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.
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. Gribble1,2,3,*
1The Brain and Mind Institute, The University of Western Ontario, London, ON N6A 5B7, Canada
2Department of Psychology, The University of Western Ontario, London, ON N6A 5B7, Canada
3Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, The University of Western Ontario, London, ON N6A 5B7, Canada
4Graduate Program in Neuroscience, The University of Western Ontario, London, ON N6A 5B7, Canada
*Correspondence: paul@gribbelab.org
http://dx.doi.org/10.1016/j.cub.2016.01.064

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 deliverafferentinputs 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
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 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
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, additional 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) = 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) = −0.22, \( p = 0.83 \)) 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, 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. SEPs 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).
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
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 sensory 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.
The robotic arm altered limb dynamics by applying velocity-dependent FFs, which pushed the hand. FFs were applied according to the following equation:

\[
F_x \frac{F_y}{F_r} = \begin{bmatrix} 0 & dk & 0 \\ -dk & 0 & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix},
\]

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, \( k = 14 \text{ Ns/m} \), 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 unlearnable 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

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 counteracting 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 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 counteracting 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].

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 stimulus onset (−10 to 70 ms). We subtracted pre-stimulus baseline from each epoch and excluded epochs in which signal voltages exceeded ±50μV 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.

AUTHOR CONTRIBUTIONS

H.R.M. and J.G.C. collected the data. H.R.M. performed analyses and drafted the manuscript, and H.R.M., J.G.C., and P.L.G. edited the manuscript. H.R.M., J.G.C., and P.L.G. designed the experiments.

ACKNOWLEDGMENTS

This research was supported by grants to P.L.G. from the Canadian Institutes of Health Research (CIHR) and the Natural Sciences and Engineering Council of Canada (NSERC).

Received: September 11, 2015
Revised: November 8, 2015
Accepted: January 25, 2016
Published: March 10, 2016

REFERENCES


