Tools and the Extended Body Representation: Blurred Boundaries between the Models for Perception and Action.

Veronica Uriel Weser
Santa Fe, New Mexico

M.A., University of Virginia, 2015
B.A., Vassar College, 2012

A Dissertation presented to the Graduate Faculty of the University of Virginia
in Candidacy for the Degree of Doctor of Philosophy

Department of Psychology

University of Virginia
May, 2018

Abstract

The embodiment of tools and rubber hands is believed to involve the modification of 2 separate body representations. Tools are embodied motorically in the body schema following tool use, while rubber hands are embodied perceptually in the body image during the rubber hand illusion (RHI). The embodiment of tools is based in action and requires tool use, while the embodiment of rubber hands is based in perception and requires identification with the rubber hand. Although these processes have been investigated separately in the past, there is evidence that some, but not all, tools can alter the body image. This research examines 3 mechanisms that cause tool-use dependent changes to the body image: tool morpho-functional and sensorimotor match, tool expertise, and tool characteristics such as shape and function. Self-reported identification with the rubber hand was largely unaffected by the tool, but tool-use did impact proprioceptive drift, a behavioral measure of the body image. Proprioceptive drift occurred when the tool had morpho-functional and sensorimotor match, suggesting that this factor may be necessary for a tool-version of the RHI to succeed.

Keywords: tools, rubber hand illusion, embodiment, body representation, expertise

Tools and the Extended Body Representation:

Blurred Boundaries between the Models for Perception and Action

Introduction

Two bodies of literature have run in parallel for nearly two decades: tool use and body representation. Both fields employ overlapping terminology and examine the ways in which non-corporeal tools or prosthetics are incorporated into and extend bodily representations. Though there has been some effort to compare the two areas of research from a speculative standpoint, only minimal headway has been made to bridge the literatures experimentally. On one hand, the investigation of human tool use demonstrates that tools are incorporated into at least some form of representation of the user's body. However, researchers who use multisensory bodily illusions like the rubber hand illusion (RHI) (Botvinick and Cohen, 1998) to examine bodily representations have repeatedly shown that the feeling of body-ownership can be extended only to objects that resemble human body parts. Thus research on tools and research using rubber hands stand in direct opposition, with many arguing that rubber hands are *incorporated* into the body, while tools merely *extend* the body.

In an effort to reconcile this division in the literature experimentally, Weser et al. (2017) used a novel RHI paradigm in which both the participant and the rubber hand were equipped with tools. In the classic RHI, simultaneous visuo-tactile stimulation of a rubber hand and the participant's hidden hand induces feelings of ownership of the rubber hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005; Tsakiris, 2016). Importantly, the illusion also results in a change in the felt position of the hand undergoing stimulation known as proprioceptive drift: stronger subjective ownership of the rubber hand coincides with the feeling that the participant's real hand is located closer to the rubber hand. In Weser et al., it was not the rubber hand and the participant's hand that received simultaneous tactile stimulation, but rather the tools held by both. The illusion was successfully induced when the tool in question was a pair of chopsticks, but not when it was a teacup. Moreover, the proprioceptive drift was greater for participants who practiced using chopsticks immediately prior to experiencing the illusion than for those who did not. Remarkably, the proprioceptive drift also increased as a function of chopstick skill, such that those who were highly skilled with chopsticks tended to perceive their hand as even closer to the location of the rubber hand than those who were less skilled.

The sensitivity of the illusion to type of tool, recency of tool use, and even tool skill indicates that the success of the tool-version of the RHI is not so straightforwardly dependent on the match-to-template process thought to underpin the classic version of the illusion. The RHI is typically 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 when both comparisons pass, can a feeling of ownership arise. In the classical RHI illusion paradigm, a rubber hand matches the internal representation of the body and so simultaneous multisensory stimulation leads to its incorporation. In the classic control condition, a wooden block fails the top-down match process and so the illusion does not succeed even though the simultaneous visual-tactile stimulation is applied to both hidden participant hand and seen wooden block.

In Weser et al., participants were looking at a rubber hand holding the tool while holding an identical tool in their own hand. In other words, the template matching between the participant's hand holding a tool and the external object (a rubber hand holding a tool) was preserved, yet the success of the illusion depended on type of tool. If the presence of a hand alone is all that is required for the template match to succeed, then teacup holders and chopstick holders alike should have experienced the illusion. As this was not the case, there must be factors at work other than the top-down template matching and bottom-up multisensory integration investigated in previous work.

Body Representations: On Tools and Rubber Hands

The literature on the effect of tool use on body representations owes its theoretical underpinnings to the ways in which perception of the environment is mediated by one's capacity for action, that is, James Gibson's classic theory of affordances (1986). Affordances are properties of objects that are perceived in relation to an agent's capacity for action. If the environment is perceived in terms of one's ability to act, then objects that are within reach will appear closer than objects beyond reachable space. The use of a tool to expand the area within reach should thereby alter the distance estimates of tool users, since the tool has expanded its wielder's capacity for action. Participants in a series of studies by Witt et al. perceived a target that was within reach as closer when they did have a tool, than the same target when it was beyond reach without the tool. Furthermore, distance estimations are not altered when people hold a tool but never use it to reach (Witt, Proffitt, & Epstein, 2005).

This finding is representative of a large body of literature that suggests tools alter body representations by expanding what researchers have dubbed peripersonal space (Cardinali, Brozzoli, & Farnè, 2009). Peripersonal space is the area that is occupied by the body and represented by the brain using information from proprioception, haptics, and visual information about the position of the body. Peripersonal space is thought to extend beyond the body to include the area reachable by the hand without moving the trunk. The concept of peripersonal space and its mutability in the case of tool use was born from the discovery of bimodal neurons that respond to both somatosensory information at a given body region and to visual information from the space adjacent to it (Maravita & Iriki, 2004).

In a pioneering physiological study, Iriki, Tanaka, and Iwamura discovered the modulation of visuotactile integration at the single-cell level by the active wielding of a long rake. They trained Japanese macaque monkeys in the use of a rake to retrieve food and found that some of the visual receptive fields (vRFs) of bimodal neurons that respond to both somatosensory stimuli at the hand and to visual stimuli near the hand expand to include the distal end of the rake (1996). It has since been demonstrated that vRFs of this class of bimodal neurons encode for the area approximately 20 cm around the corresponding somatosensory receptive fields (sRFs) of the hand (Graziano & Botvinick, 2002). These neurons are known as ‘distal type neurons’ and are distinct from the ‘proximal type neurons’ with vRFs that encode for the area of space that can be reached without bending the torso (peripersonal space). Distal type neurons have sRFs located around the monkey’s shoulder and neck (Maravita & Iriki, 2004). After tool training, the vRFs of proximal type neurons also expand to include the area that the monkey can reach using a tool. Like the Witt et al. experiments described above, the expansion of the vRFs of both proximal and distal type neurons does not occur unless the tool is used in self-initiated, goal-directed behavior (Maravita & Iriki, 2004).

This suggests that at least in monkeys, these bimodal neurons are responsible for combining information from proprioception and vision into a cohesive representation of the body’s position in space (Gaziano & Botvinick, 2002). Single neuron recording studies have shown this egocentrically represented, peripersonal space can be expanded through tool use. When researchers discuss the findings of their work on the modification of the body representation as a result of tool use, it is generally assumed that the mechanism is a modification of peripersonal space.

Researchers who study the concept of ‘embodiment’—the bodily aspects of human subjectivity—also speak of the modification of body representations to include prosthetics like rubber hands. However, the modification of body representations following exposure to a multisensory illusion like the RHI is not thought to relate to changes in peripersonal space. These changes are dependent more on the subjective feeling of body-ownership. People who experience the RHI illusion do not report feeling as though they have 3 hands, but rather that the rubber hand has replaced their hand (Longo et al. 2008). This indicates that the illusion is not expanding the body representation as is thought to happen during tool use, but rather directly incorporating the rubber hand into the body representation by replacing the limb receiving the tactile stimulation. Indeed, skin temperature of the real hand has been shown to decrease during the illusion, but only for participants who report a subjective feeling of ownership of the rubber hand, suggesting that this finding is not simply the result of multisensory integration (Moseley et al., 2008). Since the illusion is abolished when the rubber hand is replaced with a neutral, non-body-shaped object (Taskiris & Haggard, 2005; Tsakiris et al. 2008), multisensory stimulation appears to be necessary but not sufficient for inducing the subjective feeling of ownership of the rubber hand or other body-shaped object. However, the results of Weser et al. leave open the possibility that in the case of a tool-version of the rubber hand illusion, a match between tools is all that is required. In other words, given that the tactile stimulation is applied to the tool and not to the hand, the presence or absence of a hand holding the tool may be optional. Study 1 addresses this supposition by comparing the success of the illusion when participants view an amorphous blob-like structure holding a pair of chopsticks to the same rubber hand holding chopsticks used in Weser et al. (2017).

The success of the traditional RHI is contingent on the visual similarity, postural congruency, body part identity and laterality of the seen object and the body part receiving tactile stimulation (e.g. Haans, IJsselsteijn, & de Kort, 2008; Costantini & Haggard, 2007; Holms, Snijders & Spence, 2006). Tsakiris and Haggard have proposed that body ownership arises due to the modification of an abstract body representation that persists through time and contains a reference description of the visual, anatomical, and postural properties of the body (De Preester & Tsakiris, 2009). This body representation would appear to be the polar opposite of the ever-changing representation of the body's position in space that is easily modified to include a handheld tool. The two body representations at the heart of each of the literatures on tool use and multisensory illusions of body ownership (e.g. RHI) have become intimately tied to the two aspects of the dyadic model of body representation proposed in the seminal neurophysiological work of Head and Holmes (1911): the body schema—a representation for action, and the body image—a representation for perception.

The dissociation between body schema and body image is supported by neurophysiological work demonstrating a double-dissociation of impairment reported by Anema et al. (2009): two stroke patients suffering from left parietal lesions were asked to localize tactile stimuli delivered to their unseen contralesional hand either by pointing with their other hand directly to the spot where they had been stimulated or by pointing to the spot on an illustration of a hand. The first task is thought to tap the body schema—the representation for action—since it relies on the unconscious and online integration of tactile information with proprioceptive information. The second task is thought to require access to the body image—the representation for perception—because it requires that the felt touch be consciously integrated with a stored representation of the hand's visual features in order to match the tactile stimulus to the visual representation of a human hand. One of the stroke patients was impaired in the first task, but not the second, and the other patient displayed the opposite pattern.

Comparing and contrasting RHI illusion and tool use work provides further support for a division between body representations for action and perception. Even though participants report feeling as if the rubber hand has become a part of their body, the reaching actions of participants who experience proprioceptive drift following the RHI remain accurate (Kammers et al., 2009). In other words, even though they report feeling as though their hand is located closer to the rubber hand, they can still accurately reach and grasp an object with the hand that was supposedly replaced by the rubber hand during the illusion. This suggests that the RHI is only modifying the perceptual representation of the body, as movements executed by the replaced hand are still accurate. This finding can be directly contrasted with work on tool use paradigms that demonstrate using tools will alter the kinematics of reach to grasp movements (Cardinali et al., 2011, 2012).

Moreover, tools have a similar null effect on the perceptual body image representation. Cardinali et al. (2011) demonstrated that the use of a reach-extending tool increases participants' indirect length estimates of their forearms, but only when the body schema was accessed to provide the estimates. In this study, participants used a 40 cm mechanical grabbing device to reach for, grasp, lift up, and replace an object. Participants then localized one of three positions on their arm (the tip of the index finger, the wrist or the elbow) by naming the position on a scale that represented the length of the arm in response to a cue from an experimenter that was either delivered verbally (by naming either finger, wrist, or elbow) or through direct tactile stimulation of the body part. The tool-using arm was kept out of the participant's sight behind a barrier throughout the experiment. Cardinali found that after tool use, participants overestimated the distance between their wrist and elbow if the body part was *touched* but not *named*. In contrast, localizing named body parts was not affected by tool use, suggesting that using a tool may change the relationship between sRFs and vRFs, (i.e. the peripersonal space, the body representation for action; the body schema) but not necessarily a more abstract understanding of the relative location of body parts contained in the body image (Cardinali et al. 2011).

Weser et al. provided the first empirical exploration of whether it was possible to update the body's perceptual representation to include a hand-held tool using the multisensory stimulation typical of body ownership research rather than tool use research. They found evidence that chopsticks were integrated into the perceptual representation of the body. Participants held a pair of chopsticks, viewed a rubber hand with chopsticks, and received tactile stimulation at the tips of their chopsticks. Identical stimulation on the rubber hand's chopsticks caused participants to report that their hand felt like it was closer to the rubber hand. Interestingly, motor experience using the tool impacted the amount of proprioceptive drift that the participants experienced, suggesting a role of the action-mediating body representation as well. In Weser et al.'s investigation, participants who used the chopsticks immediately prior to undergoing the illusion procedure experienced higher proprioceptive drift than those who were not given the chance to use the chopsticks productively. Practice using a tool to achieve a productive end is frequently cited in the tool use literature as a necessary component for a modification of peripersonal space, the body representation, or the body schema to occur (Witt, Proffitt, & Epstein, 2005; Maravata & Iriki, 2004). Brown et al. demonstrated that the adaptation of the motor system, as opposed to visual familiarity with the tool, is necessary for changes in peripersonal space to take place. Active training participants completed a task with a reach-extending tool that had novel mass distribution while passive holding participants used the same tool while both the weight of the tool and the participant's arm were entirely supported in a mechanical device. The active training participants were much quicker at detecting targets that appeared near the tip of the tool than were passive training participants. This suggests that when divorced from motor control, the visual experience of tool-wielding is not enough to induce tool-related spatial adaptation (Brown et al., 2011). Moreover, Costantini et al. demonstrated that observing tool actions extends the representation of reachable space, but only when the observer is also holding the tool (2011). This suggests that the facilatory effect of tool use prior to the illusion relies on both the motor experience of holding the tool and the visual experience of seeing the tool in action. To disentangle the contributions of visual and motor tool experience, Study 2 compares the strength of the chopstick version of the RHI for participants who either watched an experimenter use chopsticks prior to undergoing the illusion, watched and held chopsticks, or merely held chopsticks without using them.

The facilitatory effect of tool use prior to the illusion is in keeping with the literature that examines action-specific body representations. However, this finding is also at odds with the majority of the literature demonstrating a strict separation between body image and schema, representations for perception and action. Since the work by Weser et al. represents a first attempt at documenting an interaction between the two body representations in the case of multisensory interaction with tools, it is imperative to discover the necessary conditions and constraining factors of the tool version of the RHI. Therefore, the remainder of this introduction is devoted to a careful analysis of the possible mechanisms behind the success of the chopstick version and the failure of the teacup version of the RHI. Along with the description of each mechanism, justifications for the additional studies conducted to test these mechanisms are provided. As the terminology used in the tool use and multisensory illusions of prosthetic embodiment literatures are not consistent, the more general term “body representation” will be used throughout the remainder of the paper.

Tool Morpho-functional and Sensorimotor Match

In Weser et al. (2017) chopsticks and teacup were selected as comparison tools because they have different degrees of “morpho-functional match” and identical sensorimotor match (Cardinali et al. 2016). Morpho-functional refers to the output of the tool: its shape and the action it affords. Sensorimotor refers to the input provided to the tool: the motor actions of the wielder and the actions the tool affords. Tools can match on one or both dimensions. The match (or lack thereof) between tool morphology and arm movement/grasp mechanics is thought to play a deterministic role in whether or not the use of a tool will cause a modulation of the wielder’s body representation (Cardinali et al. 2016; Miller, Longo, & Saygin, 2014). Broadly speaking, tools that extend one’s reach (such as mechanical grabbers) influence the wielder's representation of the length of his or her arm, but not the size of his or her hand (Cardinali et al., 2009, Miller, Longo, & Saygin, 2014). In contrast, tools that expand the grasp of the hand but not the length of the wielder’s reach specifically alter the implicit representation of the size of the hand, but not the length of the arm (Miller, Longo, & Saygin, 2014). This finding demonstrates that tools specifically alter the representation of the body part that they are functionally augmenting, but does not speak to whether or not small hand-held tools also alter the representation of the hand in a manner specific to the grip used to wield the tool (i.e. precision vs. power grips). In other words, morpho-functional match has a clear impact on the effect of a tool on one’s body representation, but sensorimotor match between the type of grip used to manipulate the tool and the type of action the tool affords must be investigated by comparing small handheld tools wielded with varying grips.

While the difference between reach-lengthening and grip-widening tools and how they affect body representations may seem obvious, finer-grained comparisons are needed to assess whether it is the shape of the tool or the grip used to wield the tool that has the greater impact on the body representation. Cardinali et al. (2016) found that sticks attached to the thumb and index finger and pliers both cause an increase in the represented length of the wielder's fingers. However, the pliers caused a global increase in finger length while the two sticks specifically lengthened the representation of the wielder's thumb and index finger. Thus Cardinali et al. concluded that the power grip aspect of using the pliers caused the representation of the hand to shift to one where only the fingers as a unit moving in opposition to the thumb (similar to the two prongs of the pliers) were relevant. However, when using the sticks, the middle, ring and pinkie finger remained separable from the index finger as the two digits moved alone in a precision grip action. Even though both tools offered a precision grip action, the level of morpho-functional and sensorimotor match between the tools differed.

For example, if the tool is held with a precision grip hand position and the function of the tool is to act on the environment in a precision manner, the tool is said to match at the morpho-functional and sensorimotor level. Chopsticks match, as they are used with a precision grip of the thumb and index finger and serve to pick up objects using a precision action. The teacup in Weser et al. was similarly held by the handle with a precision grip, but the function of a teacup is not a precision action but rather an extension of the whole hand cupping action used to transport liquids. Chopsticks possess a morpho-functional match, but teacups do not. Therefore, while

Cardinali et al. (2016) examined a morpho-functional match between tools (both offered a precision function) Weser et al. investigated a sensorimotor match (both tools were wielded with a precision grip). This difference presents a promising avenue for investigation of the role morpho-functional and sensorimotor match plays in the extension or incorporation of tools into body representations as measured by proprioceptive drift in tool versions of the RHI.

Studies 3 and 4 expand on this premise by using the tool-version of the RHI to compare two tools that differ in their morpho-functional match and a sensorimotor mismatch, as in Cardinali et al. (2016). For example, pliers and tweezers are both precision tools, but pliers are used with a whole-hand power grip while tweezers are wielded with only the thumb and index finger in a precision grip. If tool morpho-functional and sensorimotor match is a constraining factor on whether or not the tool-version of the RHI succeeds, then there should be a difference between these two tools. The tweezers (Study 5) should result in high proprioceptive drift following the illusion while the proprioceptive drift in the case of the pliers (Study 4) will not significantly differ from zero. This finding would bring a new level of nuance to the literature on the effects of tools on body representation, as it would indicate an advantage for morpho-functional and sensorimotor match when it comes to altering the proprioceptive information about the location of a tool and the hand wielding it. It would suggest that though a match is not necessary for a modification of the hand representation to occur (see Cardinali et al. 2016), it is required for an update to be made to the model of the body’s location in space following simultaneous multisensory stimulation. This would indicate that, as in the classic RHI, match allows for more than just the extension of the body to include the tool, but perhaps also the incorporation of the tool into the body.

General Tool Morphology

When using a tool to touch objects in the environment, one subjectively feels the stimulation at the tip of the tool, even though the mechanoreceptors that process the tactile information are located in the hand (Gibson 1966; Head and Holms, 1911). Yamamoto and Kitazawa (2001b) elegantly demonstrated that tactile stimulation at the tips of tools is not perceived at the hands, but rather at the tool-tip by delivering tactile stimuli to an unseen pair of drumsticks (one held in each hand) and asking the wielder to judge the temporal order of the stimulation. Participants were accurate when their arms and drumsticks were uncrossed, but reversed the order after either crossing the arms or crossing the sticks (see Figure 1). This mirrors the tendency for temporal order judgements to reverse when delivered directly to crossed hands (Yamamoto & Kitazawa, 2001a). The authors suggest that this occurs because the tactile stimulation of unseen hands and tools stimulate bimodal neurons that have cutaneous receptive fields located on the hands, but organized cortically in spatial coordinates (Yamamoto & Kitazawa 2001a). Crossing tools or hands therefore requires a dynamic remapping of cutaneous inputs, and when taps are delivered in quick succession (< 300 ms intervals) as they were in this study, there is not enough time to accurately remap the spatial coordinates. Thus the default assumption that a stimulus detected in one spatial area originated from the hand or tool on the same side operates. Using this paradigm, temporal order judgements are restored when participants cross both their arms and the shafts of their drumsticks (Yamamoto & Kitazawa, 2001b). Although the double crossing of arms and tools removes the tool-tip from alignment with the hand, it restores the tool-tip to the same brain hemisphere where processing takes place. This means that somatosensory signals evoked in the hands are referred to the spatial location of the stimulation—at the tip of the tool—prior to the cutaneous signals becoming time-ordered. If tactile stimuli were perceived exclusively at the hands, then subjective temporal order would not be altered by the configuration of the sticks (Yamamoto & Kitazawa, 2001b).

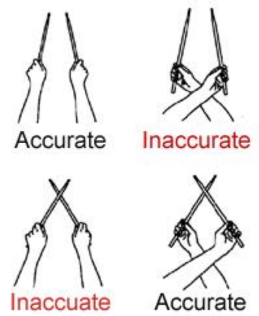

Figure 1 Temporal order judgement accuracy as a function of tool and arm position. (Adapted from Yamamoto & Kitazawa, 2001b)

The external stimulation of tools is perceived based on the stretching, compressing, twisting and bending of muscles and tendons in response to the stimulation of the tool. This kind of stimulation may increase with torque, such that contact with long slender objects like chopsticks stimulates mechanoreceptors more than contact with compact tools with handles, like teacups. The fact that the literature on tool use primarily focuses on long, slender tools and sticks may be reflective of this aspect of tool morphology. Very few investigations of tool effects on body representations have examined small tools with handles, like teacups. The tool-version of the RHI illusion might therefore succeed with chopsticks but not with teacups for the simple reason that the multisensory stimulation is easier to perceive when it is applied to an object with more torque, like a long slender chopstick. One way to check this potential confound is to investigate whether proprioceptive drift in the illusion increases as a function of the length and shape of the tool used. If long, spindly chopsticks (Studies 1, 2, 6, and 7) result in a stronger illusion than very short tweezers (Study 4), then the length of the tool may be important to its success in the illusion.

Another, perhaps more interesting, potential contribution to the success of the illusion lies in the important link between tool morphology and tool function. It is quite often the case that tactile stimulation is expected to occur at the tips of long slender objects: the canes used by the blind inform the wielder of an object in their path when the tip of the tool comes into contact with the obstacle. If the illusion does not succeed when an item not necessarily associated with any particular task is held by both a participant and a rubber hand, then it suggests that a functional match between the item and the type of stimulation applied to it is necessary for the illusion to succeed. Study 5 examines this proposal by conducting the tool-version of the RHI when a wooden block is held by both participant and rubber hand. The wooden block provides an interesting test case because it is classically used as the non-corporeal control condition in a classic RHI study. Therefore, it pits the significance of the presence of a rubber hand holding the item against the functionality of the item as a tool. Though wooden blocks can certainly be used as tools, it is unlikely that the type of tool interaction conducted with a wooden block would result in the delicate tactile stimulation at the forward edge of the block as is used in the illusion. This stands in direct contrast with chopsticks, where the tactile stimulation applied to the tip of the tool during the illusion is a close match for the pattern of use associated with chopsticks.

Chopsticks are intentionally placed in contact with food at their tips by the wielder, who intends to use tactile feedback referred to the tips of the chopsticks in order to lift the food up to his or her mouth. Except in the case of making a toast, teacups are not used to make contact with external objects in the same manner as chopsticks or other long objects used in tool studies. Perhaps the application of the tactile stimulus at the edge of the teacup in Weser et al. is the problematic element. Whereas stimulation at the tip of a chopstick is expected and provides information that is useful for wielding chopsticks, stimulation on the edge of a teacup is not a typical part of teacup use and may therefore not produce the same modification of the user's body representation. This line of reasoning suggests that the teacup version of the RHI might succeed if the tactile stimulation is delivered in a manner that matches the function of tool.

Indeed, an adaptation of the crossmodal congruency task to include a tool provides evidence to suggest that only the task-relevant portion of a tool alters the body representation. In a crossmodal congruency task, participants receive vibrotactile stimulation on the thumb or index finger of either hand in concert with a visual distracter stimulus that can appear near any of the vibrotactile stimulators on either hand. The presentation of visual stimuli at a location incongruous with the vibrotactile stimulation caused a delay in the participant's judgment of the source of the stimulation (thumb or index finger), with the greatest delays occurring when the visual distracter and the vibrotactile stimulation are presented on the same side of the body but at different locations on the hand. This trend reverses in a crossed arms posture: with the visual distracter on the left, closer to the crossed right hand, the temporal order judgment delays are greatest when either left sided visual stimuli is activated in concert with vibrotactile stimulation to the right hand at either site (Maravata & Iriki, 2004). Holmes, Calvert and Spence (2004) used a crossmodal congruency task with distracter visual stimuli located at three points along a tool held in each hand: one at each tool tip, one in the middle of each tool's shaft, and one near the thumb of each hand. To manipulate the established effect of tool-use practice on the congruency task, they interleaved their vibrotactile and visual interference trials with active tool use trials in which participants had to press a button using either the proximal end of the tool (located at the handle), the distal end of the tool (at the tip) or the shaft of the tool (a nail sticking up in the center of the tool's shaft). The visuotactile interference was dependent on the part of the tool being used during the tool-use trials: while the interference was always greatest when the visual stimuli were presented on the same side as the vibrotactile stimulation, visual distracters at the tip of the tool were not detrimental when the handle of the tool was being used to press the button, and the reverse was also true. No effect was found for visual interference at the shaft; this suggests participants only attended to the part of the tool relevant to their task, and that at least for lengthy, reach-extending tools, it is difficult to make the middle portion of the tool task-relevant (Holmes, Calvert, & Spence, 2004). By analogy to this line of research, Study 6 examines whether the functional or the structural aspect of the tool has the strongest influence on the illusion by comparing stimulation of the middle of the chopsticks to stimulation of the tips. If the illusion succeeds when the middle of the chopstick is stimulated, it suggests that the overall structure of the tool plays an important role in the success of the illusion.

Expertise

In Weser et al. (2017) an advantage was found for skilled chopstick users over unskilled users. Chopstick skill was measured by having participants use chopsticks to sort by color as many small plastic beads as possible into separate containers. The number of beads transferred in a 5-minute period was used as a proxy for chopstick skill. Weser et al. found that the more beads a participant transferred, the greater his or her proprioceptive drift in response to synchronous visuo-tactile stimulation. Greater chopstick skill is likely accompanied by increased sensitivity to tactile stimulation at the tips of the chopsticks. Indeed, more sensitivity would allow for the more skillful manipulation of beads using the chopsticks, as slippage of the bead could be accurately detected and adjusted for prior to the dropping of the bead. Greater sensitivity likely leads to increased “transparency” of the tool: when a tool is used extensively such that its properties are so fully understood that the user comes to think of the tool as a functional extension of his own body, the use of the tool is said to be "transparent" (Clark, 2003).

This line of reasoning is consistent with reports by expert tool users (such as musicians with bows and drumsticks or athletes who use rackets, clubs, etc.) of a subjective feeling of completion or wholeness when using the tools of their trade. Indeed, expert but not novice tennis players agree with the statement "the [tennis] racket is an extension of my hand," and that they can readily invoke clear, vivid kinesthetic imagery of playing tennis (Forkas et al., 2008; p. 2386). Furthermore, following the application of transcranial magnetic stimulation (TMS) over the left motor cortex, the corticospinal excitability of the muscles of the hand and forearm during the mental rehearsal of a tennis forehand differed from that measured during the mental practice of a ping-pong forehand for expert tennis players but not for novices. Similarly, badminton players have an increased cortical excitability when imagining executing a badminton-specific gesture with a badminton racket as opposed to a tennis racket (Wang et al., 2014). This convergence of neurophysiological and self-report data indicates a strong contribution of very particular long-term experience in the modulation of sensorimotor body representations.

This specificity of expert tennis player muscle activation for imagined tennis forehand as opposed to ping-pong forehand practice also speaks to why in Weser et al. (2017) chopstick skill facilitated proprioceptive drift and teacup skill (as measured with an equivalent water transfer task) did not. One could argue that surely all participants were expert teacup users given the numerous teacup use occasions they must have had throughout their lives. Even so, consider that teacups come in all shapes and sizes—from the tiny espresso cup used in Weser et al. to tea and coffee mugs, not to mention the vast array of handle sizes and shapes. In contrast, chopsticks are practical only when their dimensions fall within a particular, highly constrained range of lengths and widths.

The exact shape and dimensions of a tool may be of greater importance than researchers had previously imagined. When asked to discuss using a tennis racket that does not belong to him, expert tennis player Andre Agassi said it feels like "playing with a broomstick….as if I am playing left-handed, as if I've suffered a brain injury. Everything is slightly off" (Agassi, 2009; as cited in Biggio, et al. 2017). In a study of this phenomena, Biggio et al. (2017) found that expert tennis players are faster at perceiving a multisensory stimulus delivered to the tip of *their own personal tennis racket* as compared to a racket belonging to another player. This suggests that experienced athletes are sensitive to minute differences between the tools of their trade and are better able to incorporate into their peripersonal space the tool they have spent hours using (2017). Consider that in Japan, family members each have a designated pair of chopsticks that they use consistently at every meal. Japanese people believe that the essence of a person is transferred to their chopsticks and feel that using a utensil favored by another would contaminate it. This suggests that at least for Japanese chopsticks users, the effect in Weser et al. may have been even stronger if participants viewed the rubber hand holding their own, personal chopsticks.

Returning to Weser et al. and teacups vs. chopsticks, the differences in acceptable teacup grips as opposed to chopstick grips are also noteworthy: teacups can be held by the handle (or not), in a whole-hand power grip or a thumb and index finger opposition grip. They can be held from the top, bottom or side. Chopsticks on the other hand require a particular thumb and finger opposition grip to manipulate the top chopstick so that it can open and close against a stationary bottom chopstick. While the exact grip used to manipulate chopsticks may vary slightly among users, it is overall far more consistent than the teacup grip.

Study 7 examines the importance of tool grip on the success of the illusion by requiring participants to hold a pair of chopsticks in a novel configuration throughout the duration of the experiment. By inserting chopsticks between the fingers of a fist, one chopsticks between the knuckles of the index and middle fingers and the second chopstick between the middle and ring finger knuckles, the surface area of the fingers in contact with the tool is largely conserved, yet the grip is radically altered to the point where the tool is unusable. If the illusion fails to produce proprioceptive drift in this condition, it suggests that the configuration of the tool in the rubber hand has to match the function of the tool and the manner in which the user has experience wielding it. It may also imply that the teacup version of the illusion might succeed if a different teacup grip were to be employed.

Experts often report that their specialized tools feel like a part of their body. Frequently, this anecdote has driven the design of studies on tool effects on body representation, and yet rarely are experts used as participants (see Fourkas et al. 2008, Wang et al. 2009, and Biggio et al. 2017, for exceptions). In general, true expertise in tool use is rarely examined in the literature. Instead, novel tools and lengthy training procedures are often used to control for baseline differences in tool skill level (e.g. Farne & Ladavas, 2000; Maravita et al., 2002; Holmes, Calvert & Spence, 2004; Maravita & Iriki, 2004; Cardinali et al., 2009). This bias towards unpractical tools may contribute to the evidence against the incorporation of tools into participants' subjective reports. Weser et al. can serve as a model for future work on tool use to examine individual differences in tool skill as a variable of interest.

Previous research indicates that rubber hands are *incorporated* into the body, while tools merely *extend* the body. These two lines of research have run in parallel, each suggesting that tools and rubber hands operate on different body models: rubber hands replace real hands and alter the body image, while tools extend the affordances of the wielder and affect the body schema. The body image is thought to be a long-term model of the body shape and identity that is slow to update and available to conscious access. In contrast, the body schema changes rapidly to reflect the current state of the body and is updated unconsciously in real time. The body image has been dubbed the representation for perception, while the body schema is thought to be the representation for action.

Although it is clear that tool use changes a wielder's action capacity and therefore his body schema, there may be some conditions under which tools can also be experienced as an incorporated part of the body, perhaps reflecting a change to the body image. Weser et al. demonstrated that in some circumstances, a tool version of the RHI can be used to assess the effect a tool can have on *both* the body image and the body schema. However, not all tools are able to alter both body representations. The following 7 studies present three factors that may determine whether or not a tool-version of the RHI will be experienced by a participant: tool-grip morpho-functional and sensorimotor match (Studies 3 and 4), tool specific features such as shape and size (Studies 1, 5 and 6), and finally the wielder's tool expertise (Studies 2 and 7).

Study 1: Chopsticks with Non-hand

For a participant to experience the classic RHI, there must be visual similarity, postural congruency, body part identity and consistent laterality of the seen object and the body part receiving tactile stimulation (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005; Holms, Snijders & Spence, 2006). The classic illusion is abolished when the rubber hand is replaced with a neutral, non-body-shaped object (Haans, IJsselsteijn, & de Kort, 2008; Tsakiris et al. 2008). The extent to which the tool-version of the illusion requires the presence of a hand is unknown. Since only the tool receives tactile stimulation, a match between tools may be all that is required. **Study 1** addresses this supposition by comparing the success of the illusion when participants view an amorphous blob-like structure (Figure 2) holding a pair of chopsticks to the same rubber hand holding chopsticks used in Weser et al. (2017).

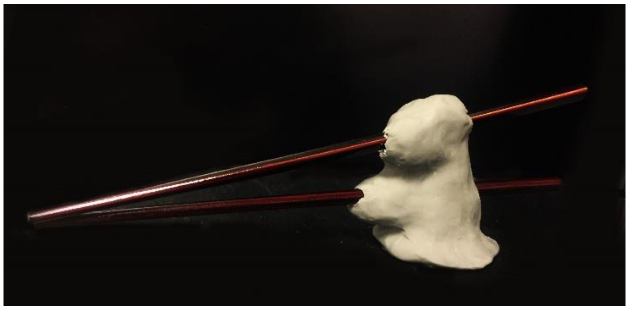

Figure 2. The amorphous, “chopstick-holding blob” created to hold chopsticks with proper form without resembling a hand or fingers

Methods

Participants

Forty-nine right-handed individuals (24 females; mean age 18.8) participated in exchange for credit in an introductory psychology course at the University of Virginia. All participants had normal or corrected to normal vision and provided written informed consent prior to participation in the study.

Materials

Chopstick Rubber Hand. The same rubber hand as was used in Weser et al. 2017: A cast of author VW’s hand holding chopsticks made from flesh-tinted plastic resin. The chopsticks were glued to the hand to minimize chopstick movement during the experimental procedure (**Figure 3**). An identical pair of chopsticks was held by the participant throughout the duration of the experiment.

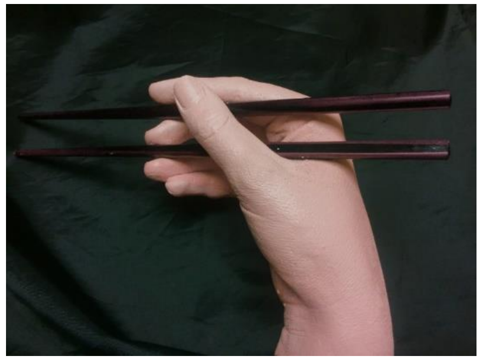

Figure 3. The resin cast of a hand holding chopsticks used in Weser et al. 2017 and Studies 1, 2 and 6.

Chopstick-Holding Blob. The other viewed item was the non-hand shaped (blob-like) object (**Figure 2**) that held chopsticks using proper from. The chopsticks were glued in place to minimize movement during the procedure.

Bead-Transfer Task. The same task used in Weser et al. was used to measure participant chopstick skill. Two-hundred seventy plastic beads of various colors that measured 0.8 cm in diameter were presented to participants in a tray. Participants used their chopsticks to transfer each bead to a container with 6 color-labeled compartments. 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 minutes to transfer as many beads as possible. The number of beads transferred was recorded and used as a proxy value for participant chopstick skill.

Rubber hand illusion questionnaire. Twenty-five questions from Longo and colleagues (Longo et al., 2008) were adapted to measure the subjective experience of the tool-version of the RHI (see Appendix A for the chopstick version of the questionnaire). In particular, the adapted questions 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.

Experimental design

A 2 x 2 design was employed. The viewed object (chopstick-holding blob vs. chopstick rubber hand) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within-subjects factors. All participants completed the tool skill task prior to undergoing the illusion induction. The 4 within-subjects conditions, completed in a random order, were: (i) chopstick-holding blob synchronous; (ii) chopstick-holding blob asynchronous; (iii) chopstick rubber hand synchronous; (iv) chopstick rubber hand asynchronous. Participants held chopsticks for all 4 illusion conditions.

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 chopsticks held by the viewed object at the same time. In the asynchronous visuo-tactile conditions, the experimenter stroked the participant's chopsticks first, while the chopsticks held by the viewed object was stroked with a latency of 500-1000 ms. Each stimulation period lasted 180 s and was timed using a stopwatch. The tip of the top chopstick was always stroked. Experimenters were instructed to apply enough pressure to the chopsticks that the contact would be felt. The paintbrush used measured 22 cm in length, with a 2 x 1 cm bristle.

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. All participants then completed the bead-transfer task. During the illusion induction phase, participants were seated across from the experimenter with their right, chopstick-holding 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 viewed object rested inside the central compartment in front of the participant's midline. The viewed object 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 chopsticks held by both of the viewed objects was kept constant at 25.5 cm. The top of the box was covered 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 (**Figure 4**).

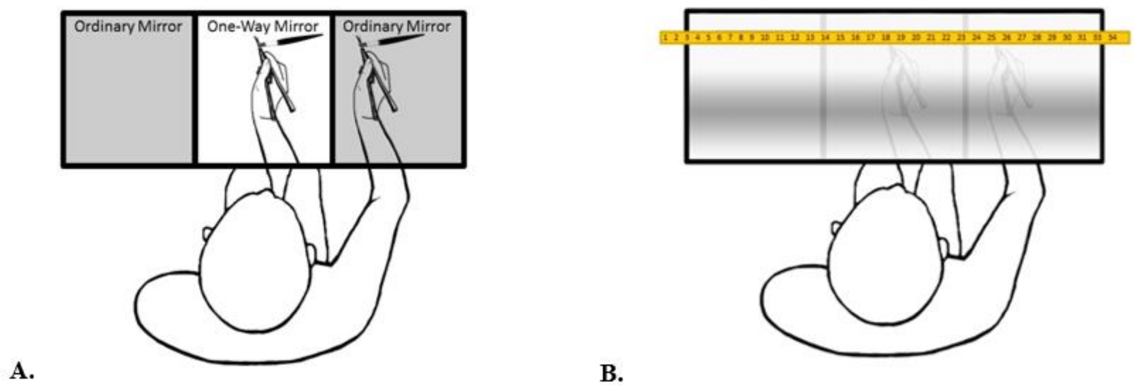

Figure 4. For each condition, the proprioceptive (B) phase was conducted before and after the illusion induction phase (A). The viewed object was visible during (A) and hidden during (B).

The lighting in the central compartment containing the viewed object was manipulated throughout the experiment. During the visuo-tactile stimulation phases, illumination from within the compartment caused the mirror to be transparent (Figure 4A), allowing the participant to view the object 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 object from view (Figure 4B).

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 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 viewed object.

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 location of the numbers the participant viewed during the judgment phases was 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 (chopstick-holding blob synchronous, chopstick-holding blob asynchronous, chopstick rubber hand synchronous, chopstick rubber hand 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 condition.

Results and Discussion

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 the viewed object, visuo-tactile stimulation, and tool skill, a linear mixed effects model was employed. Using R (R Core Team, 2013) and the *lmer*() function in the lme4 library (Bates, Maechler, Bolker, & Walker, 2014), a model was fitted to the data that predicted drift from the interaction of timing of visual-tactile stimulation (synchronous or asynchronous) and viewed object (chopstick-holding blob or chopsticks rubber hand) as between-subjects fixed effects, the amount of beads transferred during the chopsticks skill task, and a random effect of participant to account for individual differences. The main effect of timing of visuo-tactile stimulation was significant: Wald Chi-Square (1) = 13.15, $p < 0.001$. There was no effect of chopstick skill ($p = 0.83$), nor did the amount of beads transferred interact with any of the other terms in the model (all *p's* > 0.2). The interaction of timing and object (depicted in **Figure 5**) failed to reach significance ($p = 0.12$). Pairwise comparisons revealed a significant difference between the Synchronous Hand Condition ($M = 2.14$, $SE = 0.47$) and all other conditions, notably the synchronous Blob Condition ($M = 0.83$, $SE = 0.47$): $t(1,180) = 1.99$, $p = 0.048$.

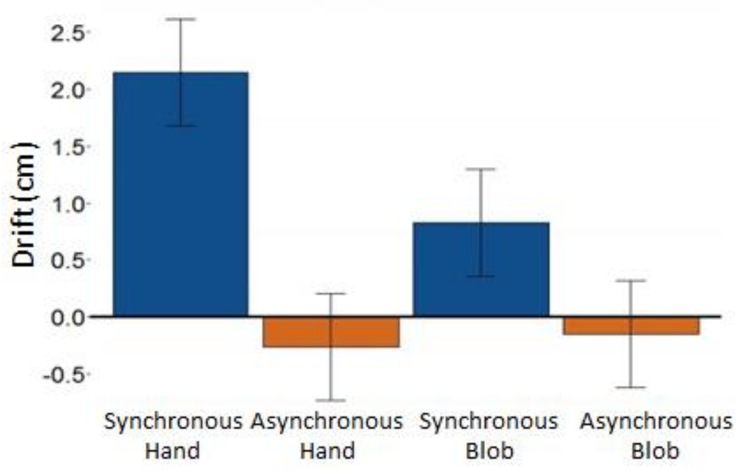

Figure 5. The non-significant interaction between viewed object and timing of visuo-tactile stimulation. Error bars represent ±1 SEM.

These findings indicate that the presence of the tool plays a stronger role in the strength of the illusion than does the presence of the hand. So long as synchronous visuo-tactile stimulation is delivered to the same tool, participants experience proprioceptive drift even when the object supporting the tool looks nothing like their own hand. This is consistent with findings from the "invisible RHI," a study in which the participants experienced the illusion while watching the experimenter move a paintbrush through empty space (Guterstam, Gentile, and Ehrsson, 2013). Importantly, Guterstam et al. moved the second paintbrush providing visuo-tactile stimulation as if it were tracing the shape of the knuckles and the angles of the invisible fingers, just in the manner that the hidden real hand was simultaneously stroked with the other paintbrush (2013). This indicates that the self-attribution mechanisms for the visuo-tactile integration of an object are independent of its actual visual presence. So long as the simultaneity of the visuo-tactile stimulation is preserved, the illusion can be felt.

In this study, the chopsticks held by the non-hand object were identical to the participants' chopsticks and were also positioned appropriately to maintain an exact match in visuo-tactile stimulation. Since only the tool is stimulated by the experimenter, the parameters for a successful illusion were met in both synchronous conditions, hence their significant difference from 0. However, the significant difference between the two synchronous conditions does indicate that the template matching hypothesis in the RHI has merit. The presence of a hand facilitates the incorporation of the tool + hand complex and the replacement of the tool + participants' own hand during the illusion over and above a viewed object lacking a hand.

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.

The ANOVA revealed significant main effects of questionnaire component ($F(4,38) = 19.21$, $p < 0.001$) and illusion condition ($F(3,39) = 16.31$, $p < 0.001$. The interaction was not significant ($F = 2.28$). Planned comparisons between illusion conditions revealed a significant difference in responses to items related to embodiment: (synchronous chopsticks rubber hand: $M = -0.17$, $SD = 1.55$; asynchronous chopsticks rubber hand: $M = -0.20$, $SD = 1.77$; synchronous chopsticks-holding blob: $M = -0.53$, SD = 1.57; asynchronous chopsticks-holding blob: $M = -1.14$, $SD = 1.71$; ($F(1,3) = 9.32$, $p = 0.02$). There was also a significant difference in responses to the movement-related items on the questionnaire: (synchronous chopsticks rubber hand: $M = -0.37$, $SD = 1.76$; asynchronous chopsticks rubber hand: $M = -0.59$, $SD = 1.69$; synchronous chopsticks-holding blob: $M = -1.15$, $SD = 1.70$; asynchronous chopsticks-holding blob: M = -

1.27, *SD* = 1.64; (*F*(1,3) = 8.57, *p* = 0.03). 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 respond slightly more positively to items related to the embodiment of the rubber hand holding the chopsticks as opposed to the blob, and moreover, to slightly positively endorse items relating to the experience of their hand and the rubber hand moving closer to one another (**Figure 6**).

This pattern of results in consistent with the findings of Weser et al. (2017). Unlike traditional RHI studies, participants in tool-versions of the illusion do not strongly endorse items with positive values on the questionnaire during synchronous conditions with a match between their hand and held object and the viewed item. Rather, they tend to strongly disagree with these items when there is no match between their tool, hand, and the viewed item. Thus significant differences between illusion conditions on each subsection of the experience survey index a difference between absolutely not experiencing the sensation queried during asynchronous, non-matching conditions, and some degree of uncertainty (represented by 0 on the -3 to 3 scale of the questionnaire) about those same sensations during the synchronous, matching conditions.

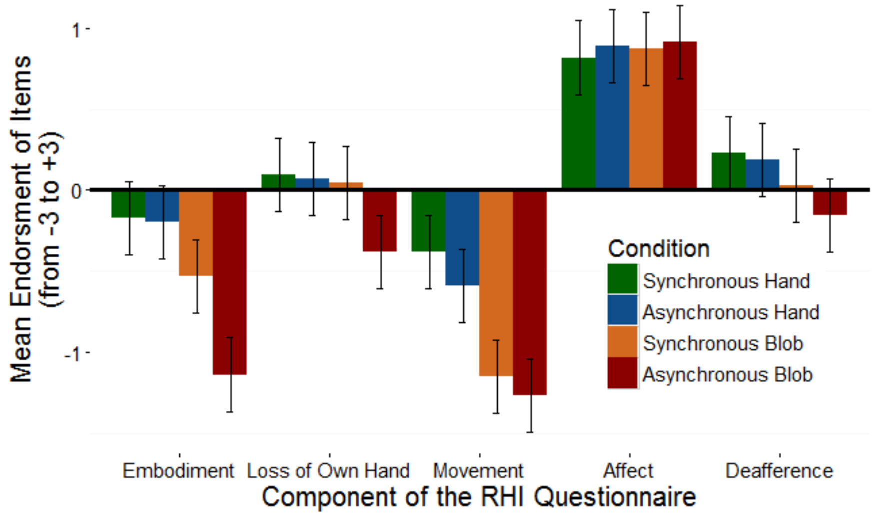

Figure 6. A comparison of illusions conditions revealed a significant difference in responses to items related to Embodiment and to the Movement-related items on the questionnaire, with a more positive mean response to these factors for conditions involving the chopsticks rubber hand. Error bars represent ±1 SEM.

Study 2: Chopsticks and Observation

Weser et al. found that participants who used the chopsticks immediately prior to undergoing the illusion procedure experienced higher proprioceptive drift than those who were not given the chance to use the chopsticks productively. This finding motivated the question of what aspect of tool use facilitated the illusion. There are 2 factors that may contribute to this facilitory effect: i) visual experience with the tool; ii) tactile experience with the tool. Visual experience of the tool may be sufficient, as it would allow the participant to more accurately determine where the tips of the chopsticks were located in relation to their own hand. However, tool effects in the various measurements of peripersonal space representation (Witt et al. 2005; Cardinali et al. 2009; Brown et al. 2011) and crossmodal correspondence paradigms (Maravita et al., 2002; Maravita, Spence, & Driver, 2003) are predicated on the participants' intentional use of the tool prior to the measurement of the effect. If the participant passively holds the tool, or in the case of Brown et al., uses the tool while the full weight of their arm and tool are suspended in a sling, tool effects are not found (2011). Thus tactile experience, as opposed to passive holding, might facilitate the illusion as it would allow the participant to learn to recognize sensations caused by touches at the tips of the chopsticks.

Given that chopstick skill also interacts with a participant's experience of the illusion, it was also of interest to examine whether or not watching a skilled chopstick user prior to experiencing the illusion would increase the strength of the illusion for a participant observing the chopstick use. Because Costantini et al. found that observing tool actions extended the representation of reachable space when the observer is also holding the tool (2011), Study 2 compares the strength of the chopstick version of the RHI for participants who either watched an experimenter use chopsticks prior to undergoing the illusion, watched and held chopsticks, or merely held chopsticks without using them.

Methods

Participants

Ninety-two right-handed individuals (35 males; mean age 18.5) participated in exchange for credit in an introductory psychology course at the University of Virginia. All participants had normal or corrected to normal vision and provided written informed consent prior to participation in the study.

Materials

Chopstick Rubber Hand. The same rubber hand as was used in Study 1. No control viewed item was employed.

Bead-Transfer Task. In two of three conditions (described below) the participant watched as the experimenter transferred beads using chopsticks into a color sorted container, following the same procedure as described in Study 1.

Rubber hand illusion questionnaire. The same 25 questions were used to measure the subjective experience of the tool-version of the RHI (see Appendix A for the chopstick version of the questionnaire).

Experimental design

A 3 x 2 mixed design was employed. The type of tool-skill task was the between-subjects factor. The tool-skill task was modified such that participants experienced one of 3 conditions prior to undergoing the illusion: visual and tactile condition, tactical only condition, visual only condition (Figure 7). The timing of visuo-tactile stimulation (synchronous versus asynchronous) was a within subject factor while the viewed object was always the rubber hand holding chopsticks.

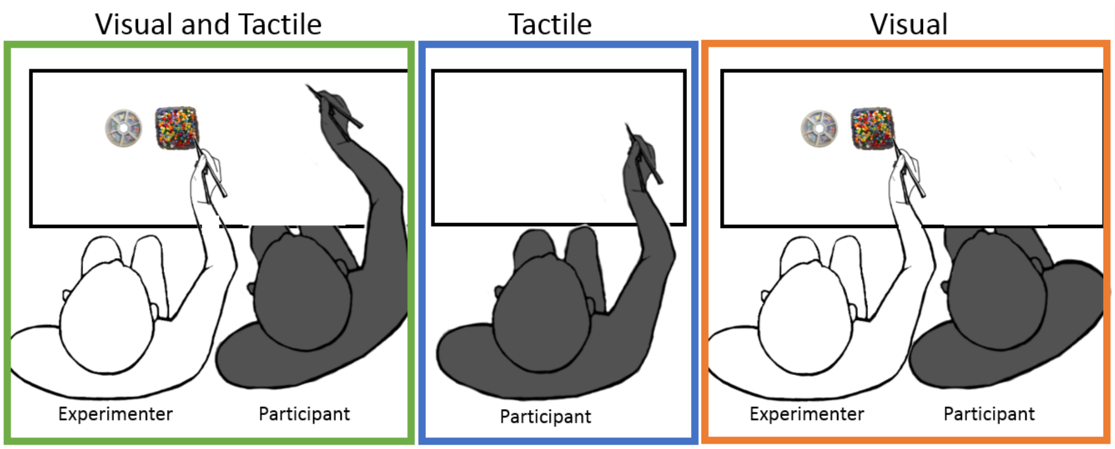

Figure 7. The 3 conditions of tool-skill task employed in Study 2: Visual and Tactile, in which the participant held chopsticks as the experimenter completed the tool skill task; Tactile, where the participant passively held the chopsticks for the same amount of time as allotted for the tool-skill task; and Visual, where the participant kept his or her hands under the table while the experimenter completed the tool-skill task.

Procedure

The procedure was identical to Study 1 with the following exceptions: Depending on his or her randomly assigned condition, a participant either held chopsticks (Tactile and Visual or Tactile Only) or folded his or her hands and kept them under the table (Visual Only). A timer was set for five minutes and the participant either watched the experimenter use chopsticks to transfer as many beads as possible from one container to the next (Tactile and Visual or Visual Only) or sat still while holding (and not manipulating) the chopsticks until the timer sounded (Tactile Only). Following the completion of the tool-skill condition, the participant and the experimenter moved to the table containing the rubber hand illusion box described in Study 1 and the participant was instructed to hold chopsticks. The procedure for the illusion induction phase was the same as Study1, except that participants experienced only the synchronous and asynchronous visuo-tactile stimulation of the rubber hand holding chopsticks. No control viewed object was employed. Participants filled out the Rubber Hand Illusion Questionnaire following the completion of each of the randomly ordered conditions (chopstick rubber hand synchronous, chopstick rubber hand asynchronous).

Results and Discussion

Proprioceptive Drift

Assumptions of normal distribution, independence of residuals, and sphericity were met. A model was computed that predicted proprioceptive drift from the interaction of timing of visual-tactile stimulation (synchronous or asynchronous) as a within-subjects fixed effect, the condition of the tool-skill task (Visual and Tactile, Tactile Only, Visual Only) as a between-subjects fixed effect, the amount of beads transferred by the experimenter (in Visual and Tactile/Tactile Only conditions), as a covariate, and a random effect of participant to account for individual differences.

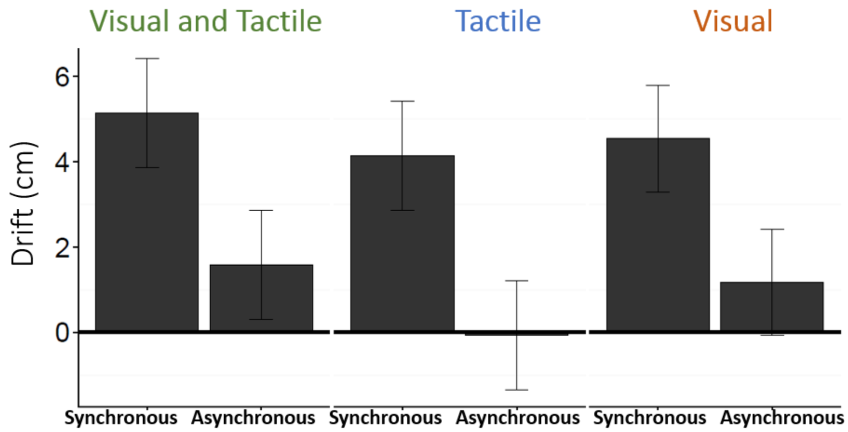

Figure 8. The non-significant interaction of timing of visuo-tactile stimulation by tool-skill condition clearly illustrates the significant difference between synchronous and asynchronous visuo-tactile stimulation. Error bars represent ±1 SEM.

The main effect of timing of visuo-tactile stimulation was significant: Wald Chi-Square (1) = 15.95, $p < 0.001$, with synchronous ($M = 4.48$, $SE = 0.84$) yielding significantly higher proprioceptive drift than asynchronous ($M = -0.05$, $SE = 0.58$). Figure 8 illustrates the high positive drift in the synchronous conditions and the null effect of tool-skill condition by depicting the interaction, which failed to reach significance ($p = 0.51$). Although there were no other significant main effects or 2-way interactions, the 3-way interaction of timing of visuo-tactile stimulation, Tool-Skill Condition (Visual and Tactile/Visual Only), and the number of beads transferred by the experimenter (i.e. the experimenter's skill with the chopsticks) did reach significance: Wald Chi-Square (1) = 5.21, $p = 0.02$. This interaction is plotted in Figure 9.

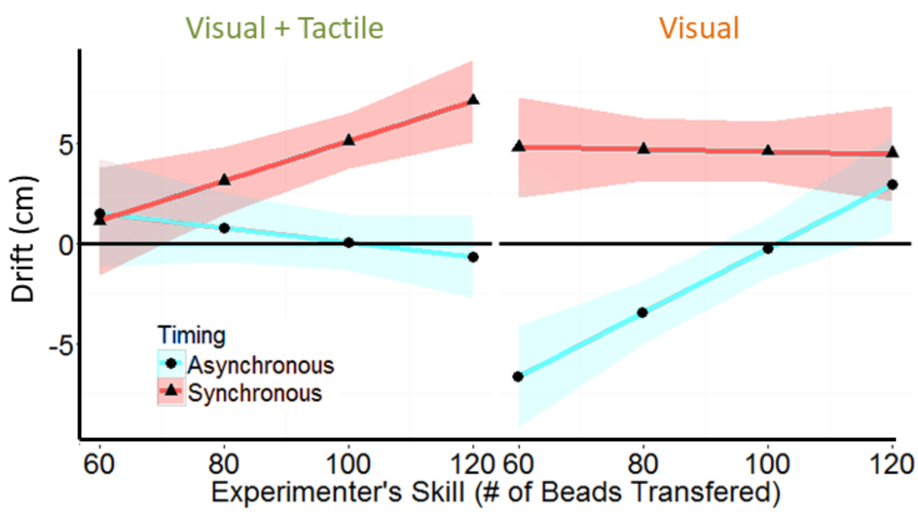

Figure 9. The significant 3-way interaction between the timing of visuo-tactile stimulation, Tool-Skill Condition, and the number of beads transferred by the experimenter (i.e. the experimenter's skill with the chopsticks). Note that beads are not transferred in the Tactile Only condition, so drift data for that condition was excluded from this plot. Shaded areas indicate ±1 SEM.

To interpret this interaction, a pairwise post-hoc tests for linear hypotheses was conducted using the *lsmeans*() function in the lsmeans library (Lenth, 2016). Custom contrasts applied to explicitly compare the difference between the proprioceptive drift outcome for Visual and Tactile synchronous visuo-stimulation and the Visual Only synchronous stimulation groups at different levels of experimenter skill (beads transferred) revealed a difference trending towards significance: $t(28)=1.65$, $p = 0.10$. Together the lack of a main effect of tool-skill task and this 3-way interaction suggest that although the three types of chopstick interaction have an equivalent effect on the participants' subsequent experience of the illusion, a participant may experience an enhanced proprioceptive drift in the synchronous visuo-tactile stimulation condition following the watching of a highly skilled experimenter use chopsticks especially when he himself is also holding chopsticks. Although the direct contrast between the Visual and Tactile group and the Visual Only group was not significant, the trending difference suggests that there may be some benefit to be had by holding a tool during tool-use viewing. This finding may have implications for the use of training procedures where experts model correct tool-use. Prospective tool-users wishing to feel more at home using the tool should consider holding the tool while watching the expert model the skill.

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 timing of visuo-tactile stimulation (synchronous vs. asynchronous) as a within subject factor and the tool-skill condition (Visual and Tactile, Visual Only, Tactile Only) as a between subjects factor. There was a significant main effect of questionnaire component

($F(4,87) = 83.16$, $p < 0.001$), timing ($F(1,90) = 44.15$, $p < 0.001$), and tool-skill condition ($F(2,89) = 11.89$, $p < 0.001$). The main effect of tool-skill condition revealed that participants who watched the experimenter use chopsticks and did not hold chopsticks themselves tended to positively endorse items more than participants who only held the chopsticks and did not see them in use (Visual Only: $M = 0.05$, $SD = 1.63$; Tactile Only: $M = -0.20$, $SD = 1.64$). Counterintuitively, participants who both held and saw chopsticks in use had the lowest mean endorsement of items on the RHI Survey ($M = -0.49$, $SD = 1.69$). This finding is difficult to interpret both because it is contrary to the predictions made at the outset of the study, and because no other studies using the RHI questionnaire examied how participant self-reported illusion experience is impacted by a manipulation prior to the illusion. In general, most differences in RHI questionnaire scores occur because of direct changes to the RHI procedure, such as altering the appearance or posture of the rubber hand, or the timing or location (finger vs. back of the hand) of the visuo-tactile stimulation.

One possibility is that the Visual and Tactilce and Tactile Only participants habituated to the feeling of chopsticks in their hand during the tool-skill task, so the subjective experience of the illusion proceedure was diminished as a result. The Visual Only group experienced an enhanced illusion relative to the Tactile Only and Visual and Tactile group because they had prolonged visual experience with a non-corporeal hand holding chopsticks (similar to the rubber hand). They also had reduced tactile information about the shape and feel of chopsticks relative to the other two groups. The lack of habituation during the tool-skill phase and the novel feeling of holding the chopsticks during the illusion proceedure may have increased the amount of attention they paid to the visuo-tactile stimulation during the illusion, which may then have enhanced their self-report of the experience.

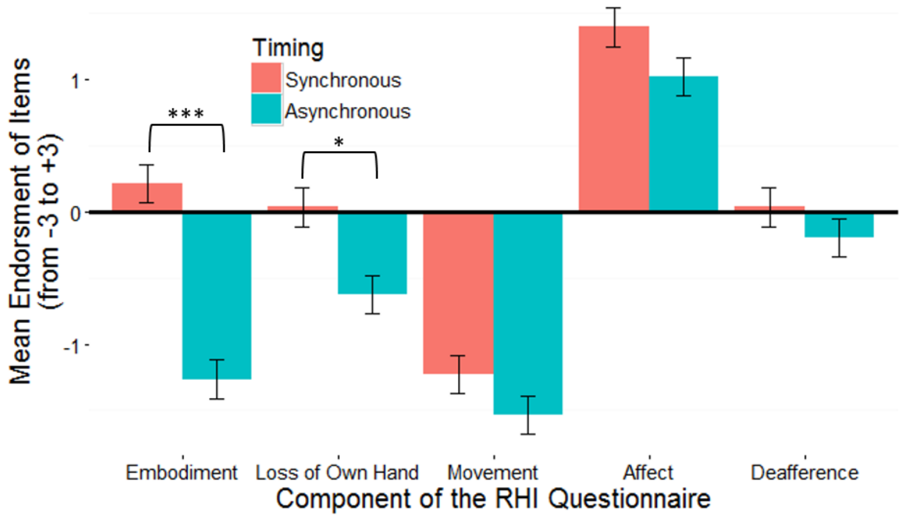

Figure 10. The significant interaction of RHI Questionnaire and Timing of visuo-tactile stimulation. Items related to Embodiment, Loss of Own Hand, and Affect differed significantly in planned comparisons, with synchronous visuo-tactile stimulation resulting in a higher mean endorsement of items. Error bars represent ±1 SEM.

In addition to these main effects, there was also a significant interaction between questionnaire component and timing ($F(4,87) = 6.24$, $p < 0.001$), which is depicted in Figure 10. No other interactions reached significance (all *F*'s < 0.5). A post hoc Tukey test showed that the endorsement of Embodiment and Loss of Own Hand items during synchronous and asynchronous visuo-tactile stimulation differed significantly at $p < .001$; the other items on the survey did not differ significantly between synchronous and asynchronous visuo-tactile stimulation. The interaction and significant difference between Embodiment and Loss of Own Hand for synchronous and asynchronous conditions dovetails with previous research using this survey (e.g. Longo et al., 2008). Synchronous visuo-tactile stimulation results in the experience of the rubber hand feeling as though it is a part of the participant's own body, and that it has replaced their own synchronously stimulated hand. Although the mean endorsement of items is lower than in previous studies using this survey, this is consistent with Weser et al. who also found that the tool version of the RHI results in lower endorsement of survey items than does classic RHI procedures.

Study 3: Rubber Hand Holding Pliers

Chopsticks and teacups were used as comparison tools in Weser et al. (2017) because the two tools have different degrees of "morpho-functional match" and identical sensorimotor match (Cardinali et al. 2016). When a tool is held with a precision grip hand position and the function of the tool is to act on the environment in a precision manner, the tool is said to match at the morpho-functional and sensorimotor level. Chopsticks match, as they are used with a precision grip of the thumb and index finger and serve to pick up objects using a precision-grip type of action. A teacup held by the handle with a precision grip does not have a morpho-functional match and sensorimotor match because the function of a teacup is not a precision-grip type of action but rather an extension of the whole hand cupping action used to transport liquids. Several researchers have proposed that the match (or lack of match) between tool morphology and grasp mechanics determines whether or not the use of a tool will cause a modulation of the wielder's body representation (Cardinali et al. 2016; Miller, Longo, & Saygin, 2014; Weser et al. 2017).

To further investigate this claim, Studies 3 and 4 were designed to compare tools with different levels of morpho-functional match and sensorimotor match. In Study 3, needle-nose pliers lack this match, as they are wielded with a full-hand power grip and act on the environment in a precision-grip type of manner. Therefore, it follows that a pliers-version of a RHI will not be as successful as a tool-version where there is both a morpho-functional match and a sensorimotor match, such as chopsticks (Weser et al. 2017, Studies 1, 2, 6, and 7) or tweezers (Study 4).

Methods

Participants

A total of 71 right-handed individuals (18 males; mean age 19.0) participated in exchange for credit in an introductory psychology course at the University of Virginia. The data from 5 participants was lost due to experimenter error (2) and participants' failure to follow instruction (3), leaving 66 participants. Thirty-one participants completed the tool-skill task prior to experiencing the illusion, while the remaining 35 completed the tool-skill task at the end of the study. All participants had normal or corrected to normal vision and provided written informed consent.

Materials

Pliers Rubber Hand. A life cast of author VW's hand holding a pair of needle nose pliers was made from flesh-tinted plastic resin (see Figure 11 A). An identical pair of pliers was provided for the participant to hold throughout the study and use during the tool-skill task. The handle of the pliers contained a small spring that caused the jaws of the pliers to open whenever the user relaxed his or her grip.

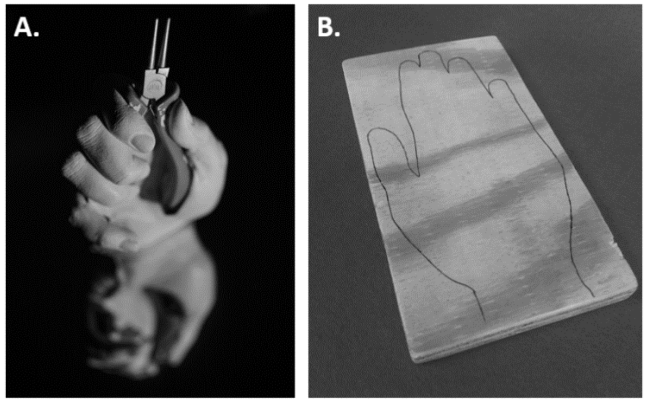

Figure 11. (A) The life cast of a hand holding needle-nose pliers. The pliers measured 13 cm in length, with a 10 cm handle and jaws 3 cm in length. (B) The wooden block used as the control viewed object in both experiments in Weser et al. (2017), and in the current work in Studies 3, 4, 5, and 7.

Wooden Block. The other viewed item was the wooden block (Figure 11 B) used in Weser et al. (2017). The piece of wood was a 9 cm x 23 cm x 2 cm block, pale and beige in color, with the outline of a hand drawn on the surface in black ink. This wooden stimulus was comparable in overall size to the chopstick rubber hand, and is comparable to the control (non-corporeal) items used in classic RHI studies (i.e. Longo et al., 2008; Haans, IJsselsteijn, & de Kort, 2008).

Tool-Skill Task. The same bead-transfer task was used, except that participants were now required to use pliers to move the beads from one container to the other, and they were assigned to complete the task either before or after the RHI procedure.

Rubber hand illusion questionnaire. The same set of 25 questions was used, except that all questions were modified to refer to the pliers held by the rubber hand, rather than to chopsticks or to the rubber hand itself.

Experimental design

A 2 x 2 x 2 mixed design was employed. The viewed object (pliers rubber hand vs. wooden block) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within subjects factors, and the group (tool-skill task prior to the illusion vs. following the illusion) was a between-subjects factor. The number of beads transferred with pliers was included as a covariate, and a random effect of participant was added to account for individual differences in pliers-skill and illusion susceptibility. The 4 within-subjects conditions, completed in a random order, were: (i) pliers rubber hand synchronous (ii) pliers rubber hand asynchronous; (iii) wooden block synchronous; (iv) wooden block asynchronous. Participants held pliers during all 4 conditions.

Procedure

Participants were greeted and informed that they would be using pliers and making self-perception estimates throughout the duration of the experiment. Upon arrival, participants were randomly assigned to either first complete the tool-skill task or to undergo the RHI procedure prior to using the pliers to transfer beads. During the illusion procedure, participants were instructed to apply light pressure to the pliers' handle and keep the jaws slightly closed. This allowed the experiment to stroke both jaws of the pliers simultaneously with the paint brush. During the wooden block condition, the front corner of the block (on the participant's right) was stroked with the paint brush. All other aspects of the procedure were identical to the studies reported previously.

Results and Discussion

Proprioceptive Drift

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 recency of tool use, a linear mixed effects model that included a random factor of participant was fitted to the data. The main effect of viewed object was significant: Wald Chi-Square (1) = 5.46, $p = 0.019$, with the pliers rubber hand ($M = 0.87$, $SE = 0.24$) yielding significantly higher proprioceptive drift than the wooden block ($M = 0.14$, $SE = 0.23$). For comparison with previous studies, Figure 12 illustrates the non-significant interaction ($p = 0.33$) between viewed object and timing of visuo-tactile stimulation.

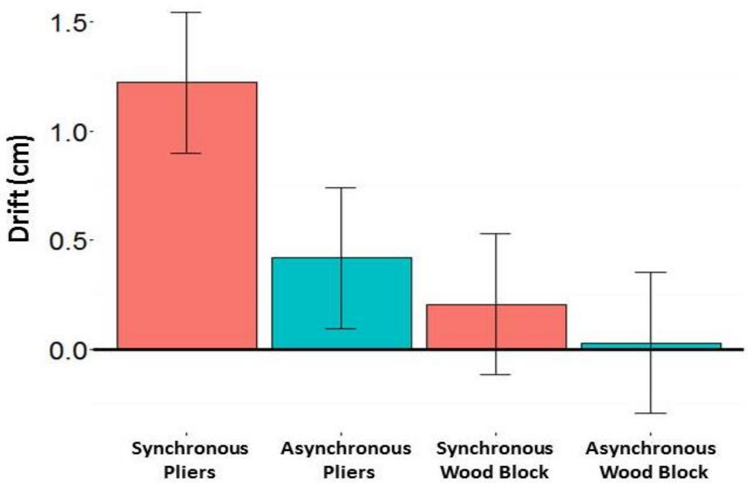

Figure 12. The non-significant interaction of timing of visuo-tactile stimulation and viewed object. The significant main effect of viewed object is apparent, as drift was larger when participants viewed a rubber hand holding pliers than when a wooden block was viewed. Error bars represent ±1 SEM.

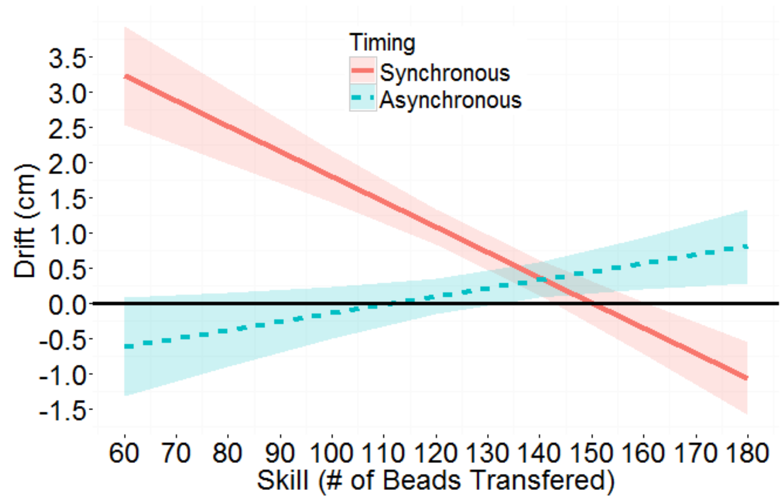

Figure 13. The significant interaction between the timing of visuo-tactile stimulation, and the number of beads transferred during the tool-skill task. Shaded areas indicate ±1 SEM.

There was also a significant interaction of timing of visuo-tactile stimulation (synchronous vs. asynchronous) and the number of beads transferred during the tool-skill task: Wald Chi-Square (1) = 13.92, $p < 0.001$. This interaction is plotted in Figure 13. There were no other main effects or interactions that reached significance. Clearly, this interaction was not predicted given the opposite findings with chopsticks; however, the pliers and chopsticks conditions differed in a number of respects. Unlike previous studies in which many participants reported that they used chopsticks daily, no participants in Study 3 reported frequently using pliers. Indeed, the majority of participants (n = 43) said they "very rarely" used pliers. Moreover, when grouping participants by their response to the pliers-use question, the 4 participants who said they "sometimes use pliers" transferred the fewest beads during the took-skill task of any group (*M* = 103, *SD* = 9.2; Occasionally: n =4, *M* = 161, *SD* = 11.7; Very Rarely: n =43, *M* = 155, *SD* = 20.9; Never: n = 15, *M* = 115, *SD* = 26.5). This suggests that the bead transfer task may not have been an ecologically valid assessment of tool skill, as it was for chopsticks. It also indicates that those performing better (e.g. transferring more beads) were not necessarily those participants with more skill and experience at using pliers. This may offer an explanation both as to why there was no effect of group (tool-skill task prior to the illusion v. after the illusion) on the illusion, and importantly why the interaction of number of beads transferred and timing of visuo-tactile stimulation was the opposite direction as previously seen in Weser et al. 2017 and Study 2. In those experiments, the tool-skill task successfully quantified the tool-users' skill with chopsticks, as participants and experimenters who reported more frequent chopstick use far outperformed those who reported never or infrequently using the tool. It is therefore a possibility that transferring beads with chopsticks was not so much a measure of skill with pliers, but rather of overall hand dexterity.

Though as of yet there is no definitive experiment that demonstrates a decrease in RHI strength for those with greater hand dexterity or awareness (dancers or pianists, for example), it has long been speculated that such individuals would have reduced susceptibility to the illusion (Tsakiris, 2010; Tsakiris & Haggard, 2005; Botvinick & Cohen, 1998). Indeed, those with lower interoceptive awareness (as measured with an established heart-rate monitoring task) were far more susceptible to the RHI than were those with high interoceptive abilities (Tsakiris, Tajadura-Jiménez, & Costantini, 2011; but see David, Fiori, & Aglioti, 2014). Therefore, the strong negative relationship seen in this study between the number of beads transferred with pliers and the amount of proprioceptive drift experienced during synchronous illusion conditions may actually index the decreased illusion susceptibility of more dexterous, bodily aware participants who are able to use an unfamiliar tool more easily than participants with less bodily awareness.

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 as within-subjects factors and a between subject factor of group (tool-skill task prior to the illusion vs. after). The analysis revealed a significant main effect of questionnaire component ($F(4,62) = 80.47$, $p < 0.001$) and of condition ($F(4,88) = 5.92$, $p < 0.001$). No other main effects of interactions reached significance (all F's > 1.0). Follow-up analyses examining each questionnaire component individually revealed no significant differences between illusion conditions, suggesting that the subjective experience of the pliers-version of the rubber hand illusion was not greatly affected by the appearance of the viewed object or by the timing of the visuo-tactile stimulation. It seems likely that participants' lack of familiarity with pliers made it just as difficult for them to embody a rubber hand holding pliers as it would be to embody a wooden block. As a result, they failed to endorse questions about the rubber hand and the wooden block at equal rates. The non-significant interaction between illusion condition and component of the RHI Questionnaire is plotted in Figure 14 for comparison with the other studies.

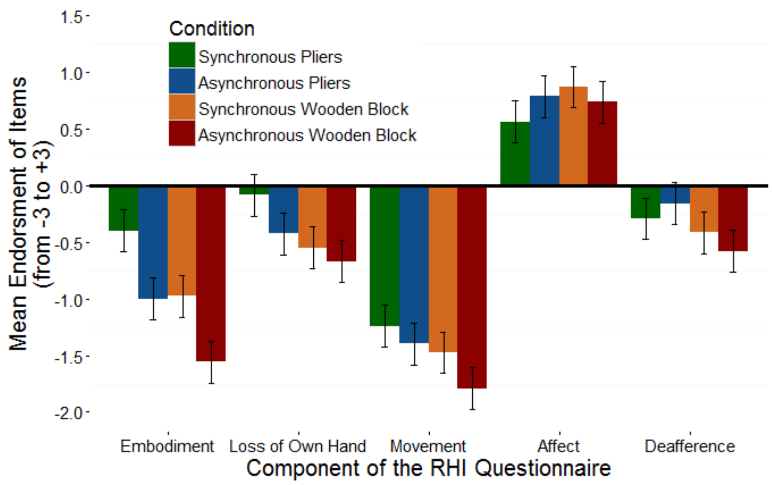

Figure 14. The non-significant interaction between RHI condition and questionnaire component for the pliers-version of the RHI. Error bars represent ±1 SEM.

Study 4: Rubber Hand Holding Tweezers

Like the chopsticks and teacups used in Weser et al. (2017), tweezers and pliers similarly differ on their level of morpho-functional match and sensorimotor match: Chopsticks and tweezers match, while teacups and pliers do not. Weser et al. examined tools with an identical sensorimotor match (both tools were held with a precision grip) while Studies 4 and 5 examine tools with an identical morpho-functional match (both tools act on the environment in a precision fashion). If the match between tool morphology and grasp mechanics determines whether or not the use of a tool will cause a modulation of the wielder's body representation (e.g. Cardinali et al. 2016; Miller, Longo, & Saygin, 2014; Weser et al. 2017), then participants in Study 4 should experience a RHI when viewing a rubber hand holding tweezers.

Methods

Participants

Data was collected from 76 right-handed participants (24 males; mean age 18.7). All participants had normal or corrected to normal vision, participated in exchange for credit in an introductory psychology course at the University of Virginia, and provided written informed consent prior to commencing the study. Data from 4 female participants was lost due to experimenter error (1) and the failure of 3 participants to follow direction. This brought the total sample size down to 72, with 37 completing the tool-skill task prior to engaging in the illusion, and the final 35 completing the tool-skill task after the completion of the illusion procedure.

Materials

Tweezers Rubber Hand. A life cast of author VW's hand holding a pair of tweezers was made from flesh-tinted plastic resin (see Figure 15). An identical pair of tweezers was provided for the participant to hold throughout the study and use during the tool-skill task.

Figure 15. The life cast of a hand holding tweezers. The tweezers measured 9 cm in length.

Wooden Block. The other viewed item was the wooden block (Figure 11 B) described in Study 3.

Tool-Skill Task. The bead-transfer task described previously was altered so that it would be more appropriate for tweezers. The beads were replaced with "seed beads," tiny plastic beads that measured 1.8 mm in diameter. As before, participants were required to use tweezers to pick up 1 bead at a time and move it from 1 container to another, sorting by color. There were 40 beads of each of 8 colors (320 beads total), and participants were allotted 5 minutes to sort as many beads as possible.

Rubber hand illusion questionnaire. The same 25 questions from Longo and colleagues (Longo et al., 2008) were used. The questions were altered so as to reference the rubber hand holding tweezers, rather than the rubber hand alone or the rubber hand holding chopsticks.

Experimental design

A 2 x 2 x 2 x 2 mixed design was employed. The viewed object (tweezers rubber hand vs. wooden block) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within-subjects factors, the group (tool-skill task prior to the illusion vs. following the illusion), and frequency of tweezers use (frequent use (n = 35) vs. little or no use (n =37)) were between-subjects factors. The number of beads transferred with tweezers was included as a covariate, and a random effect of participant was added to account for individual differences in tweezers-skill and illusion susceptibility. The 4 within-subjects conditions, completed in a random order, were: (i) tweezers rubber hand synchronous (ii) tweezers rubber hand asynchronous; (iii) wooden block synchronous; (iv) wooden block asynchronous. The participant held tweezers during all 4 conditions of the illusion.

Procedure

Upon arrival, participants were randomly assigned to either first complete the tool-skill task or to undergo the RHI procedure prior to using the tweezers to transfer seed beads. During the illusion-induction procedure, participants were instructed to apply light pressure to the tweezers handle and keep the prongs slightly closed. This allowed the experimenter to stroke both prongs of the tweezers simultaneously with a paint brush. All other aspects of the procedure were identical to the studies reported previously.

Results and Discussion

Proprioceptive Drift

Assumptions of normal distribution, independence of residuals, and sphericity were met. A linear mixed-effects model that included parameters for viewed object (tweezers rubber hand vs. wooden block), visuo-tactile stimulation (synchronous vs. asynchronous), tool skill (number of beads transferred), and recentness of tool use (tool-skill before vs. after the illusion), was fitted to the data. The model also included a random effect of participant and a between-subjects effect of whether or not participants self-reported frequent use of tweezers. The tool-use frequency data was taken from the post-experiment demographics survey in which participants also reported their age and sex. The main effect of timing of visuo-tactile stimulation was significant: Wald Chi-Square (1) = 4.65, $p = 0.031$, with synchronous stimulation ($M = 0.24$, $SE = 0.24$) yielding significantly higher proprioceptive drift than asynchronous stimulation ($M = -0.39$, $SE = 0.24$). In addition to the main effect, the interaction between viewed object, timing of visuo-tactile stimulation and tweezers use (plotted in Figure 16) was significant: Wald Chi-Square (1) = 5.57, $p = 0.018$. No other main effects or interactions were significant (all p's >

0.01). A follow-up analysis that included a factor for participant sex was conducted to ensure that the tweezers use was not sex-dependent. Indeed, sex did not significantly affect proprioceptive drift ($p > 0.3$), nor did it interact with any other factor in the model (all p's > 0.25).

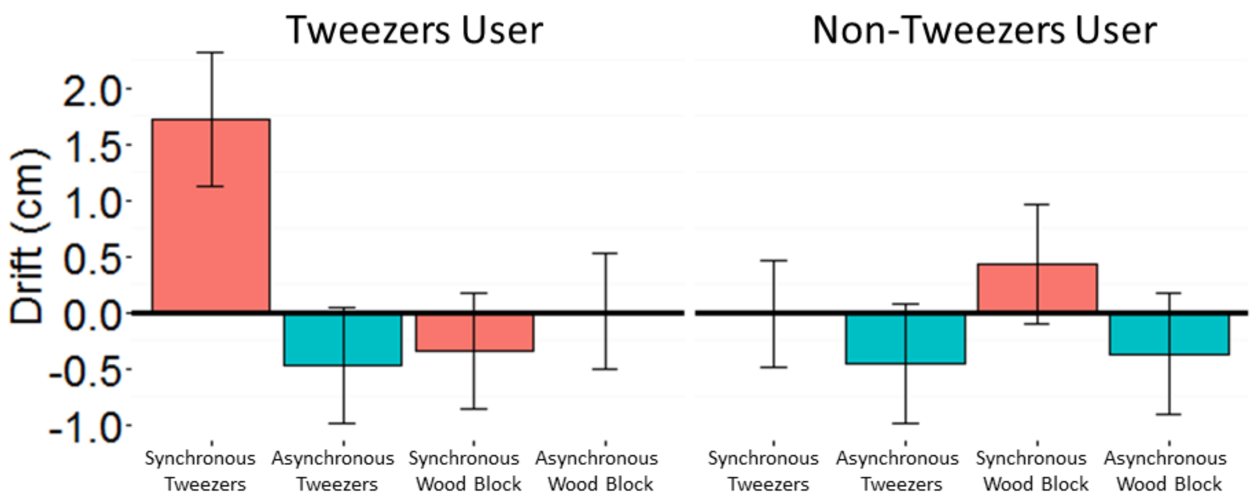

Figure 16. The significant interaction of viewed object, timing of visuo-tactile stimulation and self-report of tweezers-use. Error bars represent ±1 SEM.

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 an ANOVA with the 4 illusion conditions (Tweezers Rubber Hand Synchronous, Tweezers Rubber Hand Asynchronous, Wooden Block Synchronous, Wooden Block Asynchronous) as within-subjects factors. The ANOVA revealed a significant effect of questionnaire component ($F(4,67) = 40.53$, $p < 0.001$) and a trending effect of condition ($F(4,68) = 2.45$, $p = 0.062$). The interaction was not significant. To follow-up this finding, an ANOVA examining differences in participants' endorsement of Embodiment-related questions in the 4 conditions was conducted. This ANOVA revealed a significant effect of condition: $F(3,68) = 3.86$, $p = 0.010$, with the synchronous tweezers condition resulting in slightly more positive endorsement of embodiment items ($M = -0.26$, $SE = 0.21$) than the other conditions (asynchronous tweezers: $M = -0.61$, $SE = 0.22$; synchronous wooden block: $M = -0.92$, $SE = 0.26$; asynchronous wooden block: $M = -1.33$, $SE = 0.24$). This finding is consistent with previous studies, which similarly find a small advantage for the synchronous condition in which the viewed object matches the object held by the participant. The interaction of component of the RHI Questionnaire and the illusion condition is plotted in Figure 17 for comparison with previous studies.

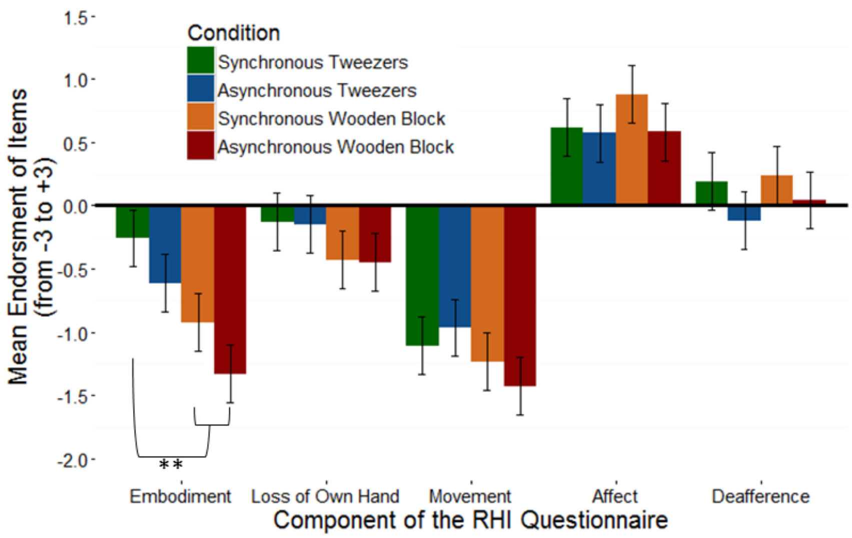

Figure 17. The non-significant interaction between RHI condition and questionnaire component for the tweezers-version of the RHI. Error bars represent ±1 SEM.

The significant interaction between viewed object, timing of visuo-tactile stimulation and tweezers-use status adds credence to the idea that morpho-functional match and sensorimotor match is an important component for the success of the illusion, and suggests that it is only the tools that match on these dimensions (chopsticks and tweezers) that integrate sufficiently with the body representation to affect an illusion of body ownership like the RHI. That the illusion only succeeds for individuals who report actual experience using the tweezers on a regular basis adds further nuance to this finding. Chopsticks are a relatively complicated tool to use, and so only those with chopsticks experience succeed at the tool skill task. On the other hand, tweezers are very simple to use and so even participants with very little real-world tweezers experience were able to transfer many beads. Therefore, the effects of the illusion emerge when participants' real world experience with tweezers are taken into account, rather than when examining their success at a somewhat arbitrary measure of tool-skill.

Study 5: Rubber Hand with Non-Tool

Study 4 demonstrated the importance of actual tool experience for the success of a tool-version of the RHI illusion. The interaction between tweezers use and illusion condition suggests that it is not enough for a tool to be easy to use: the influence of the tool on the user's body representation depends on prior experience with that tool. Thus Study 5 examines this idea by conducting the tool-version of the RHI when a wooden block is held by both participant and rubber hand. Though wooden blocks can certainly be used as tools, it is unlikely that any of the participants have extensive experience using a wooden block. Moreover, it is unlikely that the type of tool interaction conducted with a wooden block would result in the delicate tactile stimulation at the forward edge of the block as is used to induce the illusion. This stands in direct contrast with chopsticks and tweezers, where the tactile stimulation applied to the tip of the tool during the illusion is a close match for the pattern of use associated with both tools. Moreover, the wooden block is an interesting non-tool to examine because it is so often used as the non-corporeal control condition in a classic RHI study.

Methods

Participants

Seventy right-handed individuals (16 males; mean age 18.5) participated in exchange for credit in an introductory psychology course at the University of Virginia. All participants had normal or corrected to normal vision and provided written informed consent prior to participation in the study. Data from 10 participants (9 females) was excluded. Five participants were excluded due to experimenter error, 3 participants failed to follow instruction (2 females, 1 male), and due to equipment malfunction, data from a final 2 participants was excluded, leaving a total of 60 participants.

Materials

Rubber Hand Holding Wooden Block and Wooden Block. A cast was made of author VW's hand holding a wooden block (Figure 18). The wooden block held by the hand was identical in size, shape and materials to the wooden block used in Studies 3 and 4 and pictured in Figure 11 B, except that it did not have the outline of a hand traced on its surface. The very same wooden block as used in previous studies again served as the second, control viewed item in this study.

Figure 18. The piece of wood held by the hand measured 9 cm x 23 cm x 2 cm and was identical to the other wooden block used in this and previous studies as the control viewed item, except that the other wooden block had the outline of a hand drawn on its surface in black ink.

Rubber hand illusion questionnaire. The same 25 questions described previously were used, but they were adapted to refer to the wooden block held by the rubber hand, rather than to the hand itself or to any other tool.

Experimental design

A 2 x 2 design was employed. The viewed object (hand holding wooden block vs. wooden block alone) and timing of visuo-tactile stimulation (synchronous vs. asynchronous) were within-subjects factors. There was no tool-skill task in this study. The 4 within-subjects conditions, completed in a random order, were: (i) hand holding wooden block synchronous; (ii) hand holding wooden block asynchronous; (iii) wooden block synchronous; (iv) wooden block asynchronous.

Procedure

Participants were greeted and told they would be making self-perception estimates and answering a brief questionnaire about their experiences. They were seated at the RHI box and handed the wooden block which they held throughout all 4 illusion conditions. At the beginning of each condition, their grip on the block was adjusted until it matched that of the rubber hand. The block was held at about a 15° angle so that the front edge was in the air and the back edge rested on the table. This insured that the majority of the weight of the block did not need to be supported by the participant. Between illusion conditions and as they filled out the questionnaire, participants were encouraged to stretch and flex their hand to avoid fatigue.

Results and Discussion

Proprioceptive Drift

Assumptions of normal distribution, independence of residuals, and sphericity were met. A linear mixed-effects model that included parameters for viewed object (rubber hand holding wooden block vs. wooden block), visuo-tactile stimulation (synchronous vs. asynchronous), and a random effect of participant was fitted to the data. The interaction of timing of visuo-tactile stimulation and viewed object trended towards significant: Wald Chi-Square (1) = 2.75, p = 0.097, with synchronous stimulation of the rubber hand holding a wooden block (*M* = 1.57, *SE* = 0.44) yielding higher proprioceptive drift than asynchronous stimulation of the rubber hand holding the wooden block (*M* = 0.38, *SE* = 0.44) or of either of the wooden block only conditions (synchronous: *M* = 0.29, *SE* = 0.39; asynchronous: *M* = 0.46, *SE* = 0.48). Neither of the main effects reached significance (both *p*'s > 0.2). The interaction effect is plotted in Figure 19 for comparison with other studies.

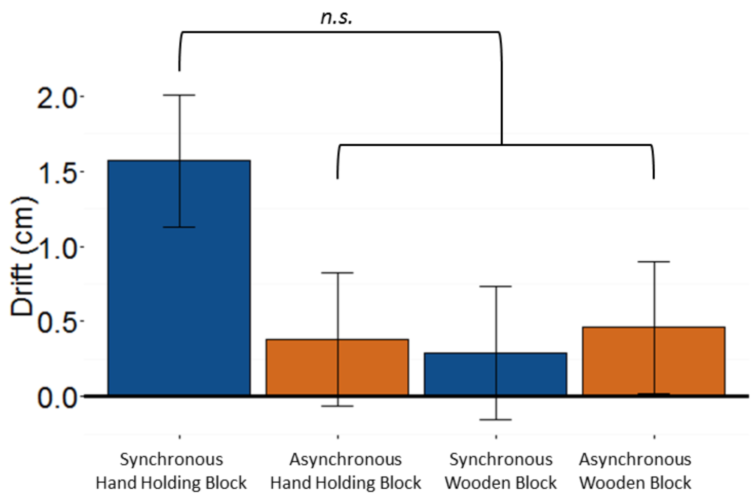

Figure 19. The non-significant interaction between the timing of the visuo-tactile stimulation and the viewed object (rubber hand holding wooden block vs. wooden block only). Error bars represent ±1 SEM.

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 hand holding wooden block, asynchronous hand holding wooden block, synchronous wooden block, and asynchronous wooden block) as within-subjects factors. The ANOVA revealed a significant main effect of questionnaire component ($F(4,55) = 24.48$, $p < 0.001$) and of illusion condition: $F(3,65) = 3.51$, $p = 0.015$. The interaction failed to reach significance. Additional planned follow-up comparisons examining differences between illusion conditions for each individual survey component revealed a significant difference between endorsement of survey items relating to embodiment in the synchronous rubber hand holding a wooden block condition: $F(3,56) = 4.03$, $p = 0.008$. The interaction of illusion condition and RHI questionnaire component is plotted in

Figure 20 for comparison with the other studies. The significant difference between illusion conditions in the embodiment component of the survey is marked with asterisks.

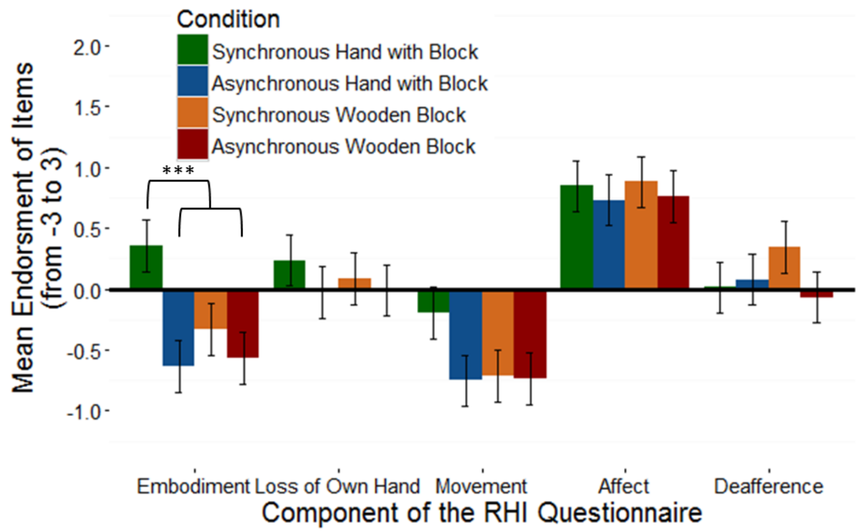

Figure 20. The non-significant interaction between illusion condition and RHI questionnaire component. Error bars represent ±1 SEM.

As expected, the wooden block held by a rubber hand stroked in synchrony with a wooden block held by the participant did not yield an illusion that differed significantly from viewing a wooden block without a hand, or from receiving asynchronous visuo-tactile stimulation. In previous work on the RHI, a lack of significant difference between the condition of interest (a viewed object that matches the participant's own hand with synchronous visuo-tactile stimulation) and the control conditions has been interpreted as a failure to induce the illusion at all. Though the difference between the condition of interest and the control conditions trended towards significance, it is noteworthy that the control conditions with asynchronous visuo-tactile stimulation and a plain wooden block without a rubber hand resulted in mean drifts close to 0.5 cm. This suggests that even when participants are not expected to be experiencing the RHI, they are slightly inaccurate at localizing the position of the held wooden block, erring on the side of underestimating the distance between their hand and the rubber hand. This may indicate that across all 4 conditions, participants had trouble localizing the front right-side corner of the wooden block they held. The wooden block was selected for its lack of resemblance to a traditional tool, and as such defining the exact area that participants should track was more difficult than with prior items used in the tool-version of the illusion.

That said, the questionnaire data for this version of the illusion did produce one of the most positive endorsement statements for items dealing with embodiment of the tool-holding rubber hand during the synchronous condition. Though the mean endorsement of embodiment-items was less than 0.5 (very low compared to embodiment scores in classic RHI designs), it is interesting that this exceeded endorsement of the same items for the chopsticks-version of the illusion. Thus, subjectively participants seemed to feel more connected to the rubber hand holding a wooden block than to a rubber hand holding chopsticks, even though the illusion employing the chopsticks-holding rubber hand had a greater effect on their proprioception as assessed through behavioral measures. It might be the case that the wooden block was easier for participants to ignore than any of the tools heretofore examined. The reason for this are twofold: the wooden block is clearly a generic item with no obvious discernable function, and unlike previous studies, the participant was never instructed to use the wooden block to complete a task. This may have better allowed participants to focus on the presence of the hand, better facilitating the connection to the body image that is believed to be tapped in the RHI Questionnaire.

Study 6: Tool Function vs. Tool Structure

Holmes, Calvert and Spence have argued that only the task-relevant, functional portion of a tool is attended to during tool use, and that attention to the tool is the driving force behind the effect a tool has on body representations (2004). Their findings applied specifically to the kind of tool typically employed in studies of tool use: a long, reach extending grabber. It is not clear whether such a dissociation would be found for the types of small, hand tools employed in the studies herein. It is also an open question as to whether researchers favor long slender tools for their studies on body representation effects because it is only these longer slender items that provide sufficient torque to make interaction with the environment at the tool tip palpable at the tool handle. It is therefore interesting to examine whether the chopsticks-version of the illusion will still succeed when the torque is reduced by stimulating the non-functional, structural shaft of the chopstick. This examination also dovetails with the work conducted by Holms and company (2004) by testing the difference between structural and functional portions of a tool in the tool-version of the RHI. If the illusion succeeds when the middle of the chopstick is stimulated, it suggests that the tool as a whole plays an important role in the success of the illusion, and that chopsticks create a compelling RHI for reasons other than the amount of torque afforded by their shape and size.

Methods

Participants

Sixty-seven right-handed individuals (17 males; mean age 18.4) participated in exchange for credit in an introductory psychology course at the University of Virginia. Data from 2 female participants was lost due to technical failure, 4 female participants' data was excluded due to loud construction noises and other disturbances during the illusion procedure, and a further 4 participants' (1 male) data was excluded due to participant failure to follow instructions, leaving a final sample of 57 participants. All participants had normal or corrected to normal vision and provided written informed consent prior to participation in the study.

Materials

Chopstick Rubber Hand. The same rubber hand holding chopsticks (pictured in Figure 3) used in previous studies was the only viewed object in this study.

Tool-Skill Task. The same bead transfer task described previously was again used to measure participant chopstick skill. All participants completed the task prior to experiencing the illusion.

Rubber hand illusion questionnaire. The 25 questions from Longo and colleagues (Longo et al., 2008) adapted to measure the chopstick-version of the RHI (Appendix A) were again used.

Experimental design and Procedure

A 2 x 2 design was employed. Location of visuo-tactile stimulation (chopsticks tip vs. chopsticks shaft) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within-subjects factors. All participants completed the tool skill task prior to undergoing the illusion. Participants were always holding a pair of chopsticks, and the viewed object was always the rubber hand holding chopsticks. What differed between conditions was the location where the visuo-tactile stimulation was delivered to both the rubber hand's held chopsticks and the participants' held chopsticks; these locations were always identical. The chopsticks "shaft" was the portion of the chopsticks just below the rubber hand and participants' fingers, extending for approximately 2.5 cm. The chopsticks "tips" were defined as the area that extended 2.5 cm from the tip of the chopsticks. Experimenters were instructed to keep the "tips" and "shafts" condition separate by selecting non-overlapping sections of the chopstick. Only the top chopstick of the pair received stimulation. The 4 within-subjects conditions, completed in a random order, were:

(i) chopstick tip synchronous; (ii) chopstick tip asynchronous; (iii) chopstick shaft synchronous; (iv) chopstick shaft asynchronous. Participants held chopsticks in all 4 illusion conditions.

Results and Discussion

Proprioceptive Drift

Assumptions of normal distribution, independence of residuals, and sphericity were met. A linear mixed-effects model that included parameters for location of visuo-tactile stimulation (chopsticks tip vs. chopsticks shaft), visuo-tactile stimulation (synchronous vs. asynchronous), chopsticks skill (the number of beads transferred in the tool-skill task) and a random effect of participant was fitted to the data. The analysis revealed only a significant main effect of timing of visuo-tactile stimulation (Wald Chi-Square (1) = 22.85, $p < 0.001$; all other *p*'s > 0.2) with synchronous stimulation resulting in greater proprioceptive drift (*M* = 2.32, *SE* = 0.41) than asynchronous stimulation (*M* = 0.19, *SE* = 0.31).

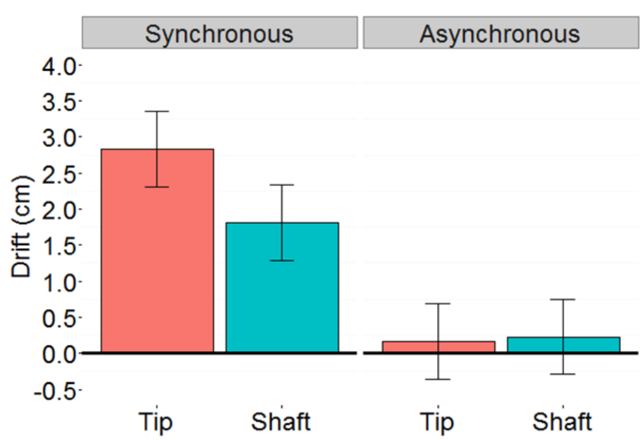

Figure 21. The main effect of timing of visuo-tactile stimulation was significant, with synchronous stimulation resulting in higher proprioceptive drift than asynchronous stimulation, across location of stimulation.

The non-significant interaction between location and timing of visuo-tactile stimulation is plotted in Figure 21, and suggests that the illusion will succeed regardless of whether the functional or structural portion of a tool is stimulated, so long as the stimulation occurs in synchrony with the stimulation of the participants' own held tool. This finding helps ease speculation that the teacup version of the RHI documented in Weser et al. 2017 may have succeeded had a more functional portion of the teacup received the visuo-tactile stimulation. It also serves to undermine the suggestion that the chopsticks version of the illusion succeeds only because the long slender shape of the tool provides stronger tactile information to the wielder than other tools. Since the illusion succeeds when the area close to a user's hand is stimulated, the success of the tool-version of the illusion is not dependent on whether or not the tool provides significant torque to strongly stimulate the hand holding the tool.

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 as within-subject factors. The analysis revealed a significant main effect of illusion questionnaire component ($F(4,52) = 120.86$, $p < 0.001$), a significant main effect of illusion condition ($F(3,56) = 87.43$, $p < 0.001$), and a significant interaction: $F(12,37) = 4.76$, $p < 0.001$. The interaction is plotted in Figure 22. Further analysis of each questionnaire component in separate ANOVAs revealed a significant difference between illusion conditions in the Affect component ($F(3,56) = 6.50$, $p < 0.001$), the Movement Component ($F(3,56) = 3.79$, $p = 0.010$), the Loss of Own Hand component ($F(3,56) = 13.36$, $p < 0.001$), and importantly, the Embodiment component: $F(3,56) = 75.17$, $p < 0.001$.

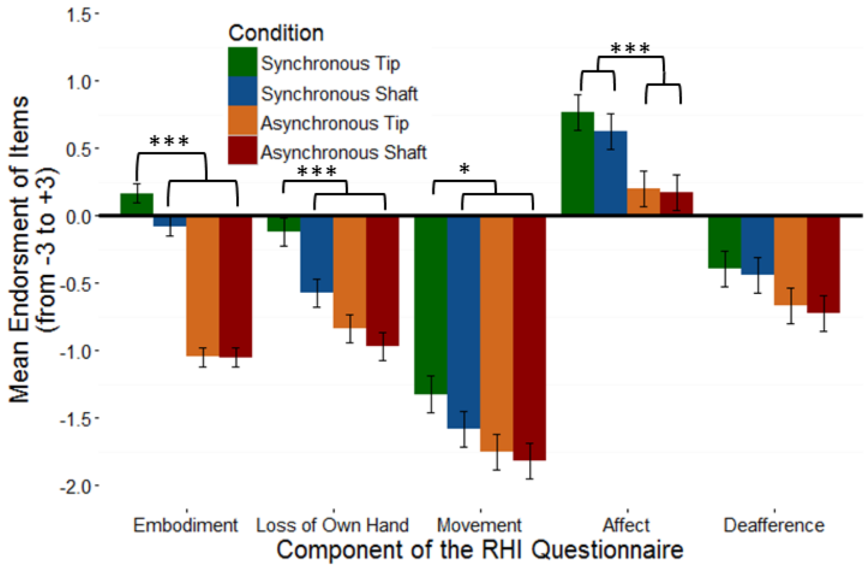

Figure 22. The interaction between illusion condition and RHI questionnaire component, with significant differences between illusion conditions for individual components marked with asterisks. Error bars represent ±1 SEM.

These results suggest that when participants experience the chopstick version of the RHI where the functional portion of the tool (the tip of the chopstick) receives synchronous visuo-tactile stimulation, they experience a stronger subjective feeling of rubber hand and tool embodiment, which likewise corresponds with a stronger feeling that their own hand holding chopsticks has been replaced. Though a weaker effect, participants in the synchronous tips condition also have a greater subjective feeling that their hand holding chopsticks is moving towards the rubber hand holding chopsticks (and visa-versa). These subjective differences between synchronous and asynchronous conditions are in line with previous research on the classic version of the RHI (Longo et al., 2008). Again, the tool-version of the illusion tends to result in a difference between conditions where the synchronous conditions have higher, not necessarily positive, endorsements of the questions relating to embodiment, movement, and loss of one's own hand. The significant difference between conditions in terms of Affect is unusual: most participants tend to report enjoying the experience regardless of condition. It is likely that participants in this experiment found viewing a rubber hand more interesting than a wooden block, and so their self-report for questions related to Affect were biased more by the visual component than the tactile component of the illusion.

It is noteworthy that participants subjectively experienced a difference between the synchronous stimulation of the functional portion of the tool (chopstick tip) and a non-function, structural portion of the tool (chopstick shaft). This stands in contrast with the behavioral measure of the illusion, where proprioceptive drift following the synchronous visuo-tactile stimulation of the chopstick tip did not differ significantly from the proprioceptive drift following synchronous visuo-tactile stimulation of the chopstick shaft. This suggests that tool-users may be consciously sensitive to the difference between functional and structural regions of a tool, but that the tool's effect on the body representation is affected less by the location of stimulation and more by whether or not it is synchronous.

Study 7: Chopsticks with Nonfunctional Grip

The specificity of the tool-version of the RHI (demonstrated in Study 4), in which only those participants with experience using tweezers experience the illusion, suggests that the illusion should not succeed when the tool is held in such a way as to compromise its function. Holding a tool like chopsticks in an inappropriate grip will strip away the previous tool experience that a user has had and should reduce the strength of the illusion. By holding the chopsticks so that they protrude from the first and second knuckles of one's fist, the amount of surface area of the fingers in contact with the tool is conserved yet the tool is rendered unusable.

If the illusion succeeds for skilled chopsticks users even under these conditions, than it may suggest top-down effects are at play, with participants able to recognize chopsticks regardless of the configuration of the hand. Otherwise, bottom-up and experience based factors likely drive the success of the illusion and prevent it from occurring when a nonfunctional grip on the tool is employed.

Methods

Participants

Sixty-five right-handed individuals (23 males; mean age 18.8) participated in exchange for credit in an introductory psychology course at the University of Virginia. Data from 4 participants (1 male) who failed to follow instructions was excluded, as was data from 3 female participants collected incorrectly due to experimenter error. Finally, data from 1 female participant was not recorded due to technical failure, which resulted in a final sample of 57 participants. All participants had normal or corrected to normal vision and provided written informed consent prior to participation in the study.

Materials

Rubber Hand with Chopstick in Nonfunctional Grip. A cast of the author's hand holding chopsticks "like Wolverine" (*X-Men* comic book character) was created from flesh-tinted plastic resin (see Figure 23). The chopsticks were held between the first and second and second and third knuckles with the fingers and thumb clenched in a fist. The pads of the index and middle finger were curled inward so as to press against the bottom of the chopstick. The rubber hand rests palm-down, with about two-thirds of the chopsticks extending forward. This nonfunctional grip was selected because it is completely nonfunctional and yet retains many of the same points of contact between hand and chopstick as does the functional chopstick grip.

Figure 23. The chopsticks extended 18 cm from the knuckles of the rubber hand. The chopsticks were held in such a way that the tips neither crossed nor touched the table at any point during the illusion procedure.

Wooden Block. The other viewed item was the wooden block (Figure 11 B) described in Study 3.

Tool-Skill Task. The same bead-transfer task described previously was used to measure participant chopstick skill. Participants held the chopsticks in the traditional, fictional grip for this task only.

Rubber hand illusion questionnaire. The same 25 questions from the Longo and colleagues (Longo et al., 2008) RHI Questionnaire adapted to measure the subjective experience of the chopstick-version of the illusion were again used (see Appendix A). The wording was not changed to reflect the change in chopstick grip.

Experimental design

A 2 x 2 design was employed. The viewed object (nonfunctional chopstick grip rubber hand vs. wooden block) and timing of visuo-tactile stimulation (synchronous versus asynchronous) were within-subjects factors. All participants completed the tool skill task prior to undergoing the illusion. The 4 within-subjects conditions, completed in a random order, were: (i) nonfunctional chopstick grip rubber hand synchronous; (ii) nonfunctional chopstick grip rubber hand asynchronous; (iii) wooden block synchronous; (iv) wooden block asynchronous.

Procedure

If upon arrival 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. Participants next completed the tool-skill task using chopsticks with the functional grip. Following the recording of the number of beads transferred, the experimenter demonstrated how to hold the chopsticks “like Wolverine from X-Men,” and then corrected the participant’s grip until his or her hand matched the rubber hand. The participant held the chopsticks in the non-functional grip for all 4 illusion conditions. The illusion induction was conducted as described in previous studies, with the experimenter always applying stimulation to the tip of the chopstick closest to the participant’s and rubber hand’s thumb.

Results and Discussion

Proprioceptive Drift

Assumptions of normal distribution, independence of residuals, and sphericity were met. A linear mixed effects model with a random factor of participant was fit to predict proprioceptive drift from the object viewed during the illusion, the timing of the visuo-tactile stimulation, and the number of beads transferred during the tool-skill task. The main effect of viewed object was significant: Wald Chi-Square (1) = 7.30, $p = 0.007$, with the non-functional chopsticks grip rubber hand ($M = 0.48$, $SE = 0.29$) yielding significantly higher proprioceptive drift than the wooden block ($M = -0.52$, $SE = 0.26$). Timing of visuo-tactile stimulation was not significant ($p = 0.16$), nor was the interaction ($p = 0.31$), which indicates that participants did not experience an illusion compelling enough to significantly alter the proprioceptively-inferred location of the hand during synchronous stroking of the rubber hand with an incorrect chopsticks grip. For comparison with previous studies, Figure 24 illustrates the non-significant interaction between viewed object and timing of visuo-tactile stimulation.

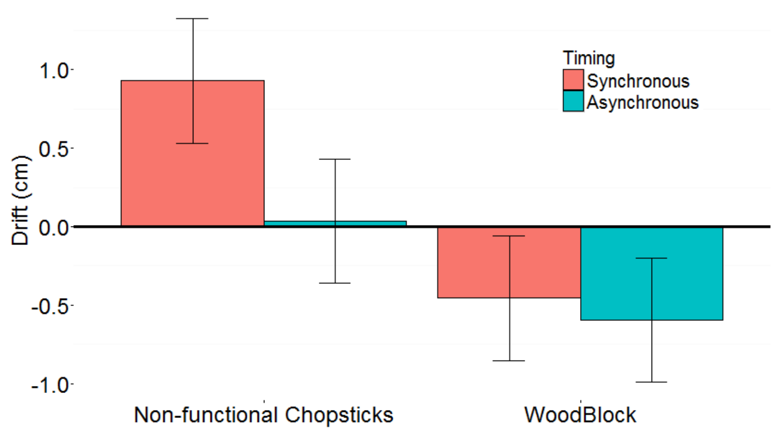

Figure 24. The non-significant interaction between the timing of the visuo-tactile stimulation and the viewed object (non-functional chopsticks grip rubber hand vs. wooden block). Error bars represent ±1 SEM.

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 as within-subject factors. The analysis revealed a significant main effect of illusion questionnaire component ($F(4,52) = 73.27$, $p < 0.001$), a significant main effect of illusion condition ($F(3,56) = 14.70$, $p < 0.001$), and a significant interaction: $F(12,37) = 10.43$, $p < 0.001$. The interaction is plotted in Figure 25. A separate ANOVA for each questionnaire component was conducted to further investigate the interaction. There was a significant difference between illusion conditions in the critical Embodiment component ($F(3,56) = 27.60$, $p < 0.001$) and also in the Movement component ($F(3,56) = 21.16$, $p < 0.001$.

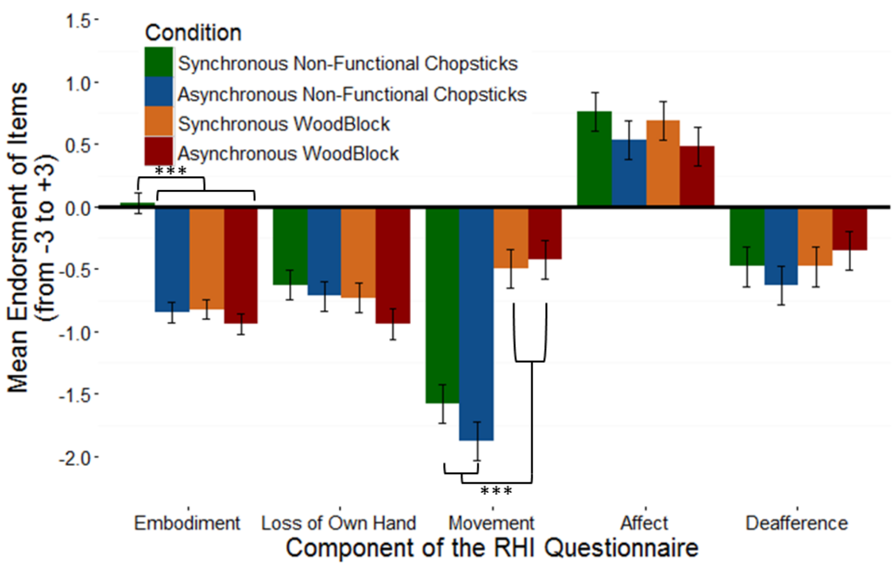

Figure 25. The significant interaction between illusion condition and RHI questionnaire component, with significant differences between illusion conditions assessed via post-hoc comparison of individual components marked with asterisks. Error bars represent ±1 SEM.

The significant difference in self-reported embodiment between the synchronous condition with a rubber hand that matched the participant's own hand and the three control conditions indicates that subjectively, participants were sensitive to the manipulation. As in the previous tool-version RHI studies, participants did not strongly endorse items related to embodiment, but rather responded more neutrally (closer to 0) than they did to the same questions addressing the asynchronous and wooden block conditions. The significant difference in subjective feelings of movement between the rubber hand conditions and the wooden block conditions is unexpected, as this effect is driven not by timing of visuo-tactile stimulation, but rather by viewed object.

In traditional RHI studies, usually synchronous visuo-tactile stimulation is associated with the subjective experience that the rubber hand and the participant's real hand are moving closer together, rather than a match between the participant's own hand and the rubber hand. Participants were not strongly expressing that the wooden block was moving towards their hand (as their responses were still negative), but they were consistent in strongly rejecting statements that suggested the feeling that the real and rubber hands were moving closer together. It may be the case that the pose selected for this experiment (with the hand clenched in a fist) was more static than the grips used in previous tool studies and traditional rubber hand studies. The static nature of the fist pose may have then reduced subjective feeling of motion towards the rubber hand, causing participants to respond more negatively when the fist-rubber hand was in view than when a neutral wooden block was present.

Conclusion

The effects of tools and rubber hands on body representations have been reported in disparate literatures since both fields began to gain traction in the past 20 years. Similarly, for over 100 years, researchers have recognized a sharp divide between the body schema, a body representation for action, and the body image, a body representation for perception and identification (Head & Holms, 1911; Anema et al. 2009). Many have argued that the embodiment of external limbs in the RHI is fundamentally different from the type of embodiment experienced by tool users (De Preester & Tsakiris, 2009; De Vingemont, 2010). Although both skilled tool users and individuals who experience the RHI report that the tool or rubber hand feels like it is a part of their body, the effects of tool-incorporation and rubber-hand incorporation on subsequent behavior are markedly different.

Tool use alters the kinematics of reach to grasp movements (Cardinali et al., 2011, 2012), but the RHI does not (Kammers et al., 2009, but see Holmes, Snijders & Spence, 2006, for a different account). Changes to grasping movements following tool use suggests a *motoric* modification of the representation of the body, caused by changes in the way the body is represented for action, i.e. the body schema (De Vignemont, 2010). On the other hand, the experience of the RHI causes a number of physiological changes such as a decrease in temperature of the real hand undergoing stimulation (Moseley et al., 2008), and an increase in skin conductance response (SCR) when the rubber hand is injured (Armel & Ramachandran, 2003), for example. These findings are different in kind than those reported for tools, and suggest that embodying the rubber hand involves the subjective experience of identifying with it, and subsequently *replacing* the stimulated hand with the rubber one (De Vignemont, 2010). This process is thought to be a perceptual one, as the illusion is induced through multisensory stimulation of an object similar in appearance to the experiencer's real hand. This perceptual modification is tapping into the representation of the body for identification, the body image. The difference in behavioral and subjective outcomes following tool use and RHI induction mirror the double dissociation of body schema and body image identified in neurophysiological patients (Anema et al., 2009).

Barring brain injury or the isolated study of a particular type of embodiment through illusion or tool training studies, the body schema and the body image must work in harmony for one to experience a coherent sense of control over and identification with one's physical form. Thus it seems likely that the two representations are not entirely separate. Weser et al. (2017) set out to examine the link between the embodiment of tools and rubber hands by adapting the classic RHI illusion to include a handheld tool. Skillfully using chopsticks prior to experiencing a RHI in which chopsticks receive the visuo-tactile stimulation increases the experience of the illusion, as measured behaviorally through proprioceptive drift (Weser et al., 2017).

Proprioceptive drift is the difference between a participant's estimate of the position of his or her own hand before and after the visuo-tactile stimulation of the real and rubber hands. Proprioceptive drift is believed to be a behavioral measure of the RHI that indexes the effect of visuo-tactile stimulation of non-corporeal objects on the body image. Since the RHI is performed with passive tactile stimulation and measured with introspective report and visual judgments of the location of one's hand, it is believed to be a purely perceptual (as opposed to motoric) illusion that only alters the body image, not the body schema (De Vingemont, 2010). In contrast, practice using a tool results in real time updates to one's capacity for action that is captured by changes to the body schema. The findings of Weser et al. were novel because the motoric changes to the body schema following chopstick use manifested in the measure of changes to the body image as assessed by perceptual drift in the RHI. Moreover, perceptual drift was even larger for participants who had a chance to use the chopsticks prior to experiencing the illusion than for participants who used chopsticks after the illusion. This indicates that motoric updates to the body schema following tool use also influence the body image.

Most researchers report a strong correlation between subjective reports of the experience of the illusion (e.g. “it felt like the rubber hand was part of my body”) and proprioceptive drift *towards* the rubber hand (e.g. Tsakiris & Haggard, 2005). In other words, participants estimate that their hand is closer to the rubber hand when they have a stronger feeling that the rubber hand is part of them. However, in both Weser et al. 2017 and the studies presented here, synchronous stimulation of a rubber hand holding a tool matching the participant’s own held tool did not result in high self-reported rubber hand embodiment, even when synchronous visuo-tactile stimulation did cause high proprioceptive drift. So although tool-versions of the RHI do provide evidence for cross-talk between the body models for perception and action, the introspective aspect of this perceptual illusion seems to be less susceptible to modification from tools. The studies presented here were designed to investigate the difference in the behavioral outcome of the chopsticks and teacup version of the RHI conducted in Weser et al., but together they also contribute to the mounting evidence that proprioceptive drift and the introspective questionnaires used in the RHI literature do not necessarily measure the same phenomena, as they are not always strongly or even positively correlated (e.g., Holmes, Snijders, & Spence, 2006; Makin, Holmes, & Ehrsson, 2008; Rohde, Di Luca, & Ernst, 2011).

The RHI is thought to be the product of the three-way interaction between vision, touch and proprioception (Botvinick & Cohen, 1998). Several findings suggest that proprioceptive drift depends upon multisensory integration (e.g. Holle, McLatchie, Maurer, & Ward, 2011), while the subjective self-report of illusory ownership of the hand involves a second mechanism which attempts to match the viewed object with the representation of the body for identification, the body image (for a review see Tsakiris, 2010). This proposal suggests that a bottom up process first checks for synchronicity in the incoming multisensory sensory stimuli (the visuo-tactile stimulation) and a top-down process next compares the viewed object with an internal representation of one's own body (Tsakiris & Haggard, 2005). If there is both synchronicity and a match between viewed object and body representation, then and only then should one experience illusory ownership of the object viewed during the illusion. Although this match is preserved in the tool-versions of the illusion (the rubber hand and the participant both held an identical tool), the results of the studies presented here indicate that this match is not enough to induce a subjective feeling of identification with the tool-holding rubber hand.

Proprioceptive drift results from the process of multisensory integration, which is prerequisite for identification with and subsequent illusory ownership of the rubber hand. Drift can occur in the absence of ownership, as it does during the chopsticks and tweezers versions of the RHI, but ownership of the rubber hand depends on both multisensory integration and a process of self-identification. Although sports players, musicians and other professional tool users may feel a strong sense of completion when holding the tool of their trade, most people do not strongly identify with tools like tweezers and chopsticks. However, the link between skilled tool use and multisensory integration runs deep through the literature, so it is not surprising that this first requirement for the RHI is met and results in the proprioceptive drift effects in the chopsticks experiment described in Weser et al. and in Studies 1, 2, 4, and 6.

Why proprioceptive drift only results from some tool-versions of the RHI but not others was the driving force behind the studies presented here. Across 7 studies, 3 mechanisms were tested to examine differences in proprioceptive drift resulting from different tools used in the RHI: tool morpho-functional and sensorimotor match, tool expertise, and more broad tool characteristics such as shape and function, as well as the role played by the effector supporting the tool (be it hand or otherwise). To assess tool morpho-functional and sensorimotor match, the outcomes of illusions conducted on rubber hands holding pliers and tweezers (Studies 3 and 4) were compared. The morpho-functional component of a tool refers to its shape and the action it affords. Sensorimotor is the wielder's actions and grip while using the tool and the resulting tool function. It has been speculated that the match or lack of match on one or both dimensions determines whether or not a modulation of the wielder's body representation occurs (Cardinali et al. 2016; Miller, Longo, & Saygin, 2014).

Studies 3 and 4 examined the difference between tools that both act on the environment in a precision manner, and therefore have the same morpho-functional attributes, but the tools are operated with either a power grip (pliers) or a precision grip (tweezers), and therefore differ at the sensorimotor level. Only the tool with a morpho-functional and sensorimotor match (tweezers: precision action, precision grip) resulted in a successful tool-version of the RHI, confirming that the same match found in chopsticks may play a deciding role in the illusion's success. That said, the tweezers version of the illusion only succeeded for participants who reported frequent tweezers use, suggesting that tool-expertise, or at least experience, also effects whether or not a tool will alter one's body representation.

Relatedly, breaking the morpho-functional and sensorimotor match between a tool and the wielder's hand by altering the grip on the tool also disrupts the illusion: Study 7, in which participants held chopsticks in a fist (like Wolverine, the comic book character), demonstrates that the illusion cannot succeed when the grip on the tool renders it non-functional. This finding also ties in with the stipulation that the tweezers-version of the illusion only succeeds for individuals who report frequent tweezers-use. Changing the grip on the chopsticks leaves them not only unusable, but also disrupts any previous chopstick experience participants may have had prior to experiencing a chopsticks-version of the RHI.

With regard to tool skill, Study 2 revealed that participants' experience of the illusion in terms of proprioceptive drift is impacted *equally* by all 3 manipulations assessed: participants experience the illusion with equivalent intensity regardless of whether they spent 5 minutes simply holding chopsticks (without using them), watching someone else use chopsticks for 5 minutes, or if they both held and watched chopsticks used by an experimenter. This is remarkable because previous literature suggests that participants both holding and watching chopsticks should have had an advantage over those who merely held or merely watched chopsticks because observing tool actions extend reachable space representations *only* when the observer is also holding the tool (Constantini et al., 2011). Moreover, tool effects on peripersonal space representation (Witt et al. 2005; Cardinali et al. 2009; Brown et al. 2011) and crossmodal correspondence paradigms (Maravita et al., 2002; Maravita, Spence, & Driver, 2003) are detected only when experimenters allow the participant to use the tool prior to measuring the effect. Thus it seems that there are fewer restrictions to the ways prior viewing or handling chopsticks facilitates the tool-version of the RHI than for other measures of tool-body representation interaction.

The effect of general tool morphology and the idiosyncrasies of the RHI in general were investigated in 3 studies: Study 6 compared the functional and structural components of the tool, in Study 5 the illusion was conducted on a non-tool wooden block, and finally Study 1 assessed the importance of the appearance of the hand holding the tool. In Study 6, the replication of the chopsticks version of the illusion with the visuo-tactile stimulation occurring on shaft of the chopstick, rather than the tip, helped to clarify the role of tool-morphology. Because synchronous tactile stimulation of both the shaft and the tip of the chopstick resulted in proprioceptive drift significantly greater than asynchronous stimulation of either section of the tool, it suggests that the success of the illusion is not contingent on the tool providing enough torque to allow a strong sensation of stimulation in the wielder’s fingers. Indeed, the success of the tweezers version of the illusion also indicates that a long, thin tool is not the only object capable of affecting body representations, although across the literature, long slender tools have received the most attention. That said, the introspective reports of participants in this illusion reveal that subjectively, people are sensitive to the distinction between the functional portion of the tool (tip) and a merely structural section of the tool (chopstick shaft). When the chopstick tip was stroked synchronously, the average endorsement of questions related to the embodiment of the chopsticks-holding rubber hand was positive, while it was negative when it was the shaft that was synchronously stroked.

Study 5 demonstrated that a reason some of the tool-versions of the illusion result in changes to proprioceptive drift is because tools have defined, functional regions to which participants can easily attend. There were no significant differences in proprioceptive drift for the 4 illusions conditions when the RHI was performed on either a rubber hand holding a wooden block (a non-tool) or when the classic control object was used—a wooden block (without a rubber hand holding it). As all conditions yielded somewhat positive drifts, it seemed likely that participants were unable to use proprioception to discern the location of the front right-corner of the wooden block they held, even before they underwent the illusion. This uncertainty speaks to the lack of familiarity participants had with wielding a wooden block, and serves to emphasize the importance of both tool familiarity and the match between participant grip and tool output, or morpho-functional and sensorimotor match (as seen in both tweezers- and chopsticks-versions of the illusion). However, participants in this study reported the highest feeling of embodiment for any of the studies presented here. Although the embodiment score was still low relative to traditional RHI studies, the lack of distinctive tool qualities may have better facilitated participants' focus on the presence of the rubber hand, allowing for a stronger sense of identification with the hand.

In Study 1, it was not necessary for the object supporting the tool to look like a hand: the presence of the tool with synchronous visuo-tactile stimulation was all that was required for proprioceptive drift to occur. Importantly, the non-hand-shaped object was holding the chopsticks with the correct posture, which preserved the correspondence between the participants' own held chopsticks and the chopsticks they observed during the induction of the illusion. Although drift occurred regardless of the presence of a hand, participants reported a stronger sense of rubber hand embodiment when they viewed a rubber hand (rather than a blob), regardless of the timing of visuo-tactile stimulation. This subjective finding is consistent with the template matching hypothesis of Tsakiris and Haggard (2005), which posits that a hand must be present for identification to occur. However, the occurrence of proprioceptive drift in both synchronous conditions fits with studies on "invisible" hands, which found proprioceptive drift following the synchronous visuo-tactile stimulation of a participants' hand and thin air, so long as the outline of a hand was traced accurately (Guterstam, Gentile, & Ehrsson, 2013).

Across all 7 studies, the dissociation between body models of action and body models of perception manifests in the differing ways proprioceptive drift is altered by tool experience. Although much of the past literature has focused on the ways in which the incorporation of rubber hands differs from that of tools, the work presented here demonstrates that the body image and the body schema do not operate in complete isolation. Body image-based identification with the rubber hand was confirmed to be largely unaffected by changes to the body schema, but tool-use did impact proprioceptive drift, the other measure of the body image.

When given the opportunity to use chopsticks prior to experiencing the tool-version of the RHI, the changes to the body schema manifested in increased proprioceptive drift relative to the drift experienced by individuals who used the tool following the illusion. Moreover, only individuals who frequently used tweezers experienced a tweezers version of the RHI, suggesting that long term tool use facilitated body image modification during synchronous visuo-tactile stimulation of real and rubber hands holding tools. Taken together, this indicates that the body image remains distinct from the body schema when it comes to introspective self-identification, but that taking action with tools can alter perceptual models of the body. The exploration of the mechanisms that contribute to and are responsible for tool-effects on body representations makes an important contribution to the literature: it is an investigation of the complex interplay between bottom-up effects such as simultaneous multisensory integration and tool experience with more top-down knowledge about body appearance, identity, position, tool function, appropriate grip, and tool expertise.

References

Anema, H. A., van Zandvoort, M. J., de Haan, E. H., Kappelle, L. J., de Kort, P. L., Jansen, B. P., et al. (2009). A double dissociation between somatosensory processing for perception and action. *Neuropsychologia*, 4 , 1615–1620.

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1523), 1499-1506.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version, 1(7), 1-23.

Biggio, M., Bisio, A., Avanzino, L., Ruggeri, P., & Bove, M. (2017). This racket is not mine: The influence of the tool-use on peripersonal space. Neuropsychologia, 103, 54-58.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, 391(6669), 756.

Brown, L. E., Doole, R., & Malfait, N. (2011). The role of motor learning in spatial adaptation near a tool. *PLoS ONE*, 6(12), 1-9.

Cardinali, L., Brozzoli, C., Urquizar, C., Salemme, R., Roy, A. C., & Farnè, A. (2011). When action is not enough: Tool-use reveals tactile-dependent access to body schema. *Neuropsychologia*, 49(13), 3750-3757.

Cardinali, L., Brozzoli & Farnè, A. (2009). Peripersonal space and body schema: Two labels for the same concept?. *Brain Topography* 21, 252–260.

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Current Biology,* 19(12), R478-R479.

Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A. C., & Farnè, A. (2012). Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Experimental Brain Research*, 218(2), 259-271.

Costantini, M., Ambrosini, E., Sinigaglia, C., & Gallese, V. (2011). Tool-use observation makes far objects ready-to-hand. *Neuropsychologia*, 49(9), 2658-2663.

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness and Cognition*, 16(2), 229-240.

Clark, A. (2008). Supersizing the mind: Embodiment, action, and cognitive extension. New York, NY: Oxford University Press.

Clark, A. (2003). Natural-Born Cyborgs. New York, NY: Oxford University Press.

De Preester, H., & Tsakiris, M. (2009). Body-extension versus body-incorporation: Is there a need for a body-model?. *Phenomenology and the Cognitive Sciences*, 8(3), 307-319.

de Vignemont F., Farné A. (2010). Widening the body to rubber hands and tools: What's the difference?. *Revue de Neuropsychologie*, 2(3), 203–211. Retrieved from http://jeannicod.ccsd.cnrs.fr/docs/00/51/23/13/PDF/RHI_and_tool.pdf

Farnè, A., & Làdavas, E. (2000). Dynamic size- change of hand peripersonal space following tool use. *Neuroreport*, 11(8), 1645-1649.

Finotti, G., Migliorati, D., & Costantini, M. (2018). Multisensory integration, body representation and hyperactivity of the immune system. Manuscript submitted for publication.

Fourkas, A. D., Bonavolont, V., Avenanti, A., & Aglioti, S. M. (2008). Kinesthetic imagery and tool-specific modulation of corticospinal representations in expert tennis players. *Cerebral Cortex*, 18(10), 2382-2390.

Graziano, M.S.A. and Botvinick, M.M. (2002). How the brain represents the body: Insights neurophysiology and psychology. Common Mechanisms in Perception and Action: Attention and Performance XIX (Prinz, W. and Hommel, B., eds), 136–157, Oxford University Press.

Guterstam, A., Gentile, G., & Ehrsson, H. H. (2013). The invisible hand illusion: multisensory integration leads to the embodiment of a discrete volume of empty space. *Journal of Cognitive Neuroscience*, 25(7), 1078-1099.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34(2-3), 102-254.

Haans, A., IJsselsteijn, W. A., & de Kort, Y. A. (2008). The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image*, 5(4), 389-394.

Holle, H., McLatchie, N., Maurer, S., & Ward, J. (2011). Proprioceptive drift without illusions of ownership for rotated hands in the “rubber hand illusion” paradigm. *Cognitive neuroscience*, *2*(3-4), 171-178.

Holmes, N. P., Calvert, G. A., & Spence, C. (2004). Extending or projecting peripersonal space with tools? multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience Letters*, 372(1-2), 62-67.

Holmes, N. P., Snijders, H. J., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception & Psychophysics*, 68(4), 685-701.

Iriki, A., Tanaka, M. and Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330.

Kammers, M., de Vignemont, F., Verhagen, L., & Dijkerman, H. C. (2008). What is embodiment?: A psychometric approach. *Cognition*, 107(3), 978-998.

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. Journal of Statistical Software, 69(1), 1-33. doi:10.18637/jss.v069.i01

Longo, M. R., Schüür, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, 107(3), 978-998.

Longo, M. R., Schüür, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. Acta psychologica, 132(2), 166-172.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, 8(2), 79-86.

Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: Close to hand and within reach. *Current Biology*, 13(13), R531-R539.

Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, 83(2), B25-B34.

Miller, L. E., Longo, M. R., & Saygin, A. P. (2014). Tool morphology constrains the effects of tool use on body representations. *Journal of Experimental Psychology: Human Perception and Performance*, 40(6), 2143.

Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., et al. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences of the USA*, 105(35), 13169–13173.

Paillard, J. (1999). Body Schema and body image-a double dissociation. *Motor control, today and tomorrow*, 197-214.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rohde M, Di Luca M, Ernst MO (2011) The Rubber Hand Illusion: Feeling of Ownership and Proprioceptive Drift Do Not Go Hand in Hand. *PLoS ONE* 6(6): e21659. https://doi.org/10.1371/journal.pone.0021659

Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703-712.

Tsakiris, M. (2016). The multisensory basis of the self: from body to identity to others. *Quarterly Journal of Experimental Psychology* (Hove), 1-28. doi: 10.1080/17470218.2016.1181768

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, 31(1), 80.

Tsakiris, M., Tajadura-Jiménez, A., & Costantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society of London B: Biological Sciences*, 278 (1717), 2470-2476.

Wang, Z., Wang, S., Shi, F. Y., Guan, Y., Wu, Y., Zhang, L. L. & Zhang, J. (2014). The effect of motor imagery with specific implement in expert badminton player. *Neuroscience*, 275, 102-112.

Weser, V., Finotti, G., Costantini, M., & Proffitt, D. R. (2017). Multisensory integration induces body ownership of a handtool, but not any handtool. *Consciousness and Cognition*, 56, 150-164.

Witt, J.K. & Proffitt, D.R. (2008) Action-specific influences on distance perception: A role for motor stimulation. Journal of Experimental Psychology*: Human Perception and Performance* 34(6): 1479-1492.

Witt, J.K., Proffitt, D.R., & Epstein, W. (2005). Tool use affects perceived distance, but only when you intend to use it. *Journal of Experimental Psychology: Human Perception and Performance* 31(5): 880-888.

Yamamoto, S., & Kitazawa, S. (2001a). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience* 4: 759-765.

Yamamoto, S., & Kitazawa, S. (2001b). Sensation at the tips of invisible tools. *Nature Neuroscience*, 4(10), 979-980.

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
It seemed like I was looking directly at my own hand holding chopsticks, rather than at a rubber hand holding chopsticks.	❍	❍	❍	❍	❍	❍	❍
It seemed like the chopsticks I was holding were in the location where the rubber hand was holding the chopsticks.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand holding chopsticks was moving towards my hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand holding chopsticks was my hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like I had three hands.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand holding chopsticks was part of my body.	❍	❍	❍	❍	❍	❍	❍
I had the sensation of pins and needles in my hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand holding chopsticks was in the location where my hand was.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand holding chopsticks belonged to me.	❍	❍	❍	❍	❍	❍	❍
I found that experience interesting.	❍	❍	❍	❍	❍	❍	❍
It seemed like I could have moved the chopsticks in the rubber hand if I had wanted.	❍	❍	❍	❍	❍	❍	❍
It seemed like my own hand became rubbery.	❍	❍	❍	❍	❍	❍	❍
It seemed like I was unable to move the chopsticks in my hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like my hand had disappeared.	❍	❍	❍	❍	❍	❍	❍
The touch of the paintbrush on my chopsticks was pleasant.	❍	❍	❍	❍	❍	❍	❍
It seemed like my hand was out of control.	❍	❍	❍	❍	❍	❍	❍
I found that experience enjoyable.	❍	❍	❍	❍	❍	❍	❍
It seemed like I could move the chopsticks in my hand if I wanted.	❍	❍	❍	❍	❍	❍	❍
It seemed like my hand was moving towards the rubber hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like I was in control of the chopsticks in the rubber hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like I couldn’t really tell where my hand was.	❍	❍	❍	❍	❍	❍	❍
It seemed like the experience of my hands was less vivid than normal.	❍	❍	❍	❍	❍	❍	❍
I had the sensation that my hand was numb.	❍	❍	❍	❍	❍	❍	❍
It seemed like the touch I felt was caused by the paintbrush touching the chopsticks held by the rubber hand.	❍	❍	❍	❍	❍	❍	❍
It seemed like the rubber hand began to resemble my real hand.	❍	❍	❍	❍	❍	❍	❍