



Long- but not short-term tool-use changes hand representation

Lara A. Coelho¹ · Jason P. Schacher^{1,2} · Cory Scammel^{1,2} · Jon B. Doan² · Claudia L. R. Gonzalez¹

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Abstract

Tool-use has been found to change body representation. For example, participants who briefly used a mechanical grabber to pick up objects perceived their forearms to be longer immediately after its use (e.g., Cardinali et al., *Curr Biol* 19(12):R478–R479, 2009; they incorporated the tool into their perceived arm size). While some studies have investigated the long-term effects of tool-use on body representation, none of these studies have used a tool that encapsulates the entire body part (e.g., a glove). Moreover, the relationship between tool-use and the body model (the representation of the body's spatial characteristics) has yet to be explored. To test this, we recruited 19 elite baseball players (EBP) and 18 age-matched controls to participate in a hand representation task. We included EBP because of their many years (8+) of training with a tool (baseball glove). The task required participants to place their hands underneath a covered glass tabletop (no vision of their hands), and to point to where they believed 10 locations (the tips and bases of each finger) were on their hands (Coelho et al., *Psychol Res* 81(6):1224–1231, 2017). Each point's XY coordinates was tracked using an Optotrak camera. From these coordinates, we mapped out the participants perceived hand size. The results showed that when compared to the controls, EBP underestimated hand width and finger length of both hands. This indicates that long-term tool use produces changes in the body model for both, the trained and untrained hands. We conducted a follow-up study to examine if 15 min of glove use would change perceived hand size in control participants. Novice baseball players (participants without baseball experience: NBP) were recruited and hand maps were derived before and after 15 min of active catching with a glove. Results showed no significant differences between the pre and post hand maps. When we compared between the two experiments, the EBP showed smaller hand representation for both hand width and finger length, than the NBP. We discuss these results in relation to theories of altered body ownership.

Keywords Body representation · Body model · Plasticity · Training · Hand

Introduction

We rely on proprioceptive signals to interact with our surroundings. The proprioceptive receptors are located in the skin, muscles, and joints of our limbs. Afferent signals generated during a movement are processed to code for an endpoint position of the limb. The term proprioception has been used loosely to describe several conscious sensations.

These include the senses involved with limb position and movement, the sense of tension or force, the sense of effort, and the sense of balance (Proske and Gandevia 2012). For the purpose of the present study we will be focusing on a subdivision of proprioception; position sense (Sherrington 1910). Position sense refers to the ability to perceive the location of our limbs in space, even when we cannot see them. Much of the research on position sense focuses on disorders that feature misrepresentations of the body, including eating disorders (Gadsby 2017; Guardia et al. 2012; Keizer et al. 2013; Metral et al. 2014; Treasure et al. 2010). Traditionally, the studies that have investigated position sense in healthy individuals focused on how position sense relates to bodily movement (Goble and Anguera 2010). These studies assumed that healthy adults have an integrated and accurate body representation of their limbs in space. However, recent evidence has shown otherwise (Longo and Haggard

✉ Lara A. Coelho
lara.coelho@uleth.ca

¹ The Brain in Action Laboratory, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada

² The Engineering and Human Performance Lab, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada

2010). In a procedure to isolate and measure position sense in healthy adults, Longo and Haggard found that the representation of the hand is distorted. They referred to this type of representation as implicit body representation (or the body model). This body model is the representation of the body's spatial characteristics. This is different from the body schema which forms a representation from constantly updating sensory information from afferent signals. Longo and Haggard asked their participants to place their hands underneath a covered tabletop (no vision of their hand), and to point to where they believed ten locations were on their hand. They found that healthy adults consistently and significantly overestimate the width of their hands and, underestimate the length of their fingers (Longo and Haggard 2010). This result has been replicated on numerous occasions, and in various different conditions (Coelho et al. 2017; Coelho and Gonzalez 2018a, b; Longo 2014, 2015; Longo and Haggard 2011, 2012a, b; Longo et al. 2015a, b; Saulton et al. 2015, 2016).

Changes to the body schema following tool-use have been documented. A tool can be defined as an object that is a physical extension of the body (Iriki et al. 1996). Many studies have shown that after tool use, there are measurable perceptual changes in the body schema (Cardinali 2011; Cardinali et al. 2009, 2012; Carlson et al. 2010; Iriki et al. 1996; Maravita and Iriki 2004; Sposito et al. 2012). For example, Cardinali asked participants to perform a reach and grasp movement using a mechanical grabber (2011). The participants were required to estimate the length of their arms before and after the grasping task. Interestingly, it was found that participants perceived their arms to be longer after they had performed the grasping task with the grabber. This result suggests that after its use, tools become integrated with the subject's own body schema, as if the tool is a physical extension of the body. Long-term tool use has also been shown to change peripersonal space representation (Serino et al. 2007) and the neural representation of the body (Fourkas et al. 2008). For example, peripersonal space plasticity was investigated in a group of blind subjects (many years of experience using a cane), and in a group of sighted participants (no experience using a cane; Serino et al. 2007). They found that the blind individual's peripersonal space extended when they held the cane, but not when they held a short handle. These authors argue that long-term exposure to a tool results in a unique representation of peripersonal space.

The effects of tool-use on the body schema, and peripersonal space have been explored previously, but what about the body model (as identified by Longo and Haggard 2010)? One previous study found that extensive practice with the hands caused the hand's body model to be more accurate (Cocchini et al. 2018). This study recruited expert magicians and a group of control participants and used the same

experimental protocol as Longo and Haggard (2010) to isolate the body model of the hand. They found that the magicians had more accurate representations of the lengths of their fingers. Although, this study showed that training leads to changes in the body model, it remains to be shown if tool-use also produces these changes.

The aim of the current study therefore was to investigate if long-term exposure to a tool would change the body model of the hand. Rather than asking participants to train with a tool for an extended period of time (likely unfeasible), we recruited a population with long-term experience using a tool; elite baseball players (EBP). EBP have many years of practice using a tool that extends the capability of their hand: a baseball glove. Based on the results of previous studies on the effects of tool use on the body schema and peripersonal space (Cardinali 2011; Cardinali et al. 2012; Carlson et al. 2010; Cocchini et al. 2018; Maravita and Iriki 2004; Schaefer et al. 2004; Sposito et al. 2012) we hypothesized changes in the body model of the hand of EBP. We present two alternate hypotheses: (1) EBP will incorporate the glove into their implicit representation of their hands and will therefore perceive their glove hand as *larger* than their non-glove hand, and larger than both hands of a control group; (2) EBP would have a *smaller* implicit representation of their glove hand because when they are not wearing it their hand appears smaller. There is also the possibility that long-term use of the glove results in no measurable changes in the body model. This would be consistent with the suggestion that experience-induced plasticity should not last in the long-term, as there would be no functional benefit to a lasting change in body representation (Cardinali et al. 2012). These authors argued that “disembodiment” of the tool should occur fast and without consequence.

Methods

Participants

Nineteen right-handed male baseball players from Prairie Baseball Academy voluntarily participated, and 18 male age matched controls from the University of Lethbridge participated in exchange for course credit. Handedness was assessed using a modified Edinburgh (Oldfield 1971) and Waterloo (Brown et al. 2006) handedness questionnaire. All but one participant self-reported as being right-handed (one baseball player reported as being ambidextrous). The baseball players also completed a questionnaire on their playing history. This questionnaire asked the players how long they had been playing, how many times a week they practice, and what hand they wore their glove on. EBP glove hand preference was consistent with being right-handed (i.e., glove being worn on the left hand by all players). We made the a

priori decision to test 19 participants per group (38 total), as there were 19 elite baseball players who volunteered to participate, and we wanted to have a close number of participants in each group. We had to exclude one participant from the control group due to hand movement during testing.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode attached to the tip of a stylus. The location of the diode was recorded for 1 s at 100 Hz for each trial.

Design and procedure

Design and procedures closely followed our previous work (Coelho and Gonzalez 2018a, b; Coelho et al. 2017). Briefly, participants were instructed to sit and place their hand palm up underneath a glass tabletop (86.5 × 41.0 cm); see Fig. 1. The original paradigm by Longo and Haggard (2010) had participants place their hands palm down against the wooden shelf (situated below the glass). However, in our original report (Coelho et al. 2017) we found no differences in distortion between a palm-up group and a palm-down group, and to keep it consistent with our own research we decided to have all our participants place their hands up against the glass. Their forearm rested on a pillow that was situated on a shelf located 12 cm below the glass. We asked participants to have their fingers spread to the maximal width that was comfortable, and we informed them that the positioned hand was to be fixed in one location for the entirety of the set of trials. When the participant was ready to begin the experiment, a black table cloth was placed over the table, occluding the hand from the participants view (occluded

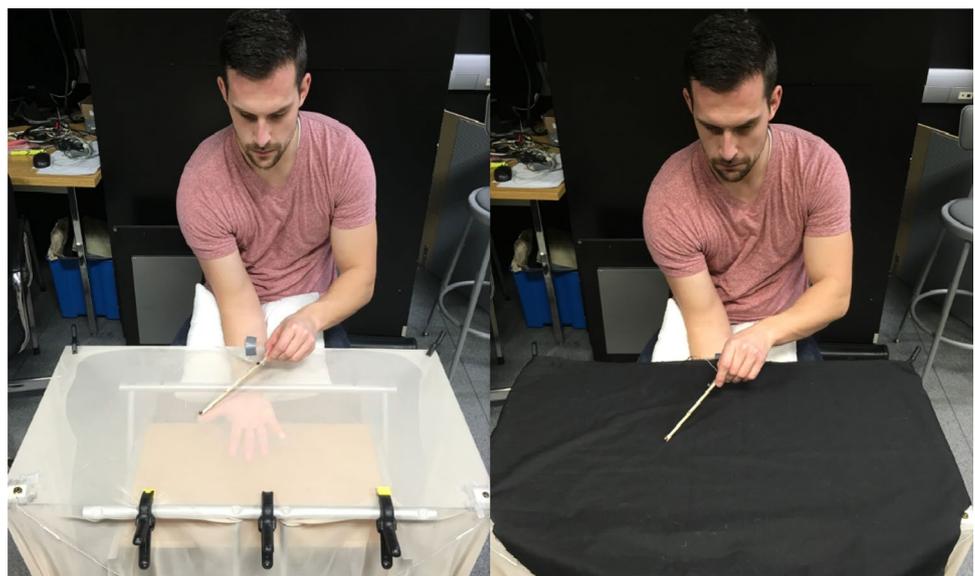
hand condition). With the unrestricted hand, participants were asked to place the tip of the stylus (with the diode attached) directly above (while contacting the top of the glass) where they believed 10 individual hand landmarks were. These landmarks consisted of the tips and the metacarpal phalangeal (mp) joints of each finger. In all cases the experimenter verbally instructed the participants as to which landmark to point to on each trial. Trials were pseudorandomized for each condition and for each participant. Following each trial participants were asked to return to a “home spot” situated directly above the participants fixed forearm. After the set of trials was completed, the black table cloth was removed from the table and the experiment was repeated again but with full vision of the hand (non-occluded hand condition). The participants repeated the experiment for both their left and right hands. Each participant completed 100 trials for each hand (200 trials total). Each set was further broken into 2 × 50 trial subsets (5 points to each landmark). The first pseudorandomized set of trials was the occluded hand condition, immediately followed by the non-occluded hand condition. This procedure was identical to that used in previous studies.

Analysis

We conducted two analyses on the data. Each of the analyses was repeated for two dependent variables: hand width, and finger length. Hand width was determined by the great span, which was defined as the sum of the distances between the tips of each digit, including the thumb. Finger length was calculated by averaging the distance from the tip to the base of each digit for all five digits.

The first analysis (occluded vs non-occluded hand) was a series of paired samples *t* tests conducted on the raw data

Fig. 1 This was the experimental setup for the experiment. The participants sat with their hand pressed up against the glass tabletop. They pointed using the wooden stylus. The black table cloth restricted vision of the participant’s hand in the occluded trials



(expressed in mm). For this analysis, we compared the occluded vs the non-occluded conditions for both measures to investigate if the perceived hand dimensions (occluded hand condition) were significantly different from the real hand dimensions (non-occluded condition).

The second analysis (effects of hand and group) was a 2×2 repeated measures ANOVA. The within variable was hand (left, right), and the between variable was group (EBP, control). This analysis was conducted on the data expressed as a percent of the non-occluded value [(occluded – non-occluded)/(non-occluded \times 100)]. This normalization was done to account for any individual differences in hand size (Coelho et al. 2017).

Data processing

Trials were excluded if participants moved the stylus before the 1 s recording was finished, or if the participant pointed to the incorrect landmark (<5% of all trials).

All data were analyzed using Matlab R2015a (Mathworks, Natick, MA), and statistics were completed using SPSS 23.

Results

Means and standard errors are reported. The analysis of occluded vs non-occluded hand was Bonferroni corrected for multiple comparisons.

Handedness questionnaires

Both groups had an average score that was consistent with being right-handed (EBP 26.6 ± 1.5 , and the control group 30.5 ± 1.7). A one-way ANOVA revealed there was not a significant difference between groups ($p = .1$).

Baseball questionnaire

The EBP had been playing baseball for an average of 12.9 ± 0.48 years, and they were playing baseball 5.1 ± 0.52 days per week at the time of testing. There were no significant correlations between the amount of time spent playing baseball and the magnitude of distortion of their hands ($p_s > 0.17$).

Analysis one: occluded vs non-occluded hand

Control group The great span of both the right and left hands was accurate [right hand $t(17) = 0.68$, $p = .51$, $d = 0.33$; left hand $t(17) = -0.24$, $p = .8$, $d = 0.12$]. Finger length, however, was significantly underestimated for both their right [$t(17) = -8.1$, $p < .01$, $d = 3.98$, CI [-16.6, -9.7]; occluded

hand = 42.9 ± 1.1 , non-occluded hand = 56.22 ± 1.2] and left hands [$t(17) = -7.8$, $p < .01$, $d = 3.64$, CI [-16.5, -7.8]; occluded hand = 44.57 ± 1.4 , non-occluded hand = 57.3 ± 1.1].

EBP Baseball players significantly underestimated the great span of their right hands [$t(18) = -3.5$, $p < .01$, $d = 1.65$, CI [-36.6, -9.2]; occluded hand = 175.1 ± 5.4 , non-occluded hand = 198.1 ± 4.45]. The great span estimations of the left hand approached significance, when compared to the non-occluded condition [$t(18) = -2.51$, $p = .09$, $d = 1.83$, CI [-23.3, -2.0]; occluded hand = 180.3 ± 4.5 , non-occluded hand = 93 ± 4.5]. Finger length was also significantly underestimated for both the right [$t(18) = -11$, $p < .01$, $d = 5.19$, CI [-23.6, -16.0]; occluded hand = 37.23 ± 1.8 , non-occluded hand = 57.04 ± 1] and left hands [$t(18) = -7.5$, $p < .01$, $d = 3.54$, CI [-22.8, -12.8]; occluded hand = 40.1 ± 1.93 , non-occluded hand = 57.92 ± 1.1].

Analysis two: effects of hand and group

Great span There was a main effect of group [$f(1, 35) = 6.4$, $p = .02$, partial $e^2 = .15$], where the EBP (-8.4 ± 2.8 , CI [-14.1, -2.7]) estimated the width of their hands to be significantly smaller than those of the control group (1.72 ± 2.9 , CI [-4.1, 7.6]). The effect of hand was non-significant [$f(1,35) = 0.00$, $p = .99$, partial $e^2 = .00$], as was the hand*group interaction [$f(1,35) = 3.2$, $p = .09$, partial $e^2 = .08$].

Finger length There was a main effect of group [$f(1, 35) = 6.8$, $p = .01$, partial $e^2 = .16$], where the EBP (-32.38 ± 2.6 , CI [-37.8, -27.0]) estimated their finger length to be significantly smaller than that of the control group (-22.53 ± 2.7 , CI [-28.0, -17.0]). The effect of hand was not significant [$f(1,35) = 1.6$, $p = .21$, partial $e^2 = .05$], as was the hand*group interaction [$f(1,35) = 0.91$, $p = .35$, partial $e^2 = .03$] (Fig. 2).

The results indicate that long-term use of a tool changes the representation of our hands. This is in line with one study that found that compared to naïve participants, experienced magicians, when compared to controls, had different representations of their hands (Cocchini et al. 2018). Previous research has found that after using a tool (for as little as 15 min), the tool becomes embodied; participant's body representation changes to incorporate (literally) that tool (Cardinali 2011; Cardinali et al. 2012; Maravita and Iriki 2004; Schaefer et al. 2004; Sposito et al. 2012). Would short-term tool use change hand representation? A follow-up study, investigated if 15 min of using a baseball glove would also produce measurable changes to the participants hand maps. To test this, we recruited a group of novice baseball players (NBP; no experience playing baseball) and asked them to complete the hand-mapping task both before

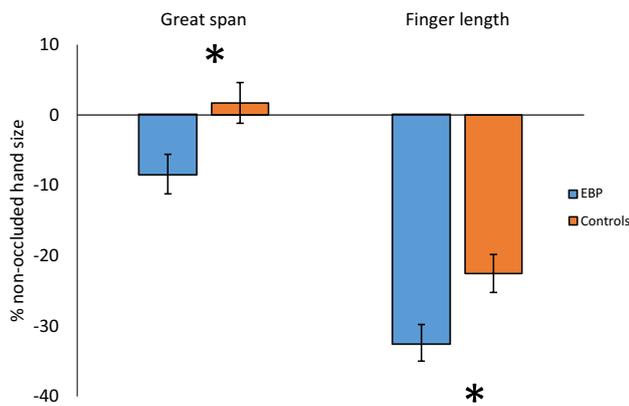


Fig. 2 Differences between the EBP and controls for both the great span and finger length. The EBP significantly underestimated both the great span and finger length in comparison to the control group

(pre-tool use) and after 15 min (post-tool use) of catching a baseball using the glove.

Follow-up: short-term effects of tool-use on hand representation

Method

Participants Eighteen male undergraduate students participated in this study. All participants received a course credit in exchange for participation. All participants self-reported as right-handed, which was confirmed via the modified version of the Waterloo–Edinburgh handedness questionnaire (mean score: 28.3 ± 1.6). We made the a priori decision to stop testing after 18 participants, so that our group sizes were the same between study 1 and study 2.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode attached to the tip of a stylus. The location of the diode was recorded for 1 s at 100 Hz for each trial.

Design and procedure

Our experimental design was similar to that used in the first study. Participants were asked to complete the hand-mapping task (pre-tool use), followed by 15 min of playing catch using a baseball glove, which was immediately followed by a repeat of the hand-mapping task (post-tool use). All participants played catch with an EBP, who pitched at a steady pace and placed the balls in easy-to-catch positions. All participants wore the glove on their left hand during

the practice trials. There was one key change to the hand-mapping process; instead of having the participants complete 50 trial subsets (5 estimations to each location, as in the first study), the participants completed 10 trial subsets (1 estimation to each location; 20 trials per hand, 40 trials in total). We decided to make this change in our protocol for sake of brevity. In none of our previous work (Coelho and Gonzalez 2018a, b, in press; Coelho et al. 2017) nor in the first study have we found differences between the maps derived from the first 10 points to each location, and any of the other 4 subsets (points #11–50). Importantly, the hand map results from control participants (first study) and from the NBP (pre-tool use) were not significantly different from each other ($p > 0.6$), indicating that the abbreviated version of the hand-mapping task yields the same results as the full version.

Analysis

We conducted three analyses on the data. Each of the analyses was repeated for two dependent variables: hand width, and finger length. These were calculated using the same methods as in the first study.

The first analysis (occluded vs non-occluded hand) was a series of paired samples t tests conducted on the raw data (expressed in mm). We conducted this analysis to examine whether the pre- and post-occluded hand values were significantly different from the non-occluded hand values both before and after the 15 min of training.

The second analysis (pre- vs post-tool use) was a 2×2 within subjects repeated measures ANOVA. Hand (left, right) and time (pre-, post-tool use), were the 2-within variables. As in the first study, the data were expressed as a percent of the non-occluded hand value (occluded – non-occluded)/(non-occluded \times 100). We chose to use this normalization to account for any differences in hand size or posture between participants. With this analysis we aimed to examine if using the baseball glove significantly changed the representation of the participant’s hands.

Lastly, we included one final analysis to compare if our EBP and our NBP had different representations of their hands. To test this possibility, we conducted a 2×2 mixed design repeated measures ANOVA. Our within variable was hand (left, right), and the between variable was group (EBP, NBP post-tool use). All the values here were expressed as a percent of the non-occluded hand value (as in our second analysis).

Data processing

Trials were excluded if participants moved the stylus before the 1 s recording was finished, or if the participant pointed to the incorrect landmark ($< 1\%$ of all trials).

Table 1 Means and standard deviations of pre- and post-tool use finger length estimations (occluded) and actual (non-occluded) finger lengths

| | Pre-tool use | | | | Post-tool use | | | |
|---------------|--------------|--------------|------------|--------------|---------------|--------------|-----------|--------------|
| | RH | | LH | | RH | | LH | |
| | Occluded | Non-occluded | Occluded | Non-occluded | Occluded | Non-occluded | Occluded | Non-occluded |
| Great span | 216.3±7.2 | 206.3±5.1 | 211.2±10.1 | 221.1±6.7 | 211.1±11.6 | 208.6±5 | 220.6±9.6 | 217.9±5.5 |
| Finger length | 46.3±1.7 | 59.9±1.2 | 46.9±2.3 | 61±1.2 | 47.6±2.8 | 58.7±1.4 | 45.6±2.4 | 59.7±1.4 |

All data were analyzed using Matlab R2015a (Mathworks, Natick, MA), and statistics were completed using SPSS 23.

Results

Analysis one: occluded vs non-occluded hand

Great span There were no significant differences between the occluded and non-occluded hand for either the pre- [right hand $t(17) = 1.6$, $p = .13$, $d = 0.78$; left hand $t(17) = -1.03$, $p = .32$, $d = 0.5$] or post- [right hand $t(17) = 0.23$, $p = .82$, $d = 0.11$; left hand $t(17) = 0.31$, $p = .76$, $d = 0.15$] tool-use.

Finger length Pre-tool use: the participants significantly underestimated the finger lengths on their right [$t(17) = -7$, $p < .01$, $d = -2.23$, CI [-17.8, -9.5]]; and left hands [$t(17) = -6.3$, $p < .01$, $d = -1.96$, CI [-18.9, -9.4]]; see Table 1 for summary of means and standard errors.

Post-tool use: the participants significantly underestimated the finger lengths on their right [$t(17) = -4.3$, $p < .01$, $d = -1.16$, CI [-16.63, -5.71]]; and left hands [$t(17) = -7$, $p < .01$, $d = -1.65$, CI [-18.3, -9.87]]; see Table 1 for summary of means and standard errors.

Analysis two: pre- vs post-tool use

Great span No significant effects were found (see Fig. 3).

Finger length No significant effects were found (see Fig. 3).

Analysis three: EBP vs NBP

Great span There was a main effect of group [$F(1,35) = 4.4$, $p = .04$, partial $e^2 = .11$], where the estimates of the EBP group (-8.4 ± 3.3 , CI [-15.2, -1.7]) were significantly smaller than those of the NBP group (1.6 ± 3.4 , CI [-5.4, 8.5]). See Fig. 4.

Finger length There was a main effect of group [$F(1,35) = 5.4$, $p = .03$, partial $e^2 = .14$], where the estimates of the EBP group (-32.4 ± 3.3 , CI [-38.98, -25.8])

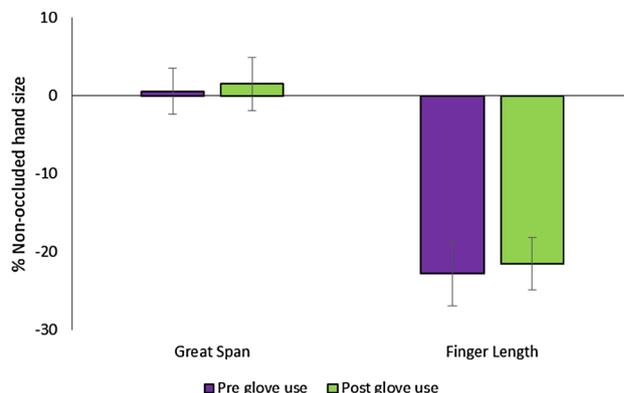


Fig. 3 This figure compares the pre-tool use to the post-tool use perceived hand size. There were no differences in hand representation pre- and post-tool use

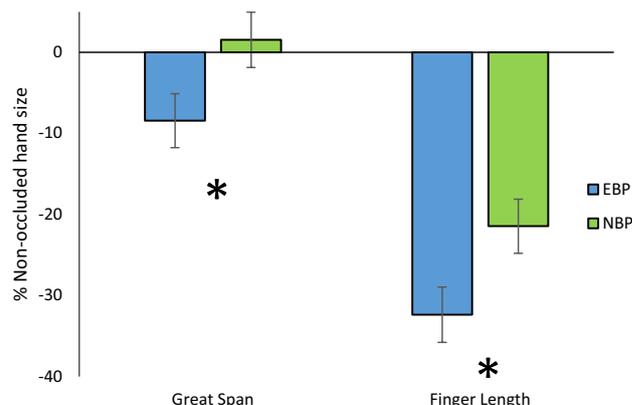
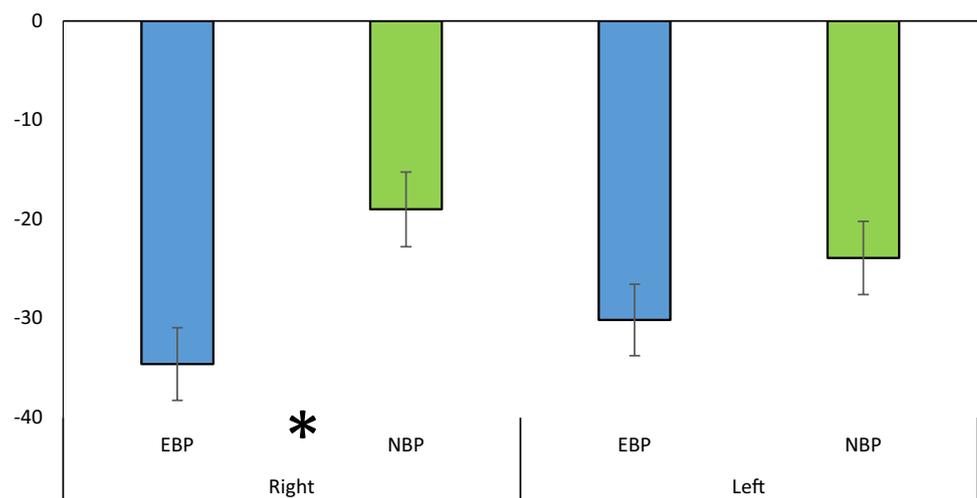


Fig. 4 This figure compares the perceived hand size of the EBP and the NBP (post-tool use). The EBP made significantly smaller estimates of both hand width and finger length compared to the NBP

were significantly smaller than those of the NBP group (-21.45 ± 3.4 , CI [-28.2, -14.7]). See Fig. 4.

The group X hand interaction approached significance [$F(1,35) = 4.1$, $p = .05$, partial $e^2 = .12$]. Follow-up one-way ANOVA's revealed that the estimated finger length of the EBP's right hand was significantly smaller than those of the NBP [$F(1,36) = 8.9$, $p < .01$]. This was not the case for the left hand ($p = .2$). See Fig. 5.

Fig. 5 The group X hand interaction. EBP made significantly smaller estimates of finger length on the right hand. However, there were no differences in perceived finger length between the EBP and NBP for the left hand



Discussion

The present studies were designed to examine if long- and short-term exposure to a tool (baseball glove) changes the body model of the hand. To investigate long-term effects, we recruited a group of male elite baseball players (EBP) and a group of age-matched male controls. We asked all participants to complete a hand-mapping task. This task involved participants pointing to ten landmarks (the tips and mp joints of their fingers), when their hands were occluded from view. XY coordinates from each point were tracked using an Optotrak camera. From the XY coordinates of these ten landmarks we created a map of how the participants perceived their hands (Coelho and Gonzalez 2018a, b, in press; Coelho et al. 2017). The results demonstrated that long-term practice with a tool (i.e., the glove) changed the body model. The results supported our second hypothesis, as the EBP significantly underestimated the width of their hands, while the male controls made accurate estimates. The EBP also underestimated the length of their fingers significantly more than the controls did.

To investigate the short-term effects of tool use, we recruited a group of novice male baseball players (NBP, no experience playing baseball). They were asked to complete the hand-mapping task both before and after 15 min of ball catching using the glove. While previous research has found changes in the body schema immediately after tool-use (Cardinali 2011; Cardinali et al. 2012; Carlson et al. 2010; Maravita and Iriki 2004; Sposito et al. 2012), our results for the body model did not align with these findings. There were no significant differences between the pre- and post-tool use hand maps. This suggests that participants did not embody the baseball glove during the 15 min of training. When we compared the results of the two studies, we found that EBP had significantly smaller estimates of hand width and finger length than NBP. Together the results suggest lasting

changes in the body model of the hand after long- but not short-term tool use.

Previous studies have demonstrated that the body model is distorted; this distortion is characterized by an overestimation of hand width and underestimation of finger length (Coelho and Gonzalez 2018a, b; Coelho et al. 2017; Longo 2014, 2015; Longo and Haggard 2010, 2011, 2012a, b; Longo et al. 2015a, b; Saulton et al. 2015, 2016). The results of the EBP in the current study did not adhere to this distortion. When compared to the non-occluded hand maps, both hand width and finger length were underestimated. This is the first report documenting an underestimation of hand width. Moreover, when compared to the maps of controls, finger length was further underestimated in the EBP. These results suggest that, after long-term training with the glove, the participants' hand perception is that of being overall smaller. This finding is somewhat surprising and we discuss it later in more detail.

The male controls in the first study and the NBP also failed to follow the characteristic distortion, with respect to hand width. Control participants and NBP made accurate estimates of hand width, while underestimating finger length. We have recently reported similar results of hand width in controls (Coelho and Gonzalez 2018). That study found that while females overestimated width, males made accurate estimates. We argued that this is in line with body dysmorphia literature which has found that females overestimate body width, whereas males underestimate body size (Fairburn and Beglin 1990; Hoek and Van Hoeken 2003; McCreary and Sasse 2000; Weltzin et al. 2005). We proposed that females and males have different underlying perceptions of their bodies (including the hands). The results from the male controls and from the NBP in the present study provide further support that males do not adhere to the previously described distortion of hand width reported when using female and male participants together. Most of the

previous studies on the body model have featured predominantly female participants, which could have hidden these sex differences. It would be interesting to investigate how long-term tool use changes hand representation in females, for example by testing softball players.

Behavioral studies have documented measurable perceptual changes in the participants' body schema following the use of a tool (Cardinali 2011; Cardinali et al. 2009, 2012; Carlson et al. 2010; Iriki et al. 1996; Maravita and Iriki 2004; Sposito et al. 2012). These studies have shown an expansion of the body schema, one that includes the tool into its representation. Surprisingly, in the present study we find that the body model of the hand is reduced in the EBP. A possible explanation for this reduction is the mechanisms of catching itself. It has been stated that the act of catching relies on visual cues and the ability to predict the path of the incoming ball (Fischman and Schneider 1985). As catching is made up of a series of complex coordinated movements involving precision and accurate timing of the limbs, the perception of having a smaller hand may in fact provide an advantage. This smaller representation could optimize hand positioning, by creating a more central position of the hand relative to the incoming ball. A conservative estimate of catching the ball, would lead to less misses and fumbles (if you perceive your hand bigger than it really is, then you are more likely to miss catching an object). Indirect evidence for this argument can be found in reach-to-grasp literature, which has found larger hand apertures, when vision is restricted or a delay is introduced (Flindall 2017; Hu et al. 1999; Hu and Goodale 2000). It has been argued that when the participant is uncertain about the target (i.e., no vision) the larger hand aperture is a way of increasing the margin of error (Jakobson and Goodale 1991). Thus, the more certain a participant is about the task, the more likely they are to reduce their hand aperture. So by perceiving their hands as smaller, the EBP would be reducing their margin of error for catching. This explanation could also address why we find differing results to another study that investigated how long-term training impacted the implicit representations of the hands (Cocchini et al. 2018). In this study, expert magicians completed a hand-mapping task. The results showed that the magicians were more accurate at estimating the lengths of their fingers. Our result from the current study show that while extensive training lead to changes in the body model, it actually caused a reduction in perceived hand size. We attribute the differing results between these two studies to the unique skill sets of the two groups (magicians and EBP). For example, magicians rely on sleight of hand tricks that require them to pretend an action, while they are actually performing a different one. This 'illusion' has been argued to require a representation of their own hand that reflects its anatomical shape and size (Cocchini et al. 2018; Cavina-Pratesi et al. 2011). EBP in contrast, would benefit

from a smaller hand representation as this could lead to more accuracy in catching.

Alternatively, it is possible that the smaller hand representation found in the EBP is a result of the fact that when they are not wearing the glove it creates the perceptual illusion that their hand is smaller. In other words, the extensive usage of the glove produces its embodiment so that when the glove is absent their hand feels incomplete. Here we quote one of the EBP who mentioned to one of the authors that "when I reach out to pick up a ball without my glove, I feel my hand is tiny and useless". In their review, Cardinali et al. (2012), argue that there is no functional benefit for lasting changes in body representation following tool use. Moreover, they state that following tool-use body ownership should rapidly revert to normal and without negative consequences (disembodiment). Our results argue otherwise, as they demonstrate that after long-term practice using a baseball glove there are lasting changes to hand representation. The relationship between tool use and the conditions upon which it is embodied and disembodied needs further investigation.

One last explanation involves the cortical representation of the hand. It has been suggested that the body model preserves characteristics of the somatosensory homunculus for both the hand (Longo and Haggard 2010) and the face (Mora et al. 2018). Although it is tempting to speculate that long-term use of the glove changes the neural representation of the hand, only future neurostimulation or imaging research could directly address this question. Nevertheless, the result that EBP have an underestimated body model of the hand could be explained in terms of changes in cortical representation. Previous work has documented that extensive training leads to less cortical activation in musicians (Jäncke et al. 2000) and in athletes (Naito and Hirose 2014). For example, Naito and Hirose (2014) found reduced recruitment in motor areas when professional soccer players rotated their feet, compared to controls (Naito and Hirose 2014). These authors argued that the long-term training controlling the ball, may have led to plastic changes in the foot's motor representation of soccer players. These studies however, did not measure body representation, so it is impossible to assert that the reduced recruitment of cortical areas leads to changes in the body model. Further research is needed to investigate this possibility.

A puzzle remains as to why we found perceptual changes in both hands if EBP consistently wear the glove on their left hand. We are unaware of any studies that have found that tool-use with one limb leads to changes in both limbs. However, one study asked participants to use (15 min) a rake with both their dominant right hand and their non-dominant left hand. They showed that training with a tool changes body representation for both the dominant and non-dominant arms (Sposito et al. 2012). It was argued that even though the dominant arm is more dexterous and trained in using tools,

the left hand is equally susceptible to changes in body representation after tool use. The fact that EBP showed changes in the representation of both hands even though they wear the glove only on the left hand, suggests that extensive training using a tool in one hand could lead to a carry-over effect to the other hand. This is reminiscent of behavioral studies that have shown that motor skills learned with one hand transfer to the other, e.g., Parlow and Kinsbourne (1989, Sainburg and Wang (2002) and Schulze et al. (2002). For example, Schulze and colleagues asked participants to train for 4 weeks on a pegboard task (pegs of different sizes had to be inserted into the appropriate holes). Some participants trained with the right hand, others with the left, and yet another group trained with both hands simultaneously. The main finding was that training had reduced the time of inserting the pegs on both the trained and the untrained hand (regardless of group). So even though only one hand did the training, movement times by the untrained hand were also faster after the training. The authors suggested that inter-hemispheric transfer must occur and they further discuss the possible neural mechanisms supporting this transfer. Based on these studies, we speculate extensive training with the glove (EBP) changes the body model of the hand and this effect can be seen in both hands.

Lastly, we found that short-term tool use with the glove did not change implicit hand representation. One likely possibility is that participants did not embody the glove during the short 15 min of active catching. As catching is a skilled movement, and using the glove requires practice, perhaps these participants did not treat the glove as something that aided their performance. This is different from the classic paradigm (mechanical grabber for example), in which the task could not be completed without the incorporation of the tool into the body schema. One previous study found similar results to ours (Biggio et al. 2017). The authors investigated if peripersonal space was modulated by tool-use (tennis racket) and found that holding onto the tennis racket only altered peripersonal space elite tennis players, but not in novices. In other words, only elite tennis players embodied the racket. The authors argue that this result means that plasticity of peripersonal space depends on familiarity with the tool, and this is gained over years of practice. Our results suggest that the same could be true for the body model, as our NBP did not demonstrate a change in the hand maps following 15 min of catching. Additionally, a study investigated the neural correlates of body representation changes in elite tennis players and controls (Fourkas et al. 2008). The authors used TMS to measure forearm and hand muscles in these groups while they mentally practiced a tennis forehand, table tennis forehand, and a golf drive. The elite tennis players showed increased corticospinal facilitation during the imagined tennis forehand, but were not different from the novices in the other two conditions. The authors

argue that their results indicate that long-term experience is crucial in modulating sensorimotor body representations. Our results suggest that long-term experience with a tool is necessary for changes in the body model. Perhaps, testing a group of participants who had played elite-level baseball for some years but did not continue playing, would yield similar results to the EBP or to other studies demonstrating changes in body representation after short-term training. It would be important to also identify how much training is necessary to see the long-term changes in hand representation; is 1 year enough? Or does it take 5+ years? Further research is needed to answer these questions.

To conclude, we investigated the long- and short-term effects of experience-based plasticity on the body model of the hand. A group of EBP (many years of baseball experience; long-term effects of tool use), a group of NBP (no experience playing baseball; short-term effects of tool use), and a group of male controls, completed an implicit hand representation task. The results show that EBP underestimated hand width and finger length more so than the NBP or controls. This result suggests that prolonged tool use produces long-lasting changes in the body model.

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