rubber hand illusion (RHI) is dependent on that object having the overall shape of a hand (Haans, IJsselsteijn, & de Kort, 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris, Costantini, & Haggard, 2008; Tsakiris & Haggard, 2005).

Although morphology constrains conscious feelings of embodiment, such as the sense of limb ownership, whether or not morphological constraints regulate plasticity induced by tool use is currently unknown. While we are certainly able to use tools that are not shaped like our body or body parts, function is often constrained by morphology. The tight coupling between a tool's shape and its usability increases the probability that tools shaped like the body can be used like the body. Here, we hypothesized that tool shape plays a role in modulating plasticity. In other words, we explored whether tool-induced representational plasticity of a body part is constrained by the tool's morphological resemblance to that body part. We tested the role of tool morphology in representational plasticity using a tactile distance judgment task (TDJ), which has been used in previous studies to measure plasticity of body representations (de Vignemont, Ehrsson, & Haggard, 2005; Tajadura-Jiménez, Väljamäe, Toshima, Kimura, Tsakiris, & Kitagawa, 2012; Taylor-Clarke, Jacobsen, & Haggard, 2004). Unlike most previous studies (though see Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013), we administered the TDJ in two orientations: proximo-distally (i.e., along the width of the hand) and medio-laterally (i.e., across the length of the hand). This allowed us to explore whether any representational plasticity we observe would be manifest as an overall size change, or a shape change.

Perceiving the size of objects touching the skin depends on an implicit representation of body form (Longo, Azanon, & Haggard, 2010). Accordingly, if tool use leads to representational plasticity, we would expect to see changes in the perceived size of objects contacting the skin surface. We measured changes in tactile size perception on the hand and arm in four experiments manipulating the morphological similarity between the tool and the effector. The tools used in each experiment differed in their morphology (hand-shaped or arm-shaped), but not in their functional "goal" (both tools were used to grasp and move objects). We predicted that the hand-shaped tool would lead to greater modulation of the implicit representation of the hand, whereas the arm-shaped tool would lead to greater modulation of the implicit representation of the arm.

Methods

Participants

Fifteen adults (14 female) between 18 and 27 years of age (mean: 21.01, SD: 2.03) participated in Experiment 1A. Fifteen adults (13 female) between 19 and 27 years of age (mean: 21.58, SD: 1.99) participated in Experiment 1B. Fourteen participants (13 female) between 18 and 34 years of age (mean: 21.15, SD: 3.96) participated in Experiment 2A. Ten participants (6 female) between 18 and 25 years of age (mean: 21.47, SD: 2.31) participated in Experiment 2B. No participant took part in more than one experiment. All participants were right-handed as indicated by self-report. The experiments were approved by the University of California, San Diego ethics committee and all participants gave informed consent.

Materials

In Experiments 1A and 2A, participants wore a custom-built plastic hand-shaped tool, which was modeled after a human hand (Figure 1.1A). Each finger of the tool contained biologically realistic, fully adjustable “joints”. The user’s fingers and those of the tool were connected via straps that allowed for control of each of the tool’s fingers individually. Thus the fingers of the hand-shaped tool were contingent upon the movement of the user’s actual fingers, and resembled the user’s fingers in their dexterity. The tool was approximately 21 cm wide, as measured from the base of the pointer finger to the base of the pinky, and 45 cm long, as measured from the base of the tool to the tip of the middle finger. In Experiment 1B and 2B, participants used an 80 cm-long arm-shaped mechanical grabber (Figure 1.1B). The grabber consisted of a handle, a long slender shaft, and pincers at its distal tip. In contrast to the hand-shaped tool, the movement of the grabber's pincers did not retain the dexterity of a human hand. To grasp an object with the grabber, participants squeezed a vertical handle in order to horizontally close pincers at its distal tip. The movement profile of the grabber's shaft, however, did resemble the user's arm during movement. In both experiments, participants used their assigned tool to pick up and move balloons.

In the tactile distance judgment task (TDJ), touch was delivered using wooden posts, each mounted on a square wooden block, and separated by three distances: 20, 30, and 40 mm. Each post was tapered to a flat point 1 mm in diameter.

Procedure

The experiments began with a pre-tool use TDJ, followed by tool use, and a post-tool use TDJ. In the TDJ (Figure 1.2), touch was administered to a target and reference surface. In Experiment 1A and 2A, the target surface was the dorsum of the hand, whereas it was the dorsum of the forearm in Experiment 1B and 2B. The reference surface was the forehead in all experiments. Participants made unspeeded two-alternative forced choice verbal judgments about which body surface was stimulated with the greatest tactile distance ("hand/arm" or "forehead"). One of five distance pairs was used to administer touch to the forehead and hand/arm on each trial (target/reference): 40/20 mm, 30/20 mm, 30/30 mm, 20/30 mm, 20/40 mm. Tactile stimulation in each trial occurred in one of two orientations: *across* (hand/arm: medio-lateral; forehead: eye-to-eye) or *along* (hand/arm: proximo-distal; forehead: nasion to hairline) the body surface. Each distance pair was applied 8 times in each orientation, yielding a total of 80 trials, 40 in each orientation. The body part that was stimulated first (target or reference) was counterbalanced for each distance combination and orientation. The procedure was split into two blocks (40 trials each), separated by an eight-minute break in the pre-tool use condition or eight minutes of tool use in the post-tool use condition. On each trial, the distance combination, stimulus orientation, and order in which body surfaces were stimulated were selected from a randomized list of all possible stimulation combinations for that block. Tactile stimuli were applied manually by the experimenter, and lasted roughly one second with an approximately two second inter-stimulus interval when switching between surfaces.

Immediately following the pre-tool use TDJ, participants were asked to use the tool. They were instructed to pick up a balloon and place it into a bucket repeatedly. The balloon was initially positioned approximately at the subject's midline and approximately 75 cm from their body in Experiment 1A and 2A, and approximately 110 cm in Experiment 1B and 2B; the bucket was placed approximately 75 cm to the right of the subject's midline. Once the balloon was placed inside the bucket by the subject, the experimenter removed it and placed it back into position. Three differently sized balloons were used during the course of the task, which were alternated to keep the task engaging. The grasping task for the two tools varied slightly due to the differences in their dexterity. The task for the hand-shaped tool was as follows: For the first three minutes, subjects picked up the balloons using a power grip. For one minute each, the subjects first picked up the largest, then medium, and then smallest balloon.

Subjects then picked up the smallest balloon using a precision grip with each thumb-finger combination (thumb-pointer, thumb-middle, thumb-ring, thumb-pinky) for one minute each, totaling four minutes. For the final minute, subjects again used a power grip to pick up the smallest balloon. The task for the mechanical grabber was as follows: For the first three minutes, subjects picked up the balloons with the grabber's pincers. For one minute each, the subjects first picked up the largest, then medium, and then smallest balloon. Subjects then spent the next four minutes alternating minutes between picking up the medium-sized and smallest balloon. The final minute was spent picking up the smallest balloon. This task was self-paced, and was done twice, each instance lasting approximately 8 minutes for a total of 16 minutes of tool use during the course of each experiment.

Analysis Methods

Psychophysical curve fitting was used to measure changes in tactile size perception on the hand following tool use. The curve-fitting procedure and all corresponding analyses were performed with MATLAB (The MathWorks, Natick, MA) using the Palamedes Toolbox (Prins, 2009). Logistic functions were fit to each participant's pre- and post-tool use response profiles using a maximum likelihood procedure (Wichmann & Hill, 2001a). We then extracted from each curve the point of subjective equality (PSE, the point on the psychometric curve that crosses 50%, and indicates the point at which the two stimuli would be perceived as equal) and the just-noticeable difference (JND). In this context, the PSE is a measure of anisotropy in tactile size perception, whereas the JND is a measure of perceptual sensitivity. We used changes to the PSE and JND in each dimension as dependent measures in repeated measures ANOVAs to evaluate the effects of tool use.

In addition to statistical analyses using dependent measures derived from the psychometric curves, we also compared the group-level curves for pre and post tool use TDJ directly using a permutation test called a likelihood ratio test (LRT; Wichmann & Hill, 2001b). P-values for the LRT correspond to the ratio of the simulated datasets that had larger likelihood values than the true data. Each LRT was based on 5000 simulations. If the number of simulated likelihood values greater than the true data exceeded 250, the pre- and post-tool use curves were not considered significantly different (i.e., $p > 0.05$).

Results

Experiment 1: Hand-shaped Tool

Experiment 1A: Hand-shaped Tool and Tactile Perception on the Hand

Significant modulations of tactile size perception on the hand were found following the use of the hand-shaped tool. Tool use changed tactile size perception on the hand in both orientations (Figure 1.3; Figure 1.5A). A 2 (tool use: pre, post) x 2 (orientation: across, along) repeated measures analysis of variance (ANOVA) with PSE as the dependent measure revealed main effects of tool use [$F(1,14) = 4.73$, $p = 0.047$, $\eta^2_p = 0.25$] and orientation [$F(1,14) = 8.83$, $p = 0.01$, $\eta^2_p = 0.38$]. We also found a highly significant interaction between the two factors [$F(1,14) = 48.88$, $p < 0.0001$, $\eta^2_p = 0.78$], which was driven by *opposing* changes in tactile size perception on the hand for each orientation. Tool use led to an increase in tactile size perception across the hand [8.9% increase, $t(14) = 3.64$, $p = 0.003$, $\eta^2 = 0.49$], and a decrease along the hand [17.3% decrease, $t(14) = -7.53$, $p < 0.001$, $\eta^2 = 0.80$].

Tool use did not change the perceptual sensitivity on the hand as measured by the JND. A 2 (tool use: pre, post) x 2 (orientation: across, along) repeated measures ANOVA revealed a main effect of orientation [$F(1,14) = 5.34$, $p = 0.037$, $\eta^2_p = 0.28$], likely reflecting pre-existing differences in the sensitivity on the hand and forehead. No other main effects or interactions were found [all F's < 1.75, all p's > 0.2].

Analysis of the group-level psychometric curves also demonstrated analogous results. LRTs demonstrated that tool use significantly changed tactile size perception across [$p = 0.02$] and along [$p < 0.001$] the hand (Figure 1.3). Significant changes in the post-tool use curves were driven by changes in the PSE [all p's < 0.05] and not the JND [all p's > 0.1].

Experiment 1B: Arm-shaped Tool and Tactile Perception on the Hand

In striking contrast to the hand shaped tool, the use of the arm-shaped mechanical grabber did not lead to tool-induced modulations on the hand in either orientation (Figure 1.5A). A repeated measures ANOVA on the PSE found no significant interactions or main effects [all F's < 0.1, all p's > 0.7]. A repeated measures ANOVA on the JND found no significant main effects or interactions [a trend for a main effect of orientation [$F(1,14) = 3.32$, $p = 0.09$, $\eta^2_p = 0.19$], other F's < 0.15, all p's > 0.7]. Analysis of the psychometric curves using LRT also found no differences between the pre- and post-tool use curves (all p's > 0.7).

Experiment 1A vs. 1B

In order to more precisely confirm our hypothesis that tool shape modulates tactile size perception, it is necessary to demonstrate that changes in TDJ following the use of the hand-shaped tool is significantly greater than that for the arm-shaped grabber. We therefore performed 2 x 2 ANOVA with the type of tool used (hand-shaped, arm-shaped) as a between-subjects factor, and the orientation of touch (across, along) as a within-subjects factor, the dependent measure being the difference between the pre- and post-tool use PSEs. Changes in tactile size perception significantly differed based on the type of tool used (Figure 1.5A). The critical interaction between tool type and orientation was significant [$F(2,28) = 17.22$, $p < 0.001$, $\eta^2_p = 0.38$]. Follow-up pairwise comparisons demonstrated a significant difference in size change between the two experiments for TDJ both across [$t(28) = 2.40$, $p = 0.02$, $\eta^2 = 0.17$], and along [$t(28) = -3.24$, $p = 0.003$, $\eta^2 = 0.27$] the hand.

Experiment 2: Arm-shaped Tool

Experiment 2A: Hand-shaped Tool and Tactile Perception on the Arm

The hand-shaped tool did not lead to significant changes in tactile size perception on the arm in either orientation (Figure 1.5B). A 2 (tool use: pre, post) x 2 (orientation: across, along) repeated measures ANOVA on the PSEs revealed a significant main effect of orientation [$F(1,13) = 10.68$, $p = 0.006$, $\eta^2_p = 0.45$] due to pre-existing orientation-specific differences in tactile size perception on the arm. No other main effects or interactions were found [all F's < 1, all p's > 0.38]. Similar results were found for the JNDs: there was a significant main effect of orientation [$F(1,13) = 28.93$, $p < 0.0001$, $\eta^2_p = 0.69$] and a marginally significant main effect of tool use [$F(1,13) = 3.59$, $p = 0.08$, $\eta^2_p = 0.22$]. However, the crucial interaction was not significant [$F(1,13) = 0.19$, $p = 0.67$]. Analysis of the psychometric curves using LRTs also found no differences between the pre- and post-tool use curves (all p's > 0.6).

Experiment 2B: Arm-shaped Tool and Tactile Perception on the Arm

In striking contrast to Experiment 2A as well as Experiment 1B, we found significant changes to tactile size perception on the arm following the use of the arm-shaped tool (Figure 1.4; Figure 1.5B). Tool use changed tactile size perception on the arm in both orientations. A 2 (tool use: pre, post) x 2 (orientation: across, along) repeated measures ANOVA on the PSEs revealed a significant main effect of orientation [$F(1,9) = 39.41$, $p < 0.0001$, $\eta^2_p = 0.81$], but no significant main effect of tool use [$F(1,9) = 0.42$, $p = 0.53$]. Like Experiment 1A, we found a significant interaction between tool use and orientation [$F(1,9) = 14.62$, $p = 0.004$, $\eta^2_p = 0.62$], demonstrating opposing changes on the arm for each orientation. Tool use led to an increase in tactile size perception across the arm [16.5% increase, $t(9) = 2.72$, $p = 0.024$, $\eta^2 = 0.45$], and a decrease along the arm [22.5% decrease, $t(9) = -2.95$, $p = 0.016$, $\eta^2 = 0.49$].

Tool use did not change the perceptual sensitivity on the arm. An ANOVA on the JNDs revealed a significant main effect of orientation [$F(1,9) = 6.44$, $p = 0.036$, $\eta^2_p = 0.42$]. No other main effects or interactions were found [all F's < 1.5, all p's > 0.25].

Analysis of the group-level psychometric curves also demonstrated that tool use modulated tactile size perception on the arm. LRTs demonstrated that tool use significantly changed tactile size perception across [$p = 0.018$] and along [$p < 0.0001$]

the arm (Figure 1.4). Significant changes in the post-tool use curves were driven by changes in the PSE [all p's < 0.001] and not the JND [all p's > 0.1].

Experiment 2A vs. 2B

As with Experiment 1A and 1B, we tested whether the measured changes following the use of the arm-shaped grabber were significantly greater than that for the hand-shaped tool. We performed 2 x 2 ANOVA with the type of tool used (hand-shaped, arm-shaped) as a between-subjects factor, and the orientation of touch (across, along) as a within-subjects factor; the dependent measure being the difference between the pre- and post-tool use PSEs. Changes in tactile size perception significantly differed based on the type of tool used (Figure 1.5B). The interaction between tool type and orientation was significant [$F(2,22) = 14.25$, $p = 0.001$, $\eta^2_p = 0.39$]. Follow-up pairwise comparisons demonstrated a significant difference in size change between the two experiments for TDJ both across [$t(22) = 2.55$, $p = 0.02$, $\eta^2 = 0.23$], and along [$t(22) = -3.01$, $p = 0.007$, $\eta^2 = 0.29$] the arm.

Experiment 1 vs. 2: Shape Modulation

Experiment 1A and 2B found that tool use led to opposing changes in tactile size perception across and along their respective target body parts. This suggests that the implicit body representation that underlies tactile size perception has changed its represented shape. To quantify this shape change for all four experiments (Figure 1.6), we calculated a *shape modulation index*, which is expressed as a ratio of change between the width and length of the hand representation (Longo & Haggard, 2010). The shape modulation index was calculated as follows:

$$\text{Shape modulation index} = \left[\left(\frac{100 + \%\ \text{change in hand width}}{100 + \%\ \text{change in hand length}}\right)\right]$$

To compare the shape modulation across all four experiments, we performed a 2 x 2 ANOVA with target body part (hand, arm) and tool shape (hand, arm) as between-subjects factors. Main effects for target body part [$F(1,53) = 3.11$, $p = 0.08$, $\eta^2_p = 0.06$], and tool shape[$F(1,53) = 3.64$, $p = 0.06$, $\eta^2_p = 0.07$] trended but did not reach significance. Crucially, the interaction between target body part and tool shape was significant [$F(1,53) = 27.65$, $p < 0.0001$, $\eta^2_p = 0.36$], indicating a relationship between the shape of the tool and the body part targeted for tool-induced representational plasticity (Figure 1.6). When the tool was hand-shaped, there was a significantly larger shape modulation on the hand than the arm [hand: 1.33 vs. arm: 1.02; $t(27) = 4.16$, $p < 0.0001$, $\eta^2 = 0.39$]; the opposite pattern of results was found for the arm-shaped tool [hand: 1.04 vs. arm: 1.66; $t(23) = 3.62$, $p = 0.001$, $\eta^2 = 0.36$].

Discussion

We investigated whether tool-induced representational plasticity, as measured by a change in tactile size perception, was contingent upon whether the tool and the effector wielding the tool were morphologically similar. Participants wielded one of two tools, a hand-shaped tool (Fig. 1.1A; Experiment 1A and 2A) or an arm-shaped grabber (Fig. 1.1B; Experiment 1B and 2B). Tactile size perception was tested before and after the use of the tool on the hand (Experiment 1A and 1B) or the forearm (Experiment 2A and 2B). We found that using a tool led to opposing changes in tactile size perception in each orientation of the target body part, namely expansion across the limb, and compression along it. However, these findings were only found when the tool and target body part were morphologically similar (e.g., for the hand-shaped tool on the hand). No plasticity was found when the shape of the tool and the target body part did not match (e.g., for the hand-shaped tool on the arm). Effects of the tool used interacted significantly with target body part. Therefore, we demonstrated that the magnitude of plasticity to the implicit representation of an effector is constrained by whether the tool morphologically resembles said effector. Taken together with previous results emphasizing the importance of functional constraints (Bonifazi et al., 2007; Farnè et al., 2005; Farnè & Làdavas, 2000; Holmes et al., 2007; Maravita et al., 2002a; Maravita et al., 2002b; Serino et al., 2007; Witt et al., 2005), we conclude both function and morphology influence tool-induced representational plasticity.

Representational Plasticity and Tool Morphology

Two aspects of morphological similarity may have driven the observed representational plasticity: similarity between the structure of the tool and the body (structural similarity), and/or the similar dexterity between the tool and the body (sensorimotor similarity). Although structural similarity, which is likely to involve visual processing, had not been studied as a modulator of tool-induced representational plasticity, it has been studied for other perceptual phenomena related to body representations. For example, in the *visual enhancement of touch* (VET) effect, tactile spatial acuity on a body part is increased when viewing that body part, but not a non-body-shaped object (Kennett, Taylor-Clarke, & Haggard, 2001).

Perhaps more relevant to the present findings is the shape specificity found for the RHI, where temporally synchronous stroking by a paintbrush applied to a prosthetic hand in view and the participant's own hand that is hidden from view gives rise to the illusion that the prosthetic hand is the participant's own hand (Botvinick & Cohen, 1998). This illusion of ownership does not occur for non-hand-shaped objects (Tsakiris et al., 2010; Tsakiris & Haggard, 2005). While the embodiment of a prosthetic hand depends on its structural similarity to the shape of a hand, it does not seem to depend on other aspects of visual similarity. For example, several studies have found that the presence of a RHI is not dependent upon whether subjects shared the same skin colour as the prosthetic hand (Farmer, Tajadura-Jimenez, & Tsakiris, 2012; Holmes, Snijders, & Spence, 2006; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009; Maister, Sebanz, Knoblich, & Tsakiris, 2013). Similarly, while the structure of our hand-shaped tool resembles that of a hand, other visual aspects of the tool are vastly different than a human hand. Whereas the skeletal structure of the tool is similar to a hand, it lacks the volumetric properties that characterize real, human hands. Further, the colour of the tool (i.e. mostly white) is significantly different than the skin colour of our participants. Similar differences exist between the arm-shaped grabber and the user's arm. As is the case in the RHI, the representation(s) involved in the embodiment of tools are likely underspecified and not self-specific.

There are a number of aspects of the tools other than shape that need to be considered in relation to the plasticity effects that are our primary interest. For example, in addition to shape, the tools also differed in size, which can modulate the magnitude of plasticity (Farnè et al., 2005; Sposito et al., 2012). In all of our experiments, the goals of the two tools were identical (i.e., picking up and moving balloons). However, each tool achieved this goal by altering body size in different ways. The hand-shaped tool did so by increasing hand size, while not increasing the reaching space of the arm—tool-object interactions still occurred within perihand space. Conversely, the arm-shaped grabber achieved its goal by extending the user's reaching space. It is therefore possible that the grabber's pincers were too distal in external space to modulate the user's hand representation. Effects of gross size are unlikely to fully explain our data however, given that previous research using a short arm-shaped tool, which was of comparable size to our hand-shaped tool (40 cm), did find plasticity to the arm representation but not the hand representation (Cardinali et al., 2011; Cardinali et al., 2009b). Nevertheless, an influence of tool size would still demonstrate that the structural morphology of the tool constrains representational plasticity, although it would not be able to speak as directly to the issue of structural and shape *similarity* between body and tool.

Another aspect to consider is somewhat separate from structural morphology: the sensorimotor similarity between the tool and the user's body. As described above, the hand-shaped tool increased the user's functional hand size, and it did so while still maintaining the dexterity of the user's own hand. The functional mapping between the user's and the tool's fingers were essentially one-to-one. In contrast to the hand-shaped tool, the distal pincers of the grabber did not map directly onto the functionality of the hand and the fingers. Because of said differences in functional mapping, each tool might have influenced different body part representations even though they were used to achieve the same goal (i.e. picking up and moving balloons). This process may also be influenced by differential patterns of proprioceptive feedback during the use of each tool. These aspects, like tool length discussed above, are broadly related to structural similarity, but need to be evaluated in more detail in future studies building on the present findings. Preliminary results appear to indicate that motor complexity of wielding the tool and proprioceptive feedback differences are unlikely to be the main driver of the representational plasticity effects observed in the present study (L.E. Miller, M.R. Longo, & A. P. Saygin, 2013).

Overall, in consideration of these data and previous research, we show that both structural and sensorimotor similarity can be potential modulators of representational plasticity. Of course, how the tool is used (i.e. its function) is often constrained by its physical structure, and vice versa. Tools that are shaped like hands will likely have a greater probability of being used like a hand than tools that are not hand-shaped. The structural and sensorimotor similarity of the tool are therefore intimately related, at least during typical use of the tool. Experimental work where these factors can be teased apart can reveal the role of each aspect of morphological similarity to quantify how much each contributes to the embodiment process.

Mechanisms Underlying Representational Plasticity

What are the mechanisms that underlie our finding that tool morphology constrains representational plasticity? One potential explanation comes from an influential hypothesis in the RHI literature, called the *body model hypothesis* (Tsakiris et al., 2010). According to this hypothesis, embodiment requires a match-to-template process where the morphology of the object is compared against a stored representation of body structure, and accordingly, representational plasticity would be constrained by whether an external object is structurally similar to the body. While several recent findings have called into question the explanatory limits of the body model hypothesis for the RHI (e.g., participants can be made to experience ownership over three arms (de Vignemont & Farnè, 2010; Ehrsson, 2009; but see Folegatti, Farnè, Salemme, & de Vignemont, 2012; Guterstam, Petkova, & Ehrsson, 2011), or even a volume of empty space (Guterstam, Gentile, & Ehrsson, 2013), our findings are nevertheless the first to implicate a match-to-template process in tool-induced plasticity. Further, while the template discussed in the RHI is often a visual one, our results leave open the possibility that tools access a *sensorimotor template* when targeting specific body parts during embodiment. This sensorimotor body template may explain how we can use certain tools despite them having little to no visual resemblance to the body (See the section "Body Representations and Tool Embodiment" for a more thorough discussion of this point).

We can gain more insight into the observed representational plasticity by considering possible neural mechanisms underlying tactile size perception. Whereas tactile size perception is dependent upon an implicit representation of body morphology (Longo et al., 2010), likely in posterior parietal cortex (PPC), it has also been tied to the geometry of receptive fields (RFs) in primary somatosensory cortex (SI) (Longo & Haggard, 2011). Visual body information from the PPC—which may store the visual body template discussed in the previous paragraph (Konen & Haggard, 2012)—can modulate levels of intracortical inhibition (Cardini, Longo, & Haggard, 2011), altering SI RF geometry (Haggard, Christakou, & Serino, 2007). Changes to intracortical inhibition often differentially affect different axes of the RF, leading to anisotropic changes in its shape (Alloway, Rosenthal, & Burton, 1989). Furthermore, neurophysiology studies have found that tool use modulates neuronal processing in both primary somatosensory cortex and posterior parietal cortex in the macaque monkey (Iriki et al., 1996; Quallo, Price, Ueno, Asamizuya, Cheng, Lemon, & Iriki, 2009). We thus suggest that top-down signals from the PPC during tool use may cause anisotropic changes in SI RF geometry, leading to the observed plasticity to tactile size perception.

The Relationship Between Plasticity and Represented Shape

Following use of the hand-shaped tool, did the underlying hand representation become short and squat, or skinny and long? The answer to this question is dependent upon on how we conceptualize the relationship between the size of an implicit limb representation and the perceived size of touch on that limb. Two opposing views have been discussed in the literature, which we summarize in Figure 1.7. In one view, there is an *inverse* relationship between representational size and perceived tactile size. As the size of the representation increases, two points of touch on the somatosensory homunculus in SI are remapped onto smaller anatomical locations on the implicit body representation in the PPC, leading them to be perceived as closer together. In the other view, there is a *proportional* relationship between representational size and perceived tactile size. As the size of the representation decreases, so does the perceived distance between two points of touch. This view is espoused by Longo & Haggard (2011), who propose that the dimensions of implicit body representations are dependent upon the geometry of receptive fields in SI. Under this view, tactile size perception is inextricably linked to the dimensions of the implicit body representation.

A recent study (Canzoneri et al., 2013) found that using a long rake led to a decrease in tactile size perception proximo-distally on the arm (consistent with our results) *and* a concurrent distal shift in tactile localization (consistent with Cardinali et al. (2009)). While these findings may lend empirical support for the inverse view, the lack of correlation between the magnitude of plasticity in the two tasks suggests caution in making a straightforward interpretation.

Although our data do not allow us to definitively resolve the issue, we are inclined to interpret our results within the framework of the proportional model. Under this view, the implicit hand representation would become short and squat following use of the hand-shaped tool. Support for the proportional view comes from studies showing a positive relationship between perceived tactile size and cortical magnification (Gibson & Craig, 2005; Taylor-Clarke et al., 2004). Increases in tactile size perception have been observed when changes in visual (Taylor-Clarke et al., 2004), auditory (Tajadura-Jiménez et al., 2012), or proprioceptive (de Vignemont et al., 2005) input led to the perception that the limb had increased in size. Further, consistent with findings from the TDJ (Longo & Haggard, 2011), a paradigm requiring participants to explicitly locate landmarks on their hand (psychomorphometric paradigm) found that the dorsal surface of the hand is perceived as short and squat (Longo & Haggard, 2010). The correspondence between findings from the psychomorphometric paradigm and the TDJ suggest that the two tasks rely on the same implicit body representation. Although this needs to be verified in future studies, we observed the same pattern of tool-induced shape plasticity for an explicit, visual body representation in a preliminary study (L.E. Miller, M. R. Longo, & A. P. Saygin, 2013).

Knowing the relationship between tactile size perception and body representation shape would help resolve an apparent conflict between our findings and previous research. How can tool use lead to an apparent lengthening of the arm representation (Cardinali et al., 2011; Cardinali et al., 2009b; Sposito et al., 2012) and compression in tactile size perception? There is no conflict if the inverse view is correct. However, if the proportional view is correct, a discrepancy exists between findings using the TDJ and other paradigms, such as tactile localization (Canzoneri et al., 2013; Cardinali et al., 2011; Cardinali et al., 2009b). One potential explanation for this discrepancy comes from the psychophysics literature on tactile localization. Tactile localization is more accurate on skin surfaces with high spatial acuity (Cody, Garside, Lloyd, & Poliakoff, 2008). Viewing the body, which increases tactile spatial acuity (Kennett et al., 2001), could also increase the speed of tactile localization (Press, Taylor-Clarke, Kennett, & Haggard, 2004) and compress tactile size perception (Longo & Sadibolova, 2013). Examination of Figure 5 in Canzoneri and colleagues (2013) reveals that the perceptual distalization of touch following tool use reflects a decrease in spatial localization error. Although the relationship between tactile size perception and localization is complicated and needs to be further specified, it is possible that both compression and distalization reflect tool-induced increases in tactile spatial acuity.

Body Representations and Tool Embodiment

How to conceptualize body representations has been a major topic of debate in psychology for decades. To date there is little agreement between researchers, both scientists and philosophers, on how many representations of the body there are and their functional properties. On the one hand, researchers hope to capture the complexities of what it is like to have a body (Longo & Haggard, 2012), while on the other hand not inventing a new body representation for every novel task (Kammers, Mulder, de Vignemont, & Dijkerman, 2010).

Perhaps the most common taxonomy divides representations of the body into those for action (*body schema*) and those for perception (*body image*) (de Vignemont, 2010; Dijkerman & de Haan, 2007; Gallagher, 1986). The body schema is conceptualized as an online sensorimotor representation of the body that is continually updated as the body's posture changes. The body image, in contrast, is conceptualized as an offline representation that structures first-person body perception in the visual and somatosensory modalities. Empirical studies of both neurological patients (Paillard, 1999; Rossetti, Rode, & Boisson, 1995) and healthy participants (e.g. Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kammers, van der Ham, & Dijkerman, 2006) have lent support to this distinction. Other researchers have sought to elaborate on this dyadic view of the body. For example, Longo and Haggard have proposed a representation that they call the *body model*, which is distinct from both the body schema and body image (Longo & Haggard, 2010, 2012b). Under this view, the body image is best conceived of as a visual representation of body shape, whereas the body model is primarily somatosensory (Longo et al., 2010).

As of now we have used the somewhat generic term *implicit body representation* when referring to the representation(s) underlying tactile perception. While our results do not directly speak to how to best divide and enumerate body representations, what levels of body-related processing are affected by tool embodiment is an important empirical question. A discussion on how to conceptualize our results in terms of a specific body representation is therefore warranted.

A recent study found that found tool-induced changes in tactile perception interpreted their effect as a modulation of a tactile body image (Cardinali et al., 2011). However, including visual and somatosensory measures of body shape under the representation “body image” ignores differences in how accurately judgments in each modality reflect actual body shape— e.g., somatosensory judgments appear to retain homuncular distortions (Longo & Haggard, 2010, 2011), whereas visual judgments are more veridical (Longo & Haggard, 2012b). We believe that this important difference is best captured by a distinction between the body image and body model. Given the distortions observed in tool-induced modulations to tactile perception (this study; Canzoneri et al., 2013; Cardinali et al., 2011; Cardinali et al., 2009b), these effects might be thought of as changes to a primarily tactile body model.

The necessary and sufficient conditions of tool embodiment likely differ between body representations. Our data suggests that representational plasticity to a body part within the body model is crucially dependent upon whether the tool is morphologically similar to that body part. This appears to be the case for the body schema as well. Cardinali and colleagues (2009) found that using an arm-shaped tool led a change to the arm—but not the hand—representation in the body schema. However, if representational plasticity is a necessary precondition for the ability to use a tool, template matching proposes a problem, as we are able to use objects whose shape does not clearly match any body part template (e.g., corkscrews). This problem may be remedied if the necessity of tool shape is dependent upon the *type of representation* undergoing embodiment. One important functional characteristic that is shared between the body model and body schema is that they are both about *the body* *itself*, and are inextricably linked to its shape. Peripersonal space, on the other hand, is not specifically about the body proper (Cardinali, Brozzoli, & Farnè, 2009a), but is instead about the space *between* the body and objects within its current action space (Brozzoli, Ehrsson, & Farnè, 2013). Embodiment of tools into peripersonal space may therefore depend more upon whether an object modifies the boundaries of the user's action space and less upon whether that object has a close physical resemblance to the body. Indeed, tools baring no resemblance to a hand (e.g., sticks) have been shown to modify the boundaries where multisensory interactions between touch *on the hand* and visual objects can take place (Farnè et al., 2005; Farnè & Làdavas, 2000; Maravita et al., 2002b). The relative indifference to the tool's shape of some representations related to the body would allow for our ability to embody and use tools that bear little to no resemblance to our own bodies.

These differences in body representations have important implications for the design of prosthetic limbs. The goal of prosthetic use—incorporation into the sense of bodily self (Murray, 2004)—is aided by the usability of the prostheses (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004), underscoring the importance of sensorimotor processes in embodiment. Our findings, on the other hand, demonstrate the importance of structural similarity in representational plasticity, especially for body representations that are specifically body-oriented (e.g., body schema and body model). This suggests that cosmetic aspects of prosthetic design may further aid in its embodiment into multiple levels of body representation, leading to less cases of prosthetic rejection.

Conclusion

We found that functional use of a tool led to representational plasticity on two body parts, the hand and arm, but only when the tool was shaped like that body part. These results demonstrate that the morphology of a tool constrains representational plasticity. Morphological similarity has previously been shown to constrain the embodiment of rubber hands, suggesting that sensitivity to shape may reflect a widespread property of body representations and embodiment. Our results indicate that both function and morphological similarity are necessary for the embodiment of tools, factors that should be taken into consideration for prosthetic design.

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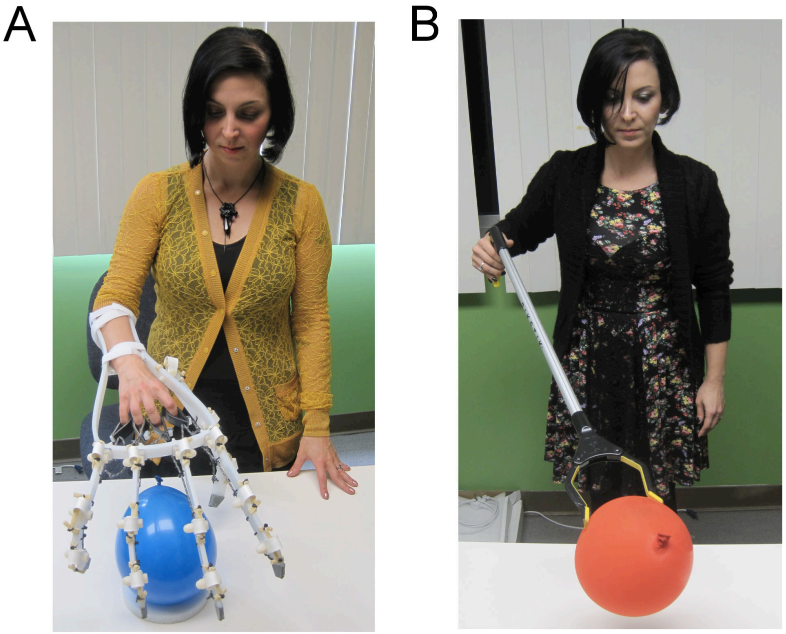

Figure 1.1: Tools used in the Experiments

Hand-shaped tool used in Experiments 1A and 2A. B) Mechanical grabber used in Experiments 1B and 2B.

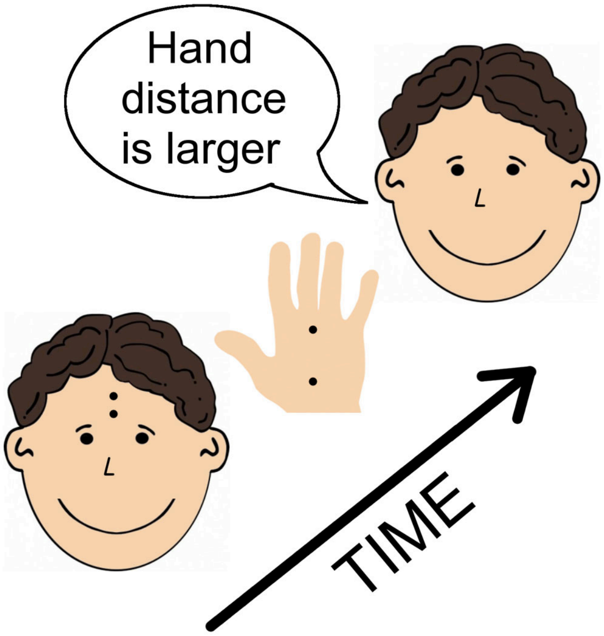

Figure 1.2: Tactile distance judgment task

Depicted is a typical trial of the tactile distance judgment task. In this case, the target body part is the hand, and the control surface is the forehead. On this trial, the participant is first presented with two tactile points along the forehead, and then, after approximately two seconds, with two points along the hand. The participant then makes a verbal judgment about which body part was touched with a greater distance. On this trial, the participant judged the two tactile points on the hand to be further apart than on the head, consistent with the actual physical difference.

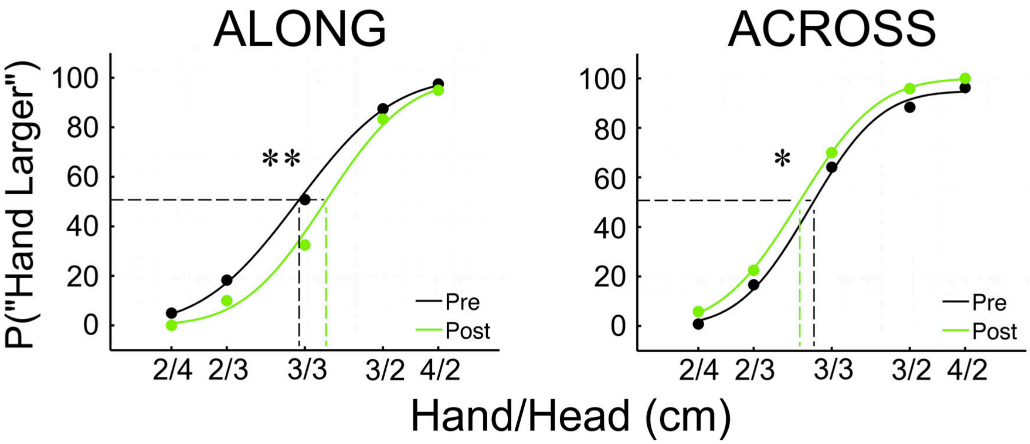

Figure 1.3: Pre and post-tool use curves for Experiment 1A

The pre-tool use (black) and post-tool use (green) curves along (left) and across (right) the hand. The y-axis is the probability that the subject responded that touch on the hand felt larger than the forehead for each distance combination (x-axis). Dashed lines of each plot correspond to the point crossing the 50% mark on the y-axis (horizontal line) and the middle distance combination (vertical line). A clear rightward shift in the along post-tool use curve indicates a compression in the perceived tactile size of stimuli. The leftward shift in the across post-tool use curve indicates an expansion in the perceived tactile size of stimuli.

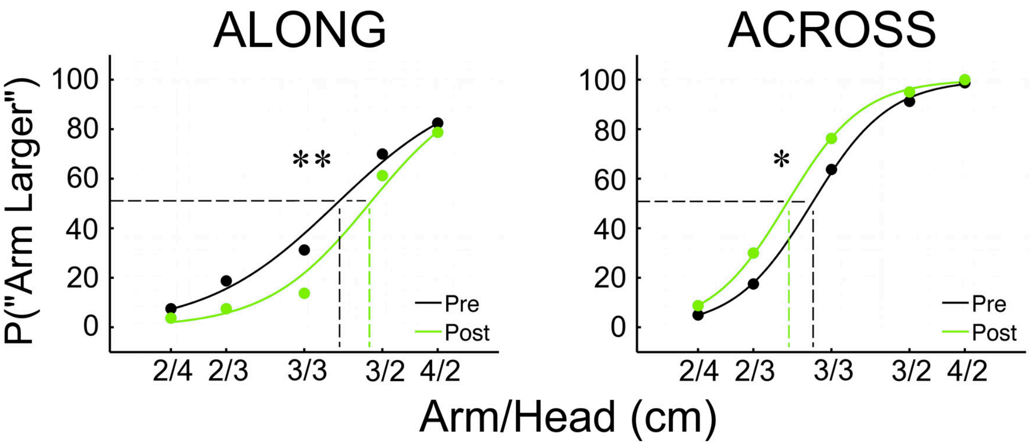

Figure 1.4: Pre and post-tool use curves for Experiment 2B

The pre-tool use (black) and post-tool use (green) curves along (left) and across (right) the hand. The y-axis is the probability that the subject responded that touch on the arm felt larger than the forehead for each distance combination (x-axis). Dashed lines in the center of each plot correspond to the point crossing the 50% mark on the y-axis (horizontal line) and the middle distance combination (vertical line). A clear rightward shift in the along post-tool use curve indicates a compression in the perceived tactile size of stimuli. The leftward shift in the across post-tool use curve indicates an expansion in the perceived tactile size of stimuli.

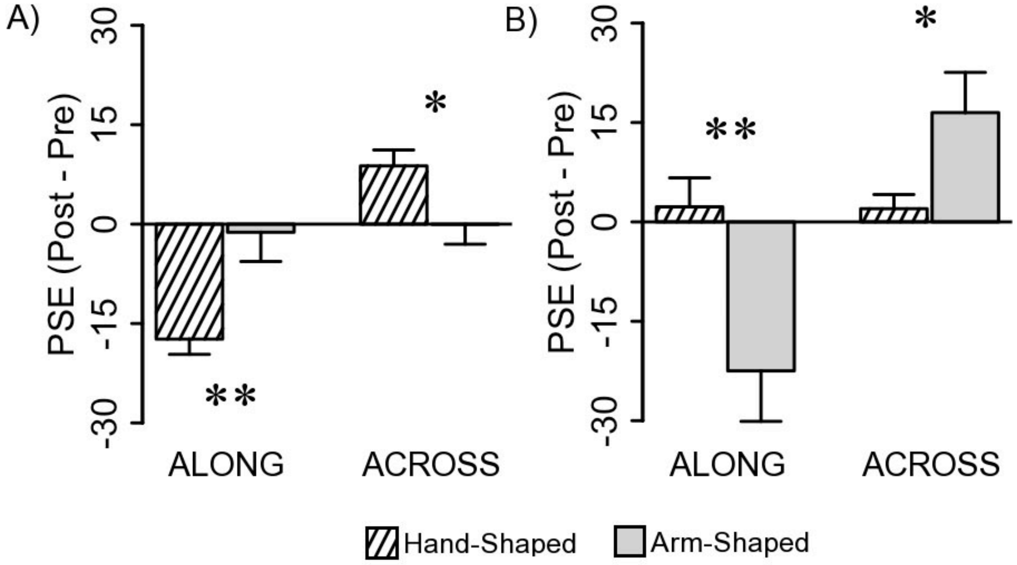

Figure 1.5: Tool-induced changes in the PSE for all experiments

A) Experiment 1: the hand was target body part. B) Experiment 2: the forearm was the target body part. Dashed bars indicate the effect of the hand-shaped tool, whereas solid gray bars indicate the effect of the arm-shaped tool. Significant changes in tactile size perception were found in both orientations for both experiments, but only when the tool was shaped like the target body part. * $p < 0.01$, ** $p < 0.001$

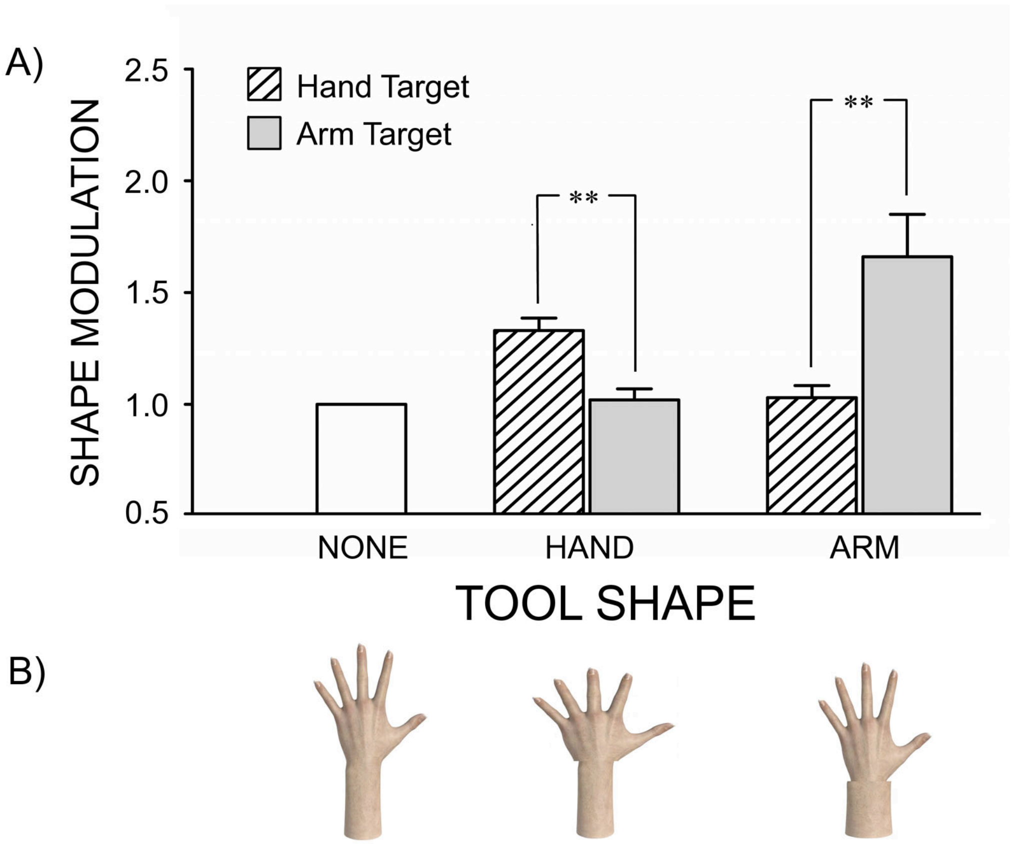

Figure 1.6: Shape Modulation Index

A) The shape modulation index for each experiment plotted as a function of tool shape (x-axis). “None” corresponds to the shape of the representation *before tool use*. Black bars with dashed lines correspond to experiments where the hand was the target body part (Experiment 1A and 2A). Solid gray bars correspond to the experiments where the arm was the target body part (Experiment 1B and 2B). B) A graphical depiction of the effect of each tool shape on the arm and hand representations. Only body parts that were shaped like the tool underwent a modulation in shape. ** $p < 0.001$

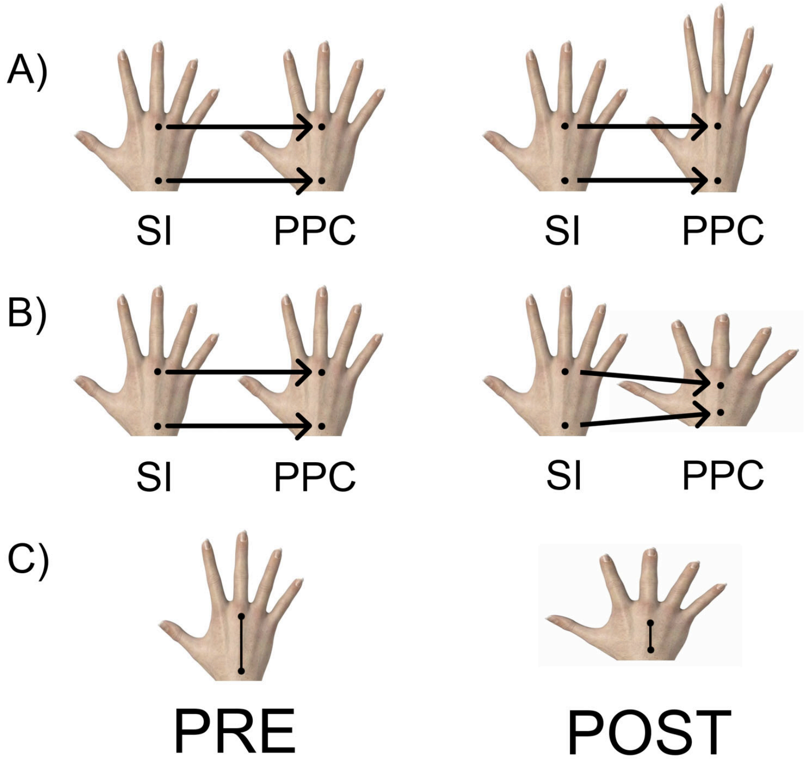

Figure 1.7: Relationship between tactile size perception and body representations

Tactile size perception may have an inverse (A) or proportional (B) relationship with the dimensions of an implicit representation of body morphology. In the pre tool use condition, two points of touch in the somatosensory homunculus of the hand in primary somatosensory cortex (SI; the hand on the left in each pairing) are mapped onto congruent locations on the implicit hand representation in the posterior parietal cortex (PPC; the hand on the right in each pairing). According to the inverse model (A) the decrease in tactile size perception observed in the post tool use condition would be the result of mapping two points of touch onto a smaller anatomical location on the implicit representation due to an *increase* in its size. Conversely, the proportional model (B) states that the decrease in tactile size perception is due to a corresponding *decrease* in the size of the implicit representation. (C) The *perceived* tactile size, represented by a line between the two points of touch, is equivalent for both models pre and post tool use.

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Chapter 2

Tool Use—In a Visual Context—Modulates Multiple Levels of Body Representation

Abstract

Representations of the body are highly plastic, changing in response to the activity of the organism as well as altered sensory feedback. Visual magnification, for example, increases the perceived distance between two tactile points. Using a tool also modulates body representations, although which representations are affected has not been thoroughly investigated. While there is considerable evidence that tool use alters the user's tactile body representation (called, the body model), whether it also affects their conscious body image—their bodily self—is unknown. We investigated this in the present study. In separate experiments, we found that tool use modulated both the body model and the body image. However, plasticity was only observed when vision was present during tool use, suggesting an important role for visual feedback in embodiment. The implications of these findings for our understanding of tool-induced plasticity are discussed.

Introduction

Having a body is a complex, multi-faceted experience (Longo & Haggard, 2012), involving several distinct levels of mental representation (de Vignemont, 2010b; Dijkerman & de Haan, 2007; Gallagher, 1986). Exactly how many representations there are is currently a matter of debate. A comprehensive model of body representation should explain a wide range of phenomena—such as, the sense of where your limbs are in space, or the feeling that your body is tied to your sense of self, i.e., the bodily self—while remaining parsimonious (Kammers, Mulder, de Vignemont, & Dijkerman, 2010).

A recent model of bodily experience (Longo, Azanon, & Haggard, 2010) postulates the existence of at least three representations of body morphology: the *body schema*, an online representation tracking the positions of the limbs in space; the *body model*, a geometric representation of the body that structures somatosensory perception; and the *body image*, a conscious (and largely visual) representation underlying the bodily sense of self. Each representation is constructed via the integration of signals from multiple sensory modalities (Blanke, 2012), underscoring the multisensory nature of body perception. Changes in sensory feedback modulate the body schema (Bernardi, Marino, Maravita, Castelnuovo, Tebano, & Bricolo, 2013), body model (de Vignemont, Ehrsson, & Haggard, 2005; Kennett, Taylor-Clarke, & Haggard, 2001; Tajadura-Jiménez, Väljamäe, Toshima, Kimura, Tsakiris, & Kitagawa, 2012; Taylor-Clarke, Jacobsen, & Haggard, 2004), and body image (Gandevia & Phegan, 1999), underscoring the multisensory nature of body perception.

For example, visually magnifying the arm “magnifies” touch on the arm, as if the body model had increased in size (Taylor-Clarke et al., 2004).

Wielding a tool also modulates the user’s body representations (Maravita & Iriki, 2004), a phenomenon known as *tool embodiment*. Iriki and colleagues uncovered the first evidence for tool embodiment in their seminal 1996 paper (Iriki, Tanaka, & Iwamura, 1996). They found that the visual receptive fields (RFs) of visuo-tactile peripersonal space neurons expanded to include the body of a rake when it was used to reach for objects in extrapersonal space. This tool-induced expansion of peripersonal space has since been found in humans using multiple behavioral paradigms (Bassolino, Serino, Ubaldi, & Làdavas, 2010; Bonifazi, Farne, Rinaldesi, & Ladavas, 2007; Farnè, Iriki, & Làdavas, 2005; Holmes, Calvert, & Spence, 2004; Maravita, Spence, & Driver, 2002; Serino, Bassolino, Farnè, & Làdavas, 2007). Tool use has also been shown to modulate the body schema (Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009; Cardinali, Jacobs, Brozzoli, Frassinetti, Roy, & Farnè, 2012) and, as we saw in Chapter 1, the body model (Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Cardinali, Brozzoli, Urquizar, Salemme, Roy, & Farnè, 2011; Cardinali et al., 2009; Miller, Longo, & Saygin, 2014; Sposito, Bolognini, Vallar, & Maravita, 2012). Whether tool use affects the user’s bodily self—their *body image*—is unknown. In fact, several researchers have claimed that embodiment is specific to sensorimotor representations(Cardinali et al., 2011; De Preester & Tsakiris, 2009; de Vignemont & Farnè, 2010), leaving the body image unaffected. However, this has never been tested directly. We sought to do just that.

The present study had two main aims: First, we investigated the role of visual feedback in the embodiment of a tool. The results presented in Chapter 1 suggest that visual feedback about the tool's shape constrains embodiment. Further, vision provides high-resolution sensory feedback of tool-object interactions, which also thought to play an important role in tool embodiment (Cardinali et al., 2012). We therefore hypothesized that visual feedback would play a critical role in modulating body representation. Second, we investigated whether tool use would modulate the user's body image, and whether it would be constrained by vision in a similar manner to the body model. To these ends, our study measured tool-induced modulation in two distinct levels of hand representation—body model and body image—and in two sensory contexts: vision-present (normal visual conditions during tool use) and vision-absent (blindfolded tool use).

Materials and Methods

We used psychophysics to measure tool embodiment in two experiments, each with two sensory contexts (vision-present, vision-absent). In *Experiment 1* we measured tool-induced modulation to the body model, a representation that underlies tactile distance perception on the hand (de Vignemont et al., 2005; Longo & Haggard, 2011, 2012b; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004). In *Experiment 2* we measured modulation of the *body image,* a representation underlying the conscious sense of the bodily self (de Vignemont, 2010a; Longo, 2014; Longo & Haggard, 2012b; Longo, Schuur, Kammers, Tsakiris, & Haggard, 2009; Paillard, 1999).

Participants

Sixty-seven right-handed adults in total participated in this study; 12 adults (6 females; Mean Age: 21.57) participated in Experiment 1A; 15 adults (10 females; Mean Age: 22.35) participated in Experiment 1B; 20 adults (12 females; Mean Age: 22.33) participated in Experiment 2A; 20 adults (15 females; Mean Age: 20.97) participated Experiment 2B. All participants gave informed consent before participating in each experiment.

Stimuli and Procedures

Tool Use Procedure

Participants used the hand-shaped tool described in Chapter 1 (Figure 2.1a). Each finger of the tool was biologically realistic, composed of three plastic “bones” connected via fully adjustable rubber “joints”. The participant’s fingers rested in leather straps attached to the tool’s fingers, allowing for their individual control; movement of each strap led to a concurrent movement of the corresponding finger of the tool. This finger-tool connection ensured that the functional precision of the tool and the user’s own hand is almost equivalent. The tool was approximately 21 cm wide, as measured from the base of the pointer finger to the base of the pinky, and 45 cm long, as measured from the base of the tool to the tip of the middle finger.

Tool use was situated in two sensory contexts: vision-present and vision-absent. Participants used the hand-shaped tool to pick up balloons (approximately 75 cm from the midline of their trunk) and put them into a bucket (approximately 75 cm laterally from the right of the body). In the vision-present condition, tool use occurred in full vision; in the vision-absent condition, participants used the tool while blindfolded. In this condition, the experimenter verbally guided the participant towards the location of the balloon and the bucket. Most participants were able to quickly learn these locations and needed minimal guidance by the experimenter. This occurred for a total of sixteen minutes in Experiment 1 (split into two sessions of eight minutes) and eight minutes in Experiment 2.

Experiment 1: Body Model

As in Chapter 1, the present study used tactile distance judgment task (TDJ; Figure 2.1b) to measure the metric properties of the user's hand representation in his or her body model (i.e., their *hand model*) (de Vignemont et al., 2005; Longo & Haggard, 2011; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004). On each trial, two pairs of tactile stimuli (two wooden posts, each tapered to a 1 mm flat point) were applied sequentially to a target surface (the hand dorsum) and to a reference surface (the forehead). The participant's task on each trial was to judge whether the distance between the two posts felt farther apart on the hand or forehead. The administered distances were 2, 3 or 4 cm, applied in five distance combinations (hand/forehead: 2/4, 2/3, 3/3, 3/2, 4/2). We manipulated the orientation of stimuli across trials: on each trial, touch was presented either *across* (hand: medio-lateral; forehead: eye-to-eye) or *along* (hand: proximo-distal; forehead: nasion to hairline) the body surface. Manipulating orientation allowed us to measure changes in each orientation separately, and thus reconstruct the hand's represented *shape*. Participants rested their arm flat on a table with their fingers splayed during the experiment. Stimuli were applied to each body surface for an average of one second with an average inter-stimulation interval of two seconds. Each distance combination was applied eight times in each orientation for a total of 40 trials per orientation, with 80 trials in all. There were a total of four runs (20 trials each), divided into two blocks of two runs. The body part stimulated first (hand or forehead) as well as stimulus orientation was pseudo-randomized across trials in each run. Eight-minute breaks were taken between each block. This procedure was performed before and after use of the hand-shaped tool.

Experiment 2: Body Image

We used a template-matching task to psychophysically estimate the shape of each participant's hand representation in his or her body image (i.e., their *hand image*) (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Longo & Haggard, 2010, 2012b). Participants were shown a picture of a hand (a realistic, computer-generated model of a male hand) on an LCD computer screen and asked to judge whether its shape was wider or more slender than how their own hand felt (Figure 2.1c). The shape of each hand image was quantified using a Shape Index (see *Shape Indices*). We used nine different shape levels, logarithmically spaced and centered on 60 (range: 40-90), the average hand shape reported by several studies (Longo, 2014; Longo & Haggard, 2010, 2012b). The shapes ranged from unrealistically slender (shape index: 40) to unrealistically wide (shape index: 90). Each hand image had an identical surface area, differing only in aspect ratio. Subjects were explicitly told to ignore the size of the hand and instead focus on its overall shape.

Each experimental session was separated into two blocks, each with 12 trials per hand shape (24 in total), for a total of 108 trials per block and 216 trials for the entire session. The hand shape displayed on each trial was randomly chosen from one of the nine hand shapes. This procedure was performed twice, once before and once after tool use. The participant's hands were hidden from view throughout the course of each session to prevent them from using visual feedback to alter their responses. A picture of the participant's own right hand was taken after the experiment in order to quantify the shape index of their own hand.

Shape Indices

Shape Index

Napier's shape index was used to quantify hand shape. The *shape index* is the ratio between the width and height of the hand (SI = 100*[width/height]), where width is defined as the distance between the knuckles of the pointer and little finger, and length is defined as the distance between the middle knuckle and tip of the middle finger.

Shape Modulation Index

The Shape Modulation Index (SMI) quantifies the change in the shape of a body representation by taking into account modulations in the proximo-distal and medio-lateral axis (Miller et al., 2014). For the tactile distance judgment task (Experiment 1), the SMI is derived from the percent change in each orientation with the following equation:

$$\textit{Shape modulation index} = \left[100 * \left(\frac{100 + \%\text{ change in hand width}}{100 + \%\text{ change in hand length}} - 1\right)\right].$$

For the template-matching task (Experiment 2), the SMI is equivalent to the percent change in shape index.

Data Analysis

Curve fitting

Each participant's responses in each experiment were fit with a logistic function using a maximum-likelihood procedure (Wichmann & Hill, 2001). We extracted two parameters from each participant's psychometric curves: the point of subject equality (PSE), a measure of perceptual threshold, and the just noticeable difference (JND), a measure of discriminative sensitivity. Differences between the pre- and post-tool use curve parameters were taken as measures of tool embodiment (Miller et al., 2014).

Correlational analysis (Experiment 2)

Correlational analyses were also performed to assess the relationship between the estimated shape of each participant's hand image and their actual hand. Previous studies have found a significant relationship between the two (Longo, 2014; Longo & Haggard, 2012b), indicating that responses in the template-matching task are based on stored self-specific knowledge of hand morphology and not just general knowledge about hand shape.

Results

Experiment 1: Body Model

Experiment 1a: Vision-present context

Tool use within a visual context significantly modulated the PSEs in both stimulus orientations. The psychometric curve for touch presented along the hand can be seen in Figure 2.2. We first conducted a 2 (*tool use*: pre, post) x 2 (*orientation*:

across, along) repeated measures ANOVA on the PSEs for Experiment 1A. We found a significant main effect of orientation ($F(1,11) = 4.87$, $p = 0.05$, $\eta^2_p=0.31$) but not tool use ($F(1,11) = 0.89$, $p = 0.37$, $\eta^2_p=0.08$). Crucially, we found an interaction between orientation and tool use ($F(1,11) = 40.08$, $p < 0.0001$, $\eta^2_p=0.79$). Follow-up post-hoc *t*-tests revealed that opposing changes in each orientation drove this interaction (Figure 2.3). Tool use led to a 13.14% *expansion* in tactile distance perception across the hand ($t(11) = 3.43$, $p < 0.01$, $d_z = 0.99$) and a 20.17% *compression* along the hand ($t(11) = -3.88$, $p < 0.005$, $d_z = 1.12$). These results replicate the pattern of tool-induced plasticity reported in Chapter 1.

We did not observe any changes to the JNDs following tool use. A 2 (*tool use*: pre, post) x 2 (*orientation*: across, along) repeated measures ANOVA revealed a significant main effect of orientation ($F(1,11) = 6.08$, $p < 0.05$, $\eta^2_p=0.36$). No other main effects or interactions were found (all Fs < 0.3, all ps > 0.8). This suggests that embodiment is limited to the represented shape of the hand while leaving discriminative sensitivity untouched.

Experiment 1b: Vision-absent context

Tool use in the vision-absent context still occurred within an experientially rich sensory environment, comprised of tactile, proprioceptive, auditory, and vestibular feedback during each individual action. However, no modulation in tactile distance perception was found when vision was removed from the sensory environment of tool use (Figure 2.2). We did not observe any main effects or interactions for either the PSEs (all $Fs<1.87$, all $ps>0.19$) or the JNDs, except for a main effect of orientation as in Experiment 1a ($F(1,14) = 31.92$, $p < 0.0001$, $\eta^2_p=0.70$; all other $Fs<0.25$, all $ps>0.6$).

Experiment 1a vs. 1b

In order to establish that visual context played an important role in tool embodiment it is necessary to establish that there were indeed differences in the magnitude of plasticity between experiments. To do so, we conducted a 2x2 mixed effects ANOVA with *orientation* (across, along) as a within-subjects factor and *visual context* (vision-present, absent) as a between-subjects factor. The dependent variable used was the difference between PSEs before and after tool use. We found the crucial interaction between factors ($F(1,25) = 29.26$, $p<0.0001$, $\eta^2_p=0.54$). This interaction was driven by highly significant differences between plasticity found in each visual context and in each orientation: along ($t(25)=-3.07$, $p=0.005$, $d = 1.18$) and across ($t(25)=3.76$, $p<0.001$, $d = 1.44$). These results can be seen in Figure 2.3.

Experiment 2: Body Image

Experiment 2a and 2b: Both contexts

We found that using a tool significantly modulated the user's conscious representation of their hand's shape (Figure 2.4a), but only when vision was present during tool use (Figure 2.4b). Using the hand-shaped tool in a visual context led to a significant increase in the PSE (+2.89; $t(19)=4.14$, $p<0.001$, $d_z=0.93$), meaning that the user's hand image expanded in width and compressed in length; this pattern of shape modulation is identical to the hand model measured in Experiment 1.

When vision was removed from the sensory environment, no changes were observed in the PSEs ($t(19)=0.72$, $p=0.48$, $d_z=0.16$), again suggesting that visual context plays a crucial role in tool embodiment. Importantly, plasticity in the two sensory contexts significantly differed ($t(38)=2.45$, $p<0.05$, $d=0.77$; Figure 2.4b). No modulation of the JNDs was observed in either sensory context (all $ps>0.1$).

Body image correlations

If our template-matching task did indeed tap into a consciously accessible representation of body shape, we would expect there to be a relationship between the shape of the representation and the actual hand. This would indicate that participant's responses were based, at least partially, on the shape of their actual hand and not just general knowledge of the way hands are shaped. Indeed, we found a significant correlation (Figure 2.5) between the SI of the participants' actual hand and their estimated SIs (PSE) before tool use in both experiments: Experiment 1 ($r(18)=0.64$, $p<0.005$); Experiment 2 ($r(19)=0.66$, $p<0.005$); Combined ($r(37)=0.60$, $p<0.001$). This significant relationship between the shape of the hand image and the actual shape of the hand replicates several previous studies (Longo, 2014; Longo & Haggard, 2012b).

Shape Modulation of Body Model and Body Image

Using the hand-shaped tool led to a similar pattern of plasticity to the shape of body hand representations. Differences may exist, however, in the *magnitude* of the plasticity for each representation. We therefore compared the changes to the shape of each representation. Tool-induced modulations of each hand representation was converted into a Shape Modulation Index (SMI) (Miller et al., 2014). When vision was present during tool use, the modulation in the shape of the implicit hand representation (SMI: 48.73) was roughly an order of magnitude greater than the observed modulation in the shape of the explicit hand representation (SMI: 4.93; $t(30)=5.06$, $p<0.0001$, *d*=1.91). No difference was observed in the vision-absent context (*p*=0.75), further suggesting that, in our experimental setup, vision played a critical role in driving plasticity to the shape of each hand representation during tool use.

Discussion

In the present study, we found evidence that tool use modulated the user's body model and body image. Our results provide the first direct evidence that tool use can modulate the user's body image. While the pattern of modulation to the shape of each representation was the same—an expansion in width and compression in length—the magnitude of modulation differed, likely reflecting intrinsic differences in plasticity between the body image and body model. Further, for both representations, this modulation only occurred when vision was present during tool use, demonstrating that the sensory context of tool use plays an important role in embodiment.

The effects of tool use are evident at multiple levels of representation. Using a hand-shaped tool modulated the shape of a tactile hand representation as measured by the TDJ (Experiment 1). The specific change in hand shape, an expansion in width and compression in length, has been found in previous experiments (Canzoneri et al., 2013; Miller et al., 2014) and might reflect plasticity occurring in SI or more posterior parietal regions (Longo et al., 2010; Longo & Haggard, 2011; Spitoni, Galati, Antonucci, Haggard, & Pizzamiglio, 2010). We also found evidence that tool use modulated the user's *conscious hand image* (Experiment 2). The body image is often affected by psychiatric conditions, such as body dysmorphic disorders (Husain, Janniger, Krysicka, Micali, & Schwartz, 2014). Here we show that it can be temporarily modulated by brief, eight-minute usage of a tool. This finding demonstrates that the effects of tool embodiment are more pervasive that previously thought (Cardinali et al., 2011; De Preester & Tsakiris, 2009; de Vignemont & Farnè, 2010).

The body model and body image differed significantly in how much tool use modulated their shape. This large difference may be due to intrinsic differences in how permeable each representation is to embodying external objects. Sensorimotor representations must adapt to the dynamics of a tool in order to successfully wield it (Cardinali et al., 2009; Ganesh, Yoshioka, Osu, & Ikegami, 2014). These dynamics are often very different than actual limbs and therefore require flexible reorganization of sensorimotor representations (Ahmed, Wolpert, & Flanagan, 2008; Baugh, Hoe, & Flanagan, 2012). Sensorimotor body representations, such as the body schema and body model, are therefore likely to be more apt to embody tools than the body image. Indeed, the conscious experience of our body would be very different if it was drastically pushed and pulled every time we used a tool.

Tool use is usually situated within an extremely rich sensory environment. Each sensory modality—for example, proprioception, audition, and vision—provides unique information about specific aspects of the tool-body system. Proprioception provides information about the user’s movements through space (Lackner, 1988; Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009; Proske & Gandevia, 2012) as well as the structural properties of the tool (Solomon, Turvey, & Burton, 1989). Audition provides temporal information about the point of contact with objects as well as spatial information about the location of contact (Serino, Canzoneri, Marzolla, di

Pellegrino, & Magosso, 2015; Tajadura-Jiménez et al., 2012). Vision provides similar spatial information as audition and proprioception, albeit with higher spatial resolution (Ernst & Bülthoff, 2004). Importantly, this includes exquisite detail about the tool and the body. The results of Chapter 1 led us to hypothesize that vision plays a crucial role in modulating body representation during tool use.

In keeping with our hypothesis, we found that modulation of both levels of body representation was dependent upon the presence of vision during tool use. There are at least three pieces of information conveyed via visual feedback during tool use: First, vision conveys information about an increase in action space, as many out-of-reach areas of the environment become reachable. Several studies have found that longer tools lead to greater modulations of body representation (Bonifazi et al., 2007; Farnè, Serino, & Ladavas, 2007; Sposito et al., 2012), a finding that is reminiscent of studies involving visual magnification of body parts (Bernardi et al., 2013; Marino, Stucchi, Nava, Haggard, & Maravita, 2010; Taylor-Clarke et al., 2004). Second, vision conveys information about tool-object interactions, a crucial component of tool embodiment (Cardinali et al., 2012). A combination of these two pieces of information—interactions with objects occurring in a space away from the physical body—is likely important for embodiment. Third, vision provides information about the shape of the tool being used, an important constraint for determining which limb representation will be modulated by tool use (see Chapter 1). We suggest that these three pieces of information are likely drivers of embodiment, regardless of the sensory modality that conveys them. Future work should investigate this hypothesis in more detail.

A recent study by Canzoneri and colleagues found significant changes to the body model when blindfolded participants used a 1–meter stick (Canzoneri et al., 2013). This finding is in contrast to the results of the present study. This discrepancy can be reconciled if embodiment is driven—at least in some conditions—by sensory information about the location of tool-object interactions. In the present study, all tool-object interactions remained very close to the user's actual hand, rendering auditory feedback uninformative to an increase in action space. The embodiment measured by Canzoneri was likely driven by auditory signals of object contact occurring far from the body (Tajadura-Jimenez, Tsakiris, Marquardt, & Bianchi-Berthouze, 2015; Tajadura-Jiménez et al., 2012), whereas our embodiment was likely driven by visual feedback of tool shape (Chapter 1). This hypothesis underscores the complexity of experimental conditions leading to tool embodiment and suggests the existence of multiple sensory routes to the modulation of body representation.

What can account for the observed modifications to each representation, specifically the similar modulation of their shape? According to recent Bayesian models of multisensory calibration, the sensory modalities constructing multisensory representations are weighted based upon their accuracy (Zaidel, Turner, & Angelaki, 2011). These multisensory representations must be calibrated over long-term development, as the brain learns the accuracy of the information carried by each sensory modality (Gori, Giuliana, Sandini, & Burr, 2012; Gori, Sandini, Martinoli, & Burr, 2010). Further, the parameters of these representations are actively recalibrated to account for real-time fluctuations in the accuracy of sensory cues (Zaidel, Ma, & Angelaki, 2013; Zaidel et al., 2011). A similar Bayesian mechanism may underlie the construction and maintenance of body representations, and may also explain how these representations change in response to tool use. Under this account of body representation, the brain attempts to construct veridical models of the body (de Vignemont, 2014) by weighting early sensory representations according to how accurately they represent the body's true dimensions.

Here we present a conceptual model of tool embodiment that is inspired by principles of multisensory integration and calibration (Figure 2.6). It is based on the assumption that the goal of a body representation is to accurately reflect the true dimensions of the body as best as possible, given the available sensory information. For simplicity we only consider the role of vision and proprioception, although other sensory modalities most certainly play an important role (Ferre, Bottini, & Haggard, 2011; Ferre, Lopez, & Haggard, 2014; Pfeiffer, Lopez, Schmutz, Duenas, Martuzzi, & Blanke, 2013; Tajadura-Jimenez et al., 2015).

We propose that tool use modifies how reliably sensory modalities represent information about the user's *physical* body. In the case of vision, the tool-body system is considerably larger than the physical body part (i.e. hand/arm) and thus visual information becomes less reliable about the user's actual body dimensions. According to our Bayesian model of tool embodiment, the weight assigned to visual information would decrease in response to a decrease in accuracy during tool use, leading to a proportional increase in the weight assigned to proprioceptive information. This recalibration in the sensory parameters of body model and body image representations of the hand would cause each to become more homuncular in shape—i.e. more short and squat (Longo & Haggard, 2010). This pattern of plasticity is exactly what was found in the present study and in Chapter 1. No recalibration in the visual weights would occur when vision is not present in the sensory environment, precluding a recalibration of body representation. This model provides a common mechanism for embodiment at multiple levels of body representation.

Conclusion

In sum, we have shown than tool use modifies multiple levels of body representation, from tactile perception to conscious bodily self-representation. The modulation of each representation was rapid, occurring during a brief eight-minute session of tool use. The rapidity of tool embodiment underscores the extreme malleability of our sense of self, despite daily experience to the contrary. Further, our results highlight the importance of the sensory context of tool use—particularly visual context—in effects of tool embodiment. We proposed a model of tool embodiment based on known principles of Bayesian multisensory calibration, providing a novel model by which to view effects of embodiment. Under this view, body representations should be viewed as finely calibrated models of the body.

Acknowledgments: Chapter 2, in full, is in preparation for publication as a manuscript with Ayse P. Saygin and Matthew R. Longo.

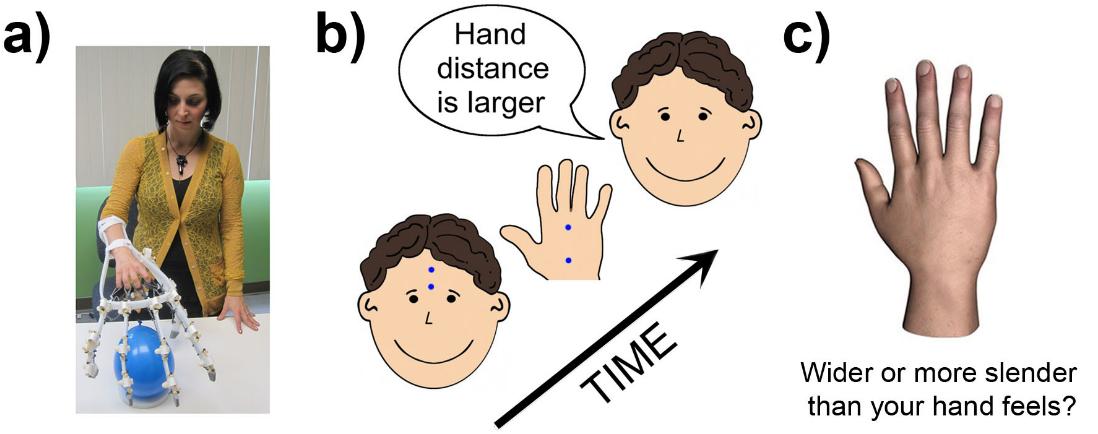

Figure 2.1. Tool and experimental paradigms

a) The hand-shaped tool used by all participants in the present study. **b)** The tactile distance judgment task: Participants made judgments about which body part, hand or forehead, was touched with the greatest tactile distance. **c)** The template matching task: Participants judged whether the shape of a right hand presented on a computer screen was wider or more slender than their actual right hand.

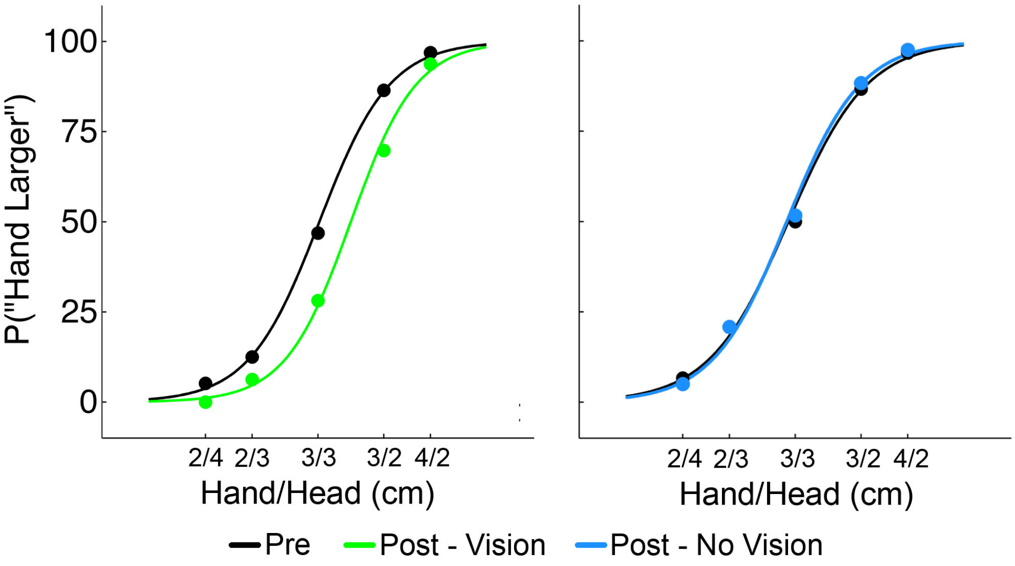

Figure 2.2. Experiment 1 psychometric curves for touch presented along the hand.

Left: When vision was present during tool use (left curve), the post-tool use psychometric curve (green) shifted to the right. This shift corresponds to a ~20% compression in perceived tactile distance. **Right**: When vision was absent during tool use (right curve), the post-tool use psychometric curve (blue) completely overlapped with the pre-tool use curve (black).

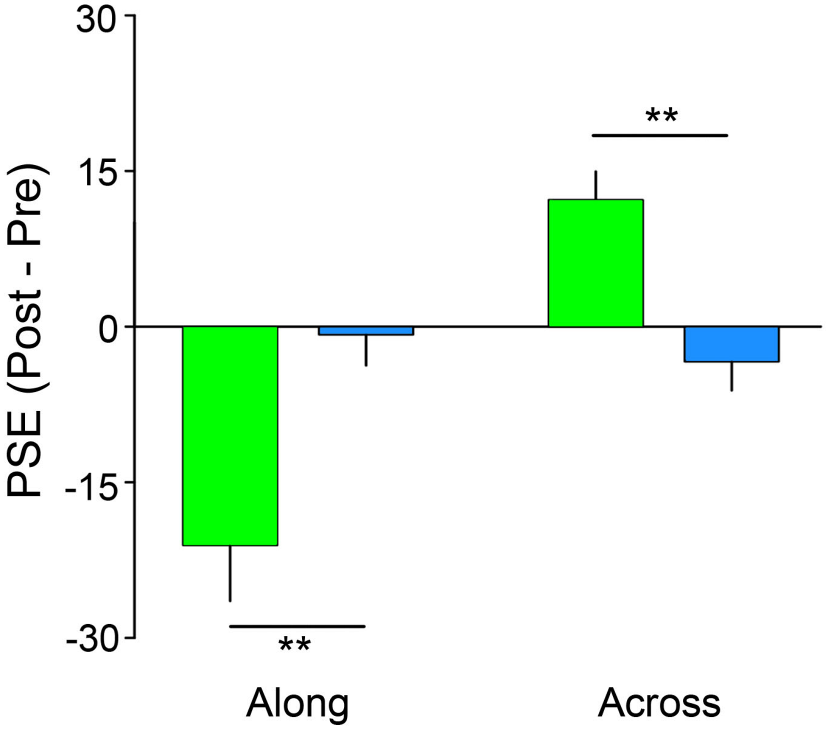

Figure 2.3. Results of Experiment 1 in both orientations.

When vision was present, tactile distance perception compressed along the hand and expanded across the hand. When vision was absent, no significant modulation in tactile distance perception was found in either orientation. ** $p<0.01$

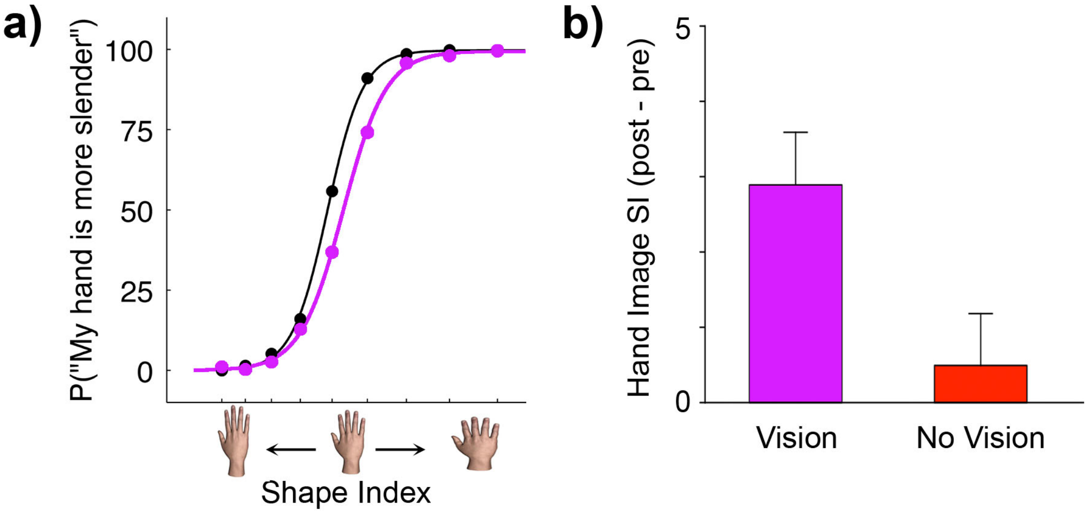

Figure 2.4. Results of Experiment 2 in both sensory contexts

a) Using a tool in full vision led to a rightward shift in the post-tool use psychometric curve (purple). Specifically, participants now judged the shape of their own hand (relative to the images on the computer screen) to be more fat and squat. This pattern of results corresponds to what we found in Experiment 1. **b)** Bar plot of the modulation of the body image's shape index in both sensory contexts.

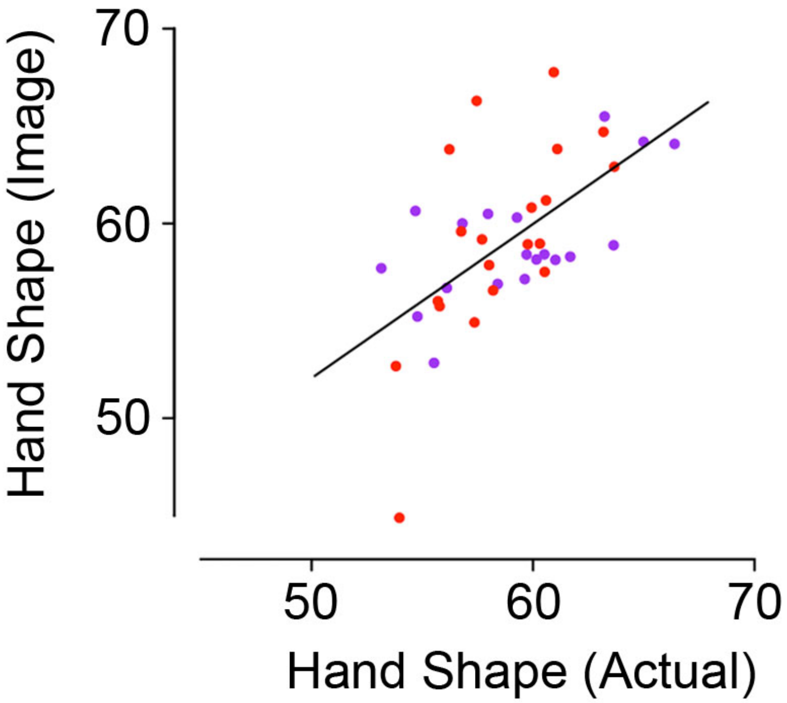

Figure 2.5. Correlation between actual and judged hand shape

We found a significant correlation between participant's actual hand shape and the shape of their pre-tool use hand image (i.e., the PSE of their psychometric curve). The present plot is a combination of both experiments (purple: Experiment 2A; red: Experiment 2B).

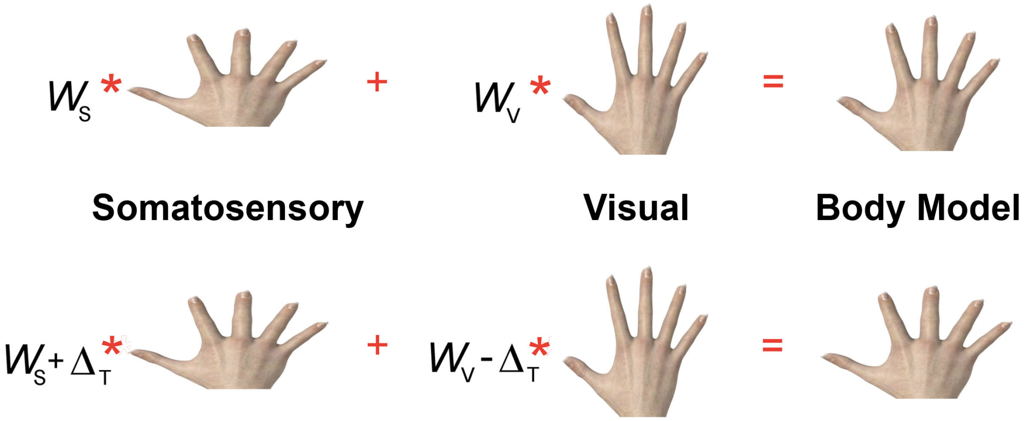

Figure 2.6. Bayesian model of tool embodiment

The present figure presents our Bayesian model of body representation. Though it depicts the body model, it applies equally well to the body image. In our model, the body model is viewed as a weighted combination of somatosensory and visual body representations, perhaps from primary sensory regions. The weights (w) assigned to each sensory representation are determined by how accurately each sensory modality reflects the hand's true shape. The top panel corresponds to the pre-tool use body model. As can be seen, the somatosensory representation is vastly more distorted in shape than the visual representation, and therefore would be assigned a weaker weight. When a tool is used with full vision (bottom panel), the visual signals include the shape of both the body and tool. We hypothesize that this combination decreases the level of accuracy inferred to the visual representation. The weight of the visual representation would therefore decrease, and the weight of the somatosensory representation would proportionally increase. This shift in weights would lead to the shape modulation (increase in width, decrease in length) that we observed in Experiment 1 and 2.

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Chapter 3

Visual Illusion of Tool Use Recalibrates Tactile Perception

Abstract

Brief use of a tool recalibrates multisensory representations of the user's body, a phenomenon called tool embodiment. Despite two decades of research, very 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 mirror-based setup to induce a vivid 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 visual-proprioceptive conflict or general interhemispheric plasticity. These results suggest visual tool-use signals play a critical—and perhaps sufficient—role in driving recalibration, a finding that challenges intuition and requires significant revision to existing models of embodiment.

Introduction

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 a). 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, Jacobs, Brozzoli, Frassinetti, Roy, & Farnè, 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, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009; Miller, Longo, & Saygin, 2014).

While tool embodiment has been studied extensively over the past two decades (Maravita & Iriki, 2004), remarkably 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 a necessary condition for embodiment (Farnè et al., 2005; 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 proprioceptive feedback—may be critical for the process (Brown, Doole, & Malfait, 2011; Rademaker, Wu, Bloem, & Sack, 2014). Here, we provide striking evidence against this widely accepted view and show that tool embodiment can be driven purely 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 moving body part from concomitant kinesthetic and motor signals. To foreshadow our results, we found that this 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.

Experiment 1: Visual Illusion of Tool Use

Methods and Materials

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 right-handed; Mean age: 21.83 SD: 2.71). 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.

Mirror Illusion Setup

A long mirror (approximately 119 by 41 cm) 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 hand palm-down behind the body of the mirror, with the elbow resting approximately 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 kinesthetically felt location of the left arm. In Experiment 1b, participants instead rested their left arm down by the left hip. This produced a complete dissociation between the mirror image and the kinesthetically felt location of the left arm.

Mechanical grabber

The tool used in the experiment was a mechanical grabber that extended the user's reach by a maximum of 40cm (Fig. 3.1a). 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.

Object interaction task and Mirror Illusion

After the initial mirror box setup, 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 to not move it. The location of the tip of the tool was marked with tape on the table and a rubber cube (approximately 5 cm^3) was placed approximately 8 cm distal to the midpoint of the tape. Participants used the tool to pick up the rubber cube. They were explicitly instructed to only focus on the content's 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 the vivid visual illusion that the participant's left arm was using a tool when it was in fact completely stationary (Fig. 3.1a). This task was self-paced, and the rate that participants picked up the object ranged from approximately 0.1 to 0.25 Hz. The task lasted for approximately 8 minutes.

Tactile Paradigm

Touch perception was measured using a tactile distance judgment task (Figure 3.1b), a standard paradigm for measuring the morphology of body representation (Canzoneri et al., 2013; Miller et al., 2014; Taylor-Clarke, Jacobsen, & Haggard, 2004). On each trial, two tactile points (wooden posts each tapered to a 1 mm flat point) were applied to the *left* forearm (target surface) and the forehead (the reference surface). Tactile stimuli were applied along the arm (proximo-distally) and across the forehead (eye-to-eye). The participant's task was to judge which body part was touched with the two tactile points of the farthest distance. The administered distances were 4, 6, or 8 cm, and were combined into five distance combinations (arm/head; 4/8, 4/6, 6/6, 6/4, 8/4). Participants rested their arm flat on a table with their fingers splayed during the experiment. Stimuli were applied to each body surface for approximately one second with an inter-stimulus interval of approximately two seconds. Each distance combination was applied eight times for a total of 40 trials. The body part stimulated first (arm or forehead) was counterbalanced across trials. This procedure was performed before and after tool use. Psychometric curves were fit to each participant's responses (see *Data Analysis* below).

Data Analysis

Logistic functions were fit to each participant's pre- and post-tool use responses using a maximum-likelihood procedure (Wichmann & Hill, 2001a). We analyzed the difference between the group level pre and post curves using a Likelihood-ratio test (LRT), which provides a robust test of the difference between two psychometric curves (Wichmann & Hill, 2001b). The LRT uses Monte Carlo simulations to simulate psychometric curves with similar parameters as the true data. We performed a total of 1000 simulations to compare to with the true likelihood-ratio (LLR). A p-value is calculated by taking the proportion of simulated LLR greater than the true LLR.

To quantify tactile distance perception pre and post-tool use, we extracted the point of subjective equality (PSE) from each participant's psychometric curves. Perceptual recalibration was numerically defined as the difference between the pre and post PSEs, the magnitude of which was assessed using a paired t-test (all p-values Bonferroni corrected). Previous studies have found that using a tool decreases the perceived distance between two tactile points on the arm in the proximo-distal orientation (Canzoneri et al., 2013; Miller et al., 2014). We therefore present our findings in units of compression, calculated by subtracting the post from the pre-tool use PSE. Positive values correspond to compression in tactile distance perception, whereas negative values correspond to expansion.

Results

Despite the absence of direct kinesthetic and motor signals from the left arm accompanying the visual feedback of tool use, we found evidence for illusion-induced perceptual recalibration of touch on the stationary arm. In Experiment 1a, there was a significant difference between the pre and post tool-use psychometric curves (Fig. 3.2a) as quantified with a Monte Carlo simulation-based likelihood-ratio test LRT; $p<0.001$ (Fig. 3.2b). Analysis and comparison of the PSE from the curves revealed a significant 20.6% (SEM: 4.30) compression in tactile distance perception on the forearm post-illusion ($t_{11}=4.80$, $p<0.005$, $d_z=1.39$, 95% CI [0.57; 2.17]). That is, after the visual illusion two tactile points applied to the arm felt closer together.

It is possible that the observed recalibration in Experiment 1a was due to an initial visuo-proprioceptive congruence at the start of each action. Experiment 1b ruled out this possibility by having participants place their left arm down by their left hip, thus ensuring complete visuo-proprioceptive incongruence throughout the tool use task. Despite this manipulation, there was still a significant difference between the pre and post tool-use psychometric curves (LRT; $p<0.01$), corresponding to a significant 15.9% (SEM: 4.28) compression in tactile distance perception on the forearm post-illusion ($t_9=3.73$, $p<0.01$, $d_z=1.18$, 95% CI [0.34; 1.98]). Crucially, there was no difference between the magnitude of recalibration found in Experiment 1a and 1b

(t_{20}=0.77, p>0.5, d=0.33, 95% CI [-0.52; 1.17]; Fig. 3c). Therefore, for all subsequent comparisons with Experiment 1, we collapse across the recalibration found in both conditions (t_{21}=6.13, p<0.001, d_z=1.31, 95% CI [0.73; 1.87]).

Experiment 2: Active Tool Use

The pattern of perceptual recalibration found in Experiment 1 for illusory tool use is consistent with the pattern found for non-illusory contexts where tactile perception is measured on the tool-using arm (Canzoneri et al., 2013; Miller et al., 2014). However, the magnitude of the effect between illusory and natural tool use may differ, which would suggest that the visual illusion lacks some crucial components for normal embodiment. This was investigated in Experiment 2.

Methods and Materials

Participants

Eleven new participants took part in Experiment 2 (9 females; 11 right-handed; Mean age: 22.38, SD: 2.44).

Object interaction task

The experimental setup was identical to Experiment 1 except that the mirror's surface was covered with an occluding board. The object interaction procedure was also identical to Experiment 1, except that participants used the tool while directly staring at their right tool-using arm (i.e., no visual illusion). This task was self-paced, and the rate that participants picked up the object ranged from approximately 0.1 to 0.25 Hz. Note that the target body part in the TDJ was the *right* arm, which used the tool.

Results

Consistent with previous studies (Canzoneri et al., 2013; Miller et al., 2014), we found a significant recalibration of tactile perception on the tool-using arm. The pre and post-tool use curves were significantly different as measured with an LRT ($p<0.05$; Fig. 3.3a). Analysis of the PSEs revealed a significant 15.0% (SEM: 3.50) compression in tactile distance perception on the right forearm post-tool use ($t_{10}=4.28$, $p<0.01$, $d_z=1.29$, 95% CI [0.46; 2.08]). Crucially, the magnitude of the recalibration found in Experiment 1 did not differ from that found in the present experiment ($t_{31}=0.71$, $p>0.5$, $d=0.26$, 95% CI [-0.47; 0.99]; Fig. 3.2d, 3.4).

Experiment 3: Passive Tool Holding

The active use of a tool (as opposed to passive handling) has been found to be necessary for tool embodiment (Farnè et al., 2005; Maravita et al., 2002; Witt et al., 2005). In Experiment 3, we tested whether this was also the case for illusory tool use. The procedures of this experiment were identical to Experiment 1, except that participants viewed the mirror reflection of their arm as they held a tool completely stationary.

Methods and Materials

Participants

Twelve new participants took part in Experiment 3 (10 females; 12 right-handed; Mean age: 21.82, SD: 1.73).

Passive holding and Mirror Illusion

The mirror box setup was identical to Experiment 1a. Participants were instructed to wrap their fingers around the handle of the tool. Unlike Experiment 1, they held this position without ever picking up or moving the tool. They were told explicitly that they would never use the tool during the task, but instead were instructed to focus their attention along the tool body and at the location of the object in the mirror. This task lasted for approximately 8 minutes.

Results

In contrast to the dynamic visual illusion (Exp. 1), passively holding a tool was not sufficient to recalibrate tactile perception on the left arm. The pre and post-tool holding curves were not significantly different as measured with an LRT (p=0.82; Fig. 3.3a). Analysis of the PSEs also failed to reveal any significant recalibration in tactile perception (Mean: -3.81%, SEM: 3.26; t_{11}=-1.17, p>0.5, d_z=-0.37, 95% CI [-0.91; 0.25]). This finding is consistent with previous studies with natural tool use, and demonstrates a central role for the illusion of *active* tool use in our effect (Exp. 1 vs. 3: t_{32}=4.26, p<0.005, d=1.53, 95% CI [0.72; 2.31]; Fig. 3.4).

Experiment 4: Visuo-Proprioceptive Conflict

Decoupling vision from proprioception has been shown to temporarily alter tactile perception (Folegatti, de Vignemont, Pavani, Rossetti, & Farnè, 2009). In Experiment 4, we ruled out the illusion-induced spatial conflict between visual and kinesthetic body signals as an explanation for our effect. Procedures were identical to

Experiment 1a, except that participants viewed their right arm in the mirror picking up an object directly (i.e., no tool).

Methods and Materials

Participants

Twelve new participants took part in Experiment 4 (8 females; 12 right-handed; Mean age: 20.91, SD: 1.47).

Object interaction task and Mirror Illusion

The mirror box setup was identical to Experiment 1a. The object interaction procedure was identical to Experiment 1 with the following exception: participants picked up the rubber cube with their right hand instead of a tool. This task was self-paced, and the rate that participants picked up the object ranged from approximately 0.1 to 0.25 Hz. The task lasted for approximately 8 minutes.

Results

In contrast to Experiment 1, where the visual illusion consisted of tool-object interactions, we found no evidence for recalibration on the stationary left arm in the present experiment. The pre and post curves were not significantly different as measured with an LRT (p=0.68; Fig. 3.3b). Analysis of the PSEs also failed to reveal any significant recalibration in tactile perception (Mean: -4.5%, SEM: 4.81; t_{11}=-0.94, p>0.5, d_z=-0.27, 95% CI [-0.84; 0.31]). This finding demonstrates that a general visual-proprioceptive conflict cannot explain the results of Experiment 1 (Exp. 1 vs. 4: t_{32}=4.70, p<0.005, d=1.69, 95% CI [0.86; 2.59]; Fig. 3.4).

Experiment 5: Interhemispheric Plasticity

Thus far, our results suggest that a dynamic visual illusion of tool use can recalibrate tactile perception on a stationary body part. It is however possible that this effect might be driven by interhemispheric transfer of somatosensory plasticity (Calford & Tweedale, 1990), independent of vision. To test this possibility, we ran a fourth experiment with all experimental procedures identical to those in Experiment 2, except that tactile perception was measured on the stationary left arm. Participants directly viewed their right arm using the tool, while keeping their left arm stationary behind an occluding board.

Methods and Materials

Participants

Eleven new participants took part in Experiment 5 (6 females; 11 right-handed; Mean age: 19.79, SD: 1.02).

Object interaction task

The mirror box setup and object interaction procedure were identical to Experiment 2. Like Experiments 1, 3, and 4, the target body part in the TDJ was the stationary left arm.

Results

In the absence of the mirror visual illusion, no perceptual recalibration was detected on the stationary left arm. The pre and post curves were not significantly different as measured with an LRT (p=0.73; Fig. 3.3c). Analysis of the PSEs also failed to reveal any significant recalibration in tactile perception (Mean: +1.9%, SEM:

3.25; t_{10}=0.56, p>0.5, d_z=0.17, 95% CI [-0.43; 0.76]). This finding rules out general interhemispheric plasticity as an explanation for the recalibration we found following illusory tool use (Exp. 1 vs. 5: t_{31}=3.42, p<0.01, d=1.26, 95% CI [0.46; 2.04]; Fig. 3.4).

We further compared the perceptual recalibration found in all experiments, with the exception of Experiment 2, using a One-way ANOVA. A significant change in the pre and post PSEs was only observed in Experiment 1 ($F(3,53)$=10.97, p<0.001); post-hoc Tukey's HSD tests demonstrated that the recalibration observed in Experiment 1 differed from all control experiments (all *ps*<0.01), and none of the control experiments differed from each other (all *ps*>0.5). Figure 3.4 displays the Cohen's *d* effect size (with 95% confidence intervals) for each experiment (Fig. 3.4a), as well as the comparisons with Experiment 1 (Fig. 3.4b).

General Discussion

We used a visual illusion to gain insight into a fundamental principle of tool embodiment, namely its boundary conditions. Participants viewed a mirror reflection of their right arm using a tool to pick up an object, giving the visual impression that the left arm was in fact doing so. This manipulation produced a significant recalibration of tactile perception on their stationary left arm.

Natural tool use involves rich somatosensory and motor feedback from the body (e.g., the hand that is wielding the tool), as well as visual input about the interaction between tool and object. In contrast, our study used the illusion such that the user had a vivid visual experience of object-directed tool use, but other sensory cues from the body part “using” the tool (i.e., the left arm) were absent. From both an experiential and neurocomputational viewpoint, the two tool use situations—natural and illusory—are substantially different, with the latter lacking the seemingly crucial direct kinesthetic and motor cues (Brown et al., 2011; Rademaker et al., 2014). Nevertheless, we found the same pattern of tactile perceptual recalibration for both situations. This suggests that natural tool use (with associated kinesthetic and motor signals) and illusory tool use (with vision of tool use as the sole feedback signal) modulates mechanisms underlying experience-dependent plasticity of body representations similarly.

The close relationship between tools and the body in the brain (Johnson-Frey, 2004) is a result of ontogenetic development (Quallo, Price, Ueno, Asamizuya, Cheng, Lemon, & Iriki, 2009), exaptation of neural structures evolved to represent the body (Gallivan, McLean, Valyear, & Culham, 2013; Peeters, Simone, Nelissen, Fabbri-Destro, Vanduffel, Rizzolatti, & Orban, 2009), as well as mechanisms that enable experience-dependent plasticity (Buonomano & Merzenich, 1998). Tool embodiment is known to be dependent upon the active *use* of the tool (Farnè et al., 2005; Maravita et al., 2002; Witt et al., 2005) and our work demonstrates for the first time that the same holds for an illusory situation; passively holding the tool does not result in embodiment (Exp. 3). Further, general hand-object interactions, which in the context of the mirror visual illusion (Exp. 4) produced a visual-proprioceptive conflict (Folegatti et al., 2009), are also not sufficient to recalibrate tactile perception (Farnè et al., 2005). Tool *use* is therefore a crucial component of the embodiment process. These results indicate that experience-dependent mechanisms of plasticity are highly sensitive to the contingencies of tool-object interactions conveyed via sensory feedback (e.g., visual biological motion signals, Blake & Shiffrar, 2007). Sensory information about these contingencies may be necessary for embodiment (Cardinali et al., 2012), a topic that deserves attention in future research.

The results of our experiments establish an essential role for vision in tool-induced recalibration. In Experiment 1, we found that visual feedback of tool use recalibrated tactile perception on the stationary arm irrespective of its actual spatial position (i.e., behind mirror, or resting by the hip). Furthermore, the perceptual recalibration we measured following the visual illusion of tool use was quantitatively *indistinguishable* from that for natural tool use (Exp. 2). A general transfer of contralateral motor and/or proprioceptive signals during tool use could not explain these results (Exp. 4). Somato-motor signals during tool use alone may therefore not play a large role in embodiment.

What role might the illusory visual feedback have played in the observed tool-induced recalibration? One possibility is that vision 'captured' the somato-motor signals from the right, tool-using arm. Indeed, visual capture is known to play an important role in the rubber hand illusion (Pavani, Spence, & Driver, 2000). It is therefore possible that vision provides the 'glue' that binds the entirety of sensory feedback into a multisensory representation of tool use, leading to recalibration. Another possibility is that recalibration was driven by the bottom-up activation of sensorimotor representations of the stationary arm by feed-forward visual signals of tool use. A recent study with patients lacking a corpus callosum found that motor learning during the mirror visual illusion transferred from the mirror-reflected body part to its stationary counterpart (Nojima, Oga, Fukuyama, Kawamata, & Mima, 2013). This finding bolsters support for the current hypothesis, as visual capture of motor signals in the hemisphere contralateral to the patient's moving limb would have been impossible. In the context of this finding, our results strongly suggest that visual tool-use signals may play a *sufficient* role in driving embodiment in both natural and illusory tool use situations. Future research should focus on distinguishing between these two possibilities.

Our experience of the world is inherently multisensory, whether with our body or in the context of tool use. Representations of the body that structure somatosensory perception are calibrated and refined through myriad interactions between different sensory modalities, particularly vision and touch (Longo, Azanon, & Haggard, 2010). In the present study, we found that visual tool use signals can recalibrate tactile perception, an interplay that highlights the multisensory nature of the embodiment process. The multisensory mechanisms underlying this interplay have still yet to be established. We suggest middle and superior temporal areas coding for tool use-related visual information such as biological motion (Beauchamp, Lee, Haxby, & Martin, 2003; Saygin, Wilson, Hagler, Bates, & Sereno, 2004) play a crucial role in tool embodiment. During tool wielding, these temporal areas transmit visual tool-use signals, via dense bidirectional white matter connections (Baizer, Ungerleider, & Desimone, 1991), to regions of the posterior parietal cortex that contain multisensory representations of the body (Bolognini & Maravita, 2007; Duhamel, Colby, & Goldberg, 1998). In addition, these parietal regions are also known to play a role in tool embodiment (Iriki et al., 1996; Quallo et al., 2009), and are functionally coupled with the primary somatosensory cortex (Cooke, Goldring, Baldwin, Recanzone, Chen, Pan, Simon, & Krubitzer, 2014). Signals from these parietal regions during tool use likely underlie the observed recalibration of body representation, perhaps by modulating receptive field properties of SI neurons through changes in intracortical inhibition (Cardini, Longo, & Haggard, 2011), a mechanism that commonly drives experience-dependent plasticity (Buonomano & Merzenich, 1998).

Conclusions

In sum, we used illusory tool use to investigate the boundary conditions of embodiment. Our results demonstrate that a visual illusion of tool use recalibrates tactile perception and strongly suggest that visual signals of tool use are a sufficient signal for embodiment. This finding represents a major shift in how we view the sensory relationship between bodies, tools and the environment, demonstrating that visual experience of our activities continuously shapes our perception of our body's dimensions.

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Chapter 3, in full, has been submitted for publication as a manuscript with Ayse P. Saygin and Matthew R. Longo.

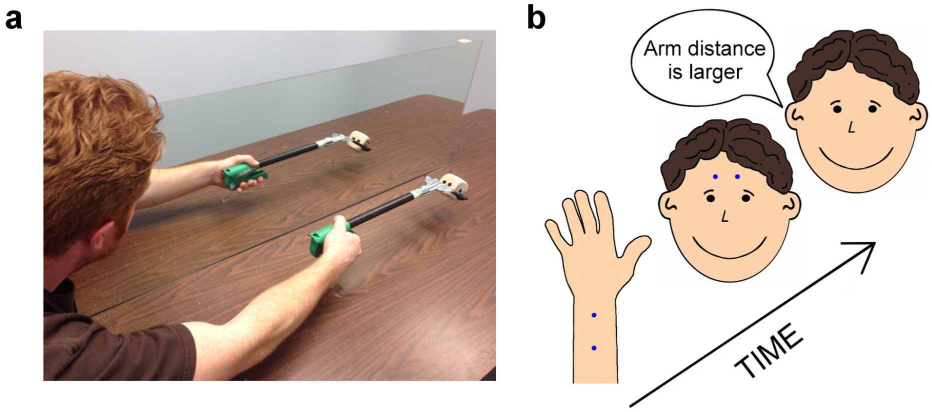

Figure 3.1: Visual illusion and tactile paradigm

(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 vivid 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.

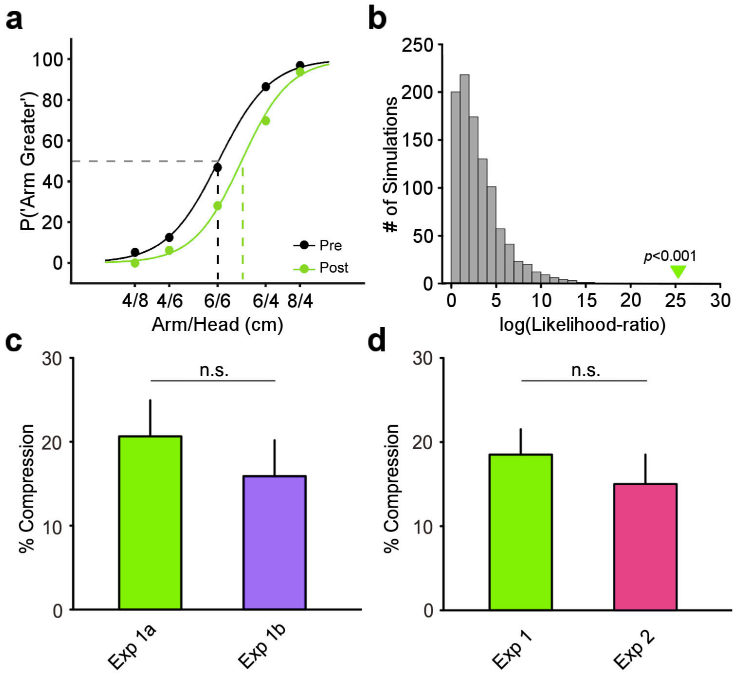

Figure 3.2: A visual illusion of tool use recalibrated tactile perception

(a) Group-level psychometric curve for Experiment 1a: Tool use led to a significant rightward shift ($p<0.001$) in the post-tool use curve (green) relative to the pre-tool use curve (black). This pattern of results was similar for both Experiment 1a and 2 (not shown). **(b)** Likelihood-ratio test histogram for Experiment 1a: The gray bars represent simulated log-likelihood ratios (LLRs) and the inverted green triangle marks the true LLR for Experiment 1. None of the simulated LLRs (max: 15.35) were greater than the true LLR (25.43), resulting in a maximal *p*-value of $p<0.001$. This pattern of results was similar for both Experiment 1a and 2 (not shown). **(c)** Comparison of arm position (Exp. 1a vs. b): As can be seen, there was no effect of arm position—recalibration occurred on the left arm irrespective of whether it was located behind the mirror (Exp. 1a) or resting down by participant's left hip (Exp. 1b). **(d)** Comparison of illusory and actual tool use (Exp. 1 vs. 2): The magnitude of the perceptual recalibration following illusory tool use (Exp. 1; collapsed across 1a and 1b) was statistically similar to actual tool use (Exp. 2). Data are presented as mean ± SEM; n.s.=not significant

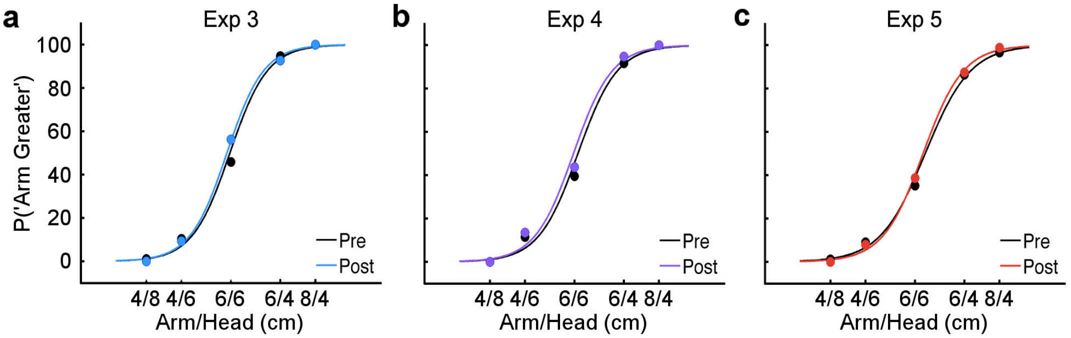

Figure 3.3: Psychometric curves for control experiments (Exp. 3-5)

No significant difference between the pre and post-tool use psychometric curves were found for any control experiment: **(a)** Experiment 3, when participants viewed a mirror reflection of their arm holding a tool stationary; **(b)** Experiment 4, when participants viewed a mirror reflection of their hand picking up an object; **(c)** Experiment 5, when tool use occurred in the absence of a mirror visual illusion.

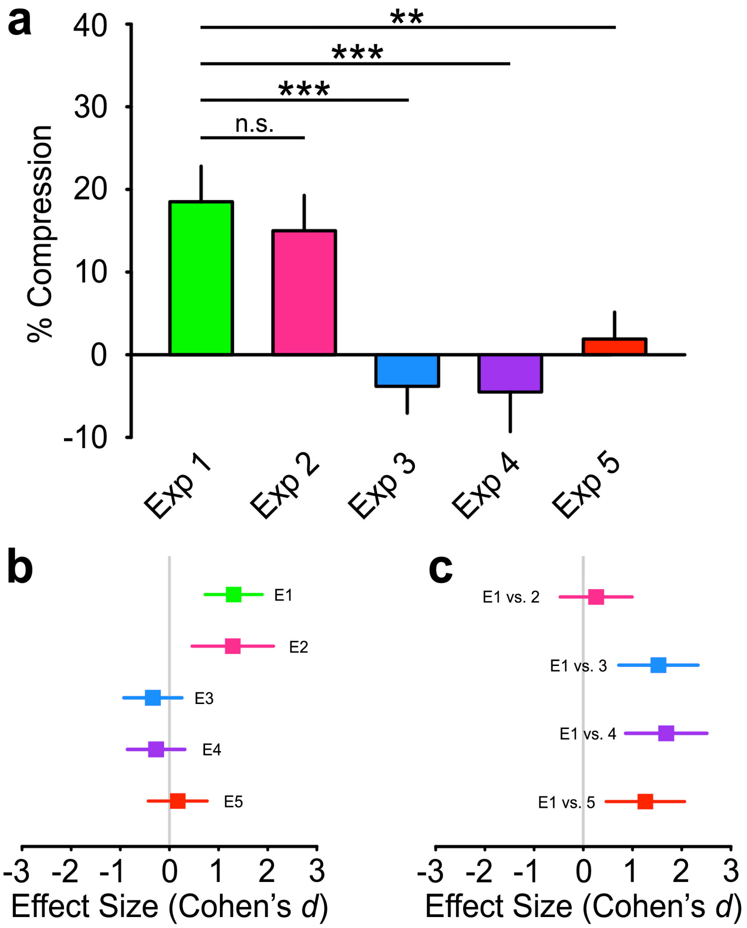

Figure 3.4: Comparison between Experiment 1 and all other experiments

(a) Perceptual recalibration for all experiments: As can be seen, a significant compression in tactile distance perception was only observed in Experiment 1 and 2, which did not differ from each other. The recalibration following illusory tool use was significantly different than found in all control conditions. Data are presented as mean ± SEM. **(b)** Forest plot of effect sizes for all experiments: The colored square is centered on the estimated Cohen's *d* and the error bars correspond to its 95% confidence interval (see the main text for the actual values). The solid gray line marks the zero point. **(c)** Forest plot of effect sizes for all comparisons with Experiment 1.
n.s.=not significant, $^{**}p<0.01$, $^{***}p<0.005$.

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Chapter 4

Using a Tool Modulates Somatosensory Cortical Processing

Abstract

Using a tool leads to plastic changes in body representations underlying tactile perception. The electrophysiological correlates of this tool-induced plasticity in humans are unknown. The present study used event-related brain potentials to investigate the stage of sensory processing modulated by tool use. Somatosensory evoked potentials, elicited by median nerve stimulation, were recorded before and after two forms of object-interaction: tool use and hand use. Using a tool, but not the hand alone, led to a modulation in the amplitude of the P100 contralateral to stimulation. The P100 has been implicated in the construction of multisensory body representations and is thought to have generators in secondary somatosensory and posterior parietal cortices. This result converges with known neural correlates of tool-induced plasticity in tool-trained macaques.

Introduction

The construction of cortical body representations involves several sensory processing stages. Somatosensory afferents are first organized into several representations of the receptor sheet (i.e., the skin surface) in the primary somatosensory cortex (SI) (Mountcastle, 2005). These representations are at least partially unified in the secondary somatosensory cortex (SII) (Fitzgerald, Lane, Thakur, & Hsiao, 2006; Murray & Mishkin, 1984), where we see the first evidence for representations that take into account volumetric properties of the body (Hsiao, 2008; Lin & Forss, 2002). Finally, regions of the posterior parietal and premotor cortices integrate signals across multiple sensory modalities (especially vision and touch) to construct supramodal representations of the body (Graziano, Hu, & Gross, 1997; Iriki, Tanaka, Obayashi, & Iwamura, 2001; Sereno & Huang, 2014) and its current postural position in external space (Azanon, Longo, Soto-Faraco, & Haggard, 2010; Graziano, 1999). Functional coupling between SII and PPC underlies the conscious experience of having a body (Limanowski & Blankenburg, 2015).

Somatosensory representations are highly sensitive to how the body is used to interact with the environment (Buonomano & Merzenich, 1998). It is well established in both human and non-human primates that the cortical magnification of limb representations in SI is dependent upon the frequency it is used (Coq & Xerri, 2001; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Jenkins, Merzenich, Ochs, Allard, & Guic-Robles, 1990). Using a tool also modulates cortical body representations (Maravita & Iriki, 2004). Studies with tool-trained macaques have found that using a tool leads to measurable functional and structural changes in anterior intraparietal sulcus (aIPS) and SII (Hihara, Notoya, Tanaka, Ichinose, Ojima, Obayashi, Fujii, & Iriki, 2006; Iriki, Tanaka, & Iwamura, 1996; Quallo, Price, Ueno, Asamizuya, Cheng, Lemon, & Iriki, 2009). Several behavioral studies in humans have found that tool use modulates tactile perception and multisensory processing around the user's body (Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013; Cardinali, Frassinetti, Brozzoli, Urquizar, Roy, & Farnè, 2009; Maravita, Spence, & Driver, 2002; Miller, Longo, & Saygin, 2014). However, the cortical mechanisms underlying tool-induced plasticity in humans are currently unknown.

In the present study, we used event-related brain potentials (ERP) to identify the stage(s) of somatosensory processing modulated by tool use in humans. ERPs are an ideal method for this research question because of their exquisite temporal resolution. Further, intracranial recordings in humans (Allison, McCarthy, Wood, & Jones, 1991) and magnetoencephalography (MEG) (Hoshiyama & Kakigi, 2001; Kakigi, 1994) have mapped out the cortical generators of several somatosensory evoked potentials (SEP). It is thought that up until around 60 ms post-stimulation, cortical somatosensory activity is specific to SI (Allison, McCarthy, & Wood, 1992; Tsuji & Murai, 1986; Yamada, Kayamori, Kimura, & Beck, 1984). Only after 60 ms does activity spread to SII, PPC, and regions of the frontal cortex (Allison et al., 1992; Forss, Hari, Salmelin, Ahonen, Hamalainen, Kajola, Knuutila, & Simola, 1994; Hamalainen, Kekoni, Sams, Reinikainen, & Naatanen, 1990; Mauguiere, Merlet, Forss, Vanni, Jousmaki, Adeleine, & Hari, 1997). Changes in the amplitude of short-latency SEPs (e.g., P45, N60) would therefore suggest that tool-induced plasticity in

SI. Conversely, changes in the amplitude of mid-latency SEPs (e.g., P100, N140) would suggest that tool use modulated representations of the body outside of SI, consistent with what is found in tool-trained macaques (Iriki et al., 1996; Quallo et al., 2009).

Methods & Materials

Participants

Twelve healthy right-handed subjects took part in the experiment. One subject was removed due to equipment failure and one was removed due to excessive eye blinks (almost every trial). The remaining ten subjects were further analyzed.

Stimuli and Apparatus

Electric shocks (0.2 ms in duration) were delivered to the right median nerve with a Digitimer DS7A constant current high-voltage stimulator. Median nerve stimulation was chosen because it is known to elicit robust SEPs (Allison et al., 1991). Each subject's median nerve was located and isolated using two criteria: 1) a single electric shock produced a noticeable tingling sensations in the right thumb, index, and middle fingers but not the two remaining digits; 2) once these sensations were reported, an involuntary thumb twitch could be elicited. The stimulation intensity used throughout the experiment was set to 120% the minimum intensity that reliably elicited a thumb twitch (Mean: 116 mV; SD: 28.9). Two subjects reported that this stimulation level caused mild discomfort. We therefore lowered their stimulation intensity to 90% the thumb-twitch threshold before the start of the experiment.

Experimental Procedure

The experiment consisted of four EEG blocks: one block before and one block after each of the two object-interaction tasks (see below). A schematic of the entire experiment can be seen in Figure 4.1.

Participants performed a target-detection task, which forced them to maintain spatial attention to their right hand and median nerve region throughout each block. They sat in a dimly lit room, both arms resting comfortably on a table and covered with a black smock; participants were asked to maintain their gaze to the location of their right hand. On each trial, the task was to distinguish between a nontarget single shock (90% probability) and infrequent target double shocks (two shocks separated by 50 ms; 10% probability), randomized across trials. Nontargets were ignored and required no overt response. When a target was detected, participants responded by lifting their left foot off of a foot pedal as quickly as possible within a set time window of 1600 ms. This long time window was chosen to minimize the probability that the proceeding trial was contaminated by residual motor activity. The inter-trial interval was randomly chosen from a uniform distribution between 400 to 600 ms. A schematic of two trials, one nontarget and one target, can be seen in Figure 4.2. Each block consisted of 800 trials, 720 nontargets and 80 targets, for a total of 3200 trials for the entire experiment.

Object-interaction Procedure

The experiment was composed of two object-interaction conditions: *tool* use and *hand* use (order counterbalanced across participants). The subject's task was to pick a balloon up to eye-level and place it back down on a table. This was performed at a comfortable pace for a total of 8 minutes. This task was identical in both object-interaction conditions, differing only in the means by which the balloons were picked up.

In the *tool* use condition, subjects used the hand-shaped tool described Chapters 1 and 2 (Figure 4.3). The tool was strapped to the subject's forearm with Velcro and their fingers were placed in straps that controlled the movements of the tool's fingers. The fingers of the tool contacted the balloons instead of the subject's actual fingers.

The *hand* use condition served as a control for general modulations of SEPs by sustained object interaction. We attempted to partially simulate the setup of the tool by strapping two large plastic pens around the sides of their forearm in the location of where the tool would have been strapped. Subjects then used their own fingers to grasp the balloon and lift it to eye-level in a similar manner as the tool use condition.

Recording and Data Analysis

EEG Recording

Neural data was recorded with a BioSemi ActiveTwo 64-channel EEG system (Biosemi B.V., Amsterdam, The Netherlands) following the international 10/20 system. Horizontal and vertical electrooculograms (EOG) were used to measure and detect horizontal eye movements and eye blinks, respectively. The offset at all recording sites was kept below 40 mV. During data acquisition, EEG and EOG signals were amplified and digitized at 2048 Hz, and low-pass filtered at 100 Hz.

EEG Preprocessing

All data was pre-processed with EEGLab (Delorme & Makeig, 2004). The electric shock creates a large ~2 ms artifact in the EEG and EOG signal. In keeping with previous studies, this artifact was removed from each trial by linearly interpolating the signal from 0 to 6 ms following the shock (Cardini, Longo, & Haggard, 2011b; Ferre, Bottini, & Haggard, 2012; Longo, Pernigo, & Haggard, 2011). The data was then down-sampled to 500 Hz, re-referenced to the average of the left and right mastoids, and band-pass filtered between 0.1 and 40 Hz. EEG and EOG signals were epoched into periods of 230 ms, starting 50 ms before and ending 180 ms after each nontarget shock. Only the nontarget trials were included in our analysis (Eimer, Cockburn, Smedley, & Driver, 2001; Gillmeister & Forster, 2012; Sambo & Forster, 2009). Data cleaning had the following steps: First, we removed large artifacts—eye movements, eye blinks, muscle activity, and alpha waves—using independent components analysis; Second, trials with activity still exceeding ±80 μV (relative to baseline) at the external electrodes or ±120 μV (relative to baseline) on the scalp were discarded (mean: 7.85; range: 0–33).

Data Analysis

As the main aim of our study was to investigate how tool use modulated somatosensory processing, we focused exclusively on electrode sites over and close to somatosensory areas (C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7). We restricted the statistical analysis of each SEP component to electrodes where its amplitude in the grand average waveform (collapsed all across subjects and experimental conditions) was largest.

Based on previous studies investigating electrophysiological signatures of somatosensory body representation, we focused on four main components of interest: First, the short-latency P45 component was calculated as the mean amplitude at C3, C5, CP3, and CP5 between 34 and 52 ms post-shock. The P45 is thought to reflect tactile spatial processing in SI (Allison et al., 1991; Cardini et al., 2011b). Second, the short-latency N60 component was calculated as the mean amplitude at C3, C5, CP3, and CP5 between 52 and 70 ms post-shock. The N60 has been localized to SI (Allison et al., 1992) and is the first component whose amplitude is modulated by sustained spatial attention (Eimer & Forster, 2003). Viewing the body modulates the amplitude of the P45 and the N60 (Cardini et al., 2011b; Taylor-Clarke, Kennett, & Haggard, 2002), demonstrating that visual signals can modulate processing in SI. Third, the mid-latency P100 component was calculated as the mean amplitude at CP1, CP3, P1, and P3 between 70 and 110 ms post-shock. The P100 is the earliest component to index visual-tactile integration (Sambo & Forster, 2009) and is thought to reflect processing in SII and PPC (Forss et al., 1994; Kany & Treede, 1997; Lin & Forss, 2002). Fourth, the mid-latency N140 component was calculated as the mean amplitude at C5, T7, CP5, TP7, P5 and P7 between 110 and 160 ms post-shock. The N140 is modulated by both unisensory and multisensory spatial attention (Eimer et al., 2001; Kennett, Eimer, Spence, & Driver, 2001; Macaluso & Driver, 2001) and is thought to have numerous cortical generators, including frontal sources (Allison et al., 1992). The scalp topography and time window of each component was consistent with prior studies.

To determine whether either object-interaction condition modulated somatosensory cortical processing, we performed a 2 (time: pre, post) x 2 (effector: tool, hand) repeated measures ANOVA on the mean amplitude of each component. The main statistic of interest is the interaction between the two factors, as this would indicate that each object-interaction condition modulated the specific component differently. Significant interactions were followed up with paired *t* tests.

Results

Behavioral Performance

All participants performed a target detection task that required them to maintain spatial attention throughout each block. Their task was to detect infrequent targets (double shocks separated by 50 ms) among frequent nontargets (single shocks). When targets were detected, participants responded by lifting their left foot off of a foot pedal as quickly as possible. Table 4.1 shows the results for each experimental condition for two dependent measures of behavioral performance: percentage of missed targets and reaction times. We did not find any statistical evidence that target detection accuracy (all $Fs < 2.1$, $ps > 0.18$) or reaction time (all $Fs < 1.3$, $ps > 0.28$) varied across blocks. This suggests that spatial attention to the location of the electric shocks was not affected by either object-interaction condition. Therefore, it is unlikely that any observed modulation in component amplitude is due to effects of spatial attention.

ERP Results

Figure 4.4 shows the grand average waveforms of each condition at the electrode sites over and close to somatosensory areas used in our analysis (C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7). Figure 4.5 shows the spread of activity across the scalp collapsed across all experimental conditions between -20 to 180 ms post-shock. Table 4.2 shows the mean modulation for each component following hand use and tool use.

P45 Results

We did not find evidence that either hand use or tool use modulated the mean amplitude of the P45 (Figure 4.6). The main effects of effector ($F(1,9) = 0.1$, $p > 0.7$, $\eta^2_p = 0.01$) and time ($F(1,9) = 0.05$, $p > 0.8$, $\eta^2_p < 0.01$) were not significant. We did find a trending significant interaction ($F(1,9) = 3.7$, $p = 0.09$, $\eta^2_p = 0.29$). However, this was driven by the fact that the non-significant (both *ps* > 0.3) modulations in mean amplitude following tool use (0.17 μV) and hand use (-0.11 μV) were opposite in sign.

N60 Results

We did not find evidence that either hand use or tool use modulated the mean amplitude of the N60 (Figure 4.7). The main effects of effector ($F(1,9) = 0.36$, $p > 0.5$, $\eta^2_p = 0.04$) and time ($F(1,9) = 0.59$, $p > 0.4$, $\eta^2_p = 0.06$) were not significant. The interaction between the two factors was also not significant ($F(1,9) = 0.17$, $p > 0.6$, $\eta^2_p = 0.02$).

P100 Results

Tool use led to a significant modulation in the amplitude of the P100 (Figure 4.8). The crucial interaction between the two factors was significant ($F(1,9) = 7.21$, $p = 0.025$, $\eta^2_p = 0.45$). Follow-up t tests revealed that this interaction was driven by a significant increase in the amplitude of the P100 following tool use (0.79 μV; $t(9) = 3.77$, $p=0.004$, $d_z = 1.19$) but not hand use (0.12 μV; $t(9) = 0.57$, $p=0.58$, $d_z = 0.19$). This can be seen clearly in the difference waves (Figure 4.9, upper panel). The increase in P100 amplitude following tool use was found in all subjects (Figure 4.9, lower panel). The scalp topography of the P100 before and after tool use (Figure 4.10) reveals that this modulation is evident in a large proportion of channels around contralateral somatosensory areas; this is also apparent in Figure 4.4. We also found a significant main effect of time ($F(1,9) = 7.55$, $p = 0.023$, $\eta^2_p = 0.46$), which was driven by the fact that the sign of the modulation following both object-interaction tasks was positive. We did not find a significant main effect of effector ($F(1,9) = 0.89$, $p > 0.3$, $\eta^2_p = 0.09$).

N140 Results

We did not find evidence that either hand use or tool use modulated the mean amplitude of the N140 (Figure 4.11). The main effects of effector ($F(1,9) = 0.02$, $p > 0.9$, $\eta^2_p < 0.01$) and time ($F(1,9) = 1.19$, $p > 0.3$, $\eta^2_p = 0.12$) were not significant. The interaction between the two factors was also not significant ($F(1,9) = 0.01$, $p > 0.9$, $\eta^2_p < 0.01$).

Discussion

In the present study, we used ERPs to investigate how using a tool modulates somatosensory cortical processing. SEPs were measured before and after two object-interaction conditions—tool use and hand use—where subjects picked up balloons for 8 minutes. As expected, sustained use of the hands to pick up the balloons did not modulate the amplitude of any SEP. Using a tool, on the other hand, modulated the amplitude of the P100 at recording sites around contralateral somatosensory areas. The implications of this finding are discussed below.

The processing of touch unfolds over several sensory processing stages in the cortex. ERPs are commonly used to investigate the temporal and functional properties of these stages (Allison et al., 1991). Short-latency SEPs—including the P45 and N60—reflect stimulus-driven responses (Lesser, Koehle, & Lueders, 1979; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006) as well as the initial integration of somatosensory sub-modalities (Dieguez, Mercier, Newby, & Blanke, 2009; Huttunen & Homberg, 1991). Mid-latency SEPs reflect later stages of processing where signals are integrated with other sensory modalities (Macaluso & Driver, 2001; Press, Heyes, Haggard, & Eimer, 2008; Sambo, Gillmeister, & Forster, 2009) and remapped from a receptor-based representation to a higher-order representation of the body (Heed & Roder, 2010; Soto-Faraco & Azanon, 2013). There is substantial evidence that these components are modulated by spatial attention (Eimer et al., 2001; Kennett et al., 2001; Macaluso & Driver, 2001).

In the present study, we found that using a tool increased the amplitude of the P100, which is the first SEP that indexes the integration of visual and tactile signals

(Sambo & Forster, 2009). The P100 likely reflects the construction of a multisensory body representation (Desmedt & Tomberg, 1989; Hogendoorn, Kammers, Haggard, & Verstraten, 2015; Sambo & Forster, 2009) that underlies conscious awareness of the body (Schubert et al., 2006). Our result is therefore in line with the findings of several human behavioral studies—including Chapters 1–3 of this dissertation— where tool use modulated the user's tactile body representation (Canzoneri et al., 2013; Cardinali et al., 2009; Miller et al., 2014). Here, we show that tool use leads to a coupling between the body and tool at the neural level.

Studies using intracranial recordings and MEG suggest that the P100 is (at least partially) generated by activity in SII (Barba, Valeriani, Colicchio, Tonali, & Restuccia, 2004; Kany & Treede, 1997) and PPC (Forss et al., 1994; Mauguiere et al., 1997). Further, monkey neurophysiology (Avillac, Ben Hamed, & Duhamel, 2007) and human TMS (Konen & Haggard, 2012; Renzi, Bruns, Heise, Zimerman, Feldheim, Hummel, & Roder, 2013) studies demonstrate that multisensory parietal regions are activated within the time window of the P100 used in the present study.

The localization of ERP components should be approached with extreme caution. However, taken at face value, the above studies suggest that the using a tool modulated sensory processing in SII and/or PPC, consistent with what is found in macaques (Hihara et al., 2006; Iriki et al., 1996; Quallo et al., 2009). The results in Chapters 1–3 demonstrate that tool-induced plasticity is driven by visual feedback, with tool shape constraining what limb representation is modulated (Chapter 1). Given that representations in PPC, but not SII, are selectively sensitive to visual signals of body shape (Cardini, Costantini, Galati, Romani, Ladavas, & Serino, 2011a; Konen &

Haggard, 2012; Taylor-Clarke et al., 2002; Tsakiris, Costantini, & Haggard, 2008), we hypothesize that the observed P100 modulation were due to plastic changes in multisensory parietal cortex. Indeed, the representations of tools and hands in these parietal regions overlap (Gallivan, McLean, Valyear, & Culham, 2013; Peeters, Simone, Nelissen, Fabbri-Destro, Vanduffel, Rizzolatti, & Orban, 2009). Future research should use fMRI and TMS to better address this hypothesis.

Several boundary conditions constrain tool-induced plasticity, including active tool wielding (Iriki et al., 1996; Maravita et al., 2002), tool-object interaction (Cardinali, Jacobs, Brozzoli, Frassinetti, Roy, & Farnè, 2012), tool shape (Chapter 1), and visual feedback (Chapter 2 and 3). It is likely that these conditions played some role in modulating the P100 during tool use. However, the tool and hand conditions differed in several ways and these variables might instead underlie our effect. First, the weight of the tool may have led to different levels of muscle fatigue between conditions. Second, both conditions likely differed in the degree of motor learning required to complete the object-interaction task. However, both muscle fatigue and motor learning *decrease* SEP amplitude (Murphy, Haavik Taylor, Wilson, Oliphant, & Mathers, 2003; Nasir, Darainy, & Ostry, 2013), making it unlikely that they can explain our effect. It is also possible that effects of spatial attention differed between blocks. However, we found no difference in behavioral performance between conditions. Further, spatial attention does not modulate the P100 when the hands are hidden from view, as they were in our experimental setup (Rigato, Bremner, Mason, Pickering, Davis, & van Velzen, 2013; Sambo et al., 2009). Future work should directly rule out these alternative explanations and investigate the aspects of tool use modulating cortical somatosensory processing.

Acknowledgments: Chapter 4, in full, is in preparation for publication as a manuscript with Ayse P. Saygin and Matthew R. Longo.

Table 4.1. Percentage of missed responses and reaction times pre- and post-tool use and hand use.

	Tool Use		**Hand Use**	
	Pre	*Pre*	*Post*	*Post*
Missed Responses (%)	3.8	2.3	3.6	1.6
Mean RTs (ms)	403.5	392.6	400.2	385.1

Table 4.2. Modulation in the mean amplitude of each SEP component following tool and hand use. * *p*<0.05, ** *p*<0.01, and — n.s.

Component	**Tool Use**	**Hand Use**	**Interaction**
P45	0.17 ± 0.17	-0.11 ± 0.13	—
N60	-0.08 ± 0.13	-0.15 ± 0.13	—
P100	0.79 ± 0.21**	0.12 ± 0.20	*
N140	0.16 ± 0.17	0.19 ± 0.25	—

EEG		EEG		EEG		EEG
Pre-Tool Use	Tool Use	Post-Tool Use	Break	Pre-Hand Use	Hand Use	Post-Hand Use
10 min.	8 min.	10 min.	5 min.	10 min.	8 min.	10 min.

Figure 4.1. Temporal structure of the experiment

The experiment was composed of four EEG blocks (~10 minutes each), one block before and one after each object-interaction condition (tool use, hand use). Each pair of object-interaction blocks was separated by a five-minute break in order to minimize carry-over effects from object interaction (especially, tool use). In the present example, the subject completed the tool use conditions first. This was counterbalanced across subjects.

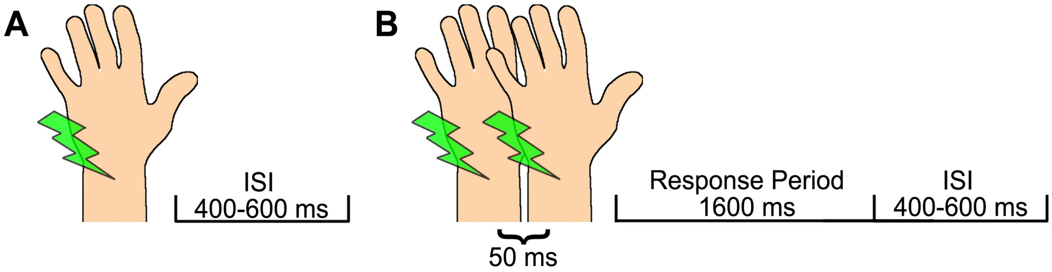

Figure 4.2. Trial structure of the target-detection task

Each block was composed of two types of trials: A) non-target trials were single shocks (green lightning bolt) and occurred on 90% of the trials (720 in total); B) target trials were double shocks (separated by 50 ms) and occurred on 10% of the trials (80 in total). Only target trials required an overt response, which subjects did during a 1600 ms response period.

Figure 4.3. Hand-shaped tool used in the current experiment.

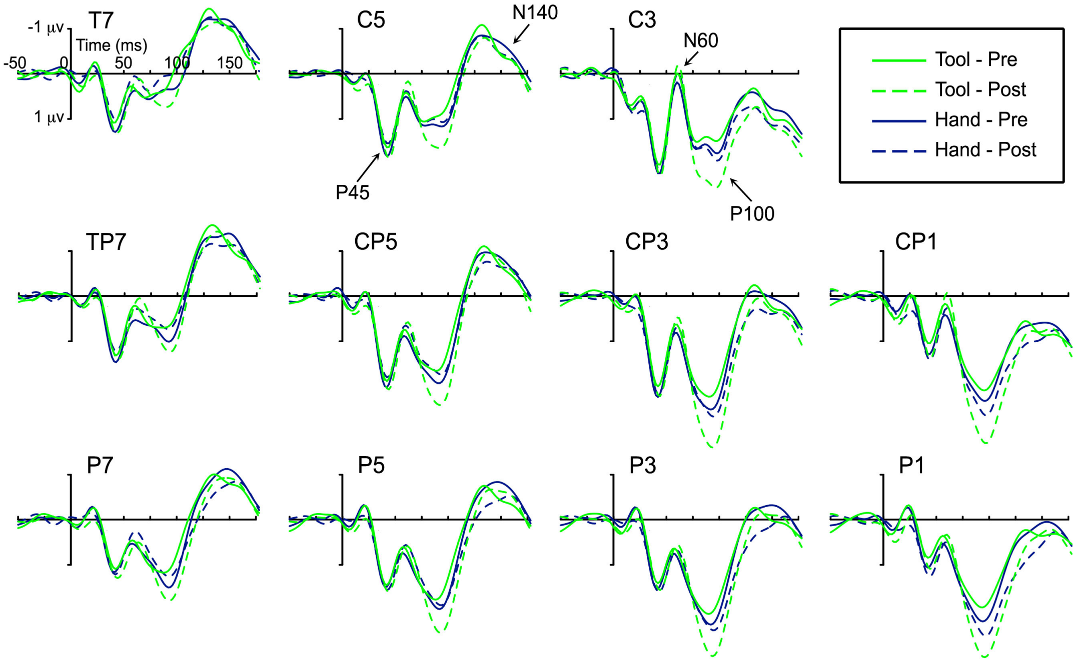

Figure 4.4. Grand average waveforms for all analyzed channels

The current figure shows the grand average SEP waveforms before (solid lines) and after (dashed lines) each object interaction condition: tool use (green) and hand use (dark blue). Our analyses were restricted to channels over and close to somatosensory areas (central, centro-parietal, and parietal channels). We focused on four components: the P45, N60, P100, and N140. As can be seen, tool use led to widespread modulation in the amplitude of the P100. Note that negative voltage is plotted up.

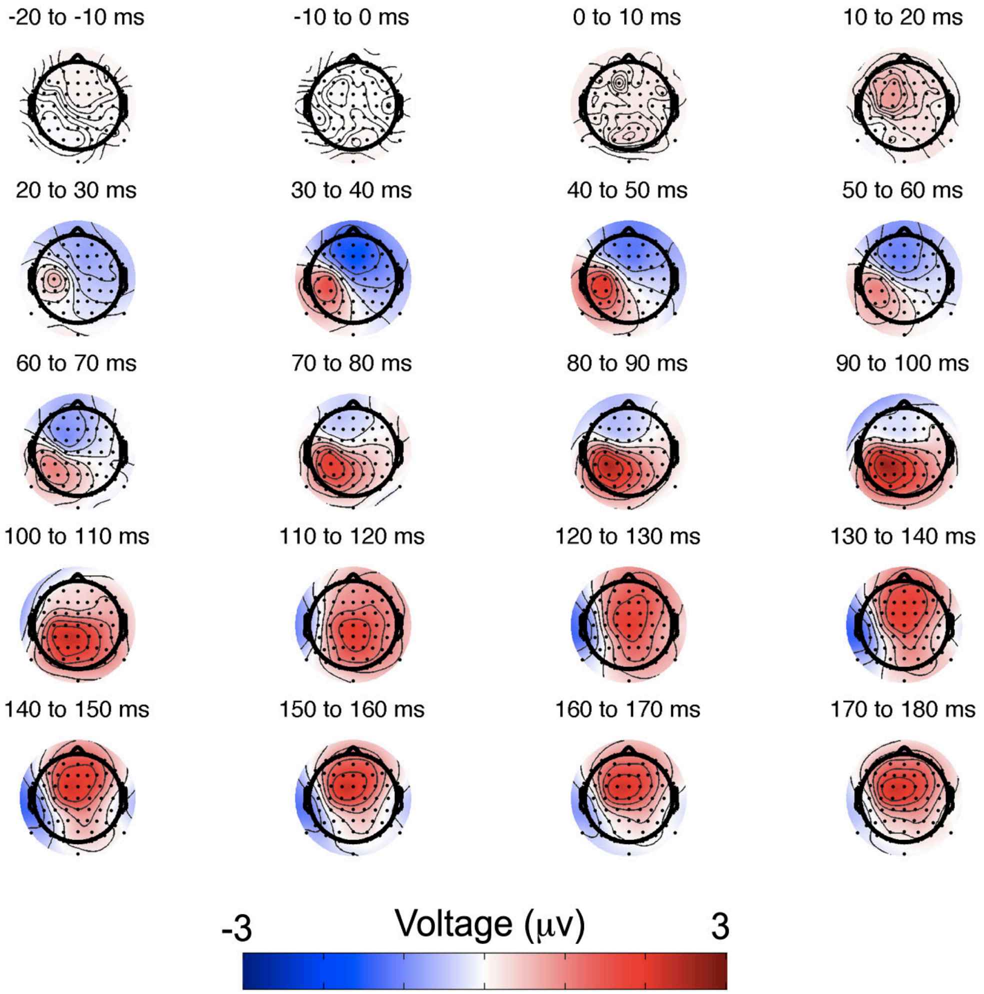

Figure 4.5. Scalp topography collapsed across all experimental conditions.

The present displays the spread of activity across the scalp between -20 to 180 ms (in periods of 10 ms). Activity is collapsed across all experimental conditions.

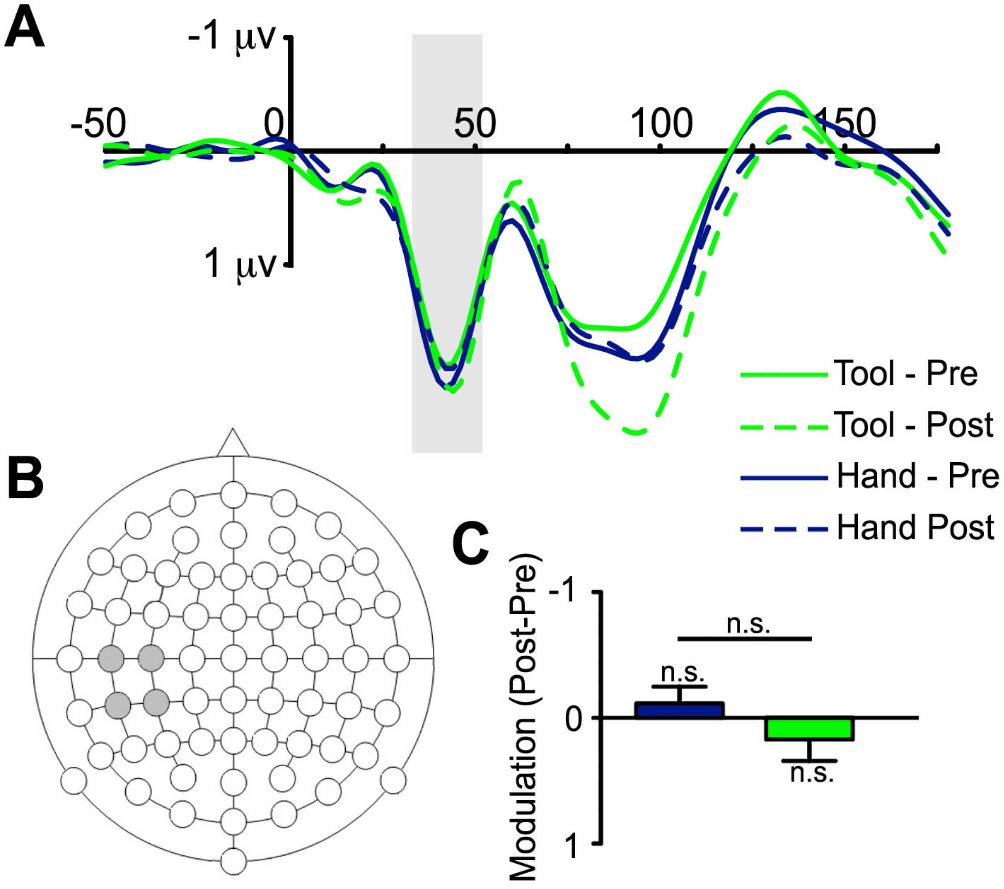

Figure 4.6. Results for the P45 component

A) Grand average SEP waveforms before (solid lines) and after (dashed lines) each object interaction condition: tool use (green) and hand use (dark blue). Note that negative voltage is plotted up. The gray block corresponds to the time window used in our analysis. **B)** The electrodes in the channel layout filled with gray correspond to C3, C5, CP3, and CP5. These channels were where the P45 amplitude was largest. For our analysis, we averaged the SEP of each channel. **C)** Bar plot displaying the average modulation in the P45 amplitude for tool use (green) and hand use (dark blue).
n.s. not significant

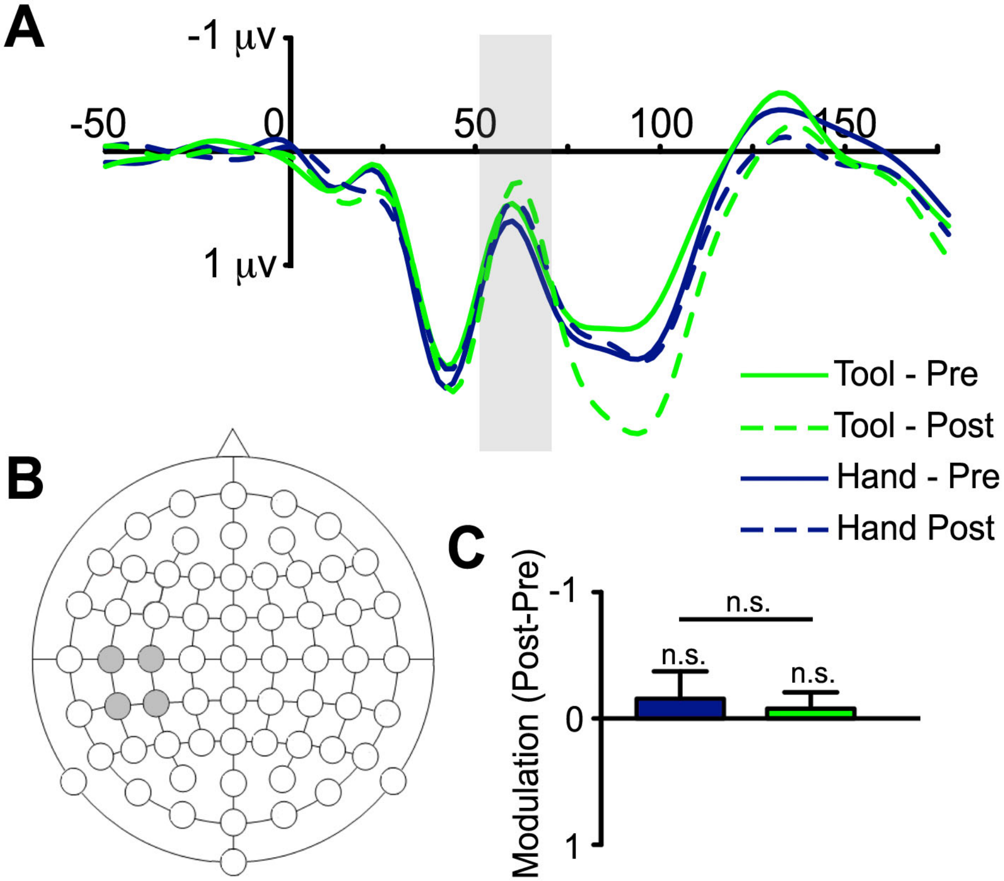

Figure 4.7. Results for the N60 component

A) Grand average SEP waveforms before (solid lines) and after (dashed lines) each object interaction condition: tool use (green) and hand use (dark blue). Note that negative voltage is plotted up. The gray block corresponds to the time window used in our analysis. **B)** The electrodes in the channel layout filled with gray correspond to C3, C5, CP3, and CP5. These channels were where the N60 amplitude was largest. For our analysis, we averaged the SEP of each channel. **C)** Bar plot displaying the average modulation in the N60 amplitude for tool use (green) and hand use (dark blue).
n.s. not significant

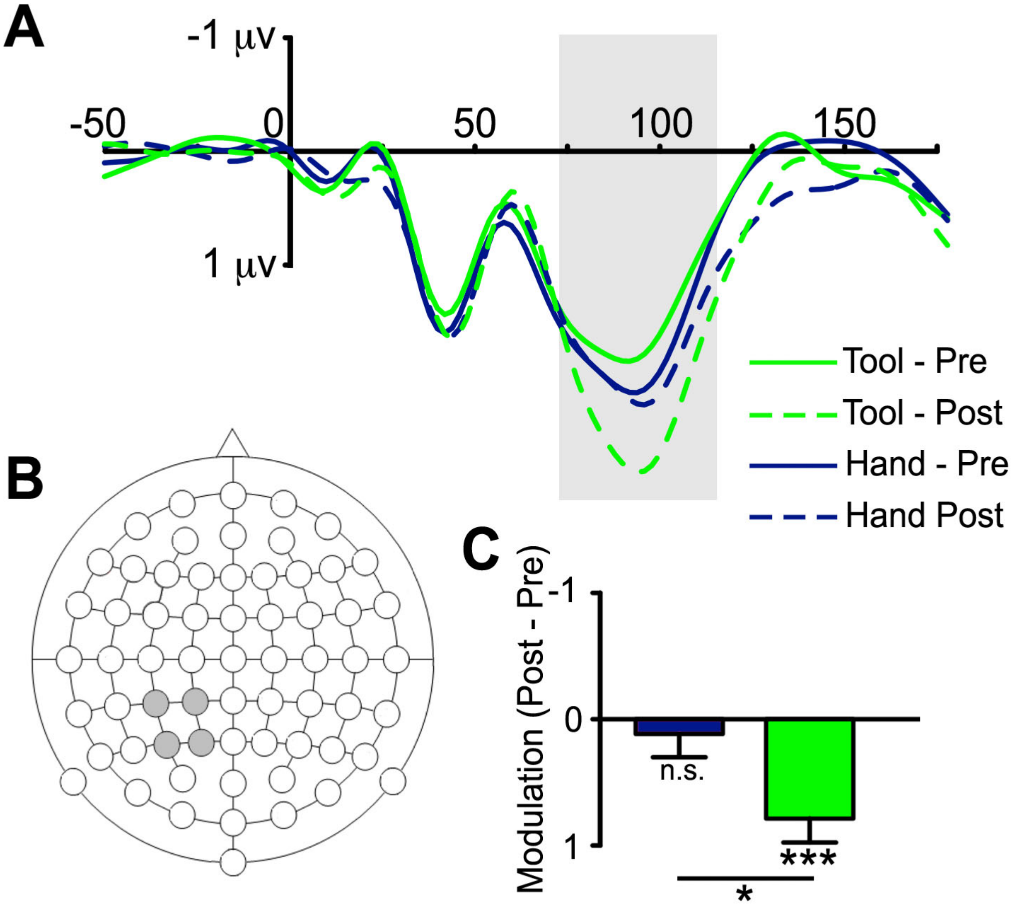

Figure 4.8. Results for the P100 component

A) Grand average SEP waveforms before (solid lines) and after (dashed lines) each object interaction condition: tool use (green) and hand use (dark blue). Note that negative voltage is plotted up. The gray block corresponds to the time window used in our analysis. **B)** The electrodes in the channel layout filled with gray correspond to CP1, CP3, P1, and P3. These channels were where the P100 amplitude was largest. For our analysis, we averaged the SEP of each channel. **C)** Bar plot displaying the average modulation in the P100 amplitude for tool use (green) and hand use (dark blue).

* *p*<0.05, ** *p*<0.01, n.s. not significant

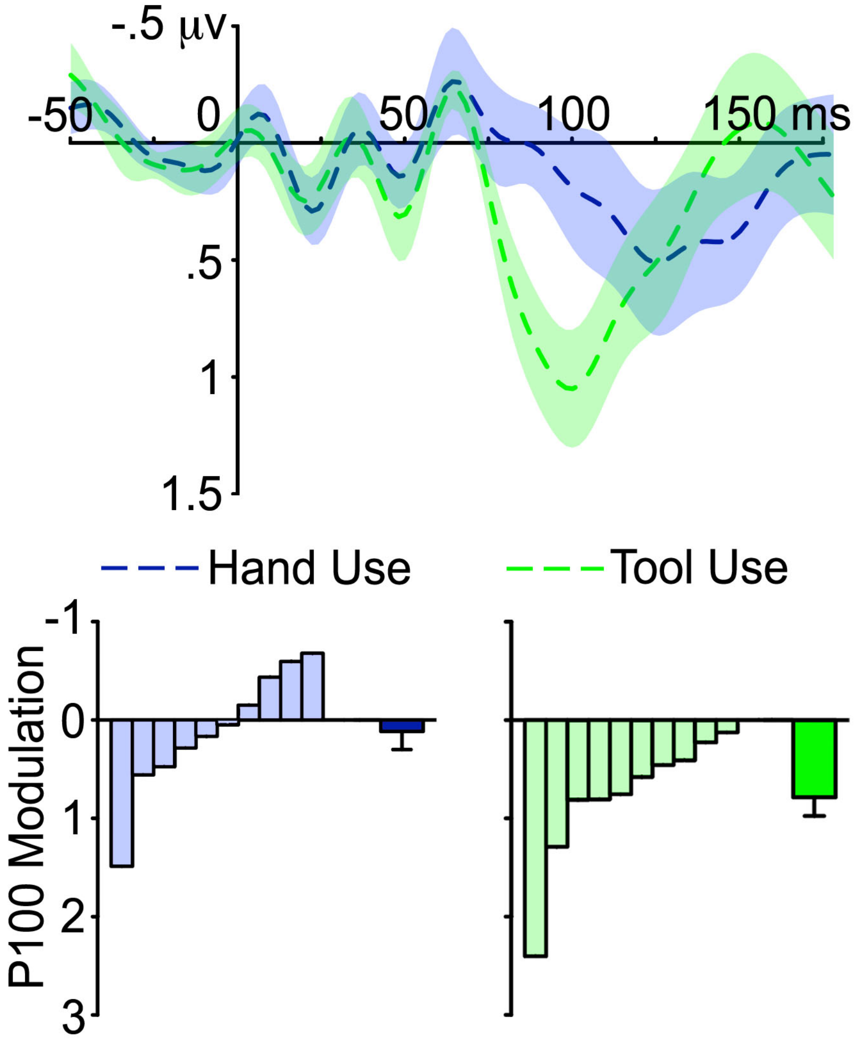

Figure 4.9. Modulation of the P100 for each subject

The upper panel displays the difference wave for tool use (green) and hand use (dark blue). Tool use led to a positive increase in amplitude starting around 70 ms and continuing until around 140 ms. This pattern of results is absent from the hand use condition. The lower panels show the rank-ordered modulation of the P100 for each individual subject. All subjects showed a positive increase in amplitude after using the tool.

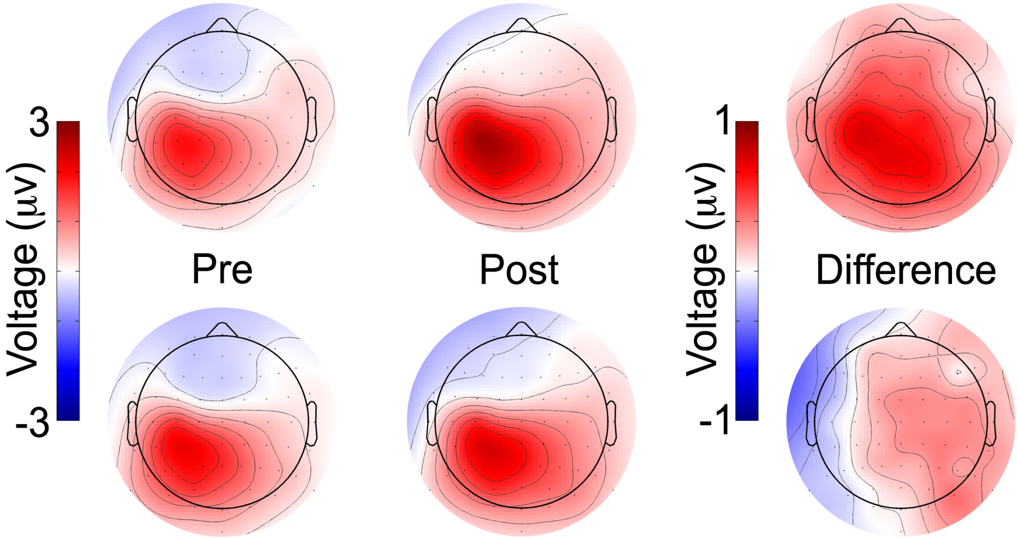

Figure 4.10. Scalp topography of the P100

The present figure shows the scalp topography between 70 to 110 ms post-electric shock—the time window of the P100—before and after tool use (upper panel) and hand use (lower panel). In all conditions, the P100 was greatest around the dorsal centro-parietal and parietal electrode sites contralateral to the electric shock. Using a tool led to a relatively focal increase in amplitude around contralateral somatosensory electrodes.

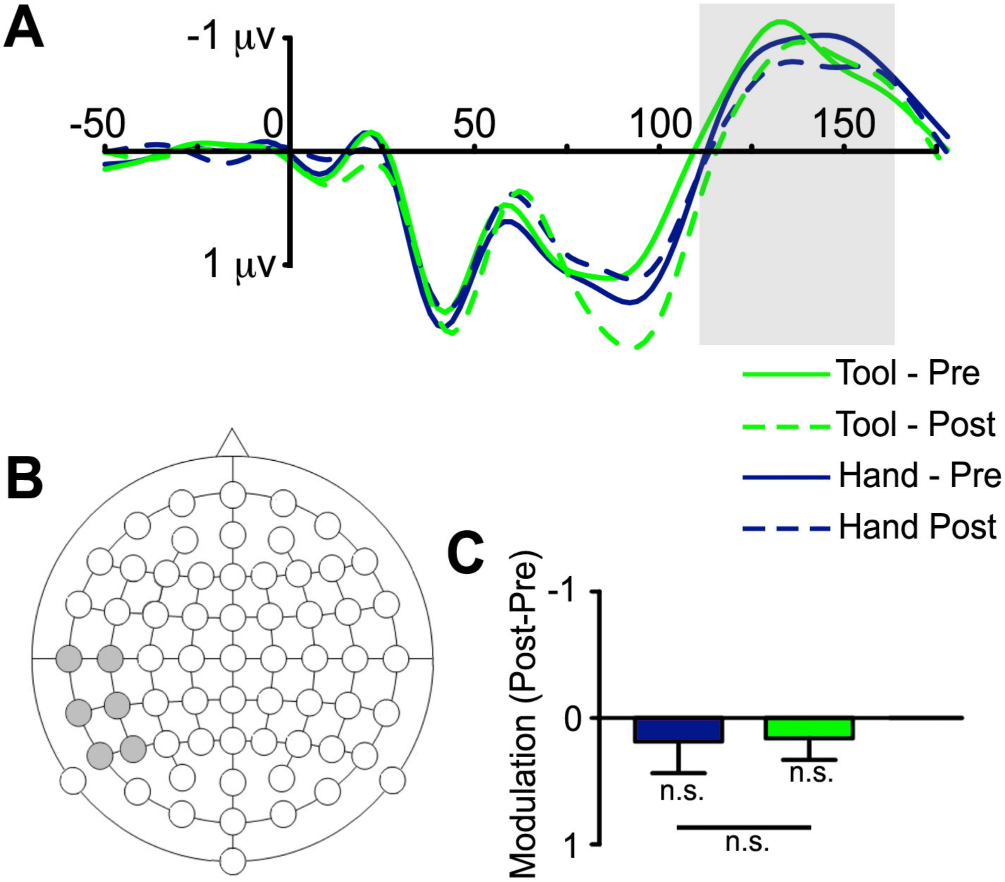

Figure 4.11. Results for the N140 component

A) Grand average SEP waveforms before (solid lines) and after (dashed lines) each object interaction condition: tool use (green) and hand use (dark blue). Note that negative voltage is plotted up. The gray block corresponds to the time window used in our analysis. **B)** The electrodes in the channel layout filled with gray correspond to C5, T7, CP5, TP7, P5, and P7. These channels were where the N140 amplitude was largest. For our analysis, we averaged the SEP of each channel. **C)** Bar plot displaying the average modulation in the N140 amplitude for tool use (green) and hand use (dark blue).

n.s. not significant

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