Current Biology

Functional Plasticity in Somatosensory Cortex Supports Motor Learning by Observing

Highlights

- Median nerve stimulation disrupts motor learning by observing

- Somatosensory evoked potentials (SEPs) increase following observation of learning

- SEP increases predict subsequent behavioral measures of motor learning

- Motor learning by observing may rely on functional plasticity in S1

Authors

Heather R. McGregor,
Joshua G.A. Cashaback,
Paul L. Gribble

Correspondence

paul@gribblelab.org

In Brief

Watching others move activates brain networks involved in producing movement. Here, McGregor et al. address the role of this action-observation link in motor learning and provide evidence that the somatosensory system, and in particular primary somatosensory cortex, is involved in motor learning by observing.

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Functional Plasticity in Somatosensory Cortex Supports Motor Learning by Observing

Heather R. McGregor,[1,2,4] Joshua G.A. Cashaback,[1,2] and Paul L. Gribble[1,2,3,*]

[1]The Brain and Mind Institute, The University of Western Ontario, London, ON N6A 5B7, Canada
[2]Department of Psychology, The University of Western Ontario, London, ON N6A 5B7, Canada
[3]Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, The University of Western Ontario, London, ON N6A 5B7, Canada
[4]Graduate Program in Neuroscience, The University of Western Ontario, London, ON N6A 5B7, Canada
*Correspondence: paul@gribblelab.org
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SUMMARY

An influential idea in neuroscience is that the sensory-motor system is activated when observing the actions of others [1, 2]. This idea has recently been extended to motor learning, in which observation results in sensory-motor plasticity and behavioral changes in both motor and somatosensory domains [3–9]. However, it is unclear how the brain maps visual information onto motor circuits for learning. Here we test the idea that the somatosensory system, and specifically primary somatosensory cortex (S1), plays a role in motor learning by observing. In experiment 1, we applied stimulation to the median nerve to occupy the somatosensory system with unrelated inputs while participants observed a tutor learning to reach in a force field. Stimulation disrupted motor learning by observing in a limb-specific manner. Stimulation delivered to the right arm (the same arm used by the tutor) disrupted learning, whereas left arm stimulation did not. This is consistent with the idea that a somatosensory representation of the observed effector must be available during observation for learning to occur. In experiment 2, we assessed S1 cortical processing before and after observation by measuring somatosensory evoked potentials (SEPs) associated with median nerve stimulation. SEP amplitudes increased only for participants who observed learning. Moreover, SEPs increased more for participants who exhibited greater motor learning following observation. Taken together, these findings support the idea that motor learning by observing relies on functional plasticity in S1. We propose that visual signals about the movements of others are mapped onto motor circuits for learning via the somatosensory system.

RESULTS

Although many of our motor skills are acquired through physical practice, we can also learn how to make movements by observing others. For instance, individuals can learn how to reach in novel dynamical environments ("force fields") by observing the movements of a tutor. Action observation promotes sensory-motor plasticity and behavioral changes in both the motor and sensory domains [3–9]. However, it remains unclear how the brain maps visual information about the movements of others onto motor circuits for learning. One possibility is the involvement of the somatosensory system. Somatosensory cortical regions have substantial anatomical connections with visual and motor areas of the brain, and so it is feasible that the somatosensory system may link visual and motor areas for motor learning by observing [10–15]. Here we present two experiments demonstrating that the somatosensory system, and more specifically primary somatosensory cortex (S1), is indeed involved in motor learning by observing.

Experiment 1

In experiment 1, we tested the hypothesis that the involvement of the somatosensory system is necessary for motor learning by observing. We used a learning task that involved holding the handle of a robotic arm with the right hand and performing straight reaches to a visual target (Figure S1). Participants first observed a learning video depicting a tutor adapting her reaches to a robot-imposed leftward force field (left FF). To test the role of the somatosensory system in motor learning by observing, we used median nerve stimulation to deliver afferent inputs to the somatosensory system that were unrelated to the observed learning task. Median nerve stimulation reliably activates S1, second somatosensory cortex, and posterior parietal cortex [16–20]. During observation, participants either received median nerve stimulation to both arms simultaneously, to the right arm only, or to the left arm only or received no stimulation. If the involvement of the somatosensory system is necessary for motor learning by observing, then we expected that occupying somatosensory cortical processing with unrelated afferent inputs during observation would disrupt learning. A control group observed, without stimulation, a control video depicting a tutor performing curved reaches in a randomly varying (and thus unlearnable) FF. All participants then performed a motor learning test in which they reached to a visual target in a right FF (Figure 1A). No nerve stimulation was applied during the motor learning test. The more participants learned about the left FF through observation, the worse (more curved) their movements would be in the right FF [3–8]. Therefore, motor learning by
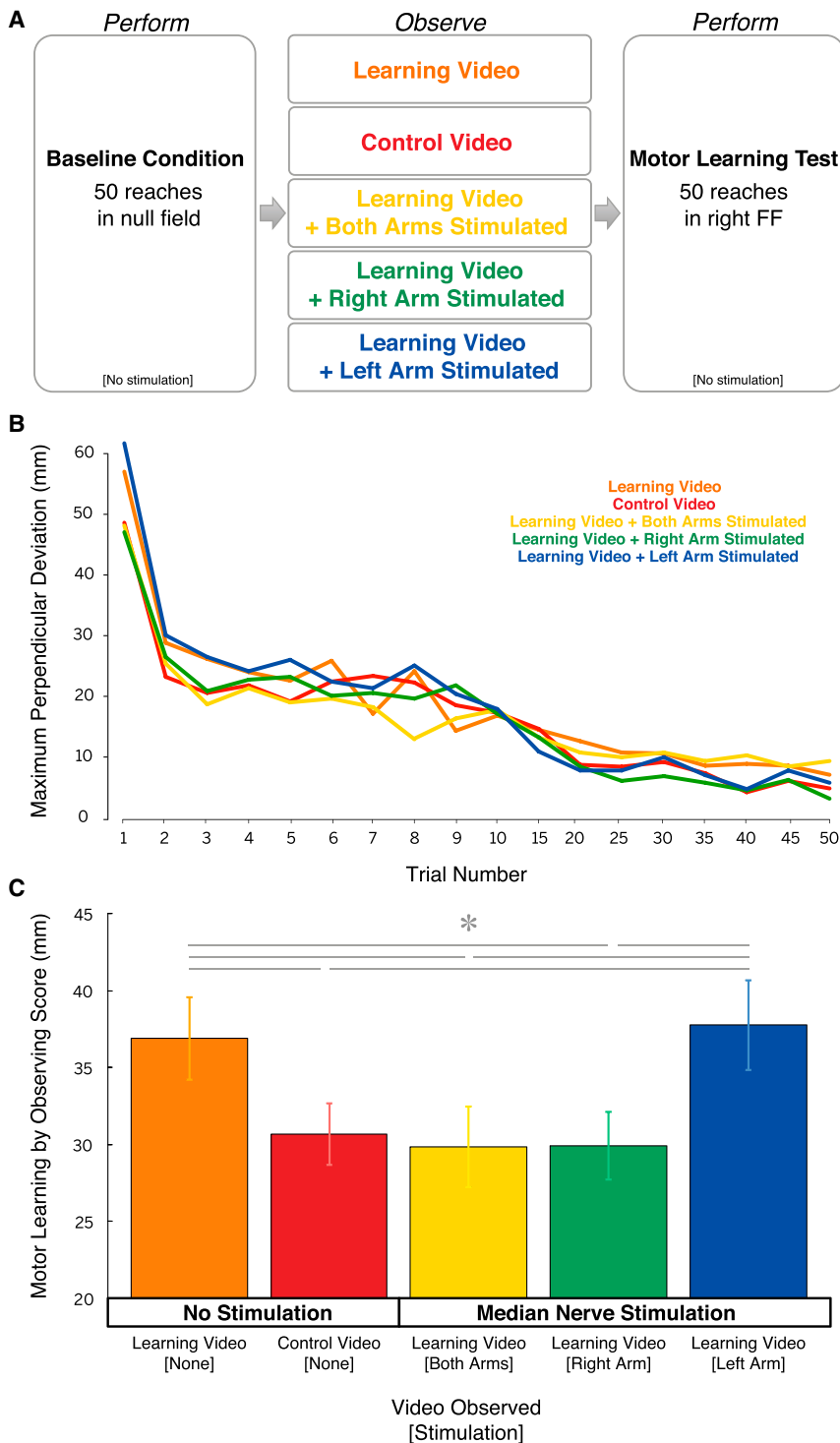
Figure 1. Experiment 1 Design and Results

(A) Participants held onto the handle of a robotic arm with the right hand (see also Figure S1). In the baseline condition, all participants performed straight reaches to a visual target in the null field in which the robot did not apply force. Participants then observed either the learning video or the control video. The learning video showed a tutor learning to reach in a leftward force field (left FF). The control video showed a tutor performing curved reaches in a randomly varying (and thus unlearnable) FF (see also Figure S2). During observation, participants received median nerve stimulation to both arms simultaneously, to the right arm only (the *same arm* used by the tutor), to the left arm only (*opposite* the arm used by the tutor), or no stimulation. Finally, as a motor learning test, all participants performed the reaching task while the robotic arm applied a rightward force field (right FF).

(B) Group average learning curves for reaches performed in the right (test) FF. The first ten movements are plotted individually and five-trial blocked averages are plotted thereafter. Greater perpendicular deviation for initial movements in the right FF indicates greater interference due to the learning of the observed left FF.

(C) Motor learning by observing scores reflecting initial interference in the right FF. Participants who observed the learning video without stimulation (orange) exhibited higher motor learning by observing scores compared to participants who observed the control video without stimulation (red). Nerve stimulation applied to both arms simultaneously (yellow) and to the right arm only (the *same* arm used by the tutor; green) during observation resulted in lower motor learning by observing scores. In contrast, participants who received nerve stimulation to the left arm only (*opposite* the arm used by the tutor; blue) exhibited higher motor learning by observing scores. Error bars represent SEM. *p < 0.05.

FF, the prediction would be that right arm stimulation during observation would diminish the benefit of observation on learning, and hence subsequent movements in the left FF would be more curved. However, in this case, it would be unclear why participants performed more poorly in the left FF. One explanation (our main hypothesis of interest) would be that the somatosensory representation of the right arm (the observed effector) was occupied during observation and was therefore unavailable for motor learning by observing. Another possibility, however, is that median nerve stimulation during observation impaired subsequent movements, for example by disrupting the basic ability to control movements of the right arm. The use of an interference paradigm allows us to rule out the latter scenario. If the somatosensory representation of the right arm (the observed effector) plays a necessary role in motor learning by observing, we expected that participants who received median nerve stimulation during
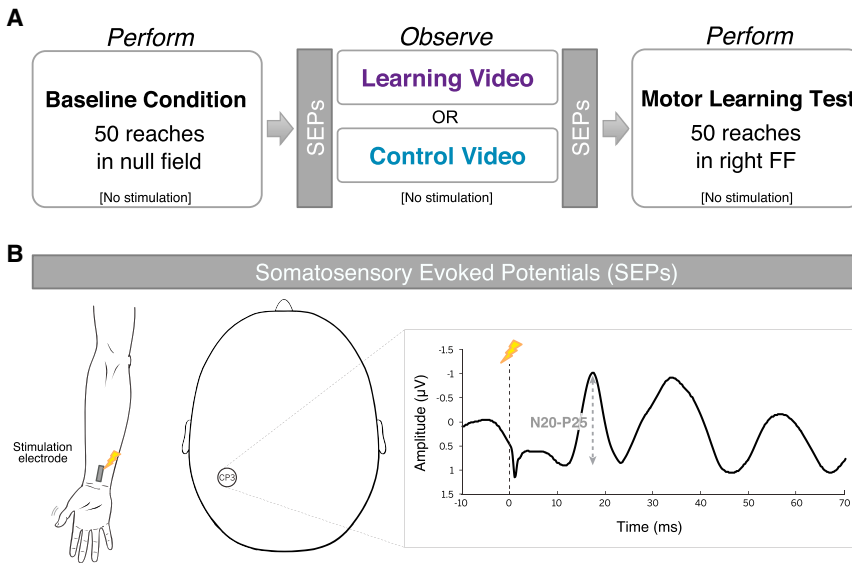
observing scores reflect interference (greater movement curvature) caused by learning to counteract the observed FF.

We chose to use an interference paradigm in experiment 1 (i.e., testing for learning in an opposite FF) because it provides a built-in control for potential non-learning-related effects of stimulation. If we had used an experimental design in which participants observed a left FF and were later tested in the same left

A

Perform

Baseline Condition
50 reaches
in null field
[No stimulation]

SEPs

Observe

Learning Video
OR
Control Video
[No stimulation]

SEPs

Perform

Motor Learning Test
50 reaches
in right FF
[No stimulation]

B

Somatosensory Evoked Potentials (SEPs)

Stimulation electrode

CP3

N20-P25

Amplitude (µV)

Time (ms)

Figure 2. Experiment 2 Design

(A) Experiment 2 used the same reaching task as in experiment 1. In the baseline condition, all participants performed straight reaches to a visual target in the null field. To assess changes in S1 cortical processing, we acquired somatosensory evoked potentials (SEPs) immediately before and after participants observed either the learning video (purple) or the control video (cyan). Finally, all participants performed a motor learning test to behaviorally assess motor learning by observing.

(B) SEP acquisition. A stimulating electrode was placed on the participant's right wrist and delivered 3-Hz electrical stimulation to the median nerve (shown at left). SEPs were recorded using an EEG electrode over left (contralateral) S1 while participants rested. The inset on the far right shows an SEP from a representative participant. The SEP trace is the average of approximately 500 stimulations, where stimulation was delivered at 0 ms (dashed line). The amplitude of the N20-P25 component of the SEP (indicated by the gray dashed arrow) reflects the earliest afferent processing in S1. SNAPs were recorded to ensure consistent stimulation across recordings (see Figure S3).

observation would perform better, straighter movements in the (opposite) right FF. An interference paradigm allows us to attribute this change in motor performance to learning resulting from observation.

Participants who observed the (left FF) learning video without nerve stimulation exhibited greater movement curvature in the right FF, and hence exhibited higher motor learning by observing scores, compared to participants who observed the control video without nerve stimulation (t(30) = 1.85, p = 0.037; Figures 1B and 1C). This is consistent with previous demonstrations that observing FF learning interferes with subsequent performance in an opposite FF [3–8]. The effects of observation seen here are unlikely to be due to changes in limb stiffness, but rather are a result of participants learning an internal model of the FF experienced by the tutor. In previous studies involving the same paradigm used here it has been shown that changes in movement curvature following observation are modulated in opposite directions based on the direction of the observed FF [3, 5, 21]. In another recent study it was shown that following observation, movements in force-channel trials exhibited systematic changes in the magnitude and direction of the force applied by participants—changes that mirrored the direction of the observed FF [9].

Median nerve stimulation applied to both arms during observation eliminated the effect of observing left FF learning. Bilateral median nerve stimulation resulted in straighter movements in the right FF compared to the group that had observed learning without nerve stimulation (t(30) = 1.88, p = 0.035). The bilateral arm stimulation group performed comparably to the control group that did not observe learning. One potential account of this result is that occupying the somatosensory cortical representation of the arms with unrelated afferent inputs during observation disrupted motor learning by observing.

It is possible that the cause of this effect is more cognitive in nature, namely that median nerve stimulation disrupted motor learning by observing because participants were distracted by the cutaneous sensation of nerve stimulation. However, addi-

tional tests allowed us to rule this out. We tested participants who received stimulation to the right arm only or to the left arm only while observing the learning video. If this effect is driven by the somatosensory system, we predicted that stimulation would disrupt learning in a limb-specific manner. That is, stimulation delivered to the right arm (the same arm used by the tutor) during observation would disrupt learning but stimulation delivered to the left arm (opposite that used by the tutor) would not. Indeed, right (same) arm stimulation resulted in lower motor learning by observing scores compared to the learning group that did not receive stimulation (t(30) = 2.01, p = 0.027). In contrast, the left (opposite) arm stimulation group performed comparably to the learning group that did not receive stimulation (t(30) = −0.22, p = 0.83). Moreover, the left arm stimulation group exhibited higher motor learning by observing scores than the right arm stimulation group (t(30) = 2.15, p = 0.02) and the both arm stimulation group (t(30) = 2.01, p = 0.027). This establishes that this effect is not driven by distraction, which would have had similar effects for both the left and right arm stimulation groups. There were no differences in stimulation intensities (t(30) = −0.74, p = 0.47) or stimulus pain ratings (t(30) = −0.53, p = 0.60) between the right and left arm stimulation groups, further supporting the idea that this effect is not due to distraction. The results of experiment 1 are consistent with the idea that a somatosensory representation of the observed effector is necessary, and therefore must be available, for motor learning by observing to occur.

Experiment 2

The findings above suggest that the somatosensory system plays a role in motor learning by observing. In experiment 2, we tested a more specific hypothesis that S1 is involved in motor learning by observing. We assessed changes in S1 cortical processing from before to after observation by measuring somatosensory evoked potentials (SEPs) (Figure 2A). SEPs were elicited by applying median nerve stimulation at the right wrist and were recorded using an EEG electrode over left S1 (Figure 2B). SEPs
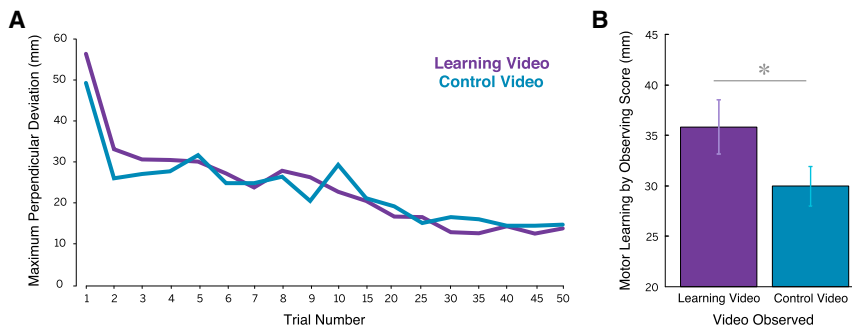
Figure 3. Experiment 2 Motor Learning Test Performance

(A) Group average learning curves for reaches performed in the right (test) FF. The first ten movements are plotted individually and five-trial blocked averages are plotted thereafter. Greater perpendicular deviation for initial movements in the right FF indicates greater interference due to the learning of the observed left FF. Participants who observed the (left FF) learning video showed greater movement curvature when first exposed to the right (test) FF compared to control participants (cyan).

(B) Average motor learning by observing scores for the learning group (purple) and control group (cyan). Motor learning by observing scores reflect interference (greater movement curvature) in the right FF caused by learning of the observed left FF. Error bars represent SEM. *p < 0.05.

were acquired before and after participants observed the learning video or the control video. No stimulation was applied during observation. Finally, participants performed reaches to a visual target in a right FF as a motor learning test.

As in experiment 1, participants who observed the tutor undergoing left FF learning performed more curved movements in the right FF (Figure 3A), exhibiting higher motor learning by observing scores compared to control participants who did not observe learning (t(30) = 1.75, p < 0.05; Figure 3B).

We assessed pre- to post-observation changes in the N20-P25 component of the SEP, occurring approximately 20–25 ms following median nerve stimulation. The N20-P25 component is a reflection of the earliest cortical processing of afferent signals by S1 [19, 20]. In addition, the N20-P25 component is highly reproducible and largely unaffected by one's cognitive state [22]. Participants who observed the tutor undergoing left FF learning exhibited reliable increases in the N20-P25 component amplitude measured over left S1 (t(30) = 2.72, p < 0.02; Figures 4A and 4B) compared to the control group that observed curved movements in an unlearnable FF. Moreover, across participants in the learning group, increases in the N20-P25 component amplitude were reliably correlated with their subsequent motor learning by observing scores (r = 0.55, p < 0.03; Figure 4C). These results are consistent with the idea that motor learning by observing involves functional plasticity in S1.

It is possible that SEP changes could have been caused by changes in applied stimulation from pre- to post-observation due to skin conductance changes or electrode slippage. To control for this possibility, we also recorded sensory nerve action potentials (SNAPs) during SEP recordings. SNAPs were recorded from the median nerve just above the right elbow (Figure S3A). This allowed us to confirm stimulus consistency between recordings. SNAP amplitude changes from the pre- to post-observation did not differ between the learning and control groups (t(28) = 0.19, p = 0.85; Figures S3B and S3C). Thus, the group differences seen in SEP changes can be attributed to changes in S1 processing, and not to changes in stimulation applied to the median nerve.

DISCUSSION

In experiment 1, we showed that the application of median nerve stimulation during observation disrupts motor learning

by observing in a limb-specific manner. This is consistent with the idea that a somatosensory representation of the observed effector is necessary and therefore must be available during observation for motor learning by observing to occur. In experiment 2 we showed that S1, in particular, is involved in motor learning by observing. SEPs recorded over S1 increased in amplitude only for those participants who observed learning. Moreover, across participants in the learning group, increases in S1 functional plasticity were positively correlated with subsequent behavioral measures of motor learning.

Much of the work on the activation of the motor system through observation has focused on so-called mirror neurons in the premotor cortex, which are activated both when observing an action and when performing the same action [23]. However, much of this work has focused on cognitive and social effects of action observation such as action understanding, empathy, and theory of mind [24]. Here we tested a different idea, namely that visual signals about the actions of others are mapped onto somatosensory and motor circuits to facilitate motor learning. Together, the results from the experiments presented here support the idea that the somatosensory system is involved in this mapping.

This idea is also supported by the existence of substantial reciprocal anatomical connections between visual, somatosensory, and motor areas of the brain. Afferent inputs are projected from primary and secondary somatosensory cortices to posterior parietal cortex (e.g., ventral intraparietal area), where they are integrated with visual inputs [10–12]. Parietal areas then project the integrated information to motor and premotor areas via S1 [13] and/or thalamic relays [14, 15].

Recent work has shown that active motor learning involving physical practice results in functional changes in somatosensory brain areas. This has been demonstrated in neuroimaging [25] and in SEP studies using EEG [26–28]. Similarly, behavioral studies have shown systematic changes in sensed limb position [29–31] and increased perceptual acuity [32] following active motor learning. If motor learning by observing involves similar neural circuitry as active motor learning, we should also see somatosensory functional plasticity and behavioral changes with observation. Although previous work has shown that observing FF learning involves concurrent changes in sensory-motor resting-state
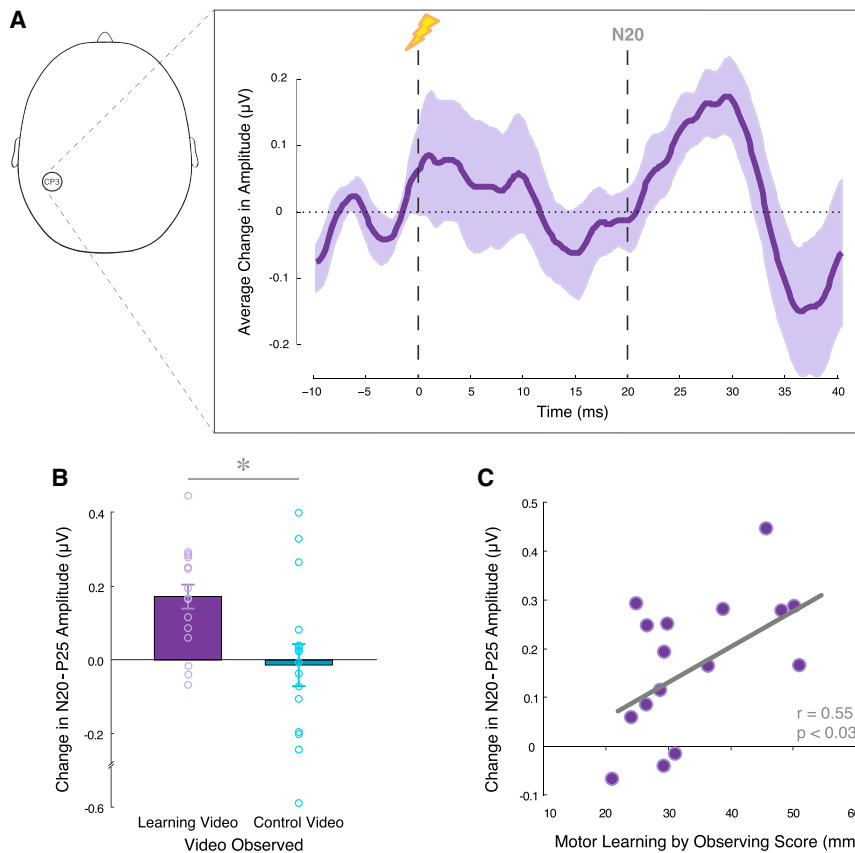
Figure 4. Motor Learning by Observing Changes in SEPs

(A) Average time-varying difference in SEP amplitudes from before to after observation for the learning group. Positive values indicate an increase in SEP amplitude following observation. Stimulation was delivered at 0 ms (vertical dashed line at left). It can be seen that the N20-P25 component amplitude (beginning at the vertical dashed line on the right) increased after observing learning. Shaded region represents SEM.

(B) Mean change in N20-P25 amplitude after participants observed the tutor learning a left FF (purple) or observed the tutor reaching in an unlearnable FF (cyan). Open circles represent changes in the N20-P25 component amplitude for individual participants. Error bars represent SEM. *p < 0.05.

(C) Across participants in the learning group, increases in the N20-P25 amplitude are correlated with subsequent behavioral motor learning by observing scores.

sory and motor plasticity contribute to motor learning by observing.

In conclusion, the results of experiment 1 are consistent with the idea that a somatosensory representation of the observed effector plays a necessary and limb-specific role in motor learning by observing. Experiment 2 demonstrated that functional plasticity in S1, in particular, supports motor learning by observing. Collectively, these results support the hypothesis that visual signals about the movements of others are mapped onto motor circuits via the somatosensory system to aid in motor learning.

EXPERIMENTAL PROCEDURES

Participants

Eighty healthy participants participated in experiment 1 (20.5 years ± 0.28 SE, 28 males, 16 participants per group). Thirty-two participated in experiment 2 (21.3 years ± 0.53 SE, 12 males, 16 participants per group). Both experiments utilized a between-participants design. Participants were right handed, had normal or corrected-to-normal vision, had no neurological or musculoskeletal disorders, and were naive to FFs. Participants provided written informed consent to experimental procedures approved by the Research Ethics Board at The University of Western Ontario.

Reaching Task

Participants grasped the handle of an InMotion2 robotic arm (Interactive Motion Technologies) with the right hand and performed straight reaches to a visual target in the horizontal plane. An air sled positioned under the elbow supported the right arm against gravity. An LCD television projected visual feedback onto a horizontal semi-silvered mirror mounted above the robot handle. Visual feedback consisted of a start position (20-mm blue circle), target (20-mm white circle), and cursor (12-mm pink circle) indicating hand position (Figure S1).

Participants were instructed to perform straight reaches from the start position to the target located 15 cm in front. Color-coded visual feedback was provided to keep movement speed consistent between trials. The target disappeared if the movement was correctly timed (450–550 ms), and turned red or green if the movement was too fast or too slow, respectively. The robot handle position and velocity were sampled at 600 Hz.

functional connectivity [7] and sensed limb position [8], these studies did not directly test the role of the somatosensory system.

There is behavioral evidence that during observation, participants use a feedforward process to predict the sensory consequences of the tutor's movement (e.g., how the movement should look) [33]. When the tutor's hand is displaced by a FF, visual feedback of kinematic errors could drive the updating of the participant's forward model [34]. It is currently unclear how motor learning by observing might differentially influence or involve feedforward versus feedback control. This is a potentially interesting avenue for future work.

Median nerve stimulation undoubtedly activates the somatosensory system [16–20]; however, it may also affect primary motor cortex excitability [35]. Although it is possible that changes in primary motor cortex (M1) may have contributed to the results of experiment 1, the primary effect of continuous stimulation to the median nerve is the activation of the somatosensory system [16–20]. Moreover, in experiment 2, we showed that observing a tutor learning to reach in a FF is associated with S1 functional plasticity that predicts, across participants, behavioral measures of learning following observation. Taken together, the results of the two experiments presented here support the idea that motor learning by observing is driven not only by activation of the motor system but also by plasticity in the somatosensory system and, in particular, S1. In future studies it would be interesting to investigate potential interactions between M1 and S1 during observation to gain a better understanding of how both sen-

The robotic arm altered limb dynamics by applying velocity-dependent FFs, which pushed the hand. FFs were applied according to the following equation:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} 0 & dk \\ -dk & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix},$$

where x and y are lateral and sagittal directions, F_x and F_y are the applied robot forces, v_x and v_y are hand velocities, $k = 14$ Ns/m, and $d = +1$ (right FF) or -1 (left FF).

Videos

The videos have been described in detail elsewhere [7]. Briefly, the videos showed a top-down view of a tutor performing the reaching task using the right arm. The learning video showed clips of a tutor adapting her reaches to a left FF, gradually progressing from curved to straight movements (Figure S2A). The control video showed clips of a tutor performing curved reaches in an un-learnable FF, which varied randomly from trial to trial between a left FF, right FF, and null field (no force applied; Figure S2B).

Experiment 1 Protocol

Participants first performed 50 baseline reaches in a null field (no applied forces). For the stimulation groups, we applied median nerve stimulation during observation to both arms simultaneously, to the right arm only, or to the left arm only. Because stimulation was applied throughout the 15-min video, we stimulated the upper arm to reduce participants' discomfort. If applicable, a bipolar bar stimulation electrode was placed (cathode proximal) over the median nerve on the anterior surface of the arm(s) 3 cm proximal to the elbow. An isolated square wave stimulator delivered 0.2-ms pulses at a rate of 3 Hz. Stimulation intensity was set to 2.5 times the participant's sensory threshold. To verify that perceived stimulation was similar across groups, participants rated the perceived stimulus pain from 0 to 10, where 0 indicated that they could not feel the stimulation and 10 corresponded to the worst pain they had ever experienced. Participants then observed either the learning video or the control video and, if applicable, stimulation was applied. Participants were not informed about FFs in the video. Participants were instructed to sit still, count the number of correctly timed reaches (indicated by the target disappearing), and report the final tally. This was done to verify that participants attended to the videos. The stimulation electrodes were then removed. Finally, as a behavioral motor learning test, participants performed 50 reaches in a right FF. The better that participants learned the muscle force pattern required for counter-acting the left FF from observing the tutor, the more curved their movements would be in the (opposite) right FF. Thus, greater rightward curvature in the motor learning test indicates greater motor learning by observing [3–8].

Experiment 2 Protocol

Participants first performed 50 baseline reaches in the null field. The bipolar stimulation electrode was then placed on the right median nerve at the wrist, and the EEG cap and SNAP electrodes were applied. We then acquired three 3-min-long SEP recordings while the participant rested with their eyes closed. As in experiment 1, stimulation consisted of 0.2-ms pulses at a rate of 3 Hz. Stimulation intensity was adjusted to elicit involuntary thumb oppositions. To ensure stimulation was consistent across SEP recordings, we also recorded SNAPs. SNAPs were recorded using two electrodes placed 2 cm apart along the median nerve on the anterior surface of the arm, just above the right elbow (Figure S3). The proximal electrode served as the reference, and a ground electrode was placed on the right olecranon. SNAPs were recorded in the same location where stimulation was applied in experiment 1. During median nerve stimulation, we acquired EEG and SNAP data using an active electrode system (g.Gamma; g.tec Medical Engineering) and amplifier (g.USBamp; g.tec Medical Engineering). Our cap-mounted montage consisted of an electrode over left S1 (site CP3) and a ground electrode on the forehead (site FPz). A reference electrode was clipped to the left earlobe. Impedances were maintained below 5 kΩ. Data were sampled at 4,800 Hz and filtered online with band-pass (0.1–1,000 Hz) and notch (60 Hz) filters. Following SEP recordings, participants observed either the learning video or the control video. No stimulation was applied during observation. As in experiment 1, participants were not informed about FFs in the video and were instructed to sit still and counted correctly timed reaches. We then acquired three 3-min-long SEP recordings

while participants rested with their eyes closed. The stimulation electrode, EEG cap, and SNAP electrodes were then removed. Finally, participants performed 50 reaches in a right FF as a motor learning test.

Behavioral Data Analysis

Positional data were low-pass filtered at 40 Hz. We computed the curvature of each movement as the maximum perpendicular deviation (PD) relative to a straight line connecting the start position and target. Motor learning by observing scores were computed as the mean PD of the first 3 right FF trials minus the mean PD of the last 25 null field trials. Motor learning by observing scores indicated the extent to which observing the left FF interfered with subsequent motor performance, in terms of movement curvature, in the right FF [3–8]. Our results for experiments 1 and 2 were consistent whether or not our motor learning by observing scores took into account the average PD of the first two through the first five right FF trials (relative to baseline).

SEP and SNAP Data Analysis

The EEG and SNAP data were band-pass filtered (between 20–100 Hz and 20–300 Hz, respectively) using second-order Butterworth filters. All signals were segmented into 80-ms epochs time locked to stimulation onset (−10 to 70 ms). We subtracted pre-stimulus baseline from each epoch and excluded epochs in which signal voltages exceeded ±50 μV from baseline. We obtained SEPs and SNAPs by averaging the remaining artifact-free epochs. SEP amplitudes were quantified as the peak-to-peak amplitude between the N20 and P25 components. SNAP amplitudes were quantified as the amplitude between the peak occurring 5 ms post-stimulation and the following peak of opposite deflection.

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.01.064.

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