

15 **Abstract**

16 Bodily boundaries are computed by integrating multisensory bodily signals and can be
17 experimentally manipulated using bodily illusions. Research on tool use demonstrates that
18 tools alter body representations motorically to account for changes in a user's action
19 repertoire. The present experiment sought to unify perceptual and motoric accounts of tool
20 embodiment using a modified Rubber Hand Illusion (RHI) that also addressed the skill and
21 practice aspects of the tool use literature. In Experiment 1, synchronous multisensory
22 stimulation induced perceptual embodiment of a tool, chopsticks. The embodiment of
23 chopsticks was stronger for more skilled participants, and if the illusion was preceded by tool
24 use. In Experiment 2, the illusion was not elicited with a different type of tool, a teacup,
25 showing that not all objects can be incorporated. This experiment helps to clarify the role of
26 perceptual and motoric embodiment and suggests future avenues for research into tools
27 embodiment using this method.
28

29 **1. Introduction**

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

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

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

49 Recent advances in our knowledge of how the brain represents the body have been
50 pioneered through the experimental use of perceptual illusions. One of the most used and best
51 known paradigms is the Rubber Hand Illusion (RHI) (Botvinick & Cohen, 1998). In its
52 classic form, synchronous visuo-tactile stimulation of a rubber hand and the participant's

53 hidden hand induces a recalibration of the proprioceptive felt position of the participants'
54 hand and a feeling ownership of the rubber hand (Botvinick & Cohen, 1998; Costantini,
55 2014; Tsakiris, 2016; Tsakiris & Haggard, 2005). This has been classically interpreted in the
56 literature as evidence that the manipulation of multisensory inputs (i.e. visual and tactile
57 stimulation), can induce the embodiment of an external, dummy hand into one's own body
58 representation (Blanke, 2012; Ehrsson, 2012), for a different view (David, Fiori, & Aglioti,
59 2014). Similar experiences of illusory ownership have been obtained, for example, for faces (
60 Tsakiris, 2008), whole bodies (Petkova & Ehrsson, 2008), and even for virtual avatars
61 (Banakou, Groten, & Slater, 2013; Hägni et al., 2008; Slater, Perez-Marcos, Ehrsson, &
62 Sanchez-Vives, 2008) and small dolls (van der Hoort, Guterstam, & Ehrsson, 2011).
63 Together, these findings show that the multisensory representation of our body is not fixed
64 and immutable, but rather extremely flexible and continuously updated through the
65 integration of multisensory information (for a review, see Costantini, 2014). This scalability
66 of the body representation is also thought to contribute to human tool use proficiency (e.g.,
67 Cardinali et al., 2012). When we use tools to manipulate the environment, the brain receives
68 somatosensory signals evoked at the hand wielding the tool. Yet, we often have the subjective
69 feeling that the touch is occurring on the tip of the tool itself. This feeling seems to be a by-
70 product of how the body representation is rescaled to incorporate the tool.

71 For instance, seminal work with both humans and primates demonstrated that the use of
72 a tool for a prolonged period of time extends the multisensory neural representations of the
73 space surrounding the hand (Bonifazi, Farnè, Rinaldesi, & Lådavas, 2007; Iriki, Tanaka, &
74 Iwamura, 1996). Similarly, Cardinali et al. showed that tool use can induce a morphological
75 update of the body representation (Cardinali et al., 2011; Cardinali et al., 2009), and of body
76 kinematics (Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Cardinali et al., 2011; Cardinali
77 et al., 2012). This modification of the body representation is likely to reflect an incorporation

78 of the tool into the body representation. For instance, a series of studies showed that the
79 tactile signals felt in the hand that occur when a held tool comes into contact with an object
80 are referred directly to the tip of the tool (Maravita et al., 2002; Yamamoto & Kitazawa,
81 2001; Yamamoto, Moizumi, & Kitazawa, 2005). Moreover, the self-produced touch
82 attenuation phenomena occurs when the participant touches his or her own limb using a tool:
83 self-produced touches are lighter than identical touches applied by another because these
84 touches have already been anticipated by a forward sensory model that takes handheld tools
85 into account (Kilteni & Ehrsson, 2017). In other words, even though the somatosensory
86 signal is originating from the receptors located on the hand, the brain treats this information
87 as if it originated from the tip of the tool.

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

98 The current experiments investigated this issue. In particular, we hypothesized the
99 importance of three factors for the modified RHI illusion to occur: a) the type of tool (and in
100 particular, the match or mismatch between the tool's function and the grip exerted to wield
101 the tool) b) one's level of proficiency in using the tool, and c) recency of experience with the

102 tool. These points are explained in greater detail in the following sections. To test these
103 hypotheses, we conducted two experiments.

104 **2. Experiment 1**

105 **2.1 Introduction**

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

119 Our choice to use chopsticks was based on several considerations. First, previous
120 studies have already shown that tools like drumsticks (e.g. Yamamoto & Kitazawa, 2001;
121 Yamamoto et al., 2005), and chopsticks (Rademaker, Wu, Bloem, & Sack, 2014) can be
122 incorporated in the body representation. Furthermore, we hypothesized that the functional
123 characteristics of a non-body shaped tool would be crucial for its incorporation, and therefore
124 for the update of the extended body representation in the RHI. This hypothesis is supported
125 by recent evidence showing that the embodiment of tools is constrained not only by the

126 morphology of the tool, but also by its functionality (Miller, Longo, & Saygin, 2014). Though
127 chopsticks violate the morphological similarity between the participant's hand and the viewed
128 object, they are manipulated using a precision grip and they function to extend the fingers in
129 a precision grip action (Goldenberg & Iriki, 2007). Thus, chopsticks are morphologically
130 dissimilar, but have a functional match with the human fingers. Past literature has focused
131 primarily on the incorporation of simple hand-held tools, such as sticks (e.g. Maravita,
132 Husain, Clarke, & Driver, 2001; Maravita et al., 2002; Neppi-Mòdona et al., 2007; Yamamoto
133 et al., 2005), rakes (e.g. Iriki et al., 1996; Farnè & Làdavvas, 2000; (Bonifazi et al., 2007;
134 Farnè & Làdavvas, 2000; Iriki et al., 1996; Jovanov, Clifton, Mazalek, Nitsche, & Welsh,
135 2015), and mechanical grabbers (e.g. Cardinali et al., 2011; Cardinali et al., 2009; Cardinali et
136 al., 2012). The use of these tools rely more on information coming from proximal parts of the
137 hand and arm representation, while chopsticks rely more on finger representation (Rademaker
138 et al., 2014). Thus, although much of the past literature on tool use has focused on larger,
139 reach extending tools like mechanical grabbers, chopsticks seem suitable for use with the
140 RHI paradigm because of the active involvement of the hand and fingers during chopstick
141 use.

142 A second aim of the experiment was to investigate the role of tool proficiency in the
143 plasticity of the body representation. We hypothesized that the update of the body
144 representation toward the external tool, as indexed by the successful induction of the RHI,
145 would be greater when participants: a) had recent practice with the tool, and b) were more
146 skilled in using the tool. Previous studies demonstrate that these two factors (practice and
147 skill) facilitate the embodiment of a tool (e.g., Rademaker et al., 2014). Thus, we predicted
148 that this facilitation would also reflect in the dynamic update of the extended body
149 representation. The choice of chopsticks was particularly conducive to addressing this aim.
150 Chopsticks are one of the most commonly used tools in the world: more than 30% of human

151 population uses chopsticks on a daily basis (Kitamura, Higashi, Masaki, & Kishino, 1999).
152 Despite their global popularity, many people struggle with chopstick use. For instance, in a
153 2014 chopstick proficiency survey of Americans, 4% of those surveyed considered
154 themselves experts at using chopsticks, 11% rated themselves as very good, 19% fair, 20%
155 not very good, 23% terrible, while 24% stated that they had never even tried them
156 (<http://www.statista.com/>, 2014). This large variation in chopstick skill within the general
157 population made it easy to test the impact of individual differences in tool skill on tool
158 embodiment. To test the relevance of both skill and recent practice, we designed a task that
159 would both measure the relative tool skill of our participants and provide them with practice
160 manipulating the tool (Bead-Transfer Task, see Methods).

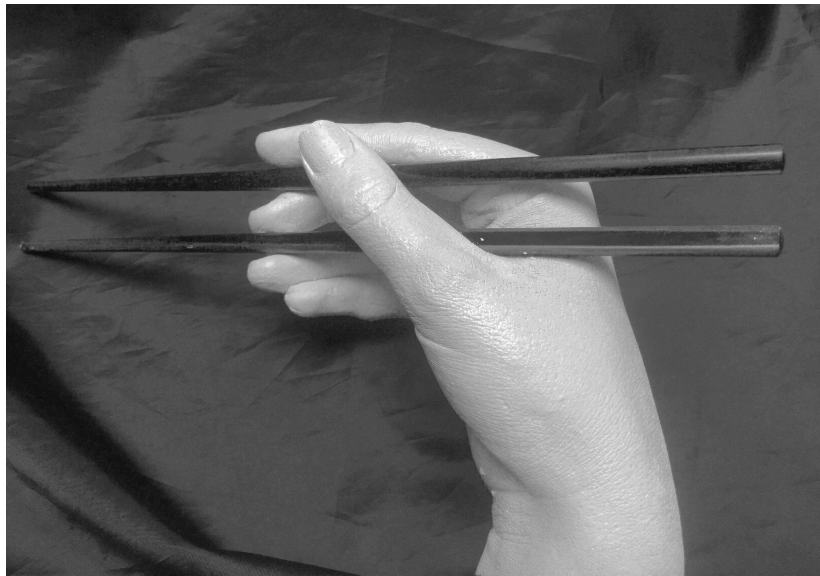
161 **2.2 Methods**

162 **2.2.1 Participants**

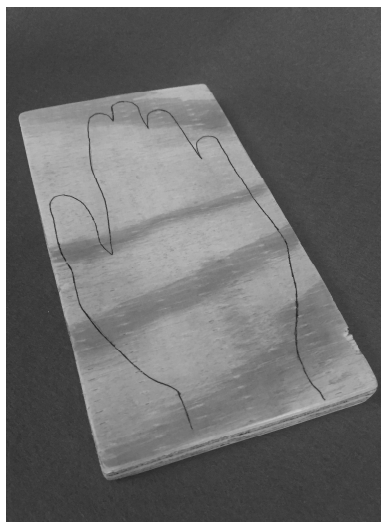
163 Fifty-seven right-handed individuals (mean age 18.8) participated in exchange for
164 credit in an introductory psychology course at the University of Virginia. Twenty-seven
165 participants (17 females) performed the bead-transfer task prior to experiencing the
166 chopstick-version of the rubber hand illusion (CRHI), while the remaining 30 participants (16
167 females) performed the bead-transfer task after undergoing the illusion. All participants were
168 right-handed, had normal or corrected to normal vision, and provided written informed
169 consent prior to participation in the study.

170 **2.2.2 Materials**

171 **Chopstick Rubber Hand.** A cast of the first author's hand holding chopsticks was
172 made from flesh-tinted plastic resin. The chopsticks were glued to the hand to minimize
173 chopstick movement during the experimental procedure (Figure 1A). An identical pair of
174 chopsticks was held by the participant throughout the duration of the experiment.



A.



B.



C.

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

175

176 **Bead-Transfer Task.** Plastic beads measuring 0.8 cm in diameter were utilized in a task
177 designed to measure participant chopstick proficiency. Participants were given a tray
178 containing 270 beads of various colors and instructed to sort by color as many beads as
179 possible by transferring them to a container with 6 compartments. Each of the six
180 compartments was designated to hold a particular color of bead. There were 30 beads of each
181 color to be sorted, and 90 “distractor beads.” Participants were required to move all beads of
182 one color to the container before starting on the next color. Participants were allotted 5

183 minutes to transfer as many beads as possible. The number of beads transferred was recorded
184 and used as a proxy value for participant chopstick skill.

185

186 **Rubber hand illusion questionnaire.** We adapted a total of 25 questions from Longo
187 and colleagues (Longo et al., 2008) to measure the subjective experience of the CRHI (See
188 Appendix A). In particular, the questions adopted referred to five different components of the
189 experience of the illusion: embodiment of the rubber hand (ten statements), loss of the real
190 hand (five statements), movement of the real or rubber hand (three statements), deafference
191 of the real hand (three statements), and affect (three statements). All questions were modified
192 to refer to the chopsticks held by the rubber hand, rather than to the rubber hand itself.

193 **2.2.3 Experimental design**

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

203 In the synchronous visuo-tactile stimulation conditions, the experimenter used 2
204 paintbrushes to manually stroke the tip of the participant's held chopsticks and the viewed
205 object at the same time. In the asynchronous visuo-tactile conditions, the experimenter
206 stroked the participant's chopsticks first, while the viewed object was stroked with a latency
207 of 500-1000 ms. Each stimulation period lasted 180 s and was timed using a stopwatch.

208 During the chopstick rubber hand condition, the tip of the chopsticks held by the rubber hand
209 were stroked, whereas the front edge of the wooden block was stroked during the wooden
210 block condition. Although participants held the tool in all 4 conditions, the chopsticks were
211 not attached to the wooden block, and so were not visible during either of the wooden block
212 conditions. Almost all participants spontaneously reported that they were surprised that they
213 could feel the touch of the paintbrush on the tip of their chopsticks. Indeed, experimenters
214 were instructed to apply enough pressure to the chopsticks that the contact would be felt.

215 **2.2.4 Procedure**

216 Participants were greeted and informed that they would be using chopsticks and
217 making self-perception estimates throughout the duration of the experiment. If participants
218 indicated that they did not know how to hold or use chopsticks, the experimenter
219 demonstrated proper chopstick technique and offered chopstick pointers as the participant
220 briefly practiced manipulating the tool. Depending on group assignment, all participants
221 either first completed the bead-transfer task or proceeded directly to the illusion phase and
222 completed the bead-transfer task upon its conclusion. During the illusion phase, participants
223 were seated across from the experimenter with their right hand placed inside a specially
224 constructed box, measuring 100 cm in width, 40 cm in height, and 20 cm in depth. The box
225 was divided into three compartments of equal size, and the rubber hand rested inside the
226 central compartment in front of the subject's midline. The rubber hand and the participant's
227 hand were aligned such that both rested at the same distance in front of the participant's
228 chest. The lateral distance between the tip of the participant's chopsticks and the tip of the
229 chopsticks held by the rubber hand was 25.5 cm. The top of the box was covered by a one-
230 way mirror. The portion of the one-way mirror above the compartment containing the
231 participant's hand was obstructed such that the interior of the compartment could not be seen

232 by the participant at any time during the experiment, and the surface always appeared to be a
233 regular, two-way mirror (Figure 2).

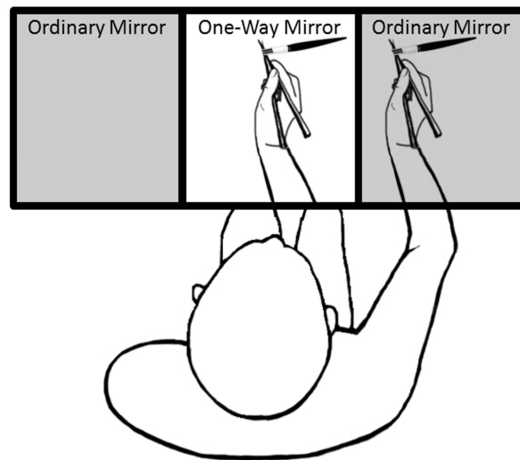


Figure 2. The top of Rubber Hand Illusion box was covered by a one-way mirror. A light inside the center portion of the box was illuminated during the illusion phase, allowing the participant to see the rubber hand holding the chopsticks. The portion of the one-way mirror above the compartment containing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

234

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

242 In the proprioceptive judgment phase, the perceived position of the participant's hand
243 and chopsticks was used as an implicit, quantitative proxy for measuring the strength of the
244 illusion. A ruler with the numbers printed in reverse was supported between two poles 45 cm
245 above the box. When illuminated from above, the mirrored surface of the box allowed for the

246 numbers to be reflected in their proper orientation and they appeared at the same gaze depth
247 as the chopstick rubber hand.

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

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

264 **2.2.5 Results**

265 **Proprioceptive Drift**

266 Participants made a baseline judgment of the location of the tip of their held chopsticks
267 before each stimulation trial, and another judgment following stimulation. The difference
268 between these two judgments represented the change in perceived hand position due to the
269 stimulation, and was used as a measure of the strength of the illusion. In the literature, this

270 difference value (post-illusion position minus pre-illusion position) is known as
271 proprioceptive drift. A positive proprioceptive drift value indicates that the participant judged
272 the position of their own hand and chopsticks as closer to the viewed object after stimulation
273 than before. In contrast, a negative proprioceptive drift corresponds to a mislocalization of
274 the participant's hand and chopsticks away from the viewed object.

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

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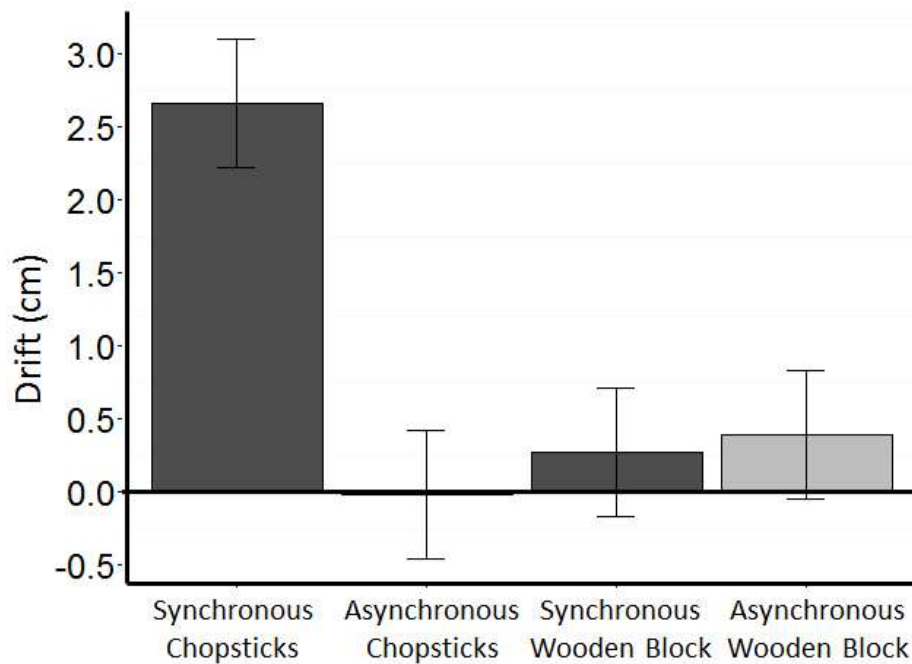


Figure 3. The significant interaction between viewed object and timing of visuo-tactile stimulation ($F(1,53) = 9.92, p < 0.01$) demonstrates that participants experienced the most proprioceptive drift when they were viewing the chopstick-holding rubber hand and viewing stroking of the rubber hand's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

286

287 The ANOVA revealed a significant main effect of viewed object ($F(1,53) = 5.74, p <$
 288 0.05) and timing of visuo-tactile stimulation ($F(1,53) = 8.44, p < 0.01$), as well as an
 289 interaction between these two conditions ($F(1,53) = 9.92, p < 0.01$), depicted in Figure 3.
 290 Pairwise comparisons statistics indicate that participants' proprioceptive drift was higher in
 291 the chopstick rubber hand synchronous condition ($M = 2.68$ cm, $SD=3.39$) than in the other
 292 experimental conditions (Rubber Hand asynchronous: $M=0.03$ cm, $SD=2.72$; $t(55)=3.47, p <$
 293 0.001 ; Wood synchronous: $M=0.25$ cm, $SD=3.29$; $t(55)=3.30, p < 0.001$; Wood
 294 asynchronous: $M= 0.36$ cm, $SD=3.79$; $t(55)=3.08, p < 0.001$). These findings indicate that the
 295 illusion was successfully induced.

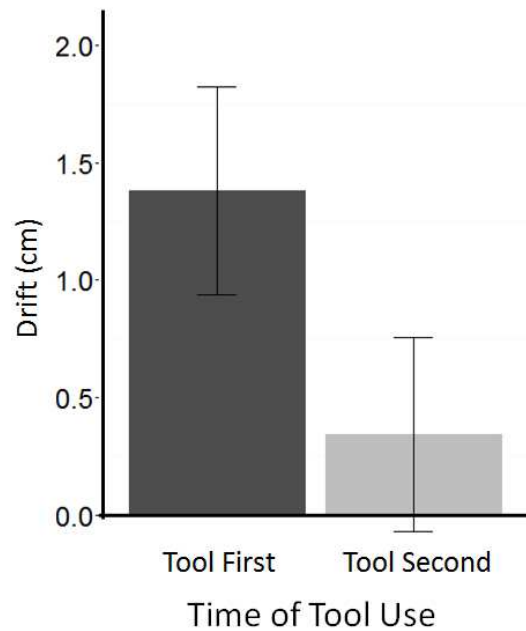


Figure 4. Participants who used the chopsticks prior to experiencing the CRHI experienced greater proprioceptive drift—regardless of timing or object—than those who used the chopsticks after the induction of the illusion. Error bars represent ± 1 SEM.

296 There was also a significant main effect of experimental group ($F(1,53) = 5.5, p < 0.05$),
 297 whereby participants who used the chopsticks prior to experiencing the CRHI experienced
 298 greater proprioceptive drift—regardless of timing or object—than those who used the
 299 chopsticks after the induction of the illusion (Figure 4). Additionally, there was a significant
 300 interaction between timing of visuo-tactile stimulation and chopstick skill: ($F(1,53) = 4.09, p$
 301 < 0.05). In the synchronous visuo-tactile condition only, participants who transferred more
 302 beads (and were therefore more skilled chopstick users) experienced more drift than
 303 participants who were less skilled in chopstick use (Figure 5).

304 The results for the linear mixed effects model with participant as a random factor
 305 resulted in comparable findings. Crucially, the interaction between viewed object and visuo-
 306 tactile stimulation was significant (Wald Chi-Square(1) = 14.09, $p < 0.001$), as was the
 307 interaction between timing of visuo-tactile stimulation and chopstick skill, (Wald Chi-
 308 Square(1) = 5.82, $p < 0.05$). Additionally, this analysis also revealed two significant three-
 309 way interactions. The first was between viewed object, timing of visuo-tactile stimulation,

310 and chopstick skill (Wald Chi-Square(1) = 4.02, $p < 0.05$). The other three-way interaction
311 was between viewed object, time of tool use, and chopstick skill (Wald Chi-Square(1) = 4.88,
312 $p < 0.05$). The data for the three-way interactions is summarized in Tables 1 and 2 in
313 Appendix B.

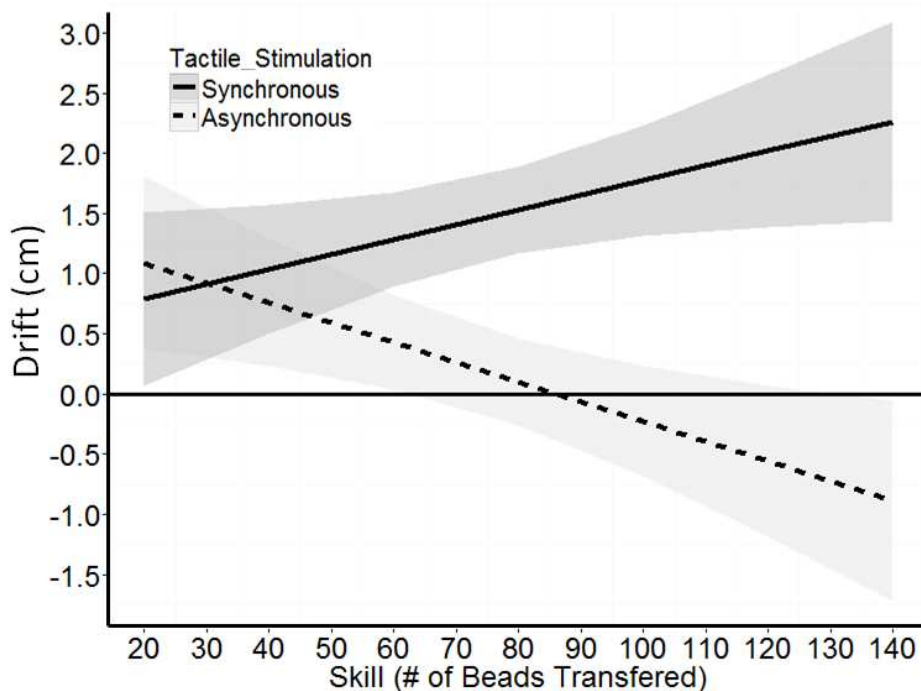


Figure 5. The significant interaction between timing of visuo-tactile stimulation and chopstick skill ($F(1,53) = 4.09$, $p < 0.05$) indicates that when visuo-tactile stimulation is synchronous, participants who transferred more beads (and were therefore more skilled chopstick users) experienced more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

314 Rubber Hand Illusion Questionnaire

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

321 The ANOVA revealed significant main effects of questionnaire component ($F(1,53) =$
322 $80.30, p < 0.001$), illusion condition ($F(1,53) = 16.16, p < 0.001$), and group ($F(1,53) =$
323 $17.87, p < 0.001$). The interactions were not significant (all F 's < 3.0).

324 Planned comparisons between illusion conditions revealed a significant difference in
325 responses to items related to Embodiment: (synchronous chopsticks: $M = -0.05, SD = 1.45$;
326 asynchronous Chopsticks: $M = -1.21, SD = 1.39$; synchronous wooden block: $M = -1.17, SD$
327 $= 1.37$; asynchronous wooden block: $M = -1.63, SD = 1.14$; ($F(1,3) = 14.23, p < 0.001$).
328 There was also a significant difference in responses to the Movement-related items on the
329 questionnaire: (synchronous chopsticks: $M = -0.98, SD = 1.30$; asynchronous Chopsticks: M
330 $= -1.45, SD = 1.31$; synchronous wooden block: $M = -1.60, SD = 1.06$; asynchronous wooden
331 block: $M = -1.70, SD = 1.16$; ($F(1,3) = 3.92, p < 0.01$). These results indicate that the
332 synchrony of visuo-tactile stimulation and the visual correspondence between the
333 participant's own hand and the viewed hand were necessary for participants to report
334 embodying the rubber hand and moreover, to endorse items relating to the experience of their
335 hand and the rubber hand moving closer to one another (Figure 6).

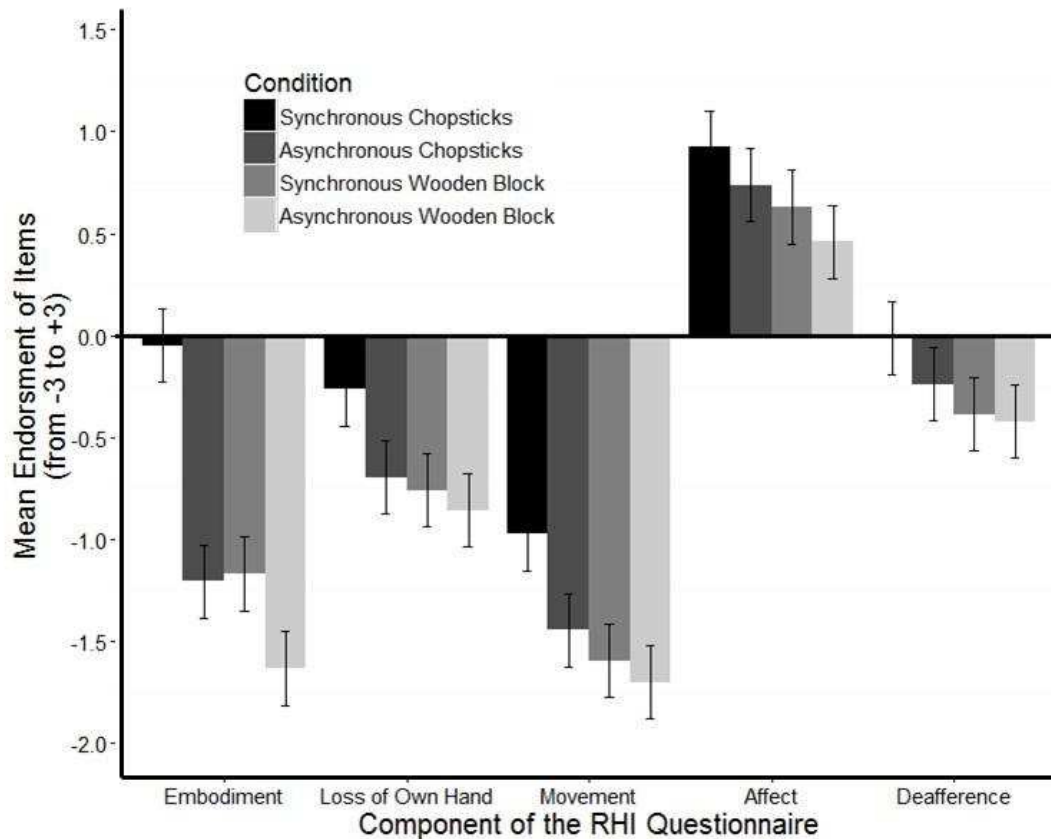


Figure 6. A comparison of illusions conditions revealed a significant difference in responses to items related to Embodiment and to the Movement-related items on the questionnaire. Differences between the critical, synchronous chopstick condition and the other conditions indicates that the synchrony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

336 3. Experiment 2

337 3.1 Introduction

338 Experiment 2 investigated the role of tool functionality in determining the modification
 339 of the body representation. In Experiment 1, multisensory stimulation caused an update of the
 340 proprioceptive felt position of the embodied tool toward an external object, but the extent of
 341 this representational plasticity is not clear. In Experiment 1, we hypothesized that the match
 342 between the tool’s function and its manner of manipulation was crucial for the embodiment of

343 the tool and the subsequent recalibration of its proprioceptive felt position following the
344 illusion. Chopsticks mimic and extend the precision grip of the hand holding them. However,
345 the results of Experiment 1 do not rule out the possibility that the observed effect is
346 independent of the type of tool in our modified RHI paradigm. Therefore, Experiment 2 used
347 the same experimental paradigm but the chopsticks were substituted with a teacup to further
348 test the role of tool functionality for the embodiment of the tool and the recalibration of its
349 proprioceptive felt position. Like chopsticks, teacups are simple, hand-held tools that
350 augment manual actions in a non-arbitrary manner (Goldenberg & Iriki, 2007). Teacups
351 mimic cupped hands to hold and transfer liquids, and like chopsticks, they rely primarily on
352 finger prehension for dexterous use, rather than on proximal information coming from the
353 forearm. However, unlike chopsticks, there is a mismatch between the way teacups are held
354 and their function. A precision grip is used to hold a teacup by its handle, but a teacup itself
355 does not imitate or extend a precision action. Rather, a teacup replicates the cupping of a
356 hand and is therefore more similar to whole hand prehension.

357 **3.2 Methods**

358 **3.2.1 Participants**

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

366 after undergoing the illusion. All participants provided written informed consent prior to
367 participation in the study and were right-handed with normal or corrected to normal vision.

368 **3.2.2 Materials**

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

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

383

384 **Rubber hand illusion questionnaire.** The same 25 questions from Longo and
385 colleagues (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009) employed in Experiment 1
386 were again used to measure the subjective experience of the TRHI. All questions were
387 modified to refer to the teacup held by the rubber hand, rather than to the rubber hand itself.
388 For example, the statements would read “the rubber hand holding the teacup belongs to me,”
389 or “I have control over the teacup the rubber hand is holding.” As in Experiment 1,
390 participants completed four versions of the questionnaire, one for each experimental

391 condition. Participants answered each statement by choosing a number from a 7-point Likert
392 Scale that ranged from -3 “strongly disagree” to +3 “strongly agree”.

393 **3.3.3 Experimental design**

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

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

411 **3.3.4 Procedure**

412 Participants were greeted and informed that they would be using a teacup and making
413 self-perception estimates throughout the duration of the experiment. Based on their group
414 assignment, all participants either first completed the water-transfer task or proceeded

415 directly to the illusion phase, completing the water-transfer task upon its conclusion. During
416 the illusion phase, participants were seated across from the experimenter with their right hand
417 placed inside the same box used in Experiment 1. As in Experiment 1, the rubber hand and
418 the participant's hand were aligned such that both rested at the same distance in front of the
419 participant's chest with a lateral distance between the front of the participant's teacup and the
420 front of the teacup held by the rubber hand set to 27 cm (Lloyd, 2007).

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

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

434 **3.3.5 Results**

435 **Proprioceptive Drift**

436 Assumptions of normal distribution, independence of residuals, and sphericity were
437 met. We began by examining how proprioceptive drift was influenced by participant hand-
438 object correspondence, the timing of visuo-tactile stimulation, success at the water transfer

439 task, and the recentness of experience with the teacup. To do so, we ran a mixed ANOVA
440 with viewed object (teacup rubber hand vs. wooden block) and timing of visuo-tactile
441 stimulation (synchronous vs. asynchronous) as within subject factors, weight of water
442 transferred as a covariate, and experimental group (water-transfer task Prior to the Illusion
443 versus After the Illusion) as the between group factor.

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

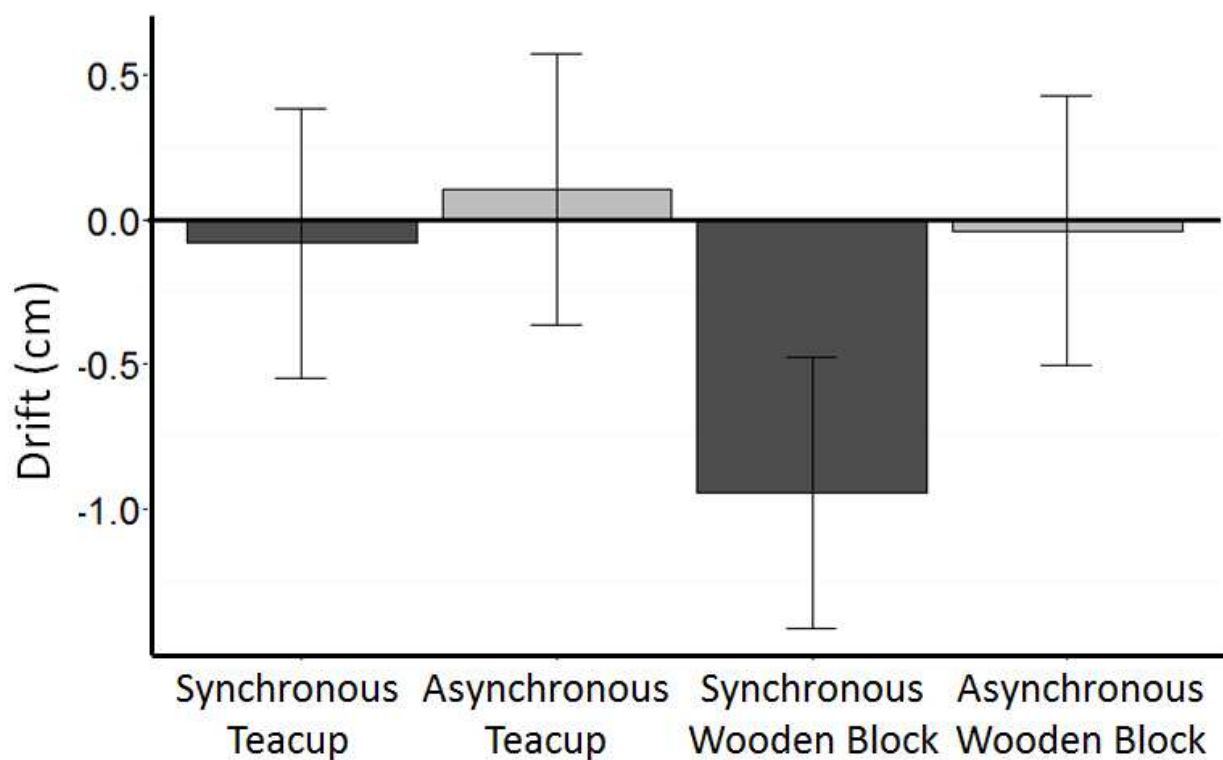


Figure 7. No interaction between viewed object and timing of visuo-tactile stimulation, ($F(1,35) = 0.67$), indicated that the illusion was not experienced by participants as strong enough to induce proprioceptive drift. Error bars represent ± 1 SEM.

449 Rubber Hand Illusion Questionnaire

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

456 The ANOVA revealed significant main effects of questionnaire component ($F(1,35) =$
457 $95.59, p < 0.001$), illusion condition ($F(1,35) = 6.96, p < 0.001$), and group ($F(1,35) = 43.04,$
458 $p < 0.001$) (Figure 8). A comparison of illusion conditions indicated that participants
459 endorsed survey statements more positively in the synchronous teacup condition ($M = -0.25,$
460 $SD = 1.61$) than in the other conditions (asynchronous teacup: $M = -0.42, SD = 1.63;$
461 synchronous wooden block: $M = -0.64, SD = 1.60;$ asynchronous wooden block: $-0.81, SD =$
462 1.63). Importantly, planned comparisons between illusion conditions revealed a significant
463 difference in responses to items related to Embodiment: (synchronous teacup: $M = -0.68, SD$
464 $= 1.57;$ asynchronous teacup: $M = -1.23, SD = 1.43;$ synchronous wooden block: $M = -1.63,$
465 $SD = 1.22;$ asynchronous wooden block: $M = -1.81, SD = 1.121;$ ($F(1,3) = 5.19, p < 0.01$).

466 There was also a significant interaction between survey component and group, $F(1,35)$
467 $= 3.26, p < 0.05$, such that individuals who used the teacup prior to experiencing the illusion
468 tended to endorse statements regarding the loss of their own hand more positively ($M = -0.07,$
469 $SD = 1.23$) than those who used the teacup after experiencing the illusion ($M = -1.00, SD =$
470 1.24). Those who used the teacup first also endorsed more statements about affect, suggesting
471 greater enjoyment of the experience (Tool Prior: $M = 1.08, SD = 1.36;$ Tool After: $M = 0.55,$
472 $SD = 1.19$). In addition, those who used the teacup before the illusion endorsed more
473 statements about deafference of their own hand during the illusion, agreeing more strongly to

474 sentiments such as the experience of pins and needles in their hand during the illusion (Tool
475 Prior: $M = 0.73$, $SD = 1.36$; Tool After: $M = -0.35$, $SD = 1.57$).

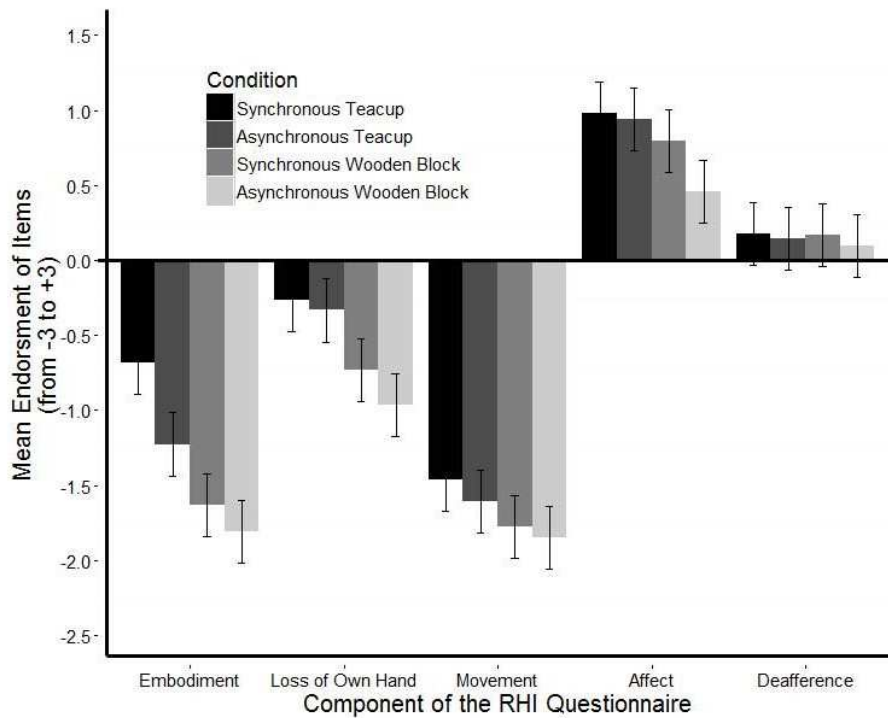


Figure 8. Comparing illusion conditions indicated that participants endorsed survey statements more positively in the synchronous teacup condition than in the other conditions. Importantly, there was also a significant difference in responses to items related to Embodiment between the synchronous teacup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

476 4. Cross-Experiment Comparison

477 In both experiments, we compared participant error in the initial estimates of the
478 position of their hand prior to inducing the illusion. The mean proprioceptive mislocalization
479 prior to the induction of the illusion was -1.3 cm ($SD = 4.9$) for Chopsticks users in
480 Experiment 1 and -2.97 cm ($SD = 4.33$) for Teacup users in Experiment 2, and the between-
481 groups mean difference, 1.58 BCa 95% CI $[-0.299, 3.446]$ was not significant ($t(97) = 1.65$, p
482 $= 0.10$, two-tailed). The absence of a significant difference suggests that participants in both

483 the chopsticks and in the teacup rubber hand experiments had comparable awareness of the
484 location of their tool-holding hand prior to the induction of the illusion.

485 In order to directly compare the success of the chopsticks and teacup versions of the
486 illusion, the difference between each participant's drift during the synchronous tool condition
487 and the asynchronous tool condition was submitted to an independent samples *t*-test. The
488 difference was found to be statistically significant, $t(97) = 3.82$, $p < .001$; $d = 0.77$; 95% CI
489 [0.36 , 1.19]. These results indicate that individuals in the chopsticks version of the illusion
490 experienced a larger difference in drift between the synchronous and asynchronous conditions
491 ($M = 2.65$, $SD = 3.55$) than did individuals in the teacup version of the illusion ($M = -0.03$,
492 $SD = 3.41$).

493 Next, we compared the embodiment component of the RHI questionnaire for the
494 synchronous tool condition for the two experiments using an independent samples *t*-test. The
495 difference was found to be statistically significant, $t(97) = 2.01$, $p < .05$; $d = 0.41$; 95% CI [0,
496 0.81]. These results indicate that individuals in the chopsticks version of the illusion
497 experienced a stronger feeling of embodiment ($M = -0.05$, $SD = 1.45$) during the synchronous
498 chopsticks condition than did individuals during the synchronous teacup condition ($M = -$
499 0.68 , $SD = 1.57$).

500 **5. Discussion**

501 The representation of the body is not fixed and immutable, but rather flexible and
502 constantly updated according to the available multisensory inputs. This process of integration
503 is pivotal both for a coherent feeling of body ownership and for the efficient use of tools.
504 When we use a tool, the brain extracts its physical properties through the dynamic
505 combination of multisensory inputs, and incorporates the object into the body representation
506 (e.g. Iriki et al., 1996; Yamamoto & Kitazawa, 2001; Yamamoto et al., 2005). The current

507 study adds to the growing literature on tool use and multisensory body representation by
508 providing evidence that the representation of an embodied tool shows a plastic property
509 similar to that of the body itself.

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

525 Previous work using the RHI paradigm has demonstrated that the illusion is successful only
526 when the external object resembles an internally stored template of the human body and is
527 placed in an anatomically plausible position (Costantini & Haggard, 2007; Tsakiris &
528 Haggard, 2005). For instance, the illusion is not successfully elicited when the rubber hand is
529 replaced with a non-hand-shaped object, such as a wooden block, as reflected by lower
530 proprioceptive drift in this condition (Haans, IJsselsteijn, & de Kort, 2008). This constraint
531 on representational plasticity is functional, as it guarantees coherence in body representation.

532 Without this constraint, coincidental multisensory stimulation might result in the perception
533 of non-corporeal objects as being part of one's own body.

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

553 Although Experiment 1 demonstrates that the representation of the extended body
554 representation can be experimentally modified, there is also evidence that the unique
555 relationship between tools and motoric body representations is also at play, as skilled
556 chopstick users and those with more recent chopstick practice experienced a stronger illusion.

557 This finding is in keeping with past experiments that consistently emphasize the necessity of
558 prolonged practice with the tool for the expansion of one's body representation to include the
559 held tool (e.g. Maravita & Iriki, 2004). For instance, in the paradigmatic Iriki et al. (1996)
560 experiment, the expansion of the visual-receptive fields was observed only after the macaque
561 monkey received weeks of practice with the tool.

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

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

579 Although tools can be rapidly incorporated, tool practice and skill still play a pivotal
580 role in their embodiment. Tool embodiment is stronger after recent use and for participants
581 who are more skilled in using the tool. For instance, Rademaker et al. (2014) provided

582 evidence of a rapid integration of objects held by chopsticks (second-order extension) into the
583 body representation. However, extensive chopstick training over a period of weeks further
584 augmented the level of integration. Moreover, greater chopstick skill was predictive of more
585 rapid integration of the second-order object held by the chopsticks. Our data support and
586 extend these findings by showing that even a short experience using the tool (as the 5-minute
587 practice session used in our Experiment) can lead to a stronger modification of the body
588 representation, as suggested by higher proprioceptive drifts and illusion scorings in the CRHI
589 compared to participants who used the chopsticks after the induction of the illusion.

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

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

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

606 The activation of CT fibers could be relevant here, because of their role in body
607 ownership. For instance, it has been shown that slow velocity touch on hairy skin produces
608 higher levels of embodiment during the RHI compared with fast, neutral touch (Crucianelli,
609 Metcalf, Fotopoulou, & Jenkinson, 2013). One could argue that the difference observed
610 between chopsticks and teacup could be explained by a differential contact with hairy skin
611 and, thus, greater or lesser involvement of CT fibers. Chopsticks mostly rest on the palmar
612 (glabrous) side of the hand. In particular, the first of the two chopsticks (the closest to the
613 handler), rests approximately on: thenar eminence (over the abductor pollicis muscle, on the
614 palm and only partially the back of the hand) and the third phalanx of the middle and ring
615 finger. The second chopsticks mostly rests on: first, second and third phalanx of the index
616 finger and the third phalanx (the fingertips) of the thumb and the middle finger (Schwarz,
617 1955) (see figure 9A). As for the teacup, the areas of contact with the skin are mostly the
618 third (distal) phalanx of the thumb (palmar side), and the second phalanx of the index, middle
619 and ring finger, both on the dorsal and palmar side of the hand (ibidem) (see figure 9B).

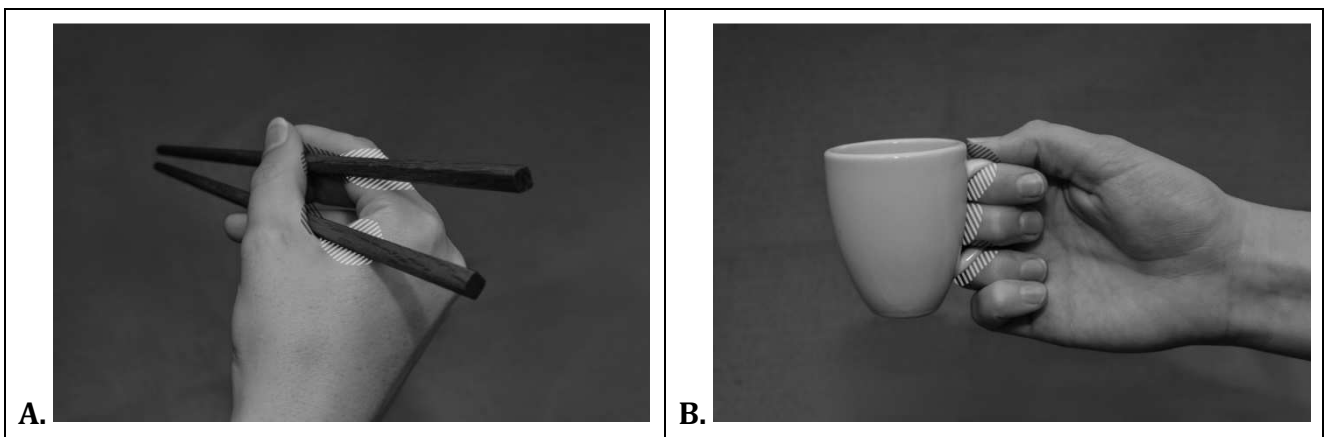


Figure 9. The manner in which participants were instructed to hold A) the chopsticks, and B) the teacup. Hashed lines demark where the tool came into contact with the participant's hand, with white lines marking glabrous skin innervated with C-fibers and black lines denoting skin on the surface of the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

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

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

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

664 A relevant question that is difficult to address with the present results regards whether
665 the position of the tool is calculated in an allocentric or egocentric frame of reference.
666 Previous evidence seems to suggest that, following tool use, the relative position of the hand
667 becomes less relevant in respect to the representation of the embodied effector. As stated
668 previously (see introduction), although somatosensory sensation necessarily originates from
669 the fingers when touching something with a too, these tactile signals are processed as if
670 referred directly to the tip of the tool (Yamamoto & Kitazawa, 2001). If this is the case, then

671 one could expect that what is been recalibrated is the coordinates of the tool itself rather than
672 the hand wielding it. In fact, previous studies with the RHI show that the illusion is restricted
673 to the locus of stimulation: only the stimulated finger is perceived to be closer to the rubber
674 hand, but not the neighbouring, unstimulated fingers (Tsakiris & Haggard, 2005). Moreover,
675 following tool use the precision of tool-related reachability judgment improves, whereas the
676 arm representation and its capabilities become less precise (Bourgeois, Farnè, & Coello,
677 2014; Costantini, Ambrosini, Sinigaglia, & Gallese, 2011). Thus, one could speculate that the
678 proprioceptive drift observed with the chopsticks pertains the coordinate of the tool itself
679 rather than its relative position with the hand. However, literature on this subject is not
680 conclusive. Most likely, the allocentric and egocentric frame of reference are not mutually
681 exclusive, but rather their relative dominance is determined by multiple factors, such as the
682 type of tool and the transformation necessary to use it (e.g., Massen & Sattler, 2010). Future
683 experiments could specifically tackle this question, for instance investigating whether in our
684 modified rubber hand with tool paradigm the representation of the hand is also recalibrated
685 along with the representation of the tool.

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

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

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833 APPENDIX A: Chopstick Version of the Rubber Hand Illusion Questionnaire

834 In the questions below, -3 corresponds to "completely disagree", while +3 corresponds to

835 "completely agree". 0 corresponds to "neither agree nor disagree".

836 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.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the chopsticks I was holding were in the location where the rubber hand was holding the chopsticks.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand holding chopsticks was moving towards my hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand holding chopsticks was my hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I had three hands.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand holding chopsticks was part of my body.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
I had the sensation of pins and needles in my hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand holding chopsticks was in the location where my hand was.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand holding chopsticks belonged to me.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
I found that experience interesting.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I could have moved the chopsticks in the rubber hand if I had wanted.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like my own hand became rubbery.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I was unable to move the chopsticks in my hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like my hand had disappeared.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
The touch of the paintbrush on my chopsticks was pleasant.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like my hand was out of control.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
I found that experience enjoyable.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I could have moved the chopsticks in my hand if I had wanted.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like my hand was moving towards the rubber hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I was in control of the chopsticks in the rubber hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like I couldn't really tell where my hand was.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the experience of my hands was less vivid than normal.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
I had the sensation that my hand was numb.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the touch I felt was caused by the paintbrush touching the chopsticks held by the rubber hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
It seemed like the rubber hand began to resemble my real hand.	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

Table 1				
<i>Descriptive Statistics for 3-way interaction of Skill, Tactile stimulation, and Viewed Object</i>				
<u>Beads Transferred</u>	<u>Tactile Stimulation</u>	<u>Viewed Object</u>	<u>M</u>	<u>SD</u>
44	Synchronous	Chopstick	2.66	0.66
		Wood	-0.59	0.66
	Asynchronous	Chopstick	0.21	0.66
		Wood	1.32	0.66
75	Synchronous	Chopstick	2.66	0.45
		Wood	0.40	0.45
	Asynchronous	Chopstick	-0.05	0.45
		Wood	0.25	0.45
106	Synchronous	Chopstick	2.66	0.78
		Wood	1.38	0.78
	Asynchronous	Chopstick	-0.30	0.78
		Wood	-0.81	0.78
<p><i>Note.</i> Skill was quantified as the number of beads participants transferred with chopsticks in a 5 minute period. The mean number of beads transferred (75) is shown here with ± 1 SD for comparison of drift at different levels of skill, timing of visuo-tactile stimulation, and viewed object.</p>				

<u>Beads Transferred</u>	<u>Time of Tool Use</u>	<u>Viewed Object</u>	<u>M</u>	<u>SD</u>
44	Tool First	Chopstick	1.27	0.77
		Wood	1.55	0.77
	Tool Second	Chopstick	1.57	0.73
		Wood	-0.66	0.73
75	Tool First	Chopstick	1.75	0.52
		Wood	1.00	0.52
	Tool Second	Chopstick	0.92	0.50
		Wood	-0.26	0.50
106	Tool First	Chopstick	2.24	0.84
		Wood	0.45	0.84
	Tool Second	Chopstick	0.26	0.92
		Wood	0.13	0.92
<p><i>Note.</i> Skill was quantified as the number of beads participants transferred with chopsticks in a 5 minute period. The mean number of beads transferred (75) is shown here with ± 1 SD for comparison of drift at different levels of skill, time of tool use (before or after the illusion), and viewed object.</p>				