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Multisensory integration induces body ownership of a handtool, but not any handtool

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ABSTRACT

Bodily boundaries are computed by integrating multisensory bodily signals and can be experimentally manipulated using bodily illusions. Research on tool use demonstrates that tools alter body representations motorically to account for changes in a user's action repertoire. The present experiment sought to unify perceptual and motoric accounts of tool embodiment using a modified Rubber Hand Illusion (RHI) that also addressed the skill and practice aspects of the tool use literature. In Experiment 1, synchronous multisensory stimulation induced perceptual embodiment of a tool, chopsticks. The embodiment of chopsticks was stronger for more skilled participants, and if the illusion was preceded by tool use. In Experiment 2, the illusion was not elicited with a different type of tool, a teacup, showing that not all objects can be incorporated. This experiment helps to clarify the role of perceptual and motoric embodiment and suggests future avenues for research into tools embodiment using this method.

1. Introduction

The representation of the body is remarkably flexible. The brain continuously integrates a complex stream of sensory inputs and uses this information to dynamically scale the representation of the body according to its current state (e.g. Botvinick & Cohen, 1998; Ehrsson, 2012, chap. 43; Tsakiris, 2008, 2010). This flexibility makes it possible to efficiently interact with the environment and is strikingly important during tool use.

Successful tool use expands the physical limits of the wielder's body and facilitates a dramatic increase in action capacity (Shumaker, Walkup, & Beck, 2011; Vaesen, 2012). Experimental research indicates that the flexibility of the body representation contributes to the human tool proficiency. Psychophysical studies demonstrate that the physical expansion afforded by a tool is accompanied by an incorporation of the tool in the body representation, such that the tool is treated as an extension of the limb wielding it (e.g. Cardinali et al., 2009; Maravita, Spence, Kennett, & Driver, 2002).

If tools are treated as an extension of the wielder's body, then might the extended body representation also demonstrate the same ability to plastically adapt to multisensory stimuli? The present work set out to shed light on this issue. In particular, we asked whether the manipulation of multisensory stimuli could induce a recalibration of the extended body representation encompassing both the tool and the effector wielding it. Furthermore, we aimed to examine whether skill and previous experience with a particular

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tool modulate the representational plasticity of the body.

Recent advances in our knowledge of how the brain represents the body have been pioneered through the experimental use of perceptual illusions. One of the most used and best known paradigms is the Rubber Hand Illusion (RHI) (Botvinick & Cohen, 1998). In its classic form, synchronous visuo-tactile stimulation of a rubber hand and the participant's hidden hand induces a recalibration of the proprioceptive felt position of the participants' hand and a feeling ownership of the rubber hand (Botvinick & Cohen, 1998; Costantini, 2014; Tsakiris, 2017; Tsakiris & Haggard, 2005). This has been classically interpreted in the literature as evidence that the manipulation of multisensory inputs (i.e. visual and tactile stimulation), can induce the embodiment of an external, dummy hand into one's own body representation (Blanke, 2012; Ehrsson, 2012, chap. 43), for a different view (David, Fiori, & Aglioti, 2014). Similar experiences of illusory ownership have been obtained, for example, for faces (Tsakiris, 2008), whole bodies (Petkova & Ehrsson, 2008), and even for virtual avatars (Banakou, Groten, & Slater, 2013; Hägni et al., 2008; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008) and small dolls (van der Hoort, Guterstam, & Ehrsson, 2011). Together, these findings show that the multisensory representation of our body is not fixed and immutable, but rather extremely flexible and continuously updated through the integration of multisensory information (for a review, see Costantini, 2014). This scalability of the body representation is also thought to contribute to human tool use proficiency (e.g., Cardinali et al., 2012). When we use tools to manipulate the environment, the brain receives somatosensory signals evoked at the hand wielding the tool. Yet, we often have the subjective feeling that the touch is occurring on the tip of the tool itself. This feeling seems to be a by-product of how the body representation is rescaled to incorporate the tool.

For instance, seminal work with both humans and primates demonstrated that the use of a tool for a prolonged period of time extends the multisensory neural representations of the space surrounding the hand (Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Iriki, Tanaka, & Iwamura, 1996). Similarly, Cardinali et al. showed that tool use can induce a morphological update of the body representation (Cardinali et al., 2009, 2011), and of body kinematics (Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Cardinali et al., 2011, 2012). This modification of the body representation is likely to reflect an incorporation of the tool into the body representation. For instance, a series of studies showed that the tactile signals felt in the hand that occur when a held tool comes into contact with an object are referred directly to the tip of the tool (Maravita et al., 2002; Yamamoto & Kitazawa, 2001; Yamamoto, Moizumi, & Kitazawa, 2005). Moreover, the self-produced touch attenuation phenomena occurs when the participant touches his or her own limb using a tool: self-produced touches are lighter than identical touches applied by another because these touches have already been anticipated by a forward sensory model that takes handheld tools into account (Kilteni & Ehrsson, 2017). In other words, even though the somatosensory signal is originating from the receptors located on the hand, the brain treats this information as if it originated from the tip of the tool.

Overall, previous studies suggest that the brain uses the available sensory information coming from different modalities to infer the structure of a wielded tool and create a unified, extended representation of the body plus the tool. If tools are treated as part of one's own body representation, one could ask to what extent the representation of the embodied tool shares similar properties with the representation of the body itself? In particular, we asked wether manipulating the multisensory stimuli perceived through the tool can induce a recalibration of this extended body representation, as assessed by the Rubber Hand Illusion. In fact, while it is well established that the manipulation of multisensory stimuli (as in the RHI) can induce a recalibration of the body representation, it is still unknown whether this is also true for the extended representation encompassing the embodied tool.

The current experiments investigated this issue. In particular, we hypothesized the importance of three factors for the modified RHI illusion to occur: (a) the type of tool (and in particular, the match or mismatch between the tool's function and the grip exerted to wield the tool) (b) one's level of proficiency in using the tool, and (c) recency of experience with the tool. These points are explained in greater detail in the following sections. To test these hypotheses, we conducted two experiments.

2. Experiment 1

2.1. Introduction

The main purpose of Experiment 1 was to investigate whether multisensory stimulation (i.e. visual and tactile) would induce a recalibration of the felt position of the body plus the tool. We used a modified version of the Rubber Hand Illusion in which the participant and the rubber hand both held a pair of chopsticks. Rather than applying stimulation to the fingers of the real and fake hand, the experimenter brushed the tip of the chopsticks held by the participant and by the rubber hand. Thus, no stimulation was delivered directly to the participant's hand, though the participant was still able to feel the contact between the brush and chopstick. As controls for multisensory stimulation and visual similarity, we manipulated the synchrony of the visuo-tactile stimulation and used a non-hand shaped object (Fig. 1B), respectively. The participant held the tool while viewing the non-hand shaped object (a block of wood with the outline of a hand) during the visual similarity control conditions. We expected participants to experience the illusion only after receiving synchronous stimulation at the tip of the chopsticks held by the rubber hand.

Our choice to use chopsticks was based on several considerations. First, previous studies have already shown that tools like drumsticks (e.g. Yamamoto & Kitazawa, 2001; Yamamoto et al., 2005), and chopsticks (Rademaker, Wu, Bloem, & Sack, 2014) can be incorporated in the body representation. Furthermore, we hypothesized that the functional characteristics of a non-body shaped tool would be crucial for its incorporation, and therefore for the update of the extended body representation in the RHI. This hypothesis is supported by recent evidence showing that the embodiment of tools is constrained not only by the morphology of the tool, but also by its functionality (Miller, Longo, & Saygin, 2014). Though chopsticks violate the morphological similarity between the participant's hand and the viewed object, they are manipulated using a precision grip and they function to extend the fingers in a precision grip



Fig. 1. (A) The rubber hand holding chopsticks used in Experiment 1. (B) The wooden block used in both Experiments 1 and 2. (C) The rubber hand holding the teacup used in Experiment 2.

action (Goldenberg & Iriki, 2007). Thus, chopsticks are morphologically dissimilar, but have a functional match with the human fingers. Past literature has focused primarily on the incorporation of simple hand-held tools, such as sticks (e.g. Maravita, Husain, Clarke, & Driver, 2001; Maravita et al., 2002; Neppi-Mòdona et al., 2007; Yamamoto et al., 2005), rakes (e.g. Bonifazi et al., 2007; Farnè & Làdavas, 2000; Iriki et al., 1996; Jovanov, Clifton, Mazalek, Nitsche, & Welsh, 2015), and mechanical grabbers (e.g. Cardinali et al., 2009, 2011, 2012). The use of these tools rely more on information coming from proximal parts of the hand and arm representation, while chopsticks rely more on finger representation (Rademaker et al., 2014). Thus, although much of the past literature on tool use has focused on larger, reach extending tools like mechanical grabbers, chopsticks seem suitable for use with the RHI paradigm because of the active involvement of the hand and fingers during chopstick use.

A second aim of the experiment was to investigate the role of tool proficiency in the plasticity of the body representation. We hypothesized that the update of the body representation toward the external tool, as indexed by the successful induction of the RHI, would be greater when participants: (a) had recent practice with the tool, and (b) were more skilled in using the tool. Previous studies demonstrate that these two factors (practice and skill) facilitate the embodiment of a tool (e.g., Rademaker et al., 2014). Thus, we predicted that this facilitation would also reflect in the dynamic update of the extended body representation. The choice of chopsticks was particularly conducive to addressing this aim. Chopsticks are one of the most commonly used tools in the world: more than 30% of human population uses chopsticks on a daily basis (Kitamura, Higashi, Masaki, & Kishino, 1999). Despite their global popularity, many people struggle with chopstick use. For instance, in a 2014 chopstick proficiency survey of Americans, 4% of those surveyed considered themselves experts at using chopsticks, 11% rated themselves as very good, 19% fair, 20% not very good, 23% terrible, while 24% stated that they had never even tried them (http://www.statista.com/, 2014). This large variation in chopstick skill within the general population made it easy to test the impact of individual differences in tool skill on tool embodiment. To test the relevance of both skill and recent practice, we designed a task that would both measure the relative tool skill of our participants and provide them with practice manipulating the tool (Bead-Transfer Task, see Methods).

2.2. Methods

2.2.1. Participants

Fifty-seven right-handed individuals (mean age 18.8) participated in exchange for credit in an introductory psychology course at

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the University of Virginia. Twenty-seven participants (17 females) performed the bead-transfer task prior to experiencing the chopstick-version of the rubber hand illusion (CRHI), while the remaining 30 participants (16 females) performed the bead-transfer task after undergoing the illusion. All participants were right-handed, had normal or corrected to normal vision, and provided written informed consent prior to participation in the study.

2.2.2. Materials

2.2.2.1. Chopstick rubber hand. A cast of the first author's hand holding chopsticks was made from flesh-tinted plastic resin. The chopsticks were glued to the hand to minimize chopstick movement during the experimental procedure (Fig. 1A). An identical pair of chopsticks was held by the participant throughout the duration of the experiment.

2.2.2.2. Bead-transfer task. Plastic beads measuring 0.8 cm in diameter were utilized in a task designed to measure participant chopstick proficiency. Participants were given a tray containing 270 beads of various colors and instructed to sort by color as many beads as possible by transferring them to a container with 6 compartments. Each of the six compartments was designated to hold a particular color of bead. There were 30 beads of each color to be sorted, and 90 "distractor beads." Participants were required to move all beads of one color to the container before starting on the next color. Participants were allotted 5 min to transfer as many beads as possible. The number of beads transferred was recorded and used as a proxy value for participant chopstick skill.

2.2.2.3. *Rubber hand illusion questionnaire*. We adapted a total of 25 questions from Longo, Schüür, Kammers, Tsakiris, and Haggard (2008) to measure the subjective experience of the CRHI (See Appendix A). In particular, the questions adopted referred to five different components of the experience of the illusion: embodiment of the rubber hand (ten statements), loss of the real hand (five statements), movement of the real or rubber hand (three statements), deafference of the real hand (three statements), and affect (three statements). All questions were modified to refer to the chopsticks held by the rubber hand, rather than to the rubber hand itself.

2.2.3. Experimental design

A 2 \times 2 \times 2 mixed design was employed. The viewed object (chopstick rubber hand versus piece of wood) and timing of visuotactile stimulation (synchronous versus asynchronous) were within subjects factors. The experimental group (Bead-Transfer Task Prior to the Illusion versus After the Illusion) was the between subjects factor. The 4 within-subjects conditions were: (i) chopstick rubber hand synchronous; (ii) chopstick rubber hand asynchronous; (iii) wooden block synchronous; and (iv) wooden block asynchronous. The piece of wood was a 9 cm \times 23 cm \times 2 cm plain wooden block, pale and beige in color, with the outline of a hand drawn on the surface in black ink (Fig. 1B). This wooden stimulus was comparable in overall size to the chopstick rubber hand.

In the synchronous visuo-tactile stimulation conditions, the experimenter used 2 paintbrushes to manually stroke the tip of the participant's held chopsticks and the viewed object at the same time. In the asynchronous visuo-tactile conditions, the experimenter stroked the participant's chopsticks first, while the viewed object was stroked with a latency of 500–1000 ms. Each stimulation period lasted 180 s and was timed using a stopwatch. During the chopstick rubber hand condition, the tip of the chopsticks held by the rubber hand were stroked, whereas the front edge of the wooden block was stroked during the wooden block condition. Although participants held the tool in all 4 conditions, the chopsticks were not attached to the wooden block, and so were not visible during either of the wooden block conditions. Almost all participants spontaneously reported that they were surprised that they could feel the touch of the paintbrush on the tip of their chopsticks. Indeed, experimenters were instructed to apply enough pressure to the chopsticks that the contact would be felt.

2.2.4. Procedure

Participants were greeted and informed that they would be using chopsticks and making self-perception estimates throughout the duration of the experiment. If participants indicated that they did not know how to hold or use chopsticks, the experimenter demonstrated proper chopstick technique and offered chopstick pointers as the participant briefly practiced manipulating the tool. Depending on group assignment, all participants either first completed the bead-transfer task or proceeded directly to the illusion phase and completed the bead-transfer task upon its conclusion. During the illusion phase, participants were seated across from the experimenter with their right hand placed inside a specially constructed box, measuring 100 cm in width, 40 cm in height, and 20 cm in depth. The box was divided into three compartments of equal size, and the rubber hand rested inside the same distance in front of the subject's midline. The rubber hand and the participant's hand were aligned such that both rested at the same distance in front of the participant's chest. The lateral distance between the tip of the participant's chopsticks and the tip of the constructed by a one-way mirror. The portion of the one-way mirror above the compartment containing the participant's hand was obstructed such that the interior of the compartment could not be seen by the participant at any time during the experiment, and the surface always appeared to be a regular, two-way mirror (Fig. 2).

The lighting in the central compartment containing the chopstick rubber hand was manipulated throughout the experiment. During the visuo-tactile stimulation phases, illumination from within the compartment caused the mirror to be transparent, allowing the participant to view the rubber hand or the wooden block as it was stimulated by the experimenter. During the proprioceptive judgment phase (described below), the surface of the mirror was illuminated from above such that the mirror was opaque and reflective, obscuring the rubber hand from view.

In the proprioceptive judgment phase, the perceived position of the participant's hand and chopsticks was used as an implicit, quantitative proxy for measuring the strength of the illusion. A ruler with the numbers printed in reverse was supported between two

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Fig. 2. The top of Rubber Hand Illusion box was covered by a one-way mirror. A light inside the center portion of the box was illuminated during the illusion phase, allowing the participant to see the rubber hand holding the chopsticks. The portion of the one-way mirror above the compartment containing the participant's hand was obstructed such that the interior of the compartment could not be seen by the participant at any time during the experiment and the surface always appeared to be an ordinary mirror. Two identical paint brushes delivered visuo-tactile stimulation to the tip of the chopsticks throughout the experiment.

poles 45 cm above the box. When illuminated from above, the mirrored surface of the box allowed for the numbers to be reflected in their proper orientation and they appeared at the same gaze depth as the chopstick rubber hand.

At the start of the judgment phase, participants were asked to report verbally the number on the ruler that was directly above the tip of their held chopsticks. They were instructed to make this judgment by projecting a parasagittal line from the tip of their chopsticks up to the ruler. Between each visuo-tactile stimulation and judgment phase, the ruler was always shifted to a different random position such that the numbers the participant viewed during the judgment phases were always different. This ensured that participants did not memorize previously stated numbers and insured that the participant estimated the proprioceptively perceived position of their hand independently during each condition.

Upon completion of each condition (Chopsticks Rubber Hand Synchronous, Chopsticks Rubber Hand Asynchronous, Wooden Block Synchronous, Wooden Block Asynchronous), participants were asked to respond to the Rubber Hand Illusion Questionnaire. A brief rest period followed each questionnaire. During the rest period, the participant was encouraged to set down their chopsticks and move their hand and body to prevent transfer of the illusion across conditions. At the start of each new condition, the experimenter then gently repositioned the participant's hand and chopsticks in the correct position in preparation for the next trial.

2.2.5. Results

2.2.5.1. Proprioceptive drift. Participants made a baseline judgment of the location of the tip of their held chopsticks before each stimulation trial, and another judgment following stimulation. The difference between these two judgments represented the change in perceived hand position due to the stimulation, and was used as a measure of the strength of the illusion. In the literature, this difference value (post-illusion position minus pre-illusion position) is known as proprioceptive drift. A positive proprioceptive drift value indicates that the participant judged the positon of their own hand and chopsticks as closer to the viewed object after stimulation than before. In contrast, a negative proprioceptive drift corresponds to a mislocalization of the participant's hand and chopsticks away from the viewed object.

Assumptions of normal distribution, independence of residuals, and sphericity were met. To examine how proprioceptive drift was influenced by participant hand-object correspondence, visuo-tactile stimulation, tool skill, and recentness of tool use, we ran a mixed ANOVA and fit a linear mixed effects model. In both analyses, viewed object (chopstick rubber hand vs. wooden block) and timing of visuo-tactile stimulation (synchronous vs. asynchronous) were within subject factors, number of beads transferred was a covariate, and experimental group (bead-transfer task Prior to the Illusion versus After the Illusion) was the between group factor. The linear mixed effects model had participant as a random factor, which facilitated the examination of individual differences in RHI susceptibility that are frequently documented throughout the literature.

The ANOVA revealed a significant main effect of viewed object (F(1,53) = 5.74, p < 0.05) and timing of visuo-tactile stimulation (F(1,53) = 8.44, p < 0.01), as well as an interaction between these two conditions (F(1,53) = 9.92, p < 0.01), depicted in Fig. 3. Pairwise comparisons statistics indicate that participants' proprioceptive drift was higher in the chopstick rubber hand synchronous condition (M = 2.68 cm, SD = 3.39) than in the other experimental conditions (Rubber Hand asynchronous: M = 0.03 cm, SD = 2.72; t(55) = 3.47, p < 0.001; Wood synchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.29; t(55) = 3.30, p < 0.001; Wood asynchronous: M = 0.25 cm, SD = 3.30, p < 0.001; Wood asynchronous: M = 0.30 cm, SD = 3.30, p < 0.001; Wood

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Fig. 3. The significant interaction between viewed object and timing of visuo-tactile stimulation (F(1,53) = 9.92, p < 0.01) demonstrates that participants experienced the most proprioceptive drift when they were viewing the chopstick-holding rubber hand and viewing stroking of the rubber hand's chopsticks that was synchronized with the stroking of their own held chopsticks. Error bars represent ± 1 SEM.

M = 0.36 cm, SD = 3.79; t(55) = 3.08, p < 0.001). These findings indicate that the illusion was successfully induced.

There was also a significant main effect of experimental group (F(1,53) = 5.5, p < 0.05), whereby participants who used the chopsticks prior to experiencing the CRHI experienced greater proprioceptive drift—regardless of timing or object—than those who used the chopsticks after the induction of the illusion (Fig. 4). Additionally, there was a significant interaction between timing of visuo-tactile stimulation and chopstick skill: (F(1,53) = 4.09, p < 0.05). In the synchronous visuo-tactile condition only, participants who transferred more beads (and were therefore more skilled chopstick users) experienced more drift than participants who were less skilled in chopstick use (Fig. 5).

The results for the linear mixed effects model with participant as a random factor resulted in comparable findings. Crucially, the interaction between viewed object and visuo-tactile stimulation was significant (Wald Chi-Square(1) = 14.09, p < 0.001), as was the interaction between timing of visuo-tactile stimulation and chopstick skill, (Wald Chi-Square(1) = 5.82, p < 0.05). Additionally, this analysis also revealed two significant three-way interactions. The first was between viewed object, timing of visuo-tactile stimulation, and chopstick skill (Wald Chi-Square(1) = 4.02, p < 0.05). The other three-way interaction was between viewed object, time of tool use, and chopstick skill (Wald Chi-Square(1) = 4.88, p < 0.05). The data for the three-way interactions is summarized in Tables 1 and 2 in Appendix B.

2.2.5.2. Rubber hand illusion questionnaire. The mean ratings for the 5 components of the rubber hand illusion questionnaire (Embodiment, Loss of one's hand, Movement, Affect, and Deafference) were submitted to a mixed ANOVA with the 4 illusion conditions (synchronous and asynchronous chopstick rubber hand vs. synchronous and asynchronous wooden block), and the 5 components of the illusion as within subject factors. Group (tool use prior vs. after the illusion) was the between subjects factor.

The ANOVA revealed significant main effects of questionnaire component (F(1,53) = 80.30, p < 0.001), illusion condition (F



Fig. 4. Participants who used the chopsticks prior to experiencing the CRHI experienced greater proprioceptive drift—regardless of timing or object—than those who used the chopsticks after the induction of the illusion. Error bars represent ± 1 SEM.

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Fig. 5. The significant interaction between timing of visuo-tactile stimulation and chopstick skill (F(1,53) = 4.09, p < 0.05) indicates that when visuo-tactile stimulation is synchronous, participants who transferred more beads (and were therefore more skilled chopstick users) experienced more drift than participants who were less skilled in chopstick use. Shaded bands represent ± 1 SEM.

(1,53) = 16.16, p < 0.001), and group (F(1,53) = 17.87, p < 0.001). The interactions were not significant (all F's < 3.0).

Planned comparisons between illusion conditions revealed a significant difference in responses to items related to Embodiment: (synchronous chopsticks: M = -0.05, SD = 1.45; asynchronous chopsticks: M = -1.21, SD = 1.39; synchronous wooden block: M = -1.17, SD = 1.37; asynchronous wooden block: M = -1.63, SD = 1.14; (F(1,3) = 14.23, p < 0.001). There was also a significant difference in responses to the Movement-related items on the questionnaire: (synchronous chopsticks: M = -0.98, SD = 1.30; asynchronous chopsticks: M = -1.45, SD = 1.31; synchronous wooden block: M = -1.60, SD = 1.06; asynchronous wooden block: M = -1.70, SD = 1.16; (F(1,3) = 3.92, p < 0.01). These results indicate that the synchrony of visuo-tactile stimulation and the visual correspondence between the participant's own hand and the viewed hand were necessary for participants to report embodying the rubber hand and moreover, to endorse items relating to the experience of their hand and the rubber hand moving closer to one another (Fig. 6).

3. Experiment 2

3.1. Introduction

Experiment 2 investigated the role of tool functionality in determining the modification of the body representation. In Experiment 1, multisensory stimulation caused an update of the proprioceptive felt position of the embodied tool toward an external object, but the extent of this representational plasticity is not clear. In Experiment 1, we hypothesized that the match between the tool's function and its manner of manipulation was crucial for the embodiment of the tool and the subsequent recalibration of its proprioceptive felt position following the illusion. Chopsticks mimic and extend the precision grip of the hand holding them. However, the results of Experiment 1 do not rule out the possibility that the observed effect is independent of the type of tool in our modified RHI paradigm. Therefore, Experiment 2 used the same experimental paradigm but the chopsticks were substituted with a teacup to further test the role of tool functionality for the embodiment of the tool and the recalibration of its proprioceptive felt position. Like chopsticks, teacups are simple, hand-held tools that augment manual actions in a non-arbitrary manner (Goldenberg & Iriki, 2007). Teacups mimic cupped hands to hold and transfer liquids, and like chopsticks, they rely primarily on finger prehension for dexterous use, rather than on proximal information coming from the forearm. However, unlike chopsticks, there is a mismatch between the way teacups are held and their function. A precision grip is used to hold a teacup by its handle, but a teacup itself does not imitate or extend a precision action. Rather, a teacup replicates the cupping of a hand and is therefore more similar to whole hand prehension.

3.2. Methods

3.2.1. Participants

Forty-six right-handed individuals (mean age 18.69) participated in exchange for payment or credit in an introductory psychology course at the University of Virginia. Data from 2 participants were excluded due to experimenter error and the data of an additional 5 participants was excluded due to excessive movement of the participant's hand during the illusion procedure. Of the remaining 39 participants, 18 participants (15 females) performed the water-transfer task prior to experiencing the teacup-version of the rubber hand illusion (TRHI), while the remaining 21 participants (17 females) performed the water-transfer task after undergoing the illusion. All participants provided written informed consent prior to participation in the study and were right-handed with normal or



Fig. 6. A comparison of illusions conditions revealed a significant difference in responses to items related to Embodiment and to the Movement-related items on the questionnaire. Differences between the critical, synchronous chopstick condition and the other conditions indicates that the synchrony of visuo-tactile stimulation and the visual correspondence between the participant's own hand were necessary for participants to report embodying the rubber hand and to report experiences of their hand and the rubber hand moving closer to one another. Error bars represent ± 1 SEM.

corrected to normal vision.

3.2.2. Materials

3.2.2.1. Teacup rubber hand. A posable hand-manikin with a realistic silicon skin designed for prosthetic use was positioned to hold a small teacup that measured 17 cm high and 16 cm in diameter (Fig. 1C). An identical teacup was held by the participant throughout the duration of the experiment.

3.2.2.2. Water-transfer task. Participants were required to transfer as much water from one location to another by carrying teacups filled to the brim. The experimenter would start a timer for 3 min as soon as participants lifted the first full teacup off the table. The experimenter would then immediately fill another teacup to the brim with water so that by the time the participant walked the 5.56 m to the dumping point and back, the next teacup was waiting. This process was repeated as many times as possible within the 3-min time limit. Participants were instructed to return to the starting point and start over with a new full teacup if any water was spilled en route. The number of spills as well as the total weight (in grams) of the water the participant transferred was used as a proxy value for participant "teacup skill," analogues to the bead-transfer task used in Experiment 1.

3.2.2.3. Rubber hand illusion questionnaire. The same 25 questions from Longo, Schüür, Kammers, Tsakiris, and Haggard (2009) employed in Experiment 1 were again used to measure the subjective experience of the TRHI. All questions were modified to refer to the teacup held by the rubber hand, rather than to the rubber hand itself. For example, the statements would read "the rubber hand holding the teacup belongs to me," or "I have control over the teacup the rubber hand is holding." As in Experiment 1, participants completed four versions of the questionnaire, one for each experimental condition. Participants answered each statement by choosing a number from a 7-point Likert Scale that ranged from -3 "strongly disagree" to +3 "strongly agree".

3.2.3. Experimental design

As in Experiment 1, a $2 \times 2 \times 2$ mixed design was employed. The viewed object (teacup rubber hand versus piece of wood) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within-subject factors. The experimental group (Water-Transfer Task Prior to the Illusion versus After the Illusion) was the between-subject factor. The four within-subject conditions were: (i) teacup rubber hand synchronous; (ii) teacup rubber hand asynchronous; (iii) wooden block synchronous; and (iv) wooden block asynchronous. The piece of wood was identical to the one used in Experiment 1.

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In the synchronous visuo-tactile stimulation conditions, the experimenter used 2 paintbrushes to manually stroke the forward edge of the participant's held teacup and the viewed object at the same time. In the asynchronous visuo-tactile conditions, the experimenter stroked the participant's teacup first, while the viewed object was stroked with a latency of 500–1.000 ms. During the teacup rubber hand condition, the forward edge of the teacup held by the rubber hand was stroked, whereas the front edge of the wooden block was stroked during the wooden block condition. Again, experimenters were instructed to apply enough pressure to the teacup that participants could feel the contact between the brush and the teacup in their fingers. Each stimulation period lasted 180 s and was timed using a stopwatch.

3.2.4. Procedure

Participants were greeted and informed that they would be using a teacup and making self-perception estimates throughout the duration of the experiment. Based on their group assignment, all participants either first completed the water-transfer task or proceeded directly to the illusion phase, completing the water-transfer task upon its conclusion. During the illusion phase, participants were seated across from the experimenter with their right hand placed inside the same box used in Experiment 1. As in Experiment 1, the rubber hand and the participant's hand were aligned such that both rested at the same distance in front of the participant's chest with a lateral distance between the front of the participant's teacup and the front of the teacup held by the rubber hand set to 27 cm (Lloyd, 2007).

The lighting in the central compartment containing the teacup rubber hand was manipulated in the same manner as in Experiment 1: the lighting within the box during visuo-tactile stimulation phases allowed the participant to view the rubber hand as it was stimulated by the experimenter, whereas the illumination from above during the position judgment phase obscured the rubber hand from view.

The proprioceptively perceived position of the participant's hand was again used as a measure of the strength of the illusion, and the same protocol used in Experiment 1 for the judgment phase was followed. As before, the ruler was always shifted to a different random position between visuo-tactile stimulation phases so that the participant viewed different numbers each time they were asked to verbally report the position that was directly above the front edge of their held teacup. This judgment was made before and after each stimulation trial, so that the difference between the judgments—the proprioceptive drift—reflected the change in perceived hand position due to the stimulation.

3.2.5. Results

3.2.5.1. Proprioceptive drift. Assumptions of normal distribution, independence of residuals, and sphericity were met. We began by examining how proprioceptive drift was influenced by participant hand-object correspondence, the timing of visuo-tactile stimulation, success at the water transfer task, and the recentness of experience with the teacup. To do so, we ran a mixed ANOVA with viewed object (teacup rubber hand vs. wooden block) and timing of visuo-tactile stimulation (synchronous vs. asynchronous) as within subject factors, weight of water transferred as a covariate, and experimental group (water-transfer task Prior to the Illusion) versus After the Illusion) as the between group factor.

The ANOVA revealed no significant main effects of viewed object, timing of visuo-tactile stimulation, recentness of tool use, or amount of water transferred, (all Fs < 1.0). There was also no interaction between the viewed object and timing of visuo-tactile stimulation, (F(1,35) = 0.67), which indicated that the illusion was not experienced by participants as strong enough to induce proprioceptive drift (Fig. 7).

3.2.5.2. Rubber hand illusion questionnaire. The mean ratings for the five components of the rubber hand illusion questionnaire (Embodiment, Loss of one's hand, Movement, Affect, and Deafference) were submitted to a mixed ANOVA with the four illusion conditions (synchronous and asynchronous teacup rubber hand vs. synchronous and asynchronous wooden block), and the five components of the illusion as within-subject factors. Group (tool use prior vs. after the illusion) was the between-subject factor.

The ANOVA revealed significant main effects of questionnaire component (F(1, 35) = 95.59, p < 0.001), illusion condition (F



Fig. 7. No interaction between viewed object and timing of visuo-tactile stimulation, (F(1, 35) = 0.67), indicated that the illusion was not experienced by participants as strong enough to induce proprioceptive drift. Error bars represent ± 1 SEM.



Fig. 8. Comparing illusion conditions indicated that participants endorsed survey statements more positively in the synchronous teacup condition than in the other conditions. Importantly, there was also a significant difference in responses to items related to Embodiment between the synchronous teacup condition and all other conditions, indicating the need for synchrony in visuo-tactile stimulation, as well as correspondence between the viewed object (the teacup rubber hand) and the participant's own hand in order for the participant to experience embodiment of the rubber hand. Error bars represent ± 1 SEM.

(1,35) = 6.96, p < 0.001), and group (*F*(1,35) = 43.04, p < 0.001) (Fig. 8). A comparison of illusion conditions indicated that participants endorsed survey statements more positively in the synchronous teacup condition (M = -0.25, SD = 1.61) than in the other conditions (asynchronous teacup: M = -0.42, SD = 1.63; synchronous wooden block: M = -0.64, SD = 1.60; asynchronous wooden block: -0.81, SD = 1.63). Importantly, planned comparisons between illusion conditions revealed a significant difference in responses to items related to Embodiment: (synchronous teacup: M = -0.68, SD = 1.57; asynchronous teacup: M = -1.23, SD = 1.43; synchronous wooden block: M = -1.63, SD = 1.22; asynchronous wooden block: M = -1.81, SD = 1.121; (*F*(1,3) = 5.19, p < 0.01).

There was also a significant interaction between survey component and group, F(1,35) = 3.26, p < 0.05, such that individuals who used the teacup prior to experiencing the illusion tended to endorse statements regarding the loss of their own hand more positively (M = -0.07, SD = 1.23) than those who used the teacup after experiencing the illusion (M = -1.00, SD = 1.24). Those who used the teacup first also endorsed more statements about affect, suggesting greater enjoyment of the experience (Tool Prior: M = 1.08, SD = 1.36; Tool After: M = 0.55, SD = 1.19). In addition, those who used the teacup before the illusion endorsed more statements about deafference of their own hand during the illusion, agreeing more strongly to sentiments such as the experience of pins and needles in their hand during the illusion (Tool Prior: M = 0.73, SD = 1.36; Tool After: M = -0.35, SD = 1.57).

4. Cross-experiment comparison

In both experiments, we compared participant error in the initial estimates of the position of their hand prior to inducing the illusion. The mean proprioceptive mislocalization prior to the induction of the illusion was -1.3 cm (SD = 4.9) for Chopsticks users in Experiment 1 and -2.97 cm (SD = 4.33) for Teacup users in Experiment 2, and the between-groups mean difference, 1.58 BCa 95% CI [-0.299, 3.446] was not significant (t(97) = 1.65, p = 0.10, two-tailed). The absence of a significant difference suggests that participants in both the chopsticks and in the teacup rubber hand experiments had comparable awareness of the location of their toolholding hand prior to the induction of the illusion.

In order to directly compare the success of the chopsticks and teacup versions of the illusion, the difference between each participant's drift during the synchronous tool condition and the asynchronous tool condition was submitted to an independent samples *t*-test. The difference was found to be statistically significant, t(97) = 3.82, p < 0.001; d = 0.77; 95% CI [0.36, 1.19]. These results indicate that individuals in the chopsticks version of the illusion experienced a larger difference in drift between the synchronous and asynchronous conditions (M = 2.65, SD = 3.55) than did individuals in the teacup version of the illusion (M = -0.03, SD = 3.41).

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Next, we compared the embodiment component of the RHI questionnaire for the synchronous tool condition for the two experiments using an independent samples *t*-test. The difference was found to be statistically significant, t(97) = 2.01, p < 0.05; d = 0.41; 95% CI [0, 0.81]. These results indicate that individuals in the chopsticks version of the illusion experienced a stronger feeling of embodiment (M = -0.05, SD = 1.45) during the synchronous chopsticks condition than did individuals during the synchronous teacup condition (M = -0.68, SD = 1.57).

5. Discussion

The representation of the body is not fixed and immutable, but rather flexible and constantly updated according to the available multisensory inputs. This process of integration is pivotal both for a coherent feeling of body ownership and for the efficient use of tools. When we use a tool, the brain extracts its physical properties through the dynamic combination of multisensory inputs, and incorporates the object into the body representation (e.g. Iriki et al., 1996; Yamamoto & Kitazawa, 2001; Yamamoto et al., 2005). The current study adds to the growing literature on tool use and multisensory body representation by providing evidence that the representation of an embodied tool shows a plastic property similar to that of the body itself.

In the first experiment, we effectively induced the Rubber Hand Illusion (Botvinick & Cohen, 1998) leading to a recalibration of the felt position of an hand held object. Our results suggest that the brain treats the representation of an embodied tool in the same way as the representation of the effector wielding it. In other words, the representation of the tool is not immutable. Results show that when the incoming visual and tactile information is synchronized, the brain will adjust the proprioceptive representation of the handheld object so that it feels closer to the seen object. Also, these data provide evidence that recentness of experience and the level of proficiency with the tool are pivotal factors in modulating the modification of the extended body representation. Participants who used the tool before the illusion and those who were more skilled users experienced significantly stronger proprioceptive drift during the illusion and responded more positively to the self-report questionnaires assessing experiences of embodiment. In Experiment 2, we demonstrated that the illusion was not elicited with a different type of tool. This shows that the plastic adaptability of the body representation has some limits which may depend on the morphology of the tool.

Previous work using the RHI paradigm has demonstrated that the illusion is successful only when the external object resembles an internally stored template of the human body and is placed in an anatomically plausible position (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). For instance, the illusion is not successfully elicited when the rubber hand is replaced with a non-hand-shaped object, such as a wooden block, as reflected by lower proprioceptive drift in this condition (Haans, LJsselsteijn, & de Kort, 2008). This constraint on representational plasticity is functional, as it guarantees coherence in body representation. Without this constraint, coincidental multisensory stimulation might result in the perception of non-corporeal objects as being part of one's own body.

In light of this, and other experiments, the RHI has been explained using a two way model where: a bottom up process compares the temporal structure of the incoming sensory stimuli and a top-down process compares these stimuli with a pre-existing internal representation of one's own body (Tsakiris & Haggard, 2005). Only if both comparisons pass, a feeling of ownership can arise. In the classical RHI illusion paradigm, a rubber hand matches the internal (visual) representation of the body. Tools do not match this template, and yet in Experiment one, the RHI was successfully induced for a hand-held tool. In keeping with this idea, in our experiment participants were looking at a rubber hand holding the chopsticks while holding an identical pair of chopsticks in their own hand. In other words, though the chopsticks alone did not match the internally stored representation of the human hand, the template matching between participants's hand (a hand holding a tool) with the external object (a rubber hand holding a tool) was preserved. Importantly, participants could feel the contact of the brush on their unseen chopsticks, so the congruency between the incoming visual and tactile inputs was also preserved—both were delivered to the chopsticks. Thus, in Experiment 1, both the template matching (top-down process) and congruency of visual and tactile inputs (bottom-up process) were similarly preserved. These two conditions were also preserved in Experiment 2, but the lack of proprioceptive drift and illusory ownership over the teacup-holding rubber hand suggests that not just any object held by a rubber hand can be successfully used to induce the RHI.

Although Experiment 1 demonstrates that the extended body representation can be experimentally modified, there is also evidence that the unique relationship between tools and motoric body representations is also at play, as skilled chopstick users and those with more recent chopstick practice experienced a stronger illusion. This finding is in keeping with past experiments that consistently emphasize the necessity of prolonged practice with the tool for the expansion of one's body representation to include the held tool (e.g. Maravita & Iriki, 2004). For instance, in the paradigmatic Iriki et al. (1996) experiment, the expansion of the visual-receptive fields was observed only after the macaque monkey received weeks of practice with the tool.

However, there is some evidence of tool embodiment and tool-dependent remapping of space, even in the absence of extensive practice with a tool (Berti & Frassinetti, 2000; Maravita et al., 2001). For instance, Naito and Ehrsson (2006) describe a modified version of the tendon vibration illusion (Goodwin, McCloskey, & Matthews, 1972) to investigate the perceptual aspect of hand-object interaction. They found that vibrating the tendon of wrist extensor while participants holding a ball induced the illusory perceived movement of the "hand-object-complex", and that this sensation is mediated by specific parietal mechanisms that seem to link the external object with our own hand when the wielded tool becomes incorporated into the body image (ibidem).

These findings are consistent with our results, which demonstrate that holding the tool while receiving visuo-tactile stimulation is sufficient to elicit the RHI for an external tool, though the illusion is enhanced if experienced immediately following practice with the tool. This result suggests that humans are able to rapidly infer the characteristics of simple tools and incorporate them into the body representation. This interpretation is also supported by previous findings showing that stimuli delivered at the tip of a tool (such as drumsticks), are perceived as occurring at the tip of the tool, even when the tool is occluded from view (Yamamoto & Kitazawa, 2001).

Although tools can be rapidly incorporated, tool practice and skill still play a pivotal role in their embodiment. Tool embodiment

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is stronger after recent use and for participants who are more skilled in using the tool. For instance, Rademaker et al. (2014) provided evidence of a rapid integration of objects held by chopsticks (second-order extension) into the body representation. However, extensive chopstick training over a period of weeks further augmented the level of integration. Moreover, greater chopstick skill was predictive of more rapid integration of the second-order object held by the chopsticks. Our data support and extend these findings by showing that even a short experience using the tool (as the 5-min practice session used in our Experiment) can lead to a stronger modification of the body representation, as suggested by higher proprioceptive drifts and illusion scorings in the CRHI compared to participants who used the chopsticks after the induction of the illusion.

Even so, the null finding in Experiment 2 indicates that the mere categorical membership in the family of 'tools' is not sufficient to allow wielders of all manner of objects to experience a modified RHI. Even though the participants have had a lifetime of experience using teacups effectively and the template matching was conserved in Experiment 2 (participants held a teacup and saw a teacup held by a rubber hand), participants did not experience the illusion. Several factors can account for the difference in results obtained from the two tools used in Experiments 1 and 2.

For instance, the difference might be explained by a different tactile feedback provided by each tool, or whether or not tactile feedback is even expected to occur during tool use.

The two tools might involve a greater or smaller contact with the skin surface and differently involve the passive stimulation of un-myelinated C tactile (CT) fibers. CT are slow conducting fibers that mostly convey information about innocuous and light tactile stimuli, particularly slow stroking (Liljencrantz & Olausson, 2014; Vallbo, Olausson, & Wessberg, 1999) and are only found in the hairy skin (Vallbo et al., 1999; Wessberg & Norrsell, 1993). Thus, this system is particularly important in conveying interoceptive and motivational information usually referred to as pleasant or affective touch.

The activation of CT fibers could be relevant here, because of their role in body ownership. For instance, it has been shown that slow velocity touch on hairy skin produces higher levels of embodiment during the RHI compared with fast, neutral touch (Crucianelli, Metcalf, Fotopoulou, & Jenkinson, 2013). One could argue that the difference observed between chopsticks and teacup could be explained by a differential contact with hairy skin and, thus, greater or lesser involvement of CT fibers. Chopsticks mostly rest on the palmar (glabrous) side of the hand. In particular, the first of the two chopsticks (the closest to the handler), rests approximately on: thenar eminence (over the abductor pollicis muscle, on the palm and only partially the back of the hand) and the third phalanx of the middle and ring finger. The second chopsticks mostly rests on: first, second and third phalanx of the index finger and the third phalanx (the fingertips) of the thumb and the middle finger (Schwarz, 1955) (see Fig. 9A). As for the teacup, the areas of contact with the skin are mostly the third (distal) phalanx of the thumb (palmar side), and the second phalanx of the index, middle and ring finger, both on the dorsal and palmar side of the hand (ibidem) (see Fig. 9B).

In both cases, the median nerve supplies all the areas of the skin in contact with the tool, although the teacup might have a slightly greater contact with hairy skin. Even though this difference looks negligible, it cannot be excluded that the two tools are partially subject to a different neural processing in the central nervous system (that is, discriminative vs emotional touch; e.g. McGlone, Vallbo, Olausson, Loken, & Wessberg, 2007). However, there are reasons to believe that this is not the case. For instance, Lloyd, Gillis, Lewis, and Farrell (2013) tested whether the embodiment of a RH was increased when slow (pleasant) touch was delivered to the back (hairy skin) of a hand (which should result in C-Fibers activation) as compared to the palm (glabrous skin) (which should not result in C-Fibers activation). Their results present a complex picture in which several factors contribute to the illusory experience. In particular, they found that pleasantness of touch and stroking speed moderate the subjective experience of body ownership (assessed by questionnaires) but not the objective measure of the illusion (proprioceptive drift). This measure was instead affected by stroking site, with greater proprioceptive drift and ratings of embodiment when stroking was applied on the back of the hand rather than the palm. According to the authors, this difference may be due to greater spatial resolution on the palm than on the back of the hand. In fact, the palm of the hand contains more bi-modal neurons that encode for both visual and tactile stimuli, which could explain the smaller error (drift) when stimulation is delivered to the palm (ibidem). Therefore, contrary to what we observed, given that the teacup involves a greater contact with the back of the hand, one would expect greater illusion with this tool then with chopsticks. Typically, chopsticks are wielded to manipulate the items on one's plate, whereas teacups are used to transport liquid to the lips. This highlights the functional difference between the two tools: we hypothesize that an important factor in determining whether or not the



Fig. 9. The manner in which participants were instructed to hold (A) the chopsticks, and (B) the teacup. Hashed lines demark where the tool came into contact with the participant's hand, with white lines marking glabrous skin innervated with C-fibers and black lines denoting skin on the surface of the palm. The middle portion of the bottom chopstick held in A also made contact with the participant's ring finger. The tip of the chopsticks rested on the surface of the table. Participants rested their pinky and the blade of their hand on the surface of the table in the teacup condition pictured in B. The bottom of the cup did not come into contact with the table. These positions were chosen in order to match the position of the rubber hands as closely as possible.

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body representation is recalibrated to include the tool is the matching between the function of the tool and the grip exerted to wield the tool itself. In the case of chopsticks, this matching criterion is met: the participant's hand operates the chopsticks using a precision grip. The chopsticks, in turn, afford precision motor actions. This is not the case for teacups. Participants use a precision grip to support the teacup's handle, but the teacup functions not as a precision grabber, but instead like cupped hands.

The importance of tool morphology is not completely novel to research on the plastic features of the body representation. For instance, Miller et al. (2014) highlighted the role of tool morphology in tool embodiment by showing that morphological similarity between the tool and the effector constrains tool-induced representational plasticity. In other words, hand-shaped tools lead to greater modulation of the implicit representation of the hand, whereas arm shaped tools lead to greater modulation of the representation of the arm. Likewise, chopsticks mimic the human precision grip and are wielded with a precision grip, which may facilitate their incorporation. This match is absent from the teacup. However, there are many ways in which chopsticks and teacups differ. Our functional matching account is speculative and in need of further research. Future experiments could address the role of tool functionality on its incorporation in the body representation (and its online update), for instance by systematically manipulating the matching between the grip necessary to operate the tool (such as precision or power grips) and the motor actions afforded by the tool itself.

A relevant question that is difficult to address with the present results regards whether the position of the tool is calculated in an allocentric or egocentric frame of reference. Previous evidence seems to suggest that, following tool use, the relative position of the hand becomes less relevant in respect to the representation of the embodied effector. As stated previously (see introduction), al-though somatosensory sensation necessarily originates from the fingers when touching something with a tool, these tactile signals are processed as if referred directly to the tip of the tool (Yamamoto & Kitazawa, 2001). If this is the case, then one could expect that what is been recalibrated is the coordinates of the tool itself rather than the hand wielding it. In fact, previous studies with the RHI show that the illusion is restricted to the locus of stimulation: only the stimulated finger is perceived to be closer to the rubber hand, but not the neighbouring, unstimulated fingers (Tsakiris & Haggard, 2005). Moreover, following tool use the precision of tool-related reachability judgment improves, whereas the arm representation and its capabilities become less precise (Bourgeois, Farnè, & Coello, 2014; Costantini, Ambrosini, Sinigaglia, & Gallese, 2011). Thus, one could speculate that the proprioceptive drift observed with the chopsticks pertains the coordinate of the tool itself rather than its relative position with the hand. However, literature on this subject is not conclusive. Most likely, the allocentric and egocentric frame of reference are not mutually exclusive, but rather their relative dominance is determined by multiple factors, such as the type of tool and the transformation necessary to use it (e.g., Massen & Sattler, 2010). Future experiments could specifically tackle this question, for instance investigating whether in our modified rubber hand with tool paradigm the representation of the hand is also recalibrated along with the representation of the tool.

To conclude, our results support the idea the body can be extended to objects that do not resemble the human body. In two experiments we showed for the first time, to the extent of our knowledge, that the perceptual binding of visual and tactile information delivered to a hand-held tool can induce an online modification of the internal representation of the tool itself. In particular, this finding is far reaching, as it shows that the body representational plasticity is even more flexible than previously expected and supports the idea that tools are treated as part of one's own body. Moreover, if the representation of our own body is constantly updated and can be modified according to the available multisensory integration, then this is also true for an embodied tool.

In addition, the present experiments shed light on the importance of recent experience and tool skill on the plasticity of the body. Participants who had a chance to practice and those who were more skilled tool users experienced a stronger illusion. Finally, we show that the illusion was not elicited with all tools, suggesting that some properties of the tool may constrain whether or not the body representation is affected by using the tool.

Appendix A. Chopstick version of the rubber hand illusion questionnaire

In the questions below, -3 corresponds to "completely disagree", while +3 corresponds to "completely agree". 0 corresponds to "neither agree nor disagree".

Please answer the following questions about your experience using the scale from -3 to +3.

-3	-2	-1	0	1	2 3
0	0	0	0	0	0 0
0	0	0	0	0	00
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
0	0	0	0	0	0 0
	-3	$\begin{array}{c c} -3 & -2 \\ \hline 0 & 0 \\ 0$	$\begin{array}{c ccccc} -3 & -2 & -1 \\ \hline 0 & 0 & 0 \\ 0 & 0 & 0 \\ \hline 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 &$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

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It seemed like I was unable to move the chopsticks in my hand	0	0	0	0000
It seemed like my hand had disappeared	0	0	0	0000
The touch of the paintbrush on my chopsticks was pleasant	0	0	0	0000
It seemed like my hand was out of control	0	0	0	0000
I found that experience enjoyable	0	0	0	0000
It seemed like I could have moved the chopsticks in my hand if I had wanted	0	0	0	0000
It seemed like my hand was moving toward the rubber hand	0	0	0	0000
It seemed like I was in control of the chopsticks in the rubber hand	0	0	0	0000
It seemed like I couldn't really tell where my hand was	0	0	0	0000
It seemed like the experience of my hands was less vivid than normal	0	0	0	0000
I had the sensation that my hand was numb	0	0	0	0000
It seemed like the touch I felt was caused by the paintbrush touching the chopsticks held by the rubber hand	0	0	0	0000
It seemed like the rubber hand began to resemble my real hand	0	0	0	0000

Appendix B. Tables of descriptive statistics for 3-way interactions

 Table 1

 Descriptive statistics for 3-way interaction of skill, tactile stimulation, and viewed object.

Beads transferred	Tactile stimulation	Viewed object	М	SD
44	Synchronous	Chopstick	2.66	0.66
	-	Wood	-0.59	0.66
	Asynchronous	Chopstick	0.21	0.66
	-	Wood	1.32	0.66
75	Synchronous	Chopstick	2.66	0.45
		Wood	0.40	0.45
	Asynchronous	Chopstick	-0.05	0.45
		Wood	0.25	0.45
106	Synchronous	Chopstick	2.66	0.78
	•	Wood	1.38	0.78
	Asynchronous	Chopstick	-0.30	0.78
	-	Wood	-0.81	0.78

Note. Skill was quantified as the number of beads participants transferred with chopsticks in a 5 min period. The mean number of beads transferred (75) is shown here with ± 1 SD for comparison of drift at different levels of skill, timing of visuo-tactile stimulation, and viewed object.

Table 2

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Descriptive statistics for 3-way interaction of skill, time of tool use, and viewed object.

Beads transferred	Time of tool use	Viewed object	М	SD
44	Tool first	Chopstick	1.27	0.77
		Wood	1.55	0.77
	Tool second	Chopstick	1.57	0.73
		Wood	-0.66	0.73
75	Tool first	Chopstick	1.75	0.52
		Wood	1.00	0.52
	Tool second	Chopstick	0.92	0.50
		Wood	-0.26	0.50
106	Tool first	Chopstick	2.24	0.84
		Wood	0.45	0.84
	Tool second	Chopstick	0.26	0.92
		Wood	0.13	0.92

Note. Skill was quantified as the number of beads participants transferred with chopsticks in a 5 min period. The mean number of beads transferred (75) is shown here with ± 1 SD for comparison of drift at different levels of skill, time of tool use (before or after the illusion), and viewed object.

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