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BRIEF REPORT

Tool Use Changes the Spatial Extension of the Magnetic Touch Illusion

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Characterizing the brain mechanisms that allow humans to use tools to interact with the environment is a major goal in neuroscience. It has been proposed that handheld tools are incorporated into the multisensory representation of the body and its surrounding (peripersonal) space, underlying our remarkable tool use ability. One single-cell recording study in tool-using monkeys provided qualitative support for this hypothesis, and the results from a vast number of human studies employing different experimental paradigms have been ambiguous. Here, we made use of the recently reported magnetic touch illusion—a perceptual correlate of peripersonal space—to examine the effect of tool use on the representation of visuotactile peripersonal space. The results showed that active tool use leads to an extension of the "illusion volume" around the entire length of a tool, which was significantly greater compared with a manual control task. These findings support the notion that the multisensory representation of peripersonal space is extended to incorporate handheld tools and provide a three-dimensional estimation of this remapping process.

Keywords: peripersonal space, tool use, body perception, space perception, multisensory integration

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Tool use is considered a main driving factor in the rapid evolution of human cognition. Characterizing the brain mechanisms underlying tool use is therefore a major goal in neuroscience and has been intensively debated over the past two decades. One influential hypothesis is that handheld tools are incorporated into the multisensory representation of the body, allowing us to use tools as extensions of our bodies (Holmes, 2012; Maravita & Iriki, 2004). This notion was initially supported by the qualitative observation in macaque monkeys that neurons integrating tactile and visual signals within the space around the body (peripersonal space) feature visual receptive fields that are dynamically extended following tool use (Iriki, Tanaka, & Iwamura, 1996; however, see Holmes, 2012, for a critical view). Evidence for a similar dynamic representation of visuotactile peripersonal space in humans is mainly derived from studies on patients with hemispatial neglect or extinction following brain damage, in which neurological deficits specific to near-personal space can be extended to far space following tool use (Berti & Frassinetti, 2000; Farnè & Làdavas, 2000; Maravita, Husain, Clarke, & Driver, 2001), and studies in healthy participants using the cross-modal congruency task showing that tool use can extend the space close to the body within which the processing of congruent visual and tactile stimuli is normally facilitated (Maravita, Spence, Kennett, & Driver, 2002; Spence, Pavani, Maravita, & Holmes, 2004). In addition to the effects on visuotactile peripersonal space, tool use influences the kinematics of grasping movements (Cardinali et al., 2009, 2012; Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016), body metrics of arm and hand size (Canzoneri et al., 2013; Cardinali et al., 2009; Garbarini et al., 2015; Miller, Longo, & Saygin, 2014, 2017; Sposito, Bolognini, Vallar, & Maravita, 2012), audio-tactile integration in the space close to the body (Canzoneri et al., 2013), and the predictive sensory attenuation of self-generated touch (Kilteni & Ehrsson, 2017), supporting the notion that tools are incorporated into multiple aspects of the body representation. However, the conclusiveness of the results from human as well as animal studies on the effect of tool use on visuotactile integration in peripersonal space has been questioned (Holmes, 2012; Holmes, Sanabria, Calvert, & Spence, 2007), highlighting the importance of developing new experimental approaches. To this end, we investigated the effect of tool use on the spatial extension of the recently reported magnetic touch illusion (Guterstam, Zeberg, Özçiftci, & Ehrsson, 2016)—a perceptual correlate of visuotactile integration in peripersonal space.

The magnetic touch illusion is elicited by the delivery of brushstrokes in midair at some distance above a rubber hand—without touching it—in synchrony with brushstrokes applied to a participant's hidden real hand. This setup results in the illusory sensation of a "magnetic force" between the brush and the rubber hand, which exhibits striking similarities to the receptive field properties of hand-centered peripersonal space neurons, being dependent on temporal visuotactile congruence, featuring a nonlinear decay at the distance of 40 cm, being independent of gaze direction, and

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following changes in the rubber hand position (Guterstam et al., 2016). In this study, we made use of motion tracking of the brush moving in midair synchronized with real-time illusion vividness ratings to systematically measure the magnetic touch illusion in seven different directions projecting from the rubber hand (see Figure 1). By first determining the illusion breaking points in three-dimensional space for each direction, we then extrapolated the "illusion volume" using procedures identical to those of Experiment 4 in Guterstam et al. (2016; see Method for details).

To estimate the effect of active tool use on the spatial extension of the illusion, we mapped out the illusion volume immediately before and after either a task involving tool use or a control task. The tool use task involved the participants using a 75-cm-long rake to collect and sort multiple small, differently colored objects placed just within the edge of their reach using the tool held in their right hand (see Figure 1). In the control task, the participants used their right hand to collect and sort the same objects placed just within their reach (see Figure 1). The duration of both tasks was 5 min, which was based on the duration used in the study of Iriki et al. (1996). Twenty-eight healthy, naïve participants were randomized to the tool use ($n = 14$) or control task group ($n = 14$). To statistically determine whether the illusion volume extended in the direction of the tool, we analyzed the shift of the geometric center of the illusion volumes before versus after tool use along a vector corresponding to the direction of the tool (in the XY-plane).

Results and Discussion

The results showed that active tool use led to a significant positive shift of the geometric center of the illusion volume along the direction of the tool (*after* vs. *before* tool use difference: $M \pm SE = 11.3 \pm 4.9$ cm; $t_{13} = 2.28$, $p = .040$, two-tailed t test). The shift along the tool direction was significantly larger compared with a random direction ($p = .004$, permutation testing with 100,000 iterations; see Figure 2A and Figure 3A). Visual inspection of the average illusion volumes before versus after tool use shows that this shift was driven by a specific extension of the illusion volume surrounding the tool (Figure 2A, red and blue represent the before and after illusion volumes, respectively). The shift along the tool direction was significantly greater in the tool use than in the control task group ($t_{15.1} = 3.34$, $p = .004$, two-tailed t test), and the difference in shift was significantly larger in the tool direction compared with a random direction ($p < .001$, permutation testing with 100,000 iterations; Figure 2B and Figure 3B). In the control task group, a general decrease in the average illusion cutoff distance before versus after was observed ($M \pm SE = 45.8 \pm 2.9$ cm vs. 38.7 ± 2.4 cm; $t_{13} = 15.80$, $p < .001$, two-tailed t test). We speculate that this 7-cm shrinkage of the illusion volume might be due to the participants becoming quicker at judging when the illusion disappears during the second repetition, which results in a slight shrinkage of the illusion volume.

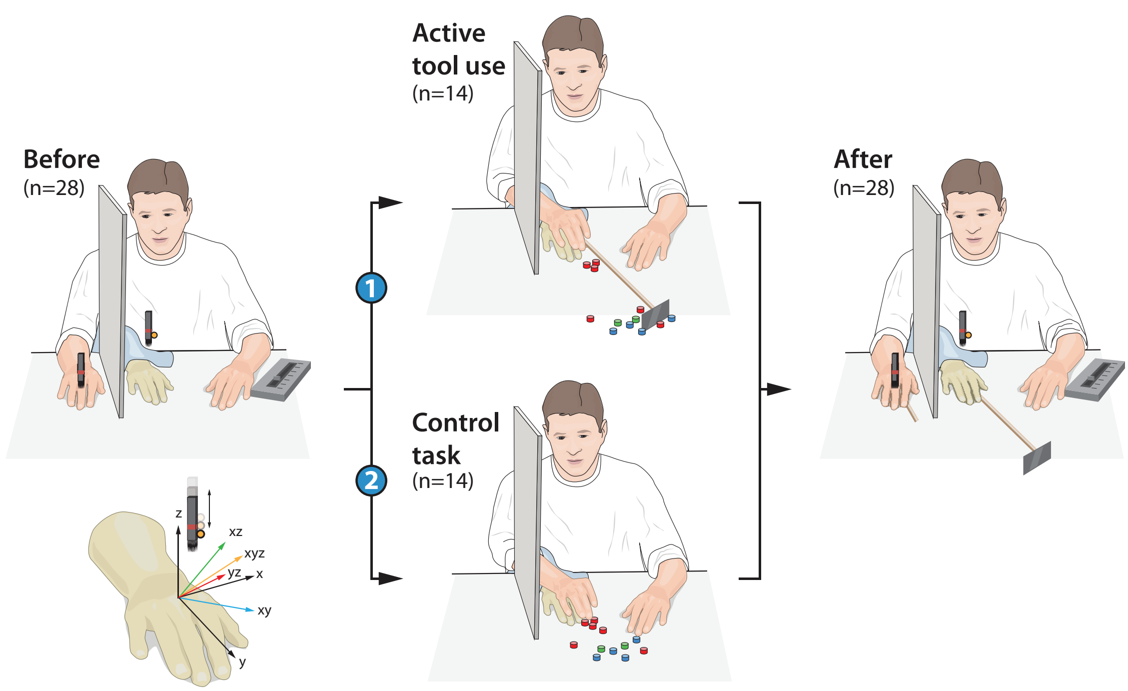

Figure 1. Experimental setup and design. The magnetic touch illusion was induced through concurrent tapping with two small brushes on the participants' real hand and in midair a couple of centimeters above a rubber hand in full view. Once the illusion was established, the distance between the rubber hand and the brush was slowly increased in one of seven directions while the tapping motions were continuously employed and the participants continuously rated the illusion strength using a sliding bar placed in their left hand. This procedure was repeated immediately before and after a task that involved collecting and sorting small objects of different colors using a 75-cm-long rake held in their right hand (Active tool use). In a control group, the participants performed the same task with their right hand but without using the rake (Control task). The rubber hand was visible during the execution of both tasks. The second repetition of the illusion procedure (After) involved the rubber hand holding the rake and the real hand holding a short stick, in both groups.

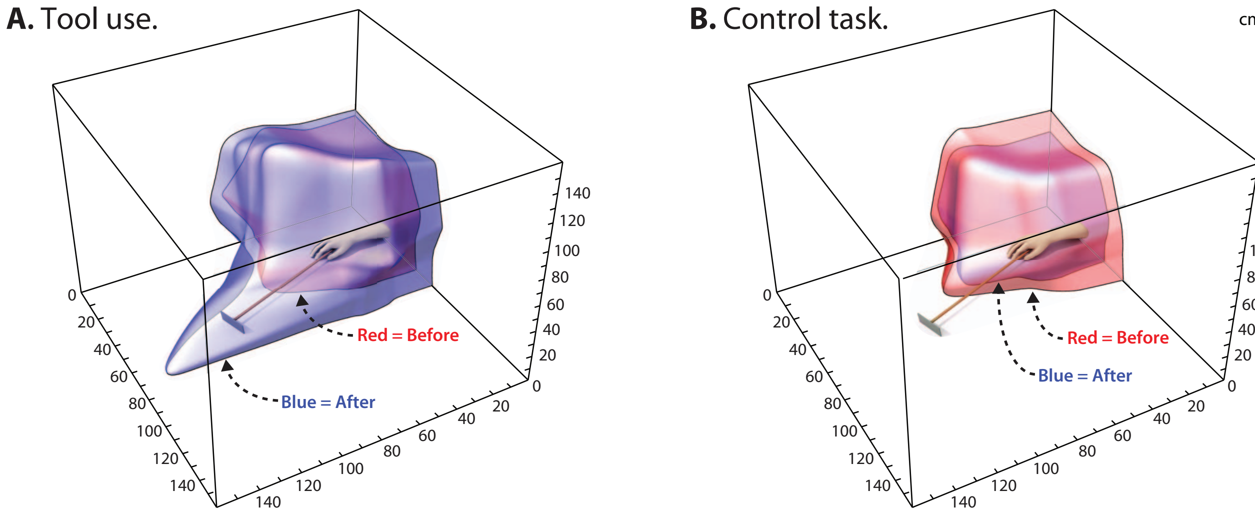

Figure 2. Illusion volume results. The average "illusion volume" for each condition was extrapolated from the illusion breaking points for each of the seven directions (for details, see Method). The results demonstrate that tool use led to a significant extension of the illusion volume along the direction of the tool, which was reflected in a significant shift of the geometric center of the illusion volume *before* versus *after* tool use ($p = .004$; A) that was significantly greater than in the control task ($p < .001$; B). These results suggest that active tool use increases the spatial boundaries of the magnetic touch illusion. The blue surface represents the *after* illusion volume and the red surface the *before* illusion volume. Please note that the red volume in panel A is engulfed entirely by the blue volume (rendering it purple) and vice versa in panel B.

Together, these findings suggest that active tool use is associated with an illusion volume increase along the tool axis that cannot be explained by general factors such as order effects, fatigue, or practice. If anything, such general factors seem to have a slightly negative effect on the illusion extension.

Our results show that active tool use leads to a spatial extension of the magnetic touch illusion. Based on our previous study showing that this illusion mirrors the receptive field properties of neurons integrating visuotactile signals within peripersonal space in a hand-centered fashion (Guterstam et al., 2016), the present findings support the hypothesis that the use of handheld tools leads to a corresponding extension of the representation of peripersonal space. This observation constitutes an important new addition to the ongoing debate regarding the neural mechanisms of tool use (Holmes, 2012; Holmes et al., 2007; Maravita & Iriki, 2004) because the magnetic touch illusion differs fundamentally from previous paradigms probing the effect of tool use on the multisensory peripersonal space representation, such as the cross-modal congruency task (Maravita et al., 2002; Spence et al., 2004). Whereas the cross-modal congruency task is based on response time differences to visuotactile stimuli presented at discrete locations in near versus far space (Holmes, 2012; Spence et al., 2004), the present illusion is a conscious perceptual effect that the participants report continuously along the trajectory of the brush moving away from the rubber hand (Guterstam et al., 2016). The configuration of the illusion volume (Figure 2A) shows that the participants reported a strong illusion along the whole length of the tool, including the shaft and the tip. This observation supports the notion that tool use leads to a redistribution of peripersonal space to surround the entire length of a tool and not merely a projection to its tip (Holmes, 2012). Moreover, whereas covert spatial attention toward the tip of the (recently used) tool might potentially impact the cross-modal congruency effect (Holmes, 2012), which is based on response time differences on the scale of 40 ms that are (most probably) subconscious, it seems less likely to impact the present illusion vividness ratings, because of the slower (second-scale) nature of the magnetic touch illusion and the fact that the participants were explicitly instructed to pay attention to the rubber hand and the brush moving in midair. In summary, our results support the notion that the multisensory representation of peripersonal space is extended to incorporate handheld tools (Maravita & Iriki, 2004), providing a potential neural mechanism for the remarkable ability of the human brain to make use of tools to interact with the environment.

Method

Participant Information

Because the experiments required the participants to experience a robust magnetic touch illusion, we first performed a screening session in which the participants were exposed to the illusion condition for 1 min and then asked to fill out a questionnaire (see (Guterstam et al., 2016, for questionnaire details). Out of a total of 39 participants, 11 (28%) individuals did not display a strong illusion experience (less than +2 rating of the statement "It seemed as though there was a 'magnetic force' or 'force field' between the brush and the rubber hand") and were excluded from further testing. This proportion of nonresponders was expected given the results of previous studies of the magnetic touch (Guterstam et al., 2016) and rubber hand illusions (Botvinick & Cohen, 1998; Guterstam, Gentile, & Ehrsson, 2013; Guterstam, Petkova,

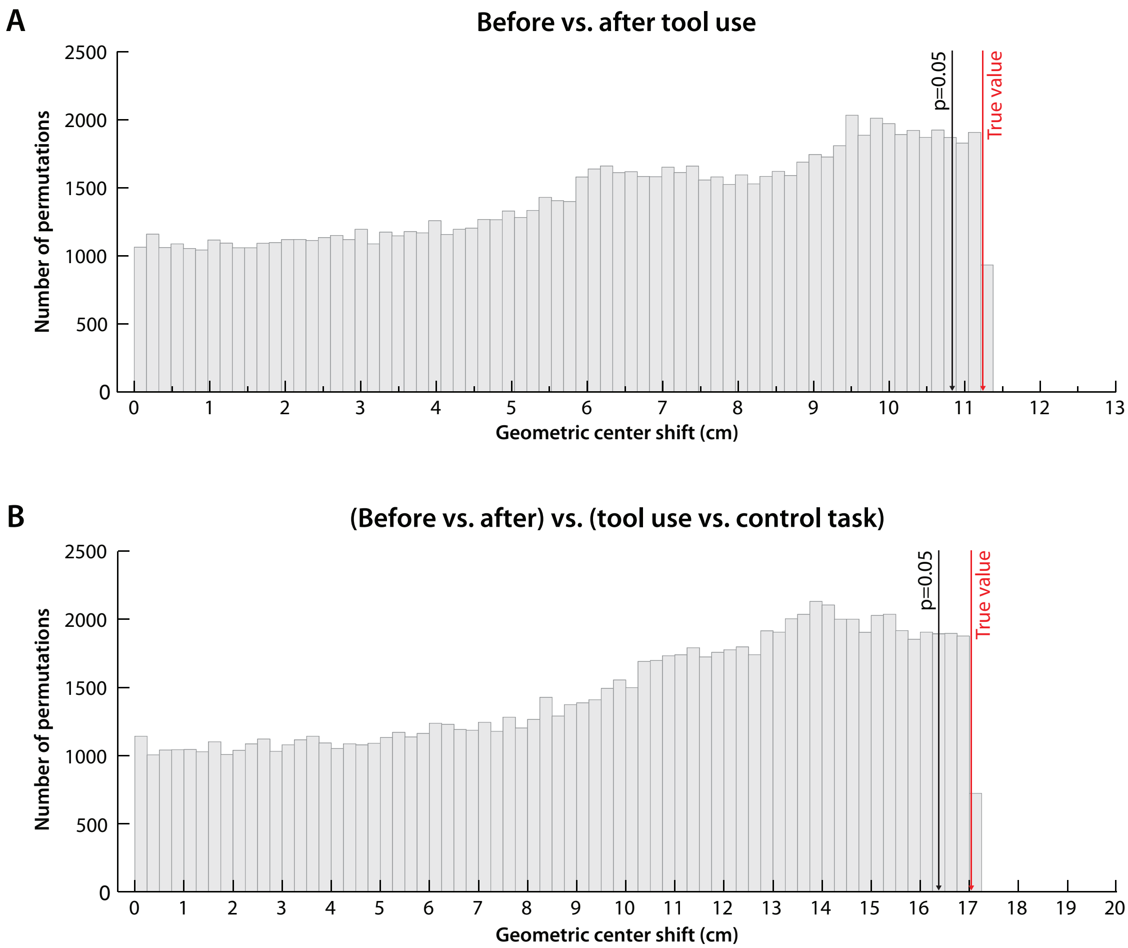

Figure 3. Permutation testing results. (A) To statistically test the hypothesis that the illusion volume is extended in the direction of the tool following tool use, we analyzed the shift of the geometric center of the illusion volumes before, compared to after, the tool use task. Specifically, we estimated the coordinates of the geometric center of the illusion volume in the before and after conditions for each participant and then projected the before-versus-after difference onto a vector that was spatially aligned with the orientation of the tool. To test for significance, we used a permutation approach in which we compared the mean before-versus-after shift along the true tool vector with the corresponding shift along a vector projected in a random direction (permutation testing using 100,000 iterations). In other words, the three-dimensional direction of the vector upon which we projected the true before-versus-after shift in geometric center was permuted. We constrained the randomly projected vectors to the polar and azimuth angle intervals 0–90° because the illusion extension in angles outside these intervals was not experimentally tested (Figure 1 and 2A, B). The p value was defined as (1 + the number of permuted shift values > true shift)/(1 + the total number of permutations). The histogram shows the results for the permuted trials, with the significance limit ($p = .05$) and the true values indicated. Thus, the tool use task was associated with a significant positive shift of the geometric center of the illusion volume along the direction of the tool. (B) To test for differences to the control task group, we repeated the same permutation procedure but using the mean difference between the before-versus-after shifts in the tool use task and the control task. The results show that there was a significantly greater task-induced shift of the illusion volume's geometric center along the tool direction in the tool use group compared with the control task group. See the online article for the color version of this figure.

& Ehrsson, 2011). It should be noted that all participants, including the ones who were excluded, received the same payment in the form of a cinema ticket and were not informed beforehand that failure to report a strong illusion would lead to a shorter experiment duration. For the main experiment, which was conducted immediately following the screening procedure, a total of 28 healthy adult volunteers (of whom 18 were female and 27 were right-handed) were recruited. Fourteen were randomized to the "active tool use" group (age: 30.3 ± 10.5 years; 7 females) and 14 to the "control task" group (age: 28.1 ± 9.5 years; 11 females). Based on the observation that illusion volumes can be reliably estimated in single subjects (Guterstam et al., 2016), we considered a sample size of $n = 14$ per group appropriate for estimating illusion volumes at the group level and examining the potential effect of tool use. All subjects gave their written informed consent prior to participation, and the Regional Ethical Review Board of Stockholm approved all the experimental procedures.

Experimental Setup

The experiments were conducted in a soundproof testing room (40-decibel noise reduction). The participants sat in a comfortable chair and rested their arms on a table in front of them. The participants' right arm was placed behind a screen and was thus hidden from view. A rubber hand was placed on the table in full view of the participant at a distance of 15 cm from the hidden real hand (see Figure 1). The experimenter, who sat opposite the participant, induced the illusion by applying synchronous tapping movements on the hidden real hand and in midair a couple of centimeters above the rubber hand. The touches were applied to all five digits and the back of the participant's right hand and the corresponding locations above the rubber hand. A small sensor that continuously recorded three-dimensional spatial coordinates at the frequency of 60 Hz (Polhemus FASTRAK, Colchester, Vermont) was attached to the tip of brush (indicated by a small yellow circle in Figure 1).

Once the participant reported illusion onset, the experimenter started to increase the distance between the brush tapping in midair and the rubber hand. To systematically map out the illusion volume, the tapping brush moved away from the rubber hand in one of seven predefined directions (see Figure 1). The participants were instructed to continuously rate the subjective strength of the magnetic touch sensation (specifically, the statement "It seemed as though there was a 'magnetic force' or 'force field' between the brush and the rubber hand") on a scale between −3 (*disagree completely*) and +3 (*agree completely*) using a sliding bar (TSD115 Variable assessment transducer; BIOPAC, Goleta, California) placed in their left hand. We used in-house software to synchronize the motion-tracking data from the sensor attached to the brush moving in midair with the input from the sliding bar representing the participant's real-time illusion vividness. As such, a given data point in three-dimensional space was assigned an illusion vividness value between −3 and +3. Finally, the location of the rubber hand itself within the coordinate system was determined by systematically moving the motion sensor across the entire rubbery skin surface. The mapping of one entire illusion volume (i.e., seven directions) took approximately 3 min in total. The order in which the seven directions were measured was randomized.

Experimental Design

The aim of the present study was to examine whether the three-dimensional spatial extension of the magnetic touch illusion is affected by active tool use. Specifically, we tested the hypothesis that a period of active tool use will lead to an extension of the illusion volume to surround the tool. To this end, we used Mathematica (Wolfram Research, Champaign, Illinois) to estimate the illusion volumes before and after the tool use or control task according to the same procedures described in Guterstam et al. (2016). Specifically, for each of the four conditions (before and after the tool use or control task), the data were extrapolated to an illusion volume in the following way: We first defined a 160-cm × 160-cm × 160-cm cube with the spatial resolution of 1 × 1 × 1 cm. The fixed location of the motion-tracking base station represented the origin coordinate [X = 1, Y = 1, Z = 1], and the knuckle of the middle finger of the rubber hand was located at [X = 20, Y = 20, Z = 5]. Within each participant, each voxel was assigned the illusion vividness value of the nearest (in terms of Euclidean distance) experimentally tested data point. At the group level, we assigned each voxel the average voxel value across participants. Because of the sparseness of the data points further away from the rubber hand, the data were then smoothened using a moving average technique in which the value of each voxel was replaced with the mean value of a 30-cm × 30-cm × 30-cm cube centered on that voxel. The smoothening procedure ensured a relatively homogeneous surface between the experimentally tested directions. In accordance with Guterstam et al. (2016), we defined the illusion breakpoint as the spatial coordinates where the rated illusion strength dropped below zero (i.e., when the participants started to deny experiencing the illusion). It should be noted that the smoothing procedure yields it impossible to detect a break in the illusion along the shaft for distances less than 15 cm (assuming that the participants' degree of agreement and disagreement during the presence and absence of the illusion is equal). However, given the fact that the distance 15 cm constitutes merely 20% of the total length of the tool shaft, we consider this limitation of our methodological approach acceptable.

The three-dimensional surface of the illusion volume for each condition and each participant was drawn using linear interpolation (Figure 2A, B), using the same procedures as described in Experiment 4 of our previous study (Guterstam et al., 2016). To statistically test the hypothesis that the illusion volume is extended in the direction of the tool following tool use, we analyzed the shift of the geometric center of the illusion volumes before, compared with after, the tool use and control tasks (for details, see Figure 3A, B). In addition to the permutation testing approach described in detail in the Results section and Figure 3A, B, we performed two *t* tests: We analyzed the mean *after-versus-before* geometric center shift along the tool axis under the null hypothesis that there was no shift (two-tailed one-sample *t* test) and compared the mean *after-versus-before* shifts in the tool use group and the control task group (two-tailed unpaired *t* test). Both data sets were normally distributed (Shapiro-Wilk test for normality: $p = .45$ and .95). However, because they did not display equal variances (Levene test: $p = .005$), we corrected for this violation by adjusting the degrees of freedom of the unpaired *t* test using the Welch-Satterthwaite method.

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