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The human somatosensory cortex contributes to the encoding of newly learned movements

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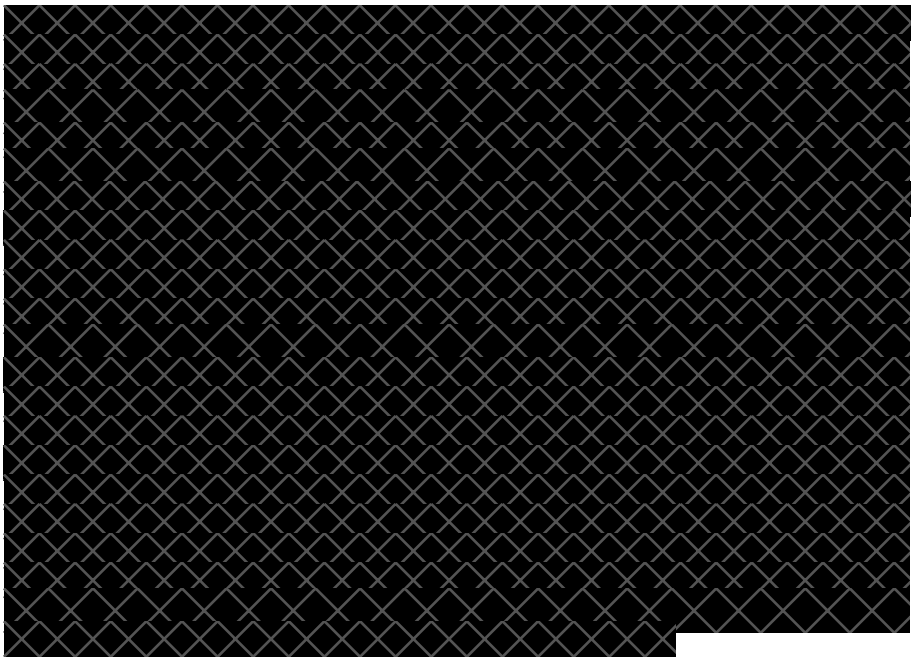

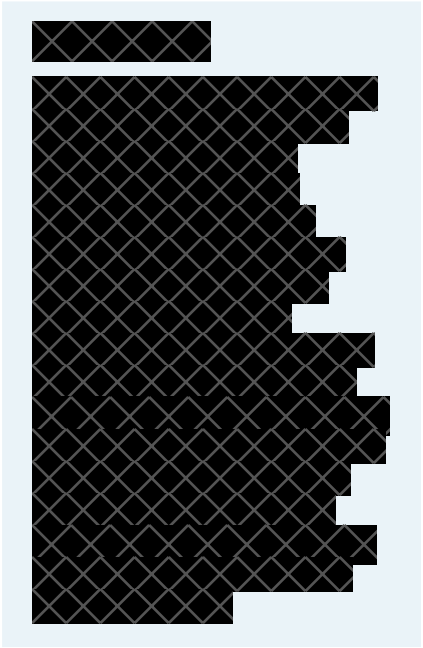

motor learning | somatosensory cortex | motor cortex | cTBS

There is accumulating evidence that motor learning is accompanied by changes to sensory systems. Somatosensory change, as reflected in sensed limb position, is observed following force-field, visuomotor, and observational learning, and there are associated changes to somatic regions of the brain, as seen in electrophysiological and neuroimaging measures (1–3). In the present paper, we test for the possible causal contribution of the motor and somatosensory cortex to motor learning and motor memory retention, using visuomotor adaptation as an experimental model. We have designed a task that permits us to distinguish whether the participation of either of these cortical zones in learning is transient, accompanying movement production, or whether, alternatively, learning results in more durable change, suggesting participation in the cortical encoding of the movement. If either the motor or somatosensory cortex contributes to the encoding of newly learned movements, then disruption of their activity once learning is complete should lead to an impairment.

In testing for the types of plasticity (somatic versus motor) which might accompany motor learning, we have designed a study that incorporates in tests of retention both active movement reproduction and recognition memory testing (4). One normally tests for retention of prior learning by asking participants to reproduce previously learned movements from memory. Testing for motor memory in this way, that is, using active movements, is analogous to recall memory testing in studies of verbal learning, and, as in verbal memory, this kind of testing may be limited by a memory access problem. That is, there may be information about previously learned movements which is available in motor memory but not accessible using tests of active movement (4). Testing for memory using recognition procedures, as is also used in tests of verbal memory, provides better access to memory and is a sensitive test of the information that is available. This is seen for example, in the ability to readily recognize a name which you are unable to retrieve and reproduce. In the context of limb movement, recognition memory testing following learning can involve passive displacements of a participant's arm and judgments by the participant as to whether the displacement corresponds to a previously learned movement direction. Using this technique, it has been found that whereas active movement testing indicated

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a substantial loss of information (memory decay) 24 h after learning, recognition tests showed almost complete retention at the same delay (4). This indicates the availability of learned information in motor memory, but a memory retrieval failure using active movement reproduction as a test of retention. The two tests in combination enable the identification of brain areas which participate in the initial retention of motor learning.

Results

The present study sought to identify the brain areas involved in the retention of motor memory by applying continuous theta-burst stimulation (cTBS) following learning to disrupt regional cortical activity in the primary motor cortex (M1), the primary somatosensory cortex (S1), or a control region over the occipital lobe. To this end, participants made reaching movements toward a visually presented target with either full or limited visual feedback (Fig. 1*A*). Prior to cTBS, subjects underwent a training block composed of a total of 150 trials (135 full feedback and 15 limited feedback), with the first 75 trials involving gradually rotated visual feedback that plateaued at 30°, followed by an additional 75 trials with feedback rotated by 30°. In full feedback trials, a cursor indicated participants' real-time hand position with a point target present throughout (Fig. 1 *F*, *Left*); in limited feedback trials, the cursor was replaced by a growing arc which provided information on movement amplitude but not direction. In these trials, the

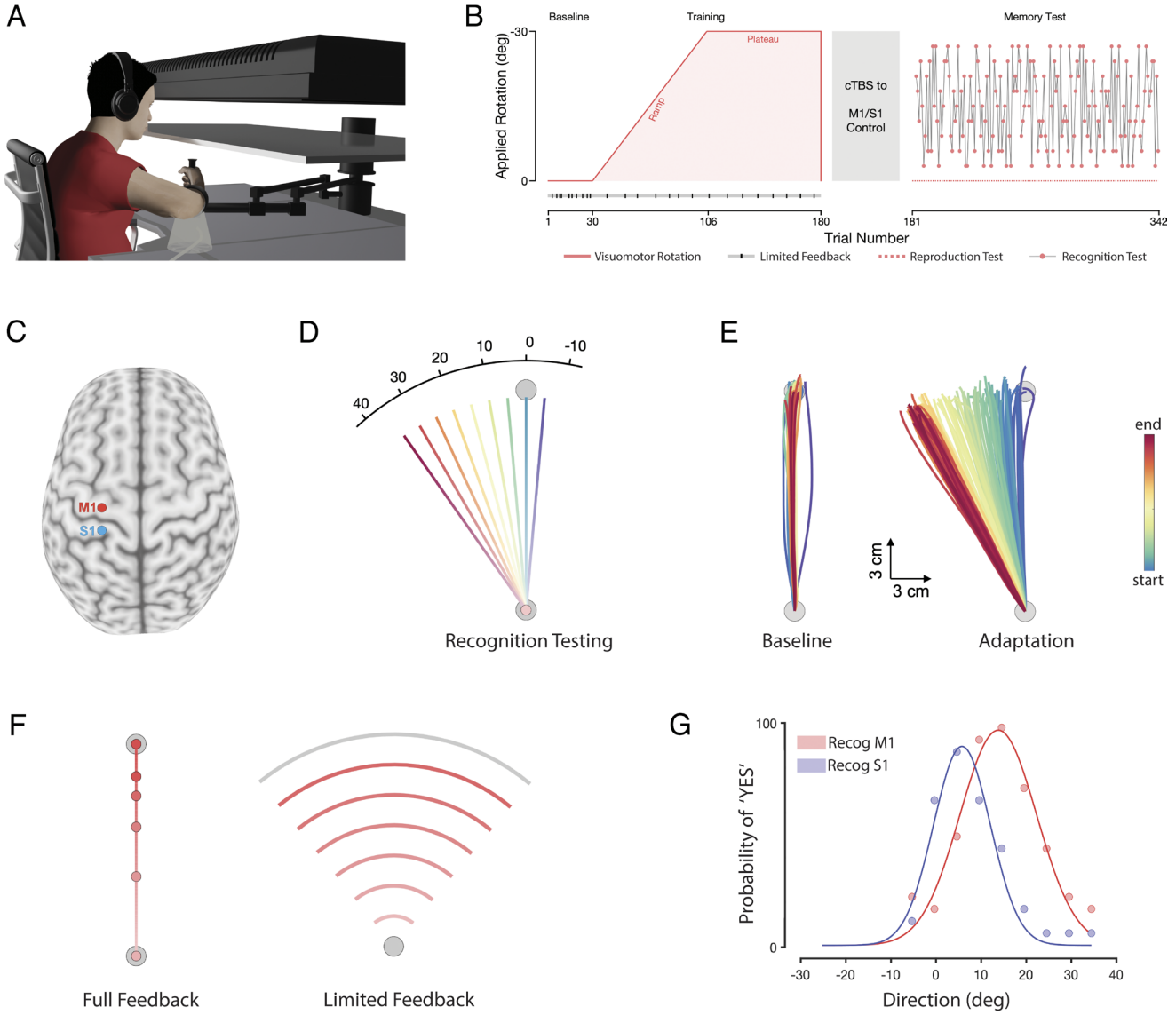

Fig. 1. Following a visuomotor adaptation task, participants were tested for retention of learning using either recognition or movement reproduction tests. (*A*) Experimental apparatus. Participants held the handle of a robot arm and made standard point-to-point reaching movements. An air sled supported the arm. (*B*) After baseline trials, participants trained with a gradually introduced 30° visuomotor rotation (shown in red). Limited feedback trials are shown with small black ticks. The adaptation task was followed by cTBS stimulation to one of three candidate regions in the brain (M1, S1, and control). Recognition or movement reproduction tests of retention tests were then performed. In tests of movement reproduction, participants were asked to move directly to the remembered position of the target point (dotted line). In recognition tests, the robot moved the participant's hand in different candidate directions, and they indicated whether this corresponded to their direction of movement (gray line with red markers). (*C*) cTBS stimulation was applied to M1, S1, or a control zone over the occipital lobe. A representative M1 hot spot is shown with a red dot. A point 2 cm posterior to the M1 hot spot was the stimulation target in S1 (blue dot). (*D*) Candidate directions in which the robot moved the participants' hand during recognition tests. (*E*) Average hand paths during baseline, training, and retention testing. (*F*) The real-time position of the participant's hand was shown in full feedback trials. Visual feedback of hand movement direction was gradually rotated in a clockwise direction over the course of training. Limited feedback trials were used both in tests of retention and in the adaptation task. During these trials, the only visual feedback was a growing semicircular arc and a target arc placed 15 cm in front of the starting point. (*G*) Gaussian fits applied to "yes" responses of two representative participants, one who underwent cTBS stimulation to S1 and the other to M1.

point target was replaced with a target arc (Fig. 1 *F*, *Right*). In a control condition, participants performed the same task with unrotated visual feedback. cTBS was applied following learning (Fig. 1*C*) and motor memory tests were subsequently performed. In a movement reproduction test involving active movement, the point target was replaced by a target arc and the cursor was replaced by an expanding arc, as in the limited feedback trials. Participants were asked to move to the remembered position of the point target. In the recognition memory test, a robot handle moved participants' arms in one of nine candidate directions, corresponding to potentially remembered movement directions (Fig. 1*D*). Visual information identical to limited feedback trials was present on the screen. Participants were instructed to respond "yes" if the displacement produced by the robot matched their own movement direction during the previous phase or "no" if it did not. Retention of motor memory was assessed by fitting a Gaussian function to a set of yes/no responses and taking the estimated mean as a measure of the remembered direction. Fig. 1*G* shows fits for two participants, one in the M1 condition and the other in the S1 condition. Across subjects, the proportion of variance accounted for by these Gaussian fits (R^2) was high, averaging 0.8638 for M1, CI [0.761, 0.966], 0.8663 for S1, CI [0.767, 0.965], and 0.8797 for control, CI [0.790, 0.969]. A summary of the different phases of the experiment is shown in Fig. 1*B*.

An example of representative hand paths during the baseline movements and adaptation task is given in Fig. 1*E*. It can be seen that participants moved straight to the target in the baseline phase and adapted to the visual perturbation over the course of the adaptation block by gradually shifting their movements in a direction opposite to the imposed perturbation, effectively compensating for the rotated visual feedback (Fig. 1 *E*, *Right*). This figure also shows that participants maintained the learned hand direction during the plateau phase of adaptation. Similar results were obtained for participants in all experimental conditions.

Fig. 2 depicts participants' hand movement direction during the adaptation task for trials in which participants received full cursor feedback (Fig. 2*A*), and for those in which they received amplitude but not direction information (Fig. 2*B*). The thin black line represents complete adaptation. It can be seen that participants in all experimental conditions displayed adaptation during the learning block and maintained movement in the learned hand direction during the plateau phase of the adaptation task. The mean hand movement direction during the baseline phase and at the end of learning (±SE) is indicated in the lower left corner and in the upper right corner of both figures, respectively. The average baseline direction was calculated based on all full and limited feedback trials and the average plateau direction was calculated based on the last 70 trials with full visual feedback and the last 8 trials with limited feedback. *SI Appendix*, Fig. S1 indicates similar results when hand directions at peak velocity are employed instead of those at the end of movement.

Statistical analysis was performed to evaluate learning by comparing the movement direction at the end of training with that observed during baseline. Tests were conducted for full and limited feedback trials separately. Mixed ANOVA was utilized to test for differences over the learning process and among the different experimental conditions. For trials involving full feedback, the data revealed a significant difference in hand movement direction between the baseline trials and the end of adaptation ($F_{[1, 66]}$ = 24923.97, $P < 0.001$, $\omega^2 = 0.993$), demonstrating learning. There were no overall significant differences in hand directions for participants that were subsequently tested for recognition versus movement reproduction memory ($P = 0.761$) or stimulated brain region ($P = 0.919$). Additionally, there was no significant

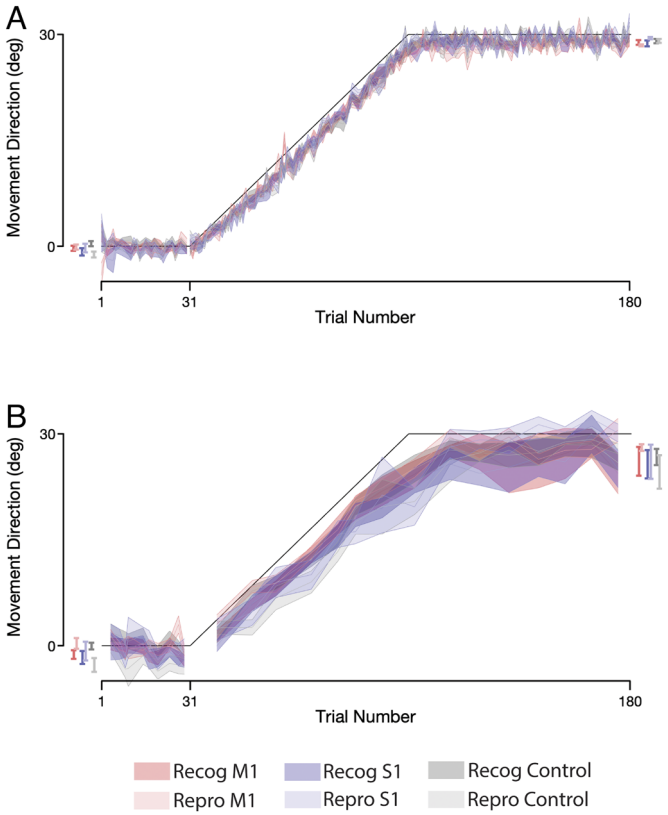

Fig. 2. Participants moved directly to the target point during baseline and compensated for the imposed visual perturbation during training. Movement direction was maintained in limited feedback trials. (*A*) Learning curves showing the average hand direction in all experimental conditions. SE are shown in shaded areas. Solid black lines show the ideal hand direction that would fully compensate for the imposed perturbation. (*B*) The mean hand direction during limited feedback trials. Error bars in (*A* and *B*) represent the mean and SE of the hand direction during baseline (*Lower Left Corner*) and plateau (*Upper Right Corner*).

interaction. Similar results were obtained for trials involving limited feedback. Specifically, no overall significant difference was found in hand direction between memory types ($P = 0.763$) or between stimulated regions ($P = 0.290$). Likewise, there was no significant interaction. However, there was a significant increase in the movement direction between the baseline and the end of the training phase ($F_{[1, 66]} = 1688.98$, $P < 0.001$, $\omega^2 = 0.901$).

Fig. 3 shows motor evoked potentials (MEPs) elicited from biceps brachii before and after cTBS stimulation. Individual participants are indicated with dots with a line connecting pre- and poststimulation MEPs. The overall mean and SE are also displayed next to the individual data points. A decrease in poststimulation MEPs can be seen in the M1 condition, whereas MEPs in the other conditions remained unchanged following stimulation. A mixed-factor ANOVA found no difference in MEP magnitude for the stimulated regions (S1, M1, and control) ($P = 0.088$). Similarly, there was no overall difference in pre- versus poststimulation MEP magnitude ($P = 0.064$). However, there was a significant interaction ($F_{[2, 69]} = 7.38$, $P = 0.001$, $\omega^2 = 0.034$). A simple main effects analysis revealed that MEPs in the M1 condition significantly decreased after cTBS stimulation ($F_{[1, 69]} = 20.50$, $P < 0.001$). The decrease was significant for the movement reproduction and recognition conditions separately ($P = 0.007$ and $P = 0.012$, respectively). Participants in the S1 condition showed slightly higher MEPs although the increase was not significant ($P = 0.150$). Likewise, there was no significant difference between pre- and post-cTBS MEPs in the control condition ($P = 0.986$).

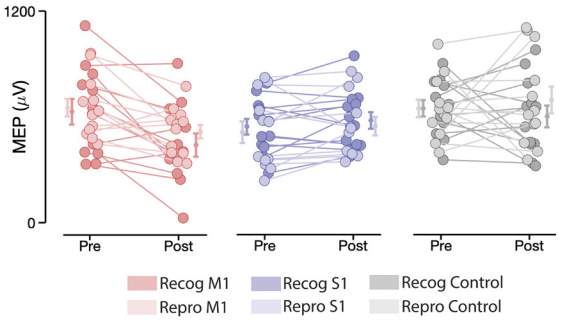

Fig. 3. MEPs were collected from the biceps brachii before and after cTBS stimulation to M1, S1, and control. The Individual MEPs are shown in dots with a straight line connecting the MEPs of each participant before and after the stimulation. Error bars represent the average and SE of each experimental condition. Statistical analysis indicated a significant decline in average MEP after cTBS stimulation to M1. No significant effect of cTBS on MEPs was found in the S1 and control conditions.

Fig. 4 shows the performance of participants during the recognition and movement reproduction tests following brain stimulation. Fig. 4*A* shows the overall Gaussian fits to the recognition judgments averaged over all individual responses for each stimulation zone separately. The peak of the Gaussian provides an estimate of the remembered direction. It is seen that relative to the other conditions, there is a displacement toward zero of the peak in the S1 condition, indicating less retention of learning. The fits for the M1 and control conditions mostly overlap. Fig. 4*B* depicts binned recognition memory performance. Each bin value was calculated by fitting a Gaussian curve over a sliding window of 36 recognition trials. It can be seen that in all experimental conditions, there is a decrease in the remembered direction relative to the estimate of adaptation at the end of learning. Participants in the S1 condition exhibited additionally degraded memory for the learned direction compared to those in the M1 and control conditions. Furthermore, as is evident in Fig. 4*B*, the remembered direction remained stable from the beginning to the end of the memory test trials. Fig. 4*C* compares the estimates of remembered direction from the overall Gaussian fits to the M1, S1, and control condition data.

Fig. 4*D* gives trial-by-trial data in the movement reproduction test of motor memory, averaged across all participants in each condition separately. As in estimates of retention based on recognition testing, it can be seen that although the overall remembered direction is less than the learned direction at the end of the adaptation task, there is a clear difference in group-level performance. As in Fig. 4 *A* and *B* for recognition testing, participants in the

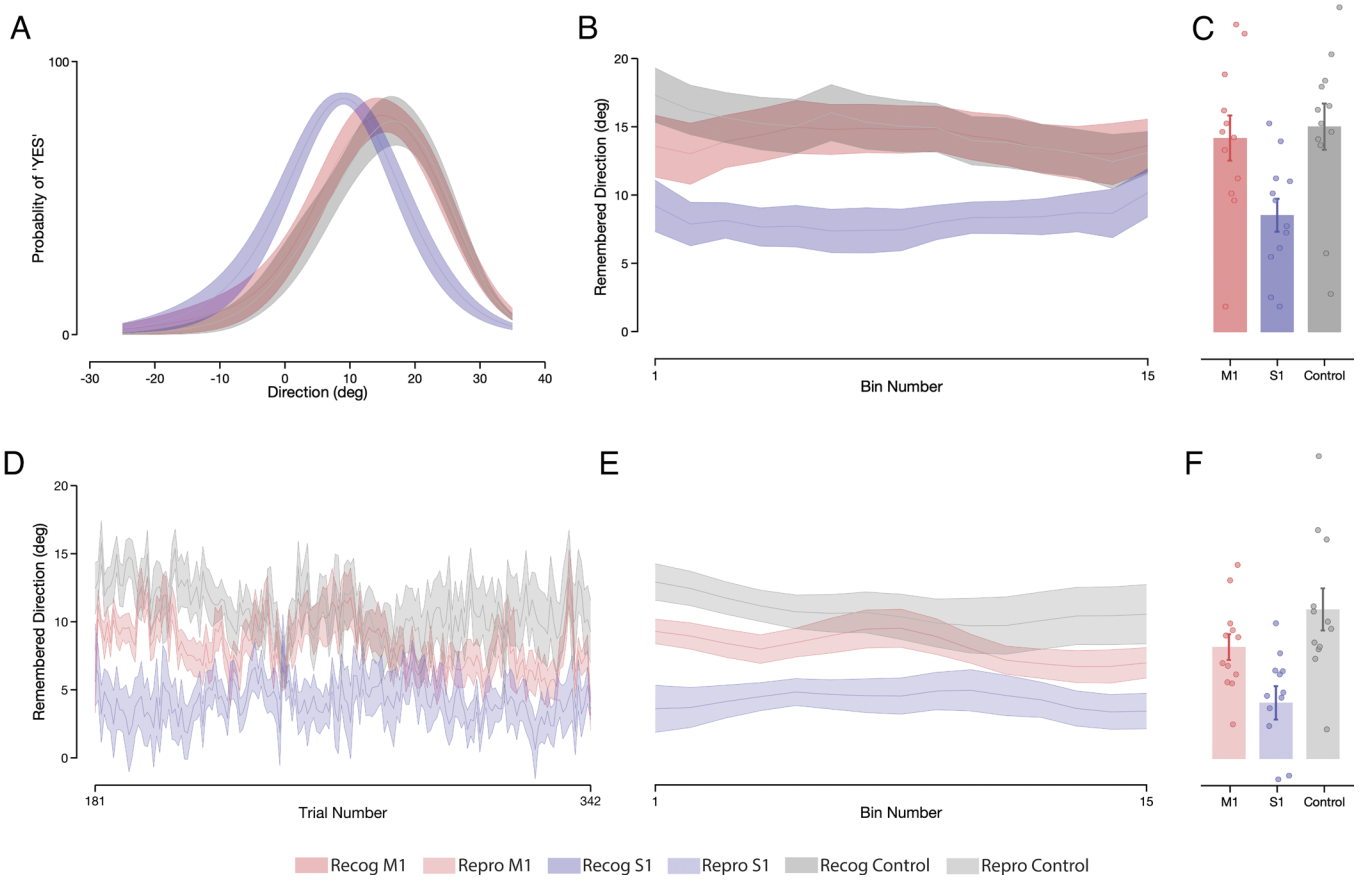

Fig. 4. Following cTBS stimulation, memory for newly learned movements was assessed using either recognition or movement reproduction tests. (*A*) Average Gaussian fits to all yes/no responses during recognition tests. The direction corresponding to the Gaussian peak provides an estimate of remembered direction. It is seen that mean retention in the S1 condition is closer to zero than in the M1 and control conditions. Fits for M1 and control conditions overlap. (*B*) Binned recognition memory performance remained stable in all conditions throughout the test. To calculate each bin value, Gaussian curves were fitted to recognition judgments over a sliding window of 36 trials (*Materials and Methods*). The remembered direction in the S1 condition is reduced compared to that in the M1 and control conditions. (*C*) A direct comparison of remembered direction estimates, using Gaussian fits for individual participants in M1, S1, and control conditions. (*D*) Trial-to-trial hand movement direction during movement reproduction tests. The remembered direction for participants in the S1 condition was reliably less than that for participants in the M1 and control conditions. The average remembered direction for M1 and control conditions mostly overlaps. (*E*) The averaged binned data in *D* over a sliding window of 36 trials. (*F*) A direct comparison in remembered direction using the average of all trial-to-trial data points for each individual in the M1, S1, and control conditions. Statistical analysis indicated a significant drop in the remembered direction for S1 relative to M1 and control, indicating an adverse effect of S1 disruption on motor memory retention. In all panels, the mean values and SE are represented with solid lines and shaded areas, respectively.

S1 condition showed less retention of prior learning than participants in the M1 and control conditions. To facilitate a comparison between reproduction tests with the binned data from recognition tests, the same binning procedure was applied to the active movement tests as well. In other words, for each participant separately, the remembered direction was estimated by averaging trials within a sliding window of 36 movements. Fig. 4*E* illustrates the average of binned data for each experimental condition over 15 bins. Additionally, Fig. 4*F* displays the average remembered direction for each participant using the average of the trial-by-trial data.

Fig. 5 presents a comparison of memory estimates based on recognition and reproduction movement testing across all experimental conditions. In Fig. 5 *A* and *B* it is seen that estimates of the remembered directions from recognition testing are consistently greater than those from movement reproduction. *SI Appendix*, Figs. S2 and S3 show similar results when hand directions at peak velocity are used instead of those at the end of movement.

For statistical analyses, we first evaluated differences in performance between the end of training and the averaged remembered direction during the memory test trials. The overall Gaussian fits and the average of the trial-by-trial values from the movement reproduction tests were used as estimates of remembered direction for movement recognition and reproduction, respectively. It was found that hand movement angles during the memory test were reliably less than those at the end of training ($F_{[1, 71]} = 644.52$, $P < 0.001$, $\omega^2 = 0.824$).

ANOVA analysis was also conducted to test for differences of the mean remembered directions between conditions. To this end, memory type (reproduction, recognition), and stimulated brain region (M1, S1, and control) were used as independent factors. Overall, there was a significant difference in remembered direction between the stimulated brain regions ($F_{[2, 66]} = 12.05$, $P < 0.001$, $\omega^2 = 0.204$). Similarly, a significant difference was found in the remembered direction between recognition and movement reproduction testing ($F_{[1, 66]} = 16.86$, $P < 0.001$, $\omega^2 = 0.146$) such that memory estimates were reliably better for recognition. There was no significant interaction between the type of memory test and the stimulated brain region ($F_{[2, 66]} = 0.20$, $P = 0.823$). Holm–Bonferroni-corrected post hoc tests indicated that the remembered direction for participants in the S1 condition was significantly less than that for participants in the M1 ($P < 0.001$) and control conditions ($P < 0.001$), indicating an adverse effect of S1 disruption on motor memory. No significant difference was found between the M1 and control groups ($P = 0.241$).

We likewise tested for the variability of remembered direction following cTBS. For the movement reproduction condition, we computed on a per-subject basis estimates of variance in the movement direction over the course of the retention test trials in each condition separately (*SI Appendix*, Fig. S4B). For recognition, again on a per-subject basis and for each condition separately, we used estimates of the width of the fitted Gaussian function (*SI Appendix*, Fig. S4A). The obtained values were compared using one-way ANOVA. No statistically significant differences were observed in either analysis (recognition: $F_{[2, 33]} = 0.57$, $P = 0.572$; active reproduction: $F_{[2, 33]} = 1.12$, $P = 0.338$).

We conducted two additional control tests in order to verify that the impairment in remembered direction following cTBS to S1 was learning specific. If so, no effect on movement direction would be expected in the absence of learning. Participants in this control condition underwent the same training task as in the main experiment but with unrotated feedback. In other words, the displayed cursor during the experiment accurately represented their actual hand position throughout. Following training, cTBS was applied to S1. Subsequently, participants underwent either movement reproduction testing or tests of recognition memory. As in the main experimental conditions, Gaussian functions were fit to the recognition memory data. The proportion of variance accounted for by the Gaussian fits averaged $R^2 = 0.9603$, with a CI of [0.946, 0.974].

Fig. 6 shows the remembered direction of participants who received unrotated feedback followed by cTBS to S1 and for comparison purposes, we also show the data for participants who received cTBS to S1 following adaptation (taken from Fig. 4). It can be seen that the remembered direction for participants that received unrotated feedback is considerably less than that in the S1 condition and comparable to that at baseline. The pattern is similar for both recognition (Fig. 6*A*), and movement reproduction testing (Fig. 6*B*). A direct comparison can be found in Fig. 6*D*. Fig. 6*C* also provides a comparison of the remembered direction for recognition and movement reproduction testing using the binning procedure (*Materials and Methods*). It should be noted that the remembered direction in the unrotated S1 is no different than the average hand direction at the end of the unrotated adaptation task. Taken together, this suggests that the effects on movement direction following the disruption of S1 are specific to the retention of newly learned movements. *SI Appendix*, Fig. S5 gives similar results, where instead of movement end, hand directions at peak velocity are employed.

A two-way ANOVA was performed to assess differences in remembered direction in the above control task. Rotation

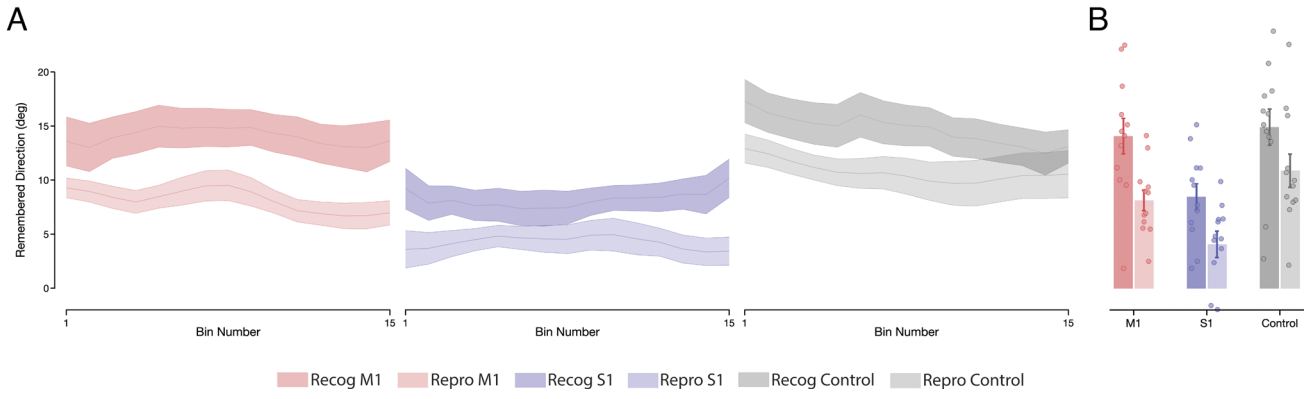

Fig. 5. To facilitate a comparison between recognition and movement reproduction tests, the same binning procedure was applied to each. (*A*) Estimates of the remembered direction in recognition tests are consistently closer to the learned direction than those in movement reproduction testing. (*B*) A direct comparison of recognition and movement reproduction scores for each participant following cTBS stimulation to each candidate brain area (M1, S1, and control). Statistical analysis found a significant difference in the remembered direction between recognition and movement reproduction tests in favor of recognition.

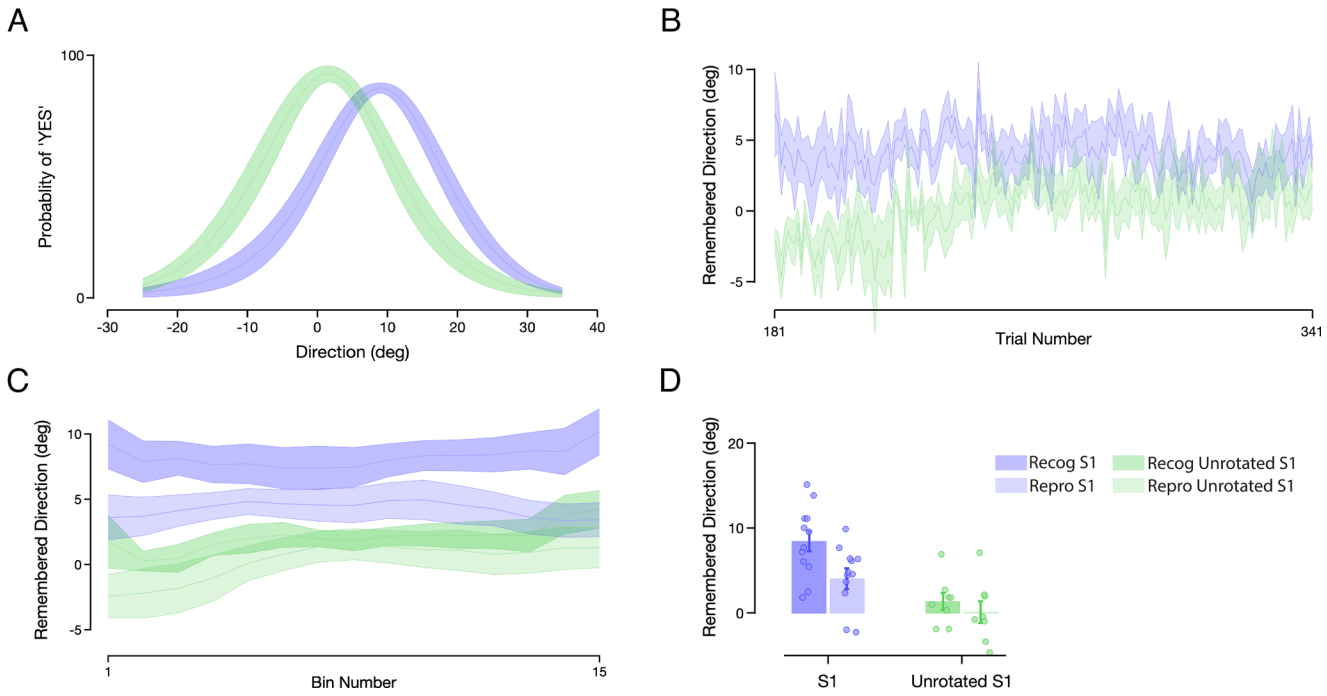

Fig. 6. Additional control tests were conducted to verify that the impairment in remembered direction after cTBS stimulation to S1 was learning specific. Using both recognition and movement reproduction tests of retention, the remembered hand direction after a null rotated training task and cTBS to S1 was compared to remembered direction estimates previously acquired following visuomotor adaptation and cTBS to S1. (*A*) Gaussian estimates of the remembered direction in the unrotated S1 condition were close to zero indicating that cTBS does not affect movement direction in the absence of learning (*B*) Similar, near-zero estimates of remembered direction, were obtained using movement reproduction tests following null-rotation training and cTBS to S1. Once again, cTBS did not affect remembered movement direction in the absence of learning. (*C*) Binned data comparison shows that remembered direction estimates from recognition and reproduction tests mostly overlap for the unrotated S1 condition. (*D*) A direct comparison of remembered direction estimates in the S1 condition following visuomotor adaptation and following unrotated S1. In unrotated S1 conditions, no difference was found between the hand direction at the end of null-rotation training and during memory tests.

(null, 30) and memory type (recognition, reproduction) were the independent variables, and remembered hand direction served as the dependent variable. The statistical analysis revealed an overall difference in remembered direction between the S1 and unrotated S1 condition ($F_{[1, 36]} = 24.17$, $P < 0.001$, $\omega^2 = 0.334$). Likewise, a significant overall statistical difference was observed between participants in recognition and reproduction movement tests ($F_{[1, 36]} = 6.97$, $P = 0.012$, $\omega^2 = 0.086$). There was no interaction ($F_{[1, 36]} = 1.15$, $P = 0.291$). Additionally, a repeated-measure ANOVA was conducted to evaluate whether the remembered direction of participants in the unrotated S1 condition was different than their own hand direction at the end of the unrotated adaptation task. No difference was found between the hand direction at the end of training and that during memory testing ($F_{[1, 14]} = 0.388$, $P = 0.543$). There was no significant effect of the type of memory test ($F_{[1, 14]} = 1.52$, $P = 0.238$) or interaction ($F_{[1, 14]} = 0.90$, $P = 0.360$).

As a further of the possibility that cTBS stimulation interfered with the movements themselves, we compared movement kinematics before and after the cTBS stimulation in the movement reproduction conditions (*SI Appendix*, Fig. S6). This analysis found minor changes to movement kinematics that were similar in all conditions and not specific to the participants in S1. Details are provided in *SI Appendix*.

Discussion

The principal objective of this study was to test the idea that the somatosensory cortex contributes to the retention of newly learned movements. Specifically, if learning-related changes to the somatosensory cortex serve to update target sensory states, then its disruption following learning should lead to an impairment. We examined our hypothesis by using a visuomotor adaptation task, followed by cTBS stimulation to disrupt activity in each of three candidate brain regions: the primary motor cortex, the somatosensory cortex, and a control zone over the occipital cortex. Tests of retention followed and were carried using both active movement reproduction and recognition memory testing.

The data are consistent with the hypothesis that plasticity in the somatosensory cortex contributes to initial stages of motor learning. An overall reduction in remembered direction relative to the end of training was observed in all experimental conditions. cTBS stimulation to the somatosensory cortex further impaired retention relative to that observed when stimulation was delivered to either the motor cortex or to the control zone. This reduction in retention was evident regardless of whether tests involved movement reproduction from memory or recognition memory tests (Fig. 4). Thus, the impairment is associated with the disruption of the somatosensory cortex and does not depend on the specific assay of memory.

Evidence of a contribution of the somatosensory cortex to motor learning and motor memory retention, in the context of force-field adaptation, has been previously reported in work with both rodents and humans when the disruption occurred prior to learning and in humans when cTBS was applied to the somatosensory cortex following learning and tests of retention were conducted 24 h later (5–7). Somatic involvement in motor learning is also seen in work in which passive arm displacements lead to the formation of motor memory comparable to that obtained when training involves active movement (8). Ohashi et al. (9) reported that the earliest changes in cortical excitability during a motor skill learning task were in the somatosensory cortex. These

changes predicted the eventual extent of learning, while those in the motor cortex did not.

The present findings indicate that disruption of the motor cortex has little impact on the retention of newly learned movements at least during the early stages of retention. As seen in Fig. 4, both recognition and movement reproduction tests consistently showed that the average remembered direction in the M1 condition was no different than that when stimulation was delivered over the occipital cortex. The present finding is in line with other studies of the effects on motor learning of TMS to M1. Specifically, single-pulse TMS to the primary motor cortex had no effect on learning with gradually introduced visuomotor (10, 11) or force field perturbations (12). Repetitive transcranial magnetic stimulation (rTMS) to M1, in the context of force-field learning, similarly had no effects on adaptation (13). Even so, several of the same studies indicate that the motor cortex is engaged in longer-term retention (11, 13). Thus, in the initial phases of motor learning, memory encoding initially occurs within the somatosensory cortex, with motor cortex participation possibly commencing at delays more typically associated with consolidation.

Motor memory encoding in the somatosensory cortex may provide desired movement states which are achieved by brain motor areas. Beyond a motor memory–related function, the somatosensory cortex may possibly be involved in the direct control of movement. There is much evidence indicating that the somatosensory cortex along with the parietal cortex more generally is involved in the control of movement and motor learning. Neural activity in the somatosensory cortex is detectable well before movement onset, and even prior to the initiation of muscle contraction (14–16). Moreover, stimulation across the somatosensory cortex and regions of the posterior parietal lobe can evoke movements (17, 18). In the context of human neuroimaging studies, preplanned movements can be decoded with comparable efficacy from the somatosensory cortex as from cortical motor areas (19, 20). This raises the possibility that the somatosensory cortex is involved not only in motor memory encoding but potentially in the direct control of movement.

As shown in Fig. 5, recognition memory estimates were closer to the learned movement direction than estimates based on active movement reproduction. A similar observation was made by Kumar et al. (4), wherein, both immediately after learning and 24 h later, recognition memory was superior to performance when movements were actively reproduced from memory. This finding is consistent with established work on human verbal memory, where recall memory, in general, underestimates how much learning is retained (21). The present results suggest that in the context of human motor learning, even shortly after the end of training, there is information available in motor memory that is not accessible in tests of active movement.

There is evidence that rTMS to the somatosensory cortex can lead to an impairment in somatosensation, a loss of movement accuracy, and, consequently, less learning (22). In contrast, movement kinematics in the present study were not adversely affected by cTBS. As a further test, we applied cTBS to S1 and assessed its effects on movement in the absence of learning. As seen in Fig. 6, movement direction which is the main dependent variable in the present study, was unaltered when cTBS was applied following null-rotation training. This indicates that the impaired remembered direction following cTBS to S1 was learning specific. The present finding is also consistent with observations by Ragert et al. (23), who observed no alteration in basic motor performance such as tapping, aiming, and grip force following S1 stimulation.

As in ref. 24, we used a target arc rather than a point target during memory test trials. This choice was designed to minimize any discrepancy between visual information and the felt position of the arm (somatic information), which when present, leads to washout. Fig. 4 shows that when memory testing was conducted in this fashion, estimates of the remembered direction, in all experimental conditions, remained stable throughout the memory tests. This was evident for both recognition tests, where participants identified previously made movements based on passive arm displacement, and in reproduction tests, where participants were required to reproduce the learned direction from memory. The present findings in conjunction with prior work using both reproduction and recognition tests (4, 5, 24) suggest that adaptation learning is durable and can remain stable for at least 24 h.

The involvement of the motor and somatosensory cortex in motor memory retention was assessed by applying cTBS to disrupt neural activity in M1 or S1 immediately following adaptation training. The M1 stimulation zone was chosen to be the same as the hotspot for MEPs. The S1 stimulation zone was 2 cm posterior to the hotspot over M1. Previous studies have used this same method to locate a somatosensory cortex stimulation site (5, 25, 26). Our results indicated that applying cTBS over the motor cortex significantly decreases MEP as evidenced by various studies (27–29). There is evidence that applying cTBS over the somatosensory cortex facilitates MEPs (26, 30). However, based on our findings, although there was a slight increase in MEP values following cTBS to S1, the difference was not significant. Several studies have found inconsistent results (29–34).

Sensorimotor adaptation is associated both with changes in movement and proprioceptive changes related to the sensed position of the limb (1–3). However, in a number of studies, it has been shown that so-called proprioceptive recalibration can be dissociated from learning (35–37), which raises the possibility that the changes seen in the present study may be related to a disruption of the recalibration process. Although we did not test for the possibility that stimulation disrupted proprioceptive shifts, we did show that disruption of the somatosensory cortex impairs motor memory retention, as measured behaviorally. Proprioceptive recalibration may also be impaired, and this would not be inconsistent with our interpretation of the findings, namely, that learning-updated sensory states (new sensory targets which guide movements) are encoded in the somatosensory cortex.

The present study found an impairment in retention when retention tests were conducted shortly after learning. The study by Kumar et al. (5) showed a similar impairment when retention tests were conducted following a 24-h delay. The immediate impairment in the present study presumably contributes to the disruption seen after 24 h. However, the relationship between immediate impairment and consolidation can be complex. For example, evidence for the involvement of M1 in learning was reported in ref. 38 where it was found that rTMS to M1 following ballistic movement practice disrupted retention. However, follow-up work showed that the effects on retention were transient (39, 40) and that memory was unimpaired following a 24-h delay. In contrast, the study by Richardson et al. (13) showed no effect of rTMS to M1 on initial motor learning in a force-field adaptation task, whereas 24 h later, there was an effect on retention.

It has been shown that there are both explicit and implicit components to motor memory retention in the context of visuomotor adaptation (41, 42). In the present study, to minimize the contribution of more cognitive or strategic components to learning, the visuomotor rotation was introduced gradually over 75 trials in a totally darkened laboratory that eliminates the potential use of extraexperimental cues. In tests of retention, subjects were instructed to point directly to the location of the remembered target and not use any previous strategies, a procedure which in other work has been shown to limit the involvement of explicit

strategies in measures of retention (41, 43). In behavioral work using the same experimental protocol as in the present study (24), this latter instruction resulted in movement directions in retention testing that were no different than when subjects might have used an explicit strategy, which suggests a limited engagement of cognitive or strategic elements in the present results.

The current studies were conducted using adaptation as an experimental model of motor learning. Consequently, the specific contribution of adaptation to learning takes the form of updates to a sensorimotor or sensory-sensory map. Future work will be needed to assess whether these findings also apply to motor learning more generally, and whether, with either longer periods of training or with tasks which necessitate fine force control for learning, evidence for motor cortex participation in retention will be obtained.

In summary, we tested the involvement of the motor and somatosensory cortex in motor memory retention by applying cTBS following learning to these areas and to a control zone over the occipital lobe. Tests of retention which were conducted afterward involved either active movement reproduction or tests of recognition of learned movement direction. Recognition testing showed better memory for learned direction in all cases. The main finding was that disruption of the somatosensory cortex impaired retention of newly learned movements, whereas disruption of the motor cortex did not. This is consistent with the idea that the somatosensory cortex is part of a circuit that participates in the encoding of learned movements.

Materials and Methods

Participants. A cohort of eighty-eight right-handed individuals, between 18 and 30 y of age, with normal or corrected-to-normal vision, participated in the study with 12 participants assigned to each of six experimental conditions, and eight participants assigned to each of two additional control conditions. This study was approved by the McGill University Faculty of Medicine Institutional Review Board (A12-B107-22A), and participants provided written informed consent.

Visuomotor Adaptation. The adaptation task employed was adapted from ref. 24. A full description of the methods used in the present study is provided at https://doi.org/10.6084/m9.figshare.24045501.

Participants were instructed to make point-to-point reaching movements from a start position, straight out, to a single visual target. Vision of the arm and the robot were blocked. Real-time visual feedback of hand position was present during the adaptation task. Limited feedback trials were interspersed. In the limited feedback trials, the cursor was replaced by an expanding arc that displayed only movement amplitude. During these trials, the point target was also replaced by a semicircular target arc. During the limited feedback trials, participants were instructed to move toward the position of the point target that they remembered from previous trials.

In the training phase, participants were instructed to perform reaching movements, while receiving clockwise rotated visual feedback of the hand position, which resulted in counterclockwise compensatory movements. The magnitude of the rotated feedback gradually increased over the course of the training phase to a maximum value of 30°. The direction of the hand movement evaluated at movement end relative to the target position served as a dependent measure of learning. Participants in all conditions underwent brain stimulation immediately after training.

Brain Stimulation Protocol. To investigate the role of candidate brain regions in the retention of motor memory, participants were then randomly assigned to one of three experimental conditions: S1, M1, and control. In the M1 condition, cTBS, which reduces the excitability of neurons in the motor cortex (44), was applied to the M1 hot spot, which is the position over M1 at which MEPs from biceps brachii were consistently elicited at the lowest stimulator output. In the S1 condition, the stimulating coil was positioned, using Brainsight, 2 cm posterior to the M1 hot spot (refer to Fig. 1*C*) which typically overlies the posterior postcentral gyrus (25, 26, 31). In the control condition, cTBS was applied to a control zone over the occipital lobe. We used two rounds of a cTBS protocol (separated by 10 min) in which 30 Hz triplets were applied 6 times per second for a total of 600 stimuli. In previous work, when applied to M1, this has been shown to produce consistent and long-lasting suppression (27, 28).

Motor Memory Testing. In an active movement test of motor memory (movement reproduction), participants were instructed to move directly to the position corresponding to the point target in the adaptation task. In a test of recognition memory, participants were instructed to hold the robot handle while being exposed passively to various candidate movement directions. These directions spanned from −5 to 35° relative to the body midline, in intervals of 5° (refer to Fig. 1*D*).

Data, Materials, and Software Availability. Anonymized digital data have been deposited in Figshare (10.6084/m9.figshare.24045501) (45). All study data are included in the main text.

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