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Sensorimotor predictions and tool use: Hand-held tools attenuate self-touch

Konstantina Kilteni *, H. Henrik Ehrsson

Brain, Body and Self Laboratory, Department of Neuroscience, Karolinska Institutet, Retzius väg 8, 17177 Stockholm, Sweden

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ABSTRACT

Human survival requires quick and accurate movements, both with and without tools. To overcome the sensorimotor delays and noise, the brain uses internal forward models to predict the sensory consequences of an action. Here, we investigated whether these sensory predictions are computed similarly for actions involving hand-held tools and natural hand movements. We hypothesized that the predictive attenuation of touch observed when touching one hand with the other would also be observed for touches applied with a hand-held tool. We first show that when touch is applied to the left index finger with the right index finger, the perceived force sensation is attenuated, only when the fingers are aligned in a manner that simulates direct physical contact and not when a distance of 25 cm is introduced between the hands. We then show that touch applied to the left index finger with a tool held in the right hand at a distance of 25 cm produces full sensory attenuation, similar to direct finger-to-finger contact. Finally, we show that touch is attenuated only when the tip of the tool is aligned with the receiving left index finger and not when the tip is placed at a distance of 25 cm. Collectively, these results suggest that tool use and natural limb movements share the same computational mechanism for sensory predictions. We submit that the brain uses effector-independent forward models: touch is predicted based on the anticipated position of the current effector (i.e., the tip of the tool) rather than the body part *per se*.

1. Introduction

The ability to perform quick and accurate body movements is fundamental for human survival. To achieve this despite the inherent delays and noise in the sensorimotor system, the brain relies on predictive internal forward models that simulate the behavior of the body and the environment (Miall & Wolpert, 1996; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Kawato, 1998; Wolpert, Miall, & Kawato, 1998). Using a copy of the motor command (efference copy), forward dynamic models predict the future state of the body (e.g., its position), while forward sensory models predict the associated sensory consequences (Wolpert & Ghahramani, 2000). Both of these predictions facilitate the effective anticipatory control of action without depending on the delayed and noisy actual sensory feedback (Flanagan, Bowman, & Johansson, 2006; Wolpert & Flanagan, 2001).

The predictions of the forward sensory models also serve to attenuate self-generated sensory feedback, thereby allowing the central nervous system to allocate more processing resources to external and unexpected information that is more critical for survival (Bays & Wolpert, 2008; Blakemore, Wolpert, & Frith, 2000; Wolpert & Flanagan, 2001). The attenuation of self-produced touch is a classic example of this phenomenon: touches applied by a participant herself feel weaker than identical touches applied by another person because the former have been already anticipated by the forward sensory model (Bays, Wolpert, & Flanagan, 2005; Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998; Shergill, Bays, Frith, & Wolpert, 2003). A well-established method to study sensory attenuation is the force-matching paradigm (Shergill et al., 2003) in which participants receive an externally generated force on their relaxed left index finger. Next, they are asked to reproduce this reference force by pressing their right index finger against their left index finger via a force sensor placed between the fingertips. Participants consistently overestimate the required forces, meaning that the self-produced force feels weaker than the externally produced reference force.

The attenuation of self-produced touch has been shown to depend on the causal relationship between the movement of the active finger and the sensation on the passive finger. Sensory attenuation is significantly reduced when the hands are placed apart from each other (Bays & Wolpert, 2008) or when delays are experimentally introduced between the force generated by the active

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* Corresponding author at: Department of Neuroscience, Karolinska Institutet, Retzius väg 8, SE-171 77 Stockholm, Sweden.

E-mail address: konstantina.kilteni@ki.se (K. Kilteni).

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finger and the force felt on the passive finger (Bays et al., 2005). Moreover, when participants reproduce the external force by moving a joystick or slider the touch is not attenuated but is perceived accurately because the relationship between the horizontal hand movement and the received force is unusual (Shergill et al., 2003). Thus, only conditions that resemble natural self-touch produce sensory attenuation.

The survival of humans depends not only on our ability to use our limbs but also on our ability to use hand-held tools. Hand-held tools enable us to achieve various tasks much more effectively than would be possible with our hands alone because they allow for greater reach, flexibility and force when interacting with objects, other individuals and animals. Several behavioral studies have suggested that using hand-held tools can expand the representation of space near the hand (Berti & Frassinetti, 2000; Farnè & Làdavas, 2000; Maravita & Iriki, 2004), influence the perceived length of the arm and hand (Cardinali, Brozzoli, Finos, Roy, & Farnè, 2016; Cardinali et al., 2009; Miller, Longo, & Saygin, 2014), and affect the kinematics of free-hand movements following tool use (Cardinali et al., 2009, 2012). Although this evidence suggests that tools are incorporated into the "body schema" to at least some degree (Head & Holmes, 1911), it remains unknown whether and how the forward sensory models predict the sensory consequences of actions involving tools.

Here, we used the force-matching paradigm to investigate whether hand-held tools attenuate self-produced touch. We found that touching oneself with a drumstick produced sensory attenuation as strong as when using the index finger. Critically, the tool acted as an "extension of the limb", overcoming the actual distance between the hands. We conclude that natural hand movements and movements with hand-held tools involve the same predictive mechanism, consisting of a common effector-independent forward sensory model.

2. Materials and methods

2.1. Participants

After providing written informed consent, 12 naïve participants (7 women and 5 men, 11 right-handed and 1 ambidextrous) aged 18–38 years old participated in Experiment 1, 12 naïve participants (4 women and 8 men, 11 right-handed and 1 ambidextrous) aged 19–39 years old participated in Experiment 2, and 12 naïve participants (7 women and 5 men, all right-handed) aged 23–40 years old participated in Experiment 3. The sample size was set based on previous studies (Bays et al., 2005; Shergill et al., 2003). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). The Regional Ethical Review Board of Stockholm approved all experiments.

2.2. General procedure

In all three experiments, participants rested their left hands palm up, with the index finger on a molded support. The distance between the participants' left index finger and their body midline was approximately 10–15 cm. In each trial, they received a constant force on the pulp of their relaxed left index finger from a cylindrical probe (25 mm height) with a flat aluminum surface (20 mm diameter) attached to a lever controlled by a DC electric motor (Maxon Motor RE 40 for Experiments 1 and 2; Maxon EC Motor EC 90 flat for Experiment 3; both manufactured in Switzerland). This *presented* force lasted 3 s. One small commercially available force sensor (FSG15N1A, Honeywell Inc., USA; diameter, 5 mm; minimum resolution, 0.01 N; response time, 1 ms; measurement range, 0–15 N) was placed inside the probe to measure the forces applied by the lever (*probe sensor*). Immediately after receiving the force produced by the lever, the participants were asked to generate a force that matched the presented force (*matched force*) by pressing another identical force sensor for 3 s (*mobile sensor*). This mobile force sensor could be placed at different locations, depending on the specific experimental conditions of each experiment, and it controlled the force output of the lever (further description below).

In all experiments, the participants wore headphones through which white noise was administered to preclude the possibility that any noise produced by the motor could serve as a cue for the task. Auditory 'go' and 'stop' signals indicated the onset and the offset of the periods of the presented and matched forces, respectively. In addition, the participants were instructed to look straight ahead at a fixation point on the wall (i.e., not look at the equipment). The equipment and the participants' hands were peripherally visible and this was matched across the conditions in all experiments.

Before the start of each experiment, the participants familiarized themselves with the equipment during five to fifteen test trials. Once the participants felt comfortable with the task, the experiment commenced. No feedback was ever provided to the participants concerning their performance during the training period and the experiments.

2.3. Experiment 1

2.3.1. Rationale

The purpose of the first experiment was to re-examine the effect of the distance between the hands on the attenuation of self-generated touch, in accordance with previous observations (Bays & Wolpert, 2008), but more importantly, to define a distance at which self-generated touch *was not* attenuated. That distance between the hands would then be used in our subsequent experiments with tools to determine whether the tool could act as an "extension of the hand" and overcome the spatial constraint of the self-touch attenuation.

2.3.2. Procedure

Experiment 1 consisted of four conditions in which the distance between the hands was varied (0 cm, 15 cm and 25 cm). Each condition included 30 trials, with each presented force level (1 N, 1.5 N, 2 N, 2.5 N, 3 N and 3.5 N) pseudorandomly presented five times. Participants reproduced the presented force by using their right index fingers to press the mobile force sensor that was placed on top of the probe sensor (0 cm lateral distance between the index fingers), 15 cm to the right of their left index fingers or 25 cm to the right of their left index fingers (Fig. 1A–C). Under all three conditions, the mobile sensor controlled the force output of the lever, with the cylindrical probe pressing on their left index fingers. That is, the on-line recordings of the mobile sensor (sensor f2 in Fig. 1) were transmitted to the controller of the motor in order to precisely move the lever to apply the same force measured by the probe sensor (sensor f1 in Fig. 1) on the participants' left index finger (intrinsic delay of the system ≃25 ms). In the fourth condition – a classical control condition that assesses force perception (Shergill et al., 2003) – the participants reproduced the presented force by using their right hands to move the slider of a 13 cm linear slide potentiometer, the midline of which was positioned 25 cm to the right of their left index fingers (Fig. 1D). The lower limit (left end) of the slider corresponded to 0 N, and the upper limit (right end) corresponded to 5 N. The reproduction period always started with the slider being at the left end (0 N). As with the mobile sensor, the slider controlled the force output of the lever pressing on the participants' left index fingers with the cylindrical probe. To