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R478

Correspondence

Tool-use induces morphological updating of the body schema

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To control bodily movements the human brain relies on a somatosensory representation referred to as the body schema [1]. The almost century-old hypothesis that tool-use induces plastic changes resulting in the tool being incorporated in the body schema is nowadays widely accepted. Whether this somatosensory representation is truly modified remains unknown, however, as tool-use has never been shown to affect arm motor behaviour. Here we report that using a mechanical grabber that physically extends the arm does alter the kinematics of subsequent free-hand grasping movements. Remarkably, tool-use after-effects generalise to pointing movements, despite the absence of specific tool-training. Furthermore, this effect is driven by an increase of the represented length of the arm: after tool-use, subjects localised touches delivered on the elbow and middle fingertip of their arm as if they were farther apart. These findings indicate that tool-use alters the body schema, and also show that what is modified is the somatosensory representation of intrinsic properties of the body morphology.

The body is not a constant object. The morphological changes it undergoes throughout life do not affect the brain's ability to accurately move limbs and grasp objects, the cerebral representation of our body-parts' dimensions and positions being constantly updated [2]. Plastic changes of the body schema have been advocated also to explain human and non-human skilful use of tools [3–6]. While tool-embodiment has been shown through perceptual changes in peripersonal space [7–9], cortical correlates of motor imagery and even time perception (see Supplemental references in the Supplemental data available online), there is no evidence that tool-use modifies the body schema. We hypothesized that, by modifying the somatosensory body schema, the use of a 40 cm-long mechanical grabber would affect the kinematics of subsequent grasping movements performed *without* the tool. Tool-use consisted of handling the grabber to reach and grasp a target object. Free-hand and tool-use grasping actions (see Supplemental Movies 1–4) were recorded in healthy subjects via a high-resolution optoelectronic three-dimensional motion tracking system by placing active infrared markers in the kinematically relevant locations on either the subject's hand or tool (Figure 1A).

In Experiment 1 ($N = 14$) separate ANOVAs with Sequence (pre/post tool-use) and target Size (small/large) as within-subject variables showed longer latencies (Velocity Latency (VL) $(1,13) = 11.62$, $p < 0.01$; Deceleration Latency (DL): $F(1, 13) = 15.11$, $p < 0.01$) and reduced maximal amplitude (peak) of reaching movement parameters after tool-use (Acceleration Peak (AP): $F(1,13) = 18.27$, $p < 0.01$; Velocity Peak (VP): $F(1,13) = 42.87$, $p < 0.01$; Deceleration Peak (DP): $F(1,13) = 21.50$, $p < 0.01$), as well as longer movement time (from action start to stable grip (MT): $F(1,13) = 15.05$, $p < 0.01$; all p-values Bonferroni corrected). Consistent with the tool property of allowing the subject to grasp objects with a 'longer' arm (see also Supplemental Figure S1), tool-use-dependent changes were selective for the transport component of the movement and independent of object size.

This pattern of results was confirmed by a replication study (Experiment 2, $N = 18$; Figure 1C), where five out of the six transport parameters shown to be affected in Experiment 1 were similarly modified. As in Experiment 1, no differences were present on the grasping phase of the movement. Critically, Experiment 3 ($N = 17$) ruled out unspecific test-retest effects possibly due to fatigue in handling the tool: when subjects performed the same tasks after training with a wrist-loaded weight (Figure 1B) identical to the tool weight (300 g), there was no change in any of the kinematic parameters (all p-values >0.4).

Our hypothesis that tool-use modifies the somatosensory representation of the subject's arm also predicts that different, previously untrained movements would be subsequently affected. We tested this prediction by assessing whether tool-use-dependent effects would affect a different type of free-hand movement, like pointing (see Supplemental Movies 5 and 6), which is composed of a transport phase, but was not trained with the tool (see Figure 1B). In Experiment 1, separate ANOVAs with Sequence and target Size as variables revealed that four out of the six transport parameters identified previously were similarly affected when free-hand pointing movements were performed after tool-use (AP: $F(1,13) = 8.07$, $p < 0.03$; VP: $F(1,13) = 16.22$, $p < 0.01$; DP: $F(1,13) = 14.15$, $p < 0.01$; MT: $F(1,13) = 24.11$, $p < 0.01$). In Experiment 2, all the six transport parameters were modified in the same direction, subjects showing longer latencies to achieve reduced peaks with longer movement duration (VL: $t(17) = -3.68$, $p < 0.01$; DL: $t(17) = -3.96$, $p < 0.01$; AP: $t(17) = 3.27$, $p < 0.01$; VP: $t(17) = 3.04$, $p < 0.01$; DP: $t(17) = -2.69$, $p < 0.03$; MT: $t(17) = -2.79$, $p < 0.02$; Bonferroni corrected p-values for both experiments). Again, no change was observed in the kinematics of pointing movements in control Experiment 3, in which the training consisted of grasping with the wrist-added weight.

The selective effects of tool-use on free-hand kinematics of grasping and their generalisation to pointing movements converge to strongly support the long-standing hypothesis that tool-use modifies the body schema. Because the object distance from the (hand and tool) starting position was fixed across experiments (Figure 1A) and within the hand reachable space, the kinematic changes can be selectively attributed to tool-use. At variance with most previous tool-use studies, in our experiments no widening of the reaching space was necessary during tool-use, ruling out any confound possibly due to perceptual differences of acting in different spaces. Moreover, we can exclude visual contributions in terms of 'shortening' of the perceived object distance [9], as acting on closer objects is known to affect kinematics in a different way, resulting in *shorter* latencies and reduced peak amplitudes.

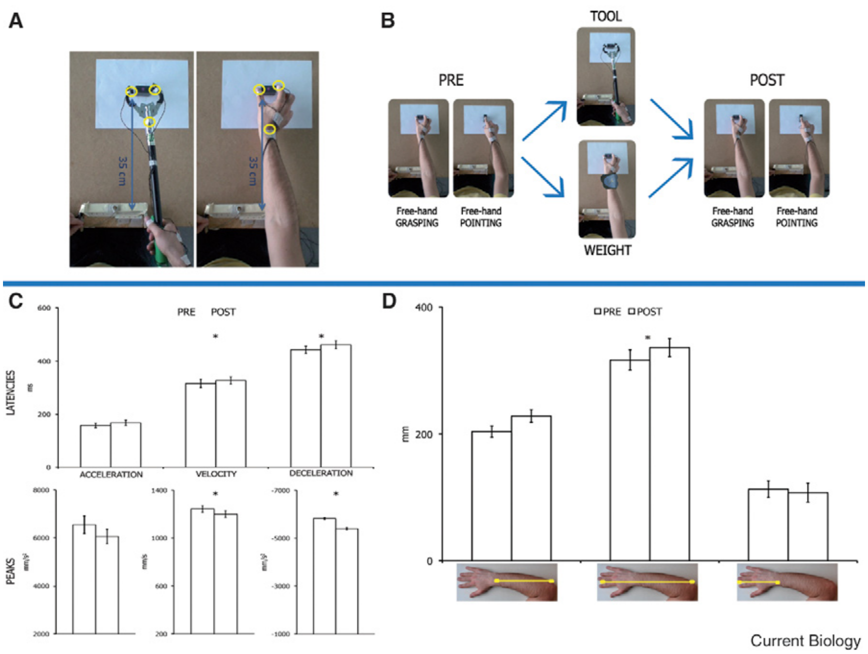

Figure 1. Tool-use modifies movement kinematics and somatosensory morphology.

(A) Infrared emitting diodes (IREDs) were located on the hand and the tool (yellow circles) for three-dimensional motion recording and off-line kinematic analysis. Three functionally homologous positions were chosen on the tool (left panel) and the hand (right panel) according to their kinematic significance: thumb and index finger-tips provide grasping information while the wrist reflects hand transport. (B) Experiment time-course: pre training (left), grasping with the tool or the weight (centre), and post training (right). A differently oriented parallepiped located 35 cm from the starting position served as large (5 cm of graspable width) and small (2 cm) target for both free-hand (grasping and pointing) and training actions. (C) After the use of the tool, most parameters of the transport component of free-hand grasping movements were modified. Subjects show longer latencies (upper graphs) and reduced peak amplitudes (lower graphs). Movement time (not shown) was also longer after tool-use ($t(17) = -2.79$, $p < 0.02$, Bonferroni corrected). (D) Mean distance between the tactually stimulated anatomical landmarks (elbow-wrist, elbow-middle fingertip, wrist-middle fingertip) as localised by subject before and after tool-use. These results clearly show that after tool-use subjects rely on a modified somatosensory representation of their arm (i.e., a longer arm). Bar graphs illustrate mean values for each parameter ± s.e.m. Asterisks denote significant differences from one-tailed Bonferroni corrected paired-sample *t*-tests.

Our hypothesis specifies that the kinematic consequences of tool-use should reflect somatosensory changes in the body schema that are consistent with an increased length of the arm. We directly tested this further prediction in Experiment 4 (N = 12, see Supplemental Experimental Procedures) by asking blindfolded subjects to point with their left (untrained) index finger directly above the location of tactile stimuli that were randomly delivered to one of three anatomical landmarks (elbow, wrist, middle fingertip) of their right (trained) arm, before and after tool-use training. Figure 1D illustrates that the mean distance among the elbow and middle fingertip locations, as indicated by the subjects ending positions, increased after tool-use (Elbow-Finger $t(11) = -2.92$, $p = 0.03$, Bonferroni corrected). This task, originally introduced in neuropsychological cases to show body schema disruption or sparing (see Supplemental References), provides here direct evidence that what is modified by tool-use is the somatosensory representation of the arm morphology. In agreement with the transport selective effects of tool-use on kinematics, this change visually appears (Figure 1D) more related to the forearm than the hand.

The morphological updating of the body schema newly reported here does not require lengthy visuomotor adaptation, as no difference potentially due to learning the use of the grabber was observed during tool-use training (see Supplemental Figure S2). Although fast, the effects produced by tool-use were not ephemeral, and persisted (at least) for the duration of the post-tool sessions across three experiments (~10–15 min). Remarkably, grasping accuracy and the molar structure of free-hand movements [10] were not altered by tool-use. This suggests that the fast dynamic updating of body morphology induced by tool-use is functional, as it does not hamper the accurate and successful control of bodily movements.

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01109-9

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