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# Motor learning and its sensory effects: time course of perceptual change and its presence with gradual introduction of load

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**Mattar AA, Darainy M, Ostry DJ.** Motor learning and its sensory effects: time course of perceptual change and its presence with gradual introduction of load. *J Neurophysiol* 109: 782–791, 2013. First published November 7, 2012; doi:10.1152/jn.00734.2011.—A complex interplay has been demonstrated between motor and sensory systems. We showed recently that motor learning leads to changes in the sensed position of the limb (Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL. *J Neurosci* 30: 5384–5393, 2010). Here, we document further the links between motor learning and changes in somatosensory perception. To study motor learning, we used a force field paradigm in which subjects learn to compensate for forces applied to the hand by a robotic device. We used a task in which subjects judge lateral displacements of the hand to study somatosensory perception. In a first experiment, we divided the motor learning task into incremental phases and tracked sensory perception throughout. We found that changes in perception occurred at a slower rate than changes in motor performance. A second experiment tested whether awareness of the motor learning process is necessary for perceptual change. In this experiment, subjects were exposed to a force field that grew gradually in strength. We found that the shift in sensory perception occurred even when awareness of motor learning was reduced. These experiments argue for a link between motor learning and changes in somatosensory perception, and they are consistent with the idea that motor learning drives sensory change.

motor learning; sensory plasticity; somatosensory perception; arm movements; psychophysics

RECENT WORK HAS SHOWN that subdividing the brain into sensory and motor systems is not a straightforward task. For example, areas of the brain classically considered to be motor areas show sensory receptive fields (Asanuma and Rosén 1972; di Pellegrino et al. 1992; Murphy et al. 1978; Rizzolatti et al. 1987, 1988; Rosén and Asanuma 1972) and neural activity related to sensory decision making (Romo et al. 2002, 2004). Motor experience has been shown to lead to selective expansions within sensory areas of the brain (Xerri et al. 1996, 1999), and, indeed, changes in motor function have been shown to affect the processing of visual (Brown et al. 2007), acoustic (Nasir and Ostry 2009; Shiller et al. 2009), and proprioceptive (Cressman and Henriques 2009, 2010; Cressman et al. 2010; Haith et al. 2008; Malfait et al. 2008; Ostry et al. 2010; Simani et al. 2007; Vahdat et al. 2011; van Beers et al. 2002) stimuli. These findings thus point to a complex interplay between motor and sensory systems within the brain.

Studies to date have revealed much about the motor learning phenomenon. For example, the psychophysical characteristics of learning (Shadmehr and Mussa-Ivaldi 1994), the rate of changes in motor performance (Krakauer et al. 2005; Smith et al. 2006), the retention of learning over time (Brashers-Krug et al. 1996; Caithness et al. 2005; Mattar and Ostry 2007a; Shadmehr and Brashers-Krug 1997), the characteristics of its generalization (Gandolfo et al. 1996; Malfait et al. 2002; Mattar and Ostry 2007b, 2010; Shadmehr and Moussavi 2000; Thoroughman and Shadmehr 2000), and the brain areas that underlie the phenomenon (Cothros et al. 2006; Gribble and Scott 2002; Shadmehr and Holcomb 1997, 1999) have all received attention in the literature. Our recent work has documented a new aspect of the motor learning phenomenon, namely, its effect on somatosensory perception (Ostry et al. 2010). Further studies from our group have identified the neural basis of the effect (Vahdat et al. 2011) and selectivity in the effect of learning on sensory perception (Wong et al. 2011). The goal of the present studies is to document further the links between motor learning and shifts in somatosensory perception. Our studies are aimed at understanding the relationship between motor learning and sensory change. Broadly speaking, our hypothesis is that motor learning drives changes in somatosensory perception. Here, we present two new pieces of data that are consistent with that idea.

In a first study, we examined the time course of changes in performance. We divided the motor learning process into consecutive segments, and between each we measured sensory performance in order to track progressive shifts in the perceptual boundary between left and right throughout the learning process. We found that the shifts in somatosensory performance developed along with subjects' ability to compensate for the forces applied to the hand. However, the rate of perceptual change was less than the rate of change in motor performance. In a second study, we assessed further the relationship between motor learning and sensory change. We examined the possibility that explicit awareness of the motor learning process is what drives changes in perceptual performance. We exposed subjects to forces that grew incrementally rather than abruptly, in order to reduce kinematic error and presumably conscious awareness of the perturbation. Previous studies have shown that patterns of generalization, and the extent to which motor learning affects subsequent performance, can be affected by the gradual versus abrupt introduction of load (Huang and Shadmehr 2009; Klassen et al. 2005; Kluzik et al. 2008; Malfait and Ostry 2004). We found that explicit knowledge of the motor learning process generated by abrupt changes in motor performance was not required for shifts in somatosensory perception to occur. These studies thus

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provide two further pieces of evidence supporting the idea that motor learning leads to changes in somatosensory perception.

## MATERIALS AND METHODS

*Participants.* Participants were recruited from the McGill University community to take part in an experimental protocol that was approved by the Research Ethics Board for the Faculty of Science. Subjects were naive to the hypotheses and to the robotic device (see below), and they were neurologically healthy and right-handed and had normal or corrected vision. Subjects provided informed consent prior to participation. In *experiment 1*, 14 subjects (13 men, 1 women) were tested. *Experiment 2* included 12 subjects (3 men, 9 women). The mean age of all subjects was 21.9 ± 4.6 yr (range 18–36 yr).

*Experimental apparatus.* In a darkened room, subjects grasped the handle of a planar, two-joint robotic manipulandum (InMotion2, IMT, Cambridge, MA) and made pointing movements to visual targets (Fig. 1*A*). The robot was fitted with 16-bit optical encoders to sense its position (Gurley Precision Instruments, Troy, NY), and a 6-axis force-torque sensor (ATI Industrial Automation, Apex, NC) that encoded forces applied to the handle. Position and force data from the robot were sampled at 400 Hz. Subjects sat in a height-adjustable chair, to which they were strapped in order to restrict movement of the upper torso. The start position for all movements was along the body midline, ~20 cm from the subject's chest. This corresponds to a shoulder angle of ~50° relative to the frontal plane and an elbow angle of ~90° relative to the upper arm. The target position was 20 cm outward from the start position. The arm was supported against gravity by an air-sled that allowed for frictionless horizontal movements. A semisilvered mirror reflected images of the start position, the target, and a cursor representing the hand's position from an LCD television (Sony, Tokyo, Japan) mounted 10 cm above the mirror. This led to the illusion that the visual stimuli were presented in the plane of the subject's movement. The start and target circles were 2 cm in diameter. The cursor was 1 cm in diameter. Prior to the experiment, each subject completed a calibration routine in which the hand was aligned with an array of visual points in order to determine the mapping between pixels on the screen and the position of the subject's hand.

*Experimental protocol.* Subjects were tested on two consecutive days. The first day served as a familiarization session in which subjects gained experience with the two experimental tasks described here. Data from the first day were not analyzed. The second day served as the experimental session.

The first task involved movements to visual targets. The start position, target, and a cursor representing the position of the hand were visible throughout the movement. The subject held his/her hand in the start location for 1,000 ± 500 ms. The start position then turned green, cuing the subject to begin a movement to the target located 20 cm away. The subject was asked to move straight to the target and to land accurately within its boundaries. Reaction time was not a factor in determining successful movements. Subjects were instructed to move at a desired velocity of 50 cm/s. Movements that fell ±7% from the desired velocity were identified with color cues. These cues were provided to encourage consistent performance, but movements that fell outside these bounds were not eliminated from analysis. At the end of each movement, the robot returned the subject's hand to the start position.

In *experiment 1*, subjects made 350 movements in total, split into 8 separate blocks (see Fig. 2*A*, *bottom*). The blocks included 150, 5, 5, 10, 20, 35, 75, and 50 movements, respectively. In the first block, the robot did not apply forces to the subject's hand during movement. In the subsequent 6 blocks, which comprised 150 movements in total, the robot applied forces according to *Eq. 1* (see below). In the eighth and final block, the aftereffects of motor learning were assessed and the robot did not apply forces.

In *experiment 2*, subjects made 300 movements in total, split into 3 separate blocks (see Fig. 2*B*, *bottom*). The first block comprised 50 movements, and the robot did not apply forces to the hand. The second block contained 200 movements during which the robot again applied forces to the hand according to *Eq. 1* (see below). Over the first 150 movements, the strength of the lateral forces (*d* in *Eq. 1*) was increased linearly from 0 on the first trial to 18 Ns/m on the 150th trial. The strength of the force field remained at 18 Ns/m for *movements 151–200*. In the third block, subjects made 50 movements to test for aftereffects of learning and the robot applied no forces.

Between blocks of movements, subjects completed the second experimental task, which has been described in detail previously (Ostry et al. 2010). This task was aimed at determining the perceptual boundary between left and right. Subjects were presented with the start and target positions as before and were asked to move toward the

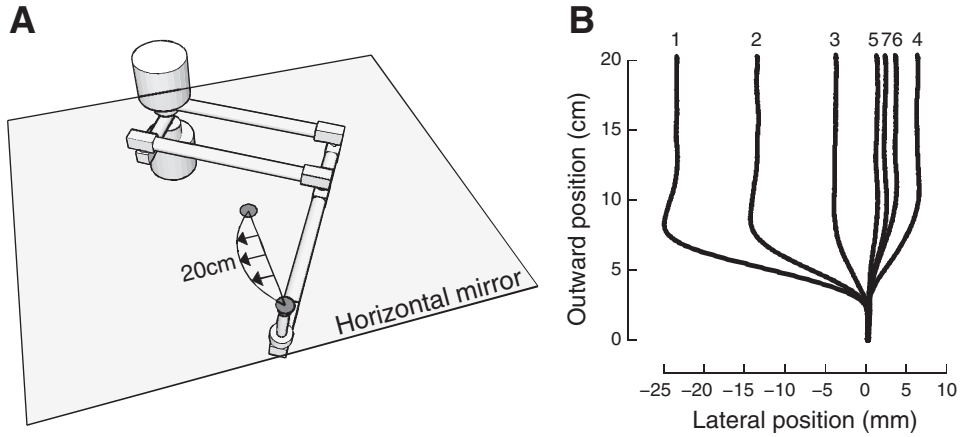


Fig. 1. Experimental apparatus and PEST procedure. *A*: subjects held the handle of a 2-joint planar robotic arm to make movements toward visual targets. Targets were presented on a television screen (not shown) mounted above a horizontal mirror. This arrangement led to the illusion that the targets were located in the plane of the hand. The position of the robot handle was represented by an on-screen cursor. Subjects made 20-cm movements from a start position, outward toward a target. When forces were applied to the hand, movements were pushed to the left as shown. *B*: during perceptual testing for the boundary between left and right, subjects made 20-cm outward movements in force channels. Channels were initially straight but then deviated laterally according to an algorithm known as PEST. The sequence began with a suprathreshold lateral deviation of 25 ± 5 mm. At the end of the movement, the subject answered the question "Was your hand moved to the right?" The subject's "yes" or "no" response determined the position of the next channel movement. Over the course of repeated movements, the position of the channel converged on the perceptual boundary. Numbers above each movement indicate the sequence of PEST trials. The sequence ended when the PEST algorithm called for a change in the lateral position of the channel of <1 mm. Perceptual testing involved sequences that began to the left and to the right (not shown) of the perceptual boundary.

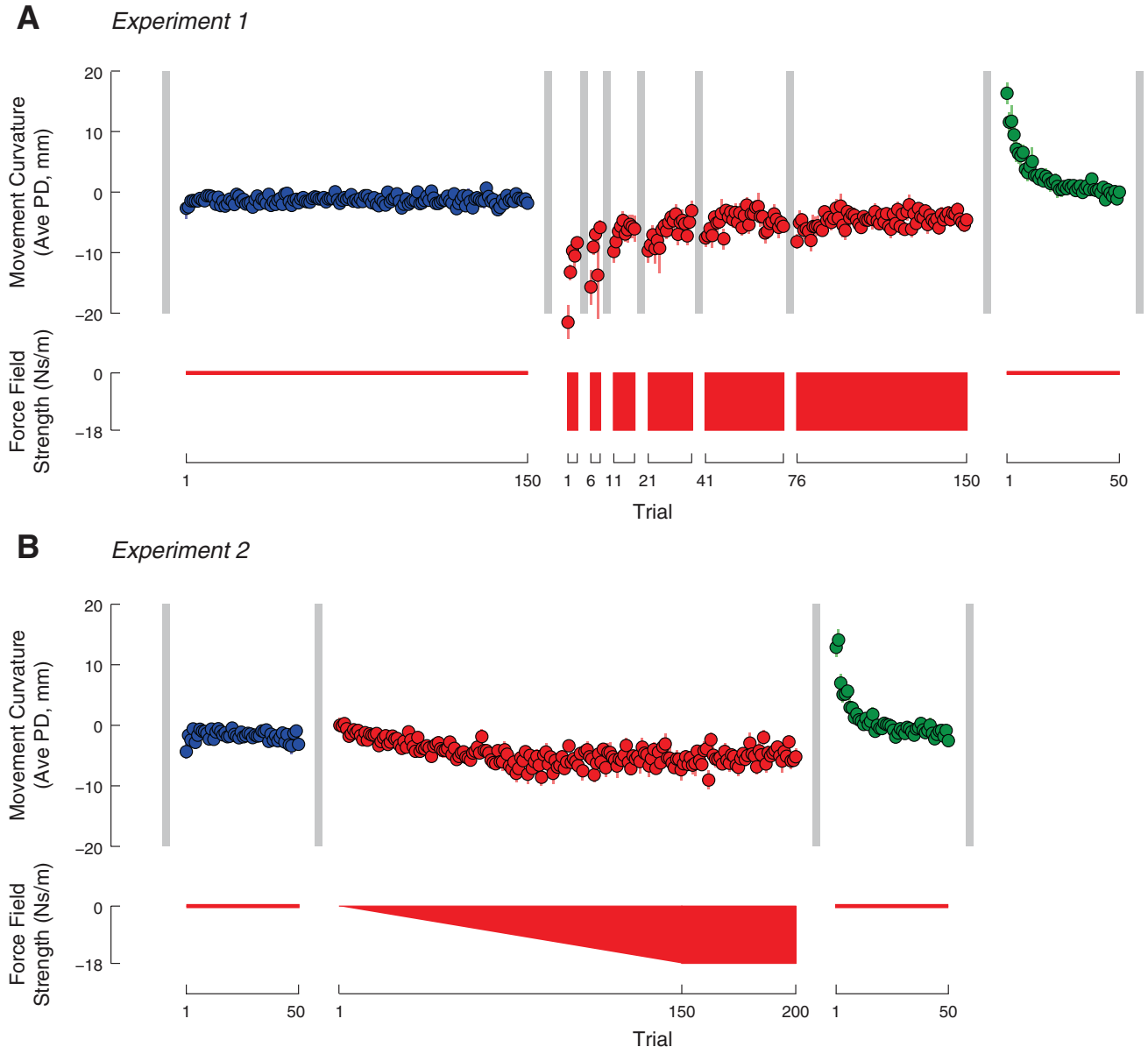


Fig. 2. Experimental sequence, kinematic results, and force field strength. *A*: *experiment 1*. Vertical gray bars indicate 9 rounds of testing for the perceptual boundary between left and right. *Bottom*: strength of the force field throughout the experiment. Subjects began by making 150 movements in a null field (blue). Subjects moved straight to the target. They then made 150 movements in a force field (red). The force field training phase was divided into 6 blocks, lasting 5, 5, 10, 20, 35, and 75 trials each. Initial movements were deviated to the left but straightened with training. The experiment ended with 50 movements in a null field to test for aftereffects (green). Initial aftereffect movements were curved to the right but straightened as the effects of learning were washed out. *B*: *experiment 2*. Vertical gray bars indicate 4 rounds of testing for the perceptual boundary between left and right. *Bottom*: strength of the force field throughout the experiment. During training the force field grew linearly from 0 to 18 Ns/m and was then held at its maximum value. Subjects began with 50 movements in a null field (blue). Movements were straight. They then made 200 movements in a force field (red). Curvature showed an initial rightward curvature but otherwise remained straight to the target, despite the increasing strength of the force field. In the final phase, the force field was eliminated to test for aftereffects (green). Movements were initially curved to the right but straightened as the effects of learning were washed out. Movements at the end of the washout phase were curved to the right, relative to the null field movements made prior to force field learning. For both *A* and *B*, data points represent the mean perpendicular deviation (PD) of each movement trajectory, averaged over subjects. Vertical lines represent 1 SE.

target. All visual feedback of the target and the hand's position was removed as soon as the subject exited the start circle. The lateral position of the hand was determined by the robot, which applied a force channel (see *Eq. 2* below) such that the movement was guided along a predetermined path. The force channel was straight for the initial 15 mm of the movement. At that point, the lateral position of the channel shifted to the right or to the left by an amount determined by an adaptive staircase procedure (see below). The shift in the lateral position was accomplished by moving the center of the force channel to the new position over the course of 300 ms according to a minimum-jerk trajectory. The lateral position of the channel was maintained at its new value for the remainder of the movement. At 20 cm outward from the start position (i.e., at the target distance) the subject encountered a viscous barrier imposed by the robot, which held the hand at that position. The subject was required to remain in that position and to provide a "yes" or "no" response to the question "Was your hand moved to the right?" The experimenter recorded the subject's response. The subject's hand was returned to the start position by the robot at the end of each trial.

The magnitude of the shift in the lateral position of the channel was determined by an adaptive staircase procedure known as PEST (Parameter Estimation by Sequential Testing; Taylor and Creelman 1967). The PEST procedure is a method for the efficient identification of psychophysical thresholds. Each set of channel movements began with a suprathreshold shift in the lateral position of the channel, to 25 ± 5 mm from the center. On each successive trial, the shift in the position of the channel was modified on the basis of the subject's response. The initial step size for the reduction in the magnitude of the shift was 10 mm. When subjects' responses shifted from "yes" to "no" (or vice versa) the step size was halved, and repetitions of the same answer led to a doubling of the step size, according to the algorithm laid out by Taylor and Creelman (1967). The maximum step size was 10 mm, and the series of trials ended when the step size fell below 1 mm. In each round of perceptual testing, subjects completed six sets of PEST trials, three beginning with shifts to the left and three with shifts to the right of the straight-ahead trajectory. Figure 1*B* shows a sequence of PEST trials beginning from the left. The number above each movement indicates its position in the PEST sequence. The series of channel trials converges on the perceptual boundary between left and right.

In *experiment 1*, subjects completed nine rounds of perceptual testing (see Fig. 2*A*, *top*, vertical gray bars): before and after initial null field movements, after each of the six blocks of force field movements, and once more after aftereffect trials. In *experiment 2*, subjects completed four rounds of perceptual testing (see Fig. 2*B*, *top*, vertical gray bars): before and after initial null field movements, after gradual force field learning, and after aftereffect trials.

*Force field.* The robot applied forces to the subject's hand during movements to visual targets. The velocity-dependent forces were applied according to *Eq. 1*:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} 0 & -d \\ d & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix} \quad (1)$$

where $x$ and $y$ are the lateral and sagittal directions, $F$ is the force in Newtons applied by the robot, and $v$ is movement velocity in meters per second. The coefficient $d$ specifies the strength of the force field. In *experiment 1* it was set to 18 Ns/m, and in *experiment 2* it grew linearly from 0 to 18 Ns/m. For outward movements along the body midline, *Eq. 1* resulted in forces that pushed the hand to the left.

*Force channels.* The robot applied force channels during tests for the perceptual boundary between left and right. The channel was applied according to *Eq. 2*:

$$F_x = S\delta_x - Dv_x \quad (2)$$

where $F_x$ is force in the lateral direction (in Newtons), $v_x$ is velocity in the lateral direction (in m/s), and $\delta_x$ is the distance of the hand from the center of the channel (in m). As described above, the center of the channel was adjusted during the movement to enact the shift in the lateral position of the hand during perceptual testing. The coefficient $S$ determines the stiffness of the channel wall and was set to 4,000 Ns/m. $D$ is a viscosity coefficient set to 40 Ns/m.

*Measures and statistical analysis.* The robot's endpoint position was recorded at 400 Hz. The position signal was filtered with a zero-lag, 2nd-order Butterworth filter at 20 Hz. Velocity signals were computed by differentiating the filtered position signal.

To quantify performance on reaching movements, we computed average perpendicular deviation (PD). To arrive at this quantity, we determined movement start and end as the points where tangential velocity exceeded and fell below 5% of its maximum value for that movement. PD at each point along the movement trajectory is the lateral deviation from a straight line linking movement start and end. We computed the average PD for each movement. Negative PD values indicate leftward movement curvature, in the direction of the force field applied by the robot (*Eq. 1*). Changes in average PD were assessed by repeated-measures analysis of variance (ANOVA) followed by Bonferroni-corrected post hoc comparisons, where appropriate.

To quantify performance on perceptual testing, we used subjects' binary responses on PEST trials to generate response curves. We recorded the lateral position of the shifted force channel and the subject's subsequent "yes" or "no" response for every individual PEST trial. We combined the binary responses from the six PEST sequences (3 beginning at the left, 3 at the right) in each round of perceptual testing. We then fit logistic curves to the entire set of individual observations, using the glmfit function in MATLAB (The MathWorks, Natick, MA). On the basis of the binomial response data, glmfit determines parameters that define the rate of change and the lateral position of the logistic curve. These curves describe the probability of responding "Yes, my hand was moved to the right" across the range of lateral channel positions, ranging from left to right. To determine the perceptual boundary between left and right, we determined the lateral position at which the probability of a "yes" response was 50%. We measured the perceptual boundary repeatedly throughout both *experiments 1* and *2*. Changes in the perceptual boundary were assessed with repeated-measures ANOVAs.

To visualize differences in the rates of change for motor and sensory performance, we fit exponential curves to the data, using the curve fitting toolbox (cftool) in MATLAB. The curves took the discrete form of an exponential function as in *Eq. 3*:

$$\hat{y} = a \cdot \left[1 - (1 - b)^x\right] + c \quad (3)$$

where $x$ is the trial number, $a$ determines the scale of the change, $b$ determines the rate of change, and $c$ is a constant term that determines the vertical offset of the function. The free parameters [$a$ $b$ $c$] are optimized according to a least-squares criterion. To obtain these curves, we expressed both the motor and sensory data as the change between initial and final performance. That is, we plotted the overall change in both movement curvature and the position of the perceptual boundary. Fits to the mean changes in motor and sensory performance are shown in Fig. 4*A*.

In *experiment 1*, our goal was to determine the time course of perceptual change as it relates to the time course of the change in motor performance that accompanies learning. We fit a curve to the change in the perceptual boundary, which was defined as the difference between the estimate measured immediately prior to learning and the six estimates measured throughout the learning process. For the change in motor performance, we determined the difference in curvature between the initial force field trial and the subsequent movements in the force field. We fit two curves to the motor performance data. One curve was fit to the full set of 150 movements. To fit a second curve, we reduced the number of data points to 7, to match the number of estimates of the perceptual boundary. For this data set, change in movement curvature was computed relative to the initial force field movement, for the bins of movements that preceded the sensory testing: *trials 1–5*, *6–10*, *11–20*, *21–40*, *41–75*, and *76–150*. For purposes of statistical analysis, we compared the $b$ parameter for the fit to the sensory data with the $b$ parameter for each of the two fits to the motor data. As noted above, the $b$ parameter describes the rate of change in the function, and thus it is the parameter of interest for evaluating differences in the time course of motor and perceptual change. Parameters were said to be statistically different if the confidence intervals of their estimated values (as determined by the cftool in MATLAB) did not overlap.

We performed a second analysis to determine the time course of perceptual change as it relates to the time course of the change in motor performance that accompanies learning. This analysis did not depend on fitting curves to the data. For each subject, we computed the overall change in sensory performance as the difference between the estimate of the perceptual boundary immediately prior to motor learning and the six estimates that occurred throughout the learning process. We also computed the overall change in motor performance, collapsed into bins to match the sensory performance data. Relative to

performance on the initial force field trial, we computed the change in movement curvature for the bins of movements that preceded sensory testing: *movements 1–5*, *6–10*, *11–20*, *21–40*, *41–75*, and *76–150*. We then performed a split-plot, repeated-measures ANOVA on the sensory and motor performance data. Our goal was to assess whether the way that sensory performance changed over the course of the experiment was different from the way that motor performance changed. Our interest was thus in whether there were differences in the slopes of the functions describing motor and sensory change (i.e., whether there were changes over the course of training in the magnitude of the difference between sensory and motor measures of performance).

We performed a correlation to determine whether there was a relationship between the extent of motor adaptation and the change in the perceptual boundary in *experiment 1*. To quantify the change in motor performance, we computed on a per-subject basis the change in movement curvature between initial and final force field movements. Sensory change was defined as the difference between the estimates of the perceptual boundary obtained before learning and after the sixth block of force field trials.

We performed a control analysis to ensure that changes in the perceptual boundary did not result from active force production during perceptual testing. In both *experiments 1* and *2*, we examined the lateral forces applied to the wall of the force channel during perceptual testing. We examined forces applied during the initial 100 ms of the first channel movement in each round of perceptual tests. We removed outlying data points, which were defined as values that were >2 standard deviations from the mean in each round of perceptual testing. This resulted in the removal of 7 data points: 5 data points (out of 125 in total) in *experiment 1* and 2 data points (out of 48 in total) in *experiment 2*. The data were compared with a repeated-measures ANOVA.

## RESULTS

The goal of *experiment 1* was to assess differences in the time course of the somatosensory and motor changes that accompany motor learning. Subjects began by making 150 baseline movements in a null field. They then made 150 force field movements, split into 6 consecutive blocks. After training, they made 50 movements in a null field to test for aftereffects. Performance throughout *experiment 1* is shown in Fig. 2*A*, *top*. Subjects showed little curvature on baseline movements. Upon the introduction of the force field, the hand was deflected to the left as subjects moved outward toward the target. Over the course of successive trials, movements straightened and regained trajectories similar to baseline. Figure 2*A* shows that interleaving sensory testing throughout the training sequence (Fig. 2*A*, *top*, vertical gray bars) resulted in a discontinuous learning curve. Nevertheless, performance changed incrementally throughout training, and the reduction in curvature was essentially maintained throughout each round of sensory testing. Overall, movement curvature decreased to an asymptotic value by the end of the 150 movements, which suggests that dividing training into an interrupted sequence did not eliminate learning. Consistent with this claim, on aftereffect trials the sudden removal of the force field resulted in movements that were curved to the right, suggesting successful learning. Over the course of 50 aftereffect movements, subjects were once again able to move straight to the target.

A repeated-measures ANOVA on the curvature data shown in Fig. 2*A* found reliable changes in movement curvature [$F_{(5,60)} = 63.629$, $P < 0.001$]. Post hoc comparisons showed that curvature on the initial and final five baseline movements did not differ ($P > 0.9$). Curvature on initial movements in the force field increased ($P < 0.001$) but decreased reliably over the course of training ($P < 0.001$). Relative to baseline movements, initial aftereffect trials were curved opposite to the direction of applied force ($P < 0.001$). Curvature returned to baseline levels by the end of the washout phase ($P > 0.9$).

We performed an analysis on movement curvature between the present experiment and our previous study (Ostry et al. 2010). The goal of this analysis was to ensure that the interleaved perceptual testing employed here had no measurable effect on the overall motor learning process. In our previous study, subjects made 150 baseline movements, followed by 150 movements during which the robot applied forces to the arm that were the same as those applied in the present experiment. At the end of the experiment subjects made 50 aftereffect trials during which no forces were applied. The experimental sequence was thus identical to the present study, except that here the learning phase was divided into six incremental blocks of trials that were separated by perceptual testing. For the analysis, we artificially divided the data collected in the learning phase of our previous study into six incremental blocks of trials, as in the present study. We then compared how curvature changes over the course of the entire experiment between the two studies. A split-plot, repeated-measures ANOVA revealed that curvature changed over the course of the experiment [$F_{(7,189)} = 88.670$, $P < 0.001$]. However, this change in curvature did not differ between the present experiment and our previous study [i.e., there was no interaction, $F_{(7,189)} = 1.012$, $P > 0.4$], nor were there overall differences in curvature between the present and previous studies [$F_{(1,27)} = 0.117$, $P > 0.7$]. These results suggest that dividing the training phase into incremental blocks of trials had little effect on the overall pattern of motor learning.

A repeated-measures ANOVA on perceptual performance in *experiment 1* revealed that the perceptual boundary between left and right changed over the course of the experiment [$F_{(8,96)} = 4.046$, $P < 0.001$]. The magnitude of the shift in the perceptual boundary relative to baseline performance increased gradually throughout training. While the magnitude of the shifts between consecutive tests of the perceptual boundary did not reach reliability, we found that the overall shift was reliably different from zero ($P < 0.05$). After washout trials, the magnitude of the shift approached significance ($P < 0.08$), suggesting some persistence of the sensory change (Fig. 3*A*).

We measured the perceptual boundary throughout the learning process, so that we could compare the time course of changes in perceptual function with that of motor learning. The perceptual data are shown in Fig. 4*A*. The red data points show the change in movement curvature from the start to the end of learning. The blue data points show the change in the perceptual boundary between left and right, measured at six time points throughout learning. The change is computed on a per-subject basis relative to the second prelearning baseline estimate of the perceptual boundary. Note the scale difference for the two sets of data shown in Fig. 4*A*; for visualization purposes the scales have been aligned, and smooth exponential curves have been fit to each data set in order to see differences in the rates of change. The curves and the statistical analysis (see below) suggest that the change in motor performance occurs in advance of changes in the perceptual boundary

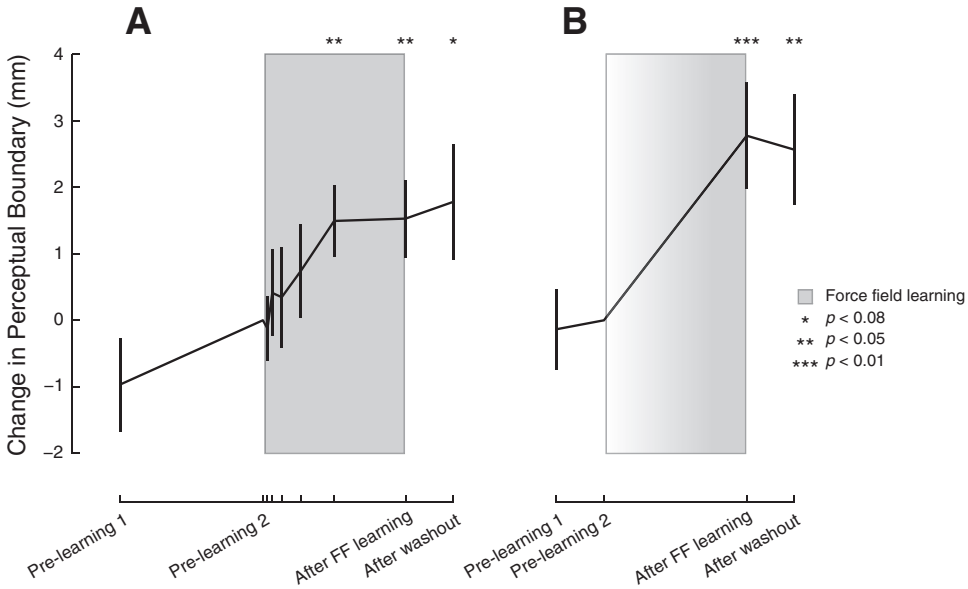


Fig. 3. Change in the position of the boundary between left and right across repeated perceptual tests. *A*: *experiment 1*. The perceptual boundary was measured 9 times: twice before and 6 times during force field learning and once after washout trials. The gray rectangle indicates the block of force field training. The perceptual boundary was stable before learning. During learning, the position of the boundary shifted incrementally to the right as learning progressed. By the end of training, the shift was reliable. After aftereffect trials, the position of the perceptual boundary remained in its shifted location. *B*: *experiment 2*. The perceptual boundary was measured 4 times: twice before and once after gradual force field learning and once after washout trials. The gray rectangle indicates the gradual force field, which grew in strength throughout training as indicated by shading. The perceptual boundary was stable before learning. After subjects learned to compensate for the gradual leftward force field, the position of perceptual boundary shifted to the right. The boundary remained in its shifted location after washout trials. Data points represent the change in the perceptual boundary, relative to the 2nd prelearning perceptual test, averaged over subjects. Vertical lines represent 1 SE. Asterisks indicate shifts whose magnitude was different from zero.

between left and right. Motor performance changes rapidly on initial trials, whereas the change in perceptual performance is slower. Changes in both motor and perceptual performance were well captured by exponential curves (see *Eq. 3*), with $r^2$ values indicating that the curves accounted for 57.2% and 93.3% of the variance for motor and perceptual learning curves, respectively. For the perceptual data, we compared exponential and linear fits to the data and found that the exponential curve provided a reliably better fit than a linear function [$F_{(1,4)} = 8.284$, $P < 0.05$].

To assess differences in the rate of change for motor and sensory performance, we performed the following analysis. We

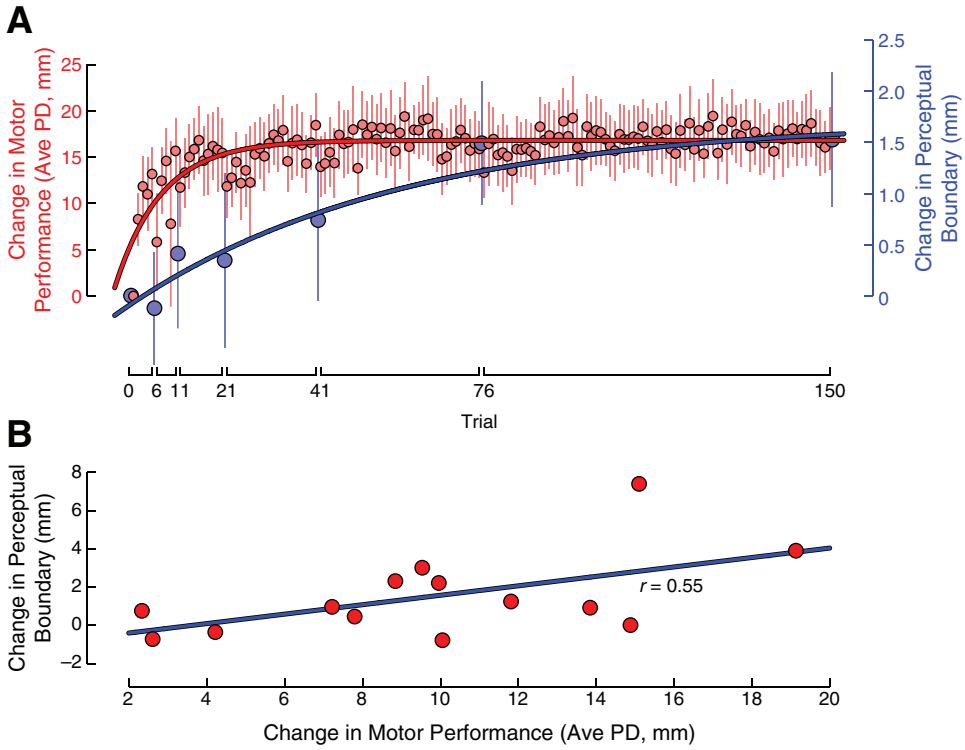


Fig. 4. Relationship between motor adaptation and sensory change. *A*: comparison of the rates of change for motor and sensory performance in *experiment 1*. Data are shown as the change in motor or sensory performance relative to the first trial in the training phase. Vertical scales for the motor (red, *left*) and sensory (blue, *right*) data have been adjusted so that each data set begins and ends at the same position on the figure. Over the course of training, movement curvature changed as subjects learned to compensate for the force field (red). The position of the perceptual boundary between left and right also shifted throughout training (blue). The figure shows that the change in motor performance preceded the shift in the perceptual boundary. Smooth curves represent exponential fits to the data. Each data point represents the change in mean perpendicular deviation, or the change in the perceptual boundary, averaged over subjects. Vertical lines represent 1 SE. *B*: a positive correlation between the extent of motor adaptation and the magnitude of the shift in the perceptual boundary in *experiment 1*. Red data points plot the change in both motor and sensory performance for each subject.

fit exponential curves to both the motor and sensory data (see *Eq. 3*) and compared the *b* parameters, which describe the rate of change for each exponential function. For the curve fit to the change in the perceptual boundary, the *b* parameter had a value of 0.017, with a 99% confidence interval ranging from −0.022 to 0.056. This estimate of the *b* parameter for the sensory data did not overlap the rates of change for curves fit to the curvature data associated with motor learning. For the curve fit to the full set of 150 trials (shown in Fig. 4*A*), the *b* parameter had a value of 0.096 and its 99% confidence interval ranged from 0.070 to 0.123. For the curve fit to the reduced set of movement trials, the *b* parameter had a value of 0.123 and its 99% confidence interval ranged 0.052 to 0.193. For the reduced data set, the $r^2$ indicates that 98.7% of the variance was accounted for by the exponential fit (data not shown). These analyses thus suggest that the rate of motor learning was greater than the rate of perceptual change.

We performed a second analysis in which we computed the change in both motor and sensory performance over the course of motor learning. We then performed a split-plot, repeated-measures ANOVA. Our goal was to determine whether the way in which motor performance changed over the course of the experiment differed from the way in which sensory performance changed. ANOVA revealed a reliable interaction [$F_{(6,156)} = 16.831$, $P < 0.001$], which indicates that the difference between motor and sensory performance changed over the course of learning. This analysis is consistent with the curve fitting analysis described above, and it suggests that the rate of change for sensory performance differed reliably from the rate of change for motor performance.

We performed a correlation to assess whether the extent of motor adaptation was associated with the magnitude of the change in the perceptual boundary; the relationship is plotted in Fig. 4*B*. We found that larger shifts in the perceptual boundary between left and right were associated with larger changes in movement curvature over the course of learning (Pearson's $r = 0.55$, $P < 0.05$). For this analysis, we computed the change in movement curvature between the initial three and final three movements in the force field. We repeated the analysis, examining different numbers of initial and final trials, and found similar results. We also found that the magnitude of the change in the perceptual boundary was 15.6% as large as the magnitude of the change in movement curvature due to motor learning.

In summary, in *experiment 1* we found that changes in perceptual function lag behind changes in motor performance. By measuring the perceptual boundary at intervals throughout the learning process, we have shown that shifts in perception occur at a slower rate than changes in motor performance associated with force field learning. The magnitude of the change in the perceptual boundary is associated with the extent of motor adaptation. These results are consistent with the idea that motor learning can drive change in sensory performance.

In *experiment 2*, we conducted a study to rule out the possibility that factors related to the cognitive awareness of the presence of the force field are at the source of the change in sensory performance that is seen in conjunction with motor learning. We employed a technique in which the forces applied to the hand increase gradually over the course of training (Huang and Shadmehr 2009; Klassen et al. 2005; Kluzik et al. 2008; Malfait and Ostry 2004). This reduces the kinematic error experienced by the subjects and, presumably, the explicit, declarative awareness of the perturbing forces as well. Moreover, the gradual introduction of perturbations has been shown to modify the extent to which motor learning affects subsequent performance (Huang and Shadmehr 2009; Klassen et al. 2005; Kluzik et al. 2008; Malfait and Ostry 2004). Here we used a gradually increasing force field to determine whether changes in sensory perception occur when awareness of the motor learning process is reduced. This would strengthen the idea that changes in sensory perception are driven by motor learning.

Figure 2*B*, *top*, shows movement curvature over the course of training. Subjects began with 50 null field movements to assess baseline performance. Movement curvature was stable across the baseline phase. The force field was then increased linearly over 150 trials, from 0 to 18 Ns/m. The force field was held at 18 Ns/m for the 151st–200th trials in the training phase. Across the training phase, initial trials showed curvature in a direction opposite to the applied force, and final movements were curved slightly in the direction of the force field. However, the magnitude of curvature across training remained stable near baseline levels, and it never approached the curvature seen after the abrupt application of force fields of the same strength (see Fig. 2*A*). After training, subjects completed 50 null field movements to assess aftereffects of learning. Initial aftereffect movements were curved in a direction opposite to the applied force, suggesting that subjects learned the force field in the absence of substantial kinematic error.

A repeated-measures ANOVA showed that there were differences in movement curvature throughout *experiment 2* [$F_{(8,88)} = 49.217$, $P < 0.001$]. Post hoc comparisons revealed that curvature on the initial and final five baseline movements did not differ ($P > 0.9$). Initial movements in the training phase, when the strength of the force field was near zero, showed a slight increase in curvature relative to baseline movements, in a direction opposite to the applied force ($P < 0.05$). As the strength of the force field grew throughout training (*movements 51–55*, *101–105*, and *151–155*), at no point did curvature differ from baseline ($P > 0.1$). This was also true at the end of training (*movements 196–200*) when the force was at its peak ($P > 0.3$). This suggests that subjects learned to compensate for the gradually increasing force field despite a lack of appreciable kinematic error. Initial aftereffect trials reveal this learning process, as curvature increased relative to baseline in a direction opposite to the applied force ($P < 0.001$). Increased curvature persisted, as final aftereffect trials remained curved relative to baseline ($P < 0.001$). A repeated-measures ANOVA showed that curvature changed over the course of the 50 aftereffect trials [$F_{(9,99)} = 47.551$, $P < 0.001$]. Curvature decreased rapidly on initial trials but then remained stable over the final aftereffect movements; Bonferroni-adjusted post hoc comparisons revealed that curvature did not change after the 11th aftereffect trial ($P > 0.05$ for all comparisons). This suggests that the curvature that remained at the end of washout was not due to an insufficient number of washout trials.

Sensory performance was measured throughout the learning process, as indicated by the gray bars in Fig. 2*B*. We measured the perceptual boundary between left and right before and after baseline movements, after gradual motor learning, and at the

end of the washout phase. The change in the perceptual boundary relative to the second baseline measure is shown in Fig. 3*B*. The boundary was stable before and after baseline movements. After force field learning, there was a rightward shift in the perceptual boundary. The rightward shift in the perceptual boundary remained after washout trials.

A repeated-measures ANOVA on the data shown in Fig. 3*B* found that there were reliable changes in the perceptual boundary [$F_{(3,33)} = 9.373$, $P < 0.001$]. After training in a gradual force field, the magnitude of the shift in the perceptual boundary relative to baseline performance was reliable ($P < 0.01$). The shift in the perceptual boundary was also reliable after washout trials ($P < 0.05$), suggesting persistence of the change in sensory performance.

In summary, the results in *experiment 2* suggest that, even in the absence of substantial kinematic error, subjects learn to compensate for forces applied to the arm by a force field whose strength increased gradually. We found that changes in the perceptual boundary between left and right accompany these changes in motor performance. These findings suggest that changes in sensory performance occur even with reduced knowledge of the effects of the force field. This is consistent with the idea that sensory change following motor learning does not require explicit knowledge of the learning process.

As a control, we analyzed the lateral forces applied to the wall of the force channel during perceptual testing, to ensure that changes in perceptual boundary did not reflect active force production. We examined forces applied during the initial 100 ms of the channel movement, prior to the leftward or rightward shift in the channel's position. We examined force production on the first movement in each sequence of perceptual testing. Overall the lateral forces produced during perceptual testing were low, averaging 0.71 N. However, in *experiment 1*, a repeated-measures ANOVA revealed that there were nevertheless differences in lateral force production in the nine rounds of perceptual testing [$F_{(8,72)} = 3.115$, $P < 0.01$]. But when post hoc tests were conducted with a Bonferroni correction for multiple comparisons, no reliable differences were obtained. That is, no reliable differences in the amount of lateral force produced among the nine rounds of perceptual testing could be identified. Forces produced before the start of force field learning, and after washout trials, were not different from zero ($P > 0.05$, $P > 0.20$, respectively).

We found similar results for *experiment 2*. Average lateral force was 0.23 N. A repeated-measures ANOVA revealed differences in lateral force production across the four rounds of perceptual testing [$F_{(3,27)} = 7.653$, $P < 0.01$]. Bonferroni-corrected post hoc tests revealed that lateral forces produced during perceptual testing increased after learning in the gradual force field; forces produced after training were greater than those produced on the initial round of perceptual testing and those produced after aftereffect trials ($P < 0.05$ for both comparisons). Forces produced during the two rounds of perceptual training before learning, and during the test that followed washout trials, did not differ from zero ($P > 0.90$, $P > 0.05$, $P > 0.90$, respectively).

Thus this control analysis reveals that in both *experiments 1* and *2* there were increases in the lateral forces produced during perceptual tests following training in the force field. However, it is important to note that lateral force production returned to baseline on the perceptual tests that followed aftereffect trials, on which a shift in the perceptual boundary could still be detected. This suggests that the shift in the perceptual boundary was not the result of active force production during perceptual testing.

## DISCUSSION

In the experiments reported here, we have explored the links between motor learning and changes in somatosensory function. These experiments follow upon our previous work, in which we showed that plasticity in motor performance, as induced by force field learning, results in changes in somatosensory perception of the hand's location in space (Ostry et al. 2010). Here we have replicated that effect; having learned to compensate for forces applied to the hand changes the perceptual boundary between left and right. We have expanded upon our previous work to show that the changes in sensory function progress incrementally throughout the learning process. In *experiment 1*, we divided motor learning into incremental phases and found that changes in sensory perception grew after changes in motor performance. In *experiment 2* we found that changes in sensory function occur despite reduced kinematic error, and presumably reduced awareness of the motor learning process. Taken together, the results from *experiments 1* and *2* strengthen the links between motor learning and changes in sensory perception. Indeed, they support the idea that sensory function is modified by motor learning.

In *experiment 1*, we found that the change in motor performance occurred more rapidly than the change in the perceptual boundary between left and right. This is consistent with the idea that plasticity in sensory function can be driven by motor learning. In our previous work, we showed that changes in the perceived location of the hand depend on learning; subjects who receive matched kinematic input but do not undergo motor learning during training do not show changes in sensory perception (Ostry et al. 2010). Similarly, while active exploration of a regionally selective portion of the workspace increases proprioceptive acuity, sensory performance is unchanged if the hand is guided passively by the robot (Wong et al. 2011). Moreover, investigations into the effect of speech motor learning on auditory perception show that control subjects and subjects who fail to adapt during the force field task do not show changes in the perception of speech sounds (Nasir and Ostry 2009). These findings, and those reported here in *experiment 1*, strengthen the case for links between motor learning and changes in sensory function.

The mechanism by which motor learning modifies sensory function is as yet unknown. One possibility is that motor learning leads to direct changes in sensory systems. Indeed, previous research has shown that primary and secondary somatosensory areas show changes in receptive field sizes after training on a motor task (Jenkins et al. 1990; Xerri et al. 1999). In this case, however, it is not clear whether the motor or the sensory aspects of the training task are responsible for the changes in sensory areas. Another possibility is that sensory processing involves a motoric reference frame that has been modified by learning (Feldman 2009). In other words, sensory information is interpreted with reference to underlying motor plans that have been changed/updated to account for the force field encountered during training. This idea is similar to the so-called motor theory of speech perception, in which the

perception of speech sounds involves the neural structures in the perceiver's brain that are involved in generating the same sounds (Liberman and Mattingly 1985; Pulvermüller et al. 2006). It is also similar to the idea that perception of the movements of others invokes the motor system in the perceiver (Rizzolatti et al. 2001). It is different, however, in that here it is perception of one's own movements, and not the movements of another individual, that may be interpreted with reference to the motor system. Resolving whether motor learning results in changes only to the motor system, or to both motor and sensory systems, could be investigated with electrophysiological or neuroimaging techniques.

Indeed, studies from our laboratory have used these techniques, and they lend support for the latter possibility, namely, that motor learning leads to changes in sensory as well as motor areas of the brain. In a recent study (Vahdat et al. 2011), we used functional magnetic resonance imaging (fMRI) and resting connectivity analyses to identify regions within the sensorimotor network that showed changes in functional connectivity that were correlated with either the magnitude of motor learning or with the associated change in sensory performance. The analysis revealed that changes in sensory performance were correlated with changes in connectivity between second somatosensory cortex (SII), ventral premotor cortex (PMv), and supplementary motor area (SMA). This suggests that the changes in sensory performance induced by motor learning are associated with changes to both motor and sensory areas of the brain. This finding supports the link between motor learning and changes in sensory systems.

In *experiment 2*, subjects were exposed to a force field that grew incrementally stronger throughout training. We measured the perceptual boundary between left and right before and after gradual learning and found a reliable rightward shift following force field adaptation. Examining the magnitude of the shift, despite the lack of a statistical difference it appears that the change in the perceptual boundary may be slightly greater after gradual learning than after training on a force field that was held at its maximum strength throughout training (compare Fig. 3, *A* and *B*). If future studies revealed this to be true, it could be consistent with other work suggesting benefits of gradual learning. These studies have shown that 24 h after initial learning retention is greater if force fields were applied incrementally rather than abruptly (Klassen et al. 2005). Studies have also shown larger aftereffects and greater transfer of learning from one context to another (Kluzik et al. 2008) after gradual learning. Differences in the decay rates of the processes underlying incremental versus abrupt learning may explain the improved retention following adaptation to gradually increasing loads (Huang and Shadmehr 2009). Here, our results suggest that gradual learning may also be associated with larger changes to the sensory system, which is consistent with our claim that changes in the sensory system are tied to, and driven by, motor learning.

Here, and in our previous study (Ostry et al. 2010), we found persistence in the changes in sensory performance. That is, shifts in the perceptual boundary could still be detected after the completion of the washout phase of the experiment. *Experiment 1* provides a possible explanation for this persistence, namely, that changes in sensory performance occur at a slower rate than changes in motor performance. That is, the rapid change in motor performance that occurs during both force field and washout trials is followed by a slower change in perceptual boundaries. This slow rate of change may reflect a need for stability in sensory systems, which may help to maintain perceptual representations in a changing environment.

Our previous findings argue against the idea that sensory performance will return to baseline after a sufficient delay. We found that changes in sensory performance were still evident 24 h after the end of washout trials (Ostry et al. 2010). Moreover, in *experiment 2* we found persistent changes in both movement trajectories and the perceptual boundary between left and right after washout trials and the restabilization of performance. That is, after the removal of the forces, outward movements converged upon a trajectory that aligned with the shifted perceptual boundary between left and right. This is consistent with the idea that both the motor and sensory effects of force field learning can still be detected long after the forces have been removed. This suggests that motor learning can lead to long-standing changes in both motor and sensory performance.

In summary, in the two experiments reported here we have replicated our earlier finding that force field learning can modify somatosensory perception (Ostry et al. 2010). Specifically, learning results in a shift in the perceptual boundary between left and right. Here, we have extended our earlier finding by demonstrating that the change in sensory performance grows incrementally throughout the learning process. We divided training into incremental phases and found that changes in motor performance occur faster than perceptual changes. We have also shown that changes in sensory performance occur even when explicit knowledge of the learning process is reduced by the gradual introduction of load. Taken together, these results suggest that the motor learning process can drive changes in sensory performance.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

Author contributions: A.A.G.M., M.D., and D.J.O. conception and design of research; A.A.G.M. and M.D. performed experiments; A.A.G.M., M.D., and D.J.O. analyzed data; A.A.G.M., M.D., and D.J.O. interpreted results of experiments; A.A.G.M., M.D., and D.J.O. prepared figures; A.A.G.M., M.D., and D.J.O. drafted manuscript; A.A.G.M., M.D., and D.J.O. edited and revised manuscript; A.A.G.M., M.D., and D.J.O. approved final version of manuscript.

## REFERENCES

**Asanuma H, Rosén I.** Functional role of afferent inputs to the monkey motor cortex. *Brain Res* 40: 3–5, 1972.

**Brashers-Krug T, Shadmehr R, Bizzi E.** Consolidation in human motor memory. *Nature* 382: 252–255, 1996.

**Brown LE, Wilson ET, Goodale MA, Gribble PL.** Motor force field learning influences visual processing of target motion. *J Neurosci* 27: 9975–9983, 2007.

**Caithness G, Osu R, Bays PM, Chase H, Klassen J, Kawato M, Wolpert DM, Flanagan JR.** Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. *J Neurosci* 24: 8662–8671, 2004.

**Cothros N, Köhler S, Dickie EW, Mirsattari SM, Gribble PL.** Proactive interference as a result of persisting neural representations of previously learned motor skills in primary motor cortex. *J Cogn Neurosci* 18: 2167–2176, 2006.

**Cressman EK, Henriques DY.** Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102: 3505–3518, 2009.

**Cressman EK, Henriques DY.** Reach adaptation and proprioceptive recalibration following exposure to misaligned sensory input. *J Neurophysiol* 103: 1888–1895, 2010.

**Cressman EK, Salomonczyk D, Henriques DY.** Visuomotor adaptation and proprioceptive recalibration in older adults. *Exp Brain Res* 205: 533–544, 2010.

**di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G.** Understanding motor events: a neurophysiological study. *Exp Brain Res* 91: 176–180, 1992.

**Feldman AG.** New insights into action-perception coupling. *Exp Brain Res* 194: 39–58, 2009.

**Gandolfo F, Mussa-Ivaldi FA, Bizzi E.** Motor learning by field approximation. *Proc Natl Acad Sci USA* 93: 3843–3846, 1996.

**Gribble PL, Scott SH.** Overlap of internal models in motor cortex for mechanical loads during reaching. *Nature* 417: 938–941, 2002.

**Haith A, Jackson C, Miall R, Vijayakumar S.** Unifying the sensory and motor components of sensorimotor adaptation. *Adv Neural Inf Process Syst* 21: 593–600, 2008.

**Huang VS, Shadmehr R.** Persistence of motor memories reflects statistics of the learning event. *J Neurophysiol* 102: 931–940, 2009.

**Jenkins WM, Merzenich MM, Ochs MT, Allard T, Guic-Robles E.** Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *J Neurophysiol* 63: 82–104, 1990.

**Klassen J, Tong C, Flanagan JR.** Learning and recall of incremental kinematic and dynamic sensorimotor transformations. *Exp Brain Res* 164: 250–259, 2005.

**Kluzik J, Diedrichsen J, Shadmehr R, Bastian AJ.** Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? *J Neurophysiol* 100: 1455–1464, 2008.

**Krakauer JW, Ghez C, Ghilardi MF.** Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J Neurosci* 25: 473–478, 2005.

**Liberman AM, Mattingly IG.** The motor theory of speech perception revised. *Cognition* 21: 1–36, 1985.

**Malfait N, Henriques DY, Gribble PL.** Shape distortion produced by isolated mismatch between vision and proprioception. *J Neurophysiol* 99: 231–243, 2008.

**Malfait N, Ostry DJ.** Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? *J Neurosci* 24: 8084–8089, 2004.

**Malfait N, Shiller DM, Ostry DJ.** Transfer of motor learning across arm configurations. *J Neurosci* 22: 9656–9660, 2002.

**Mattar AA, Ostry DJ.** Neural averaging in motor learning. *J Neurophysiol* 97: 220–228, 2007a.

**Mattar AA, Ostry DJ.** Modifiability of generalization in dynamics learning. *J Neurophysiol* 98: 3321–3329, 2007b.

**Mattar AA, Ostry DJ.** Generalization of dynamics learning across changes in movement amplitude. *J Neurophysiol* 104: 426–438, 2010.

**Murphy JT, Kwan HC, MacKay WA, Wong YC.** Spatial organization of precentral cortex in awake primates. III. Input-output coupling. *J Neurophysiol* 41: 1132–1139, 1978.

**Nasir SM, Ostry DJ.** Auditory plasticity and speech motor learning. *Proc Natl Acad Sci USA* 106: 20470–29475, 2009.

**Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL.** Somatosensory plasticity and motor learning. *J Neurosci* 30: 5384–5393, 2010.

**Pulvermüller F, Huss M, Kherif F, Moscoso del Prado Martin F, Hauk O, Shtyrov Y.** Motor cortex maps articulatory features of speech sounds. *Proc Natl Acad Sci USA* 103: 7865–7870, 2006.

**Rizzolatti G, Gentilucci M, Fogassi L, Luppino G, Matelli M, Ponzoni-Maggi S.** Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey. *Exp Brain Res* 67: 220–224, 1987.

**Rizzolatti G, Gentilucci M, Fogassi L, Luppino G, Matelli M.** Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 71: 491–507, 1988.

**Rizzolatti G, Fogassi L, Gallese V.** Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2: 661–670, 2001.

**Romo R, Hernández A, Zainos A, Lemus L, Brody CD.** Neuronal correlates of decision-making in secondary somatosensory cortex. *Nat Neurosci* 5: 1217–1225, 2002.

**Romo R, Hernández A, Zainos A.** Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron* 41: 165–173, 2004.

**Rosén I, Asanuma H.** Peripheral afferent inputs to the forelimb area of the monkey motor cortex: input-output relations. *Exp Brain Res* 14: 257–273, 1972.

**Shadmehr R, Brashers-Krug T.** Functional stages in the formation of human long-term motor memory. *J Neurosci* 17: 409–419, 1997.

**Shadmehr R, Holcomb HH.** Neural correlates of motor memory consolidation. *Science* 277: 821–825, 1997.

**Shadmehr R, Holcomb HH.** Inhibitory control of competing motor memories. *Exp Brain Res* 126: 235–251, 1999.

**Shadmehr R, Moussavi ZM.** Spatial generalization from learning dynamics of reaching movements. *J Neurosci* 20: 7807–7815, 2000.

**Shadmehr R, Mussa-Ivaldi FA.** Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.

**Shiller DM, Sato M, Gracco VL, Baum SR.** Perceptual recalibration of speech sounds following speech motor learning. *J Acoust Soc Am* 125: 1103–1113, 2009.

**Simani MC, McGuire LM, Sabes PN.** Visual-shift adaptation is composed of separable sensory and task-dependent effects. *J Neurophysiol* 98: 2827–2841, 2007.

**Smith MA, Ghazizadeh A, Shadmehr R.** Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol* 4: e179, 2006.

**Taylor MM, Creelman CD.** PEST: Efficient Estimates on Probability Functions. *J Acoust Soc Am* 41: 782–787, 1967.

**Thoroughman KA, Shadmehr R.** Learning of action through adaptive combination of motor primitives. *Nature* 407: 742–747, 2000.

**Vahdat S, Darainy M, Milner TE, Ostry DJ.** Functionally specific changes in resting-state sensorimotor networks after motor learning. *J Neurosci* 31: 16907–16915, 2011.

**van Beers RJ, Wolpert DM, Haggard P.** When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol* 12: 834–837, 2002.

**Wong JD, Wilson ET, Gribble PL.** Spatially selective enhancement of proprioceptive acuity following motor learning. *J Neurophysiol* 105: 2512–2521, 2011.

**Xerri C, Coq JO, Merzenich MM, Jenkins WM.** Experience-induced plasticity of cutaneous maps in the primary somatosensory cortex of adult monkeys and rats. *J Physiol (Paris)* 90: 277–287, 1996.

**Xerri C, Merzenich MM, Jenkins W, Santucci S.** Representational plasticity in cortical area 3b paralleling tactual-motor skill acquisition in adult monkeys. *Cereb Cortex* 9: 264–276, 1999.