

CHAPTER 2

Sensory change following motor learning

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Abstract: Here we describe two studies linking perceptual change with motor learning. In the first, we document persistent changes in somatosensory perception that occur following force field learning. Subjects learned to control a robotic device that applied forces to the hand during arm movements. This led to a change in the sensed position of the limb that lasted at least 24 h. Control experiments revealed that the sensory change depended on motor learning. In the second study, we describe changes in the perception of speech sounds that occur following speech motor learning. Subjects adapted control of speech movements to compensate for loads applied to the jaw by a robot. Perception of speech sounds was measured before and after motor learning. Adapted subjects showed a consistent shift in perception. In contrast, no consistent shift was seen in control subjects and subjects that did not adapt to the load. These studies suggest that motor learning changes both sensory and motor function.

Keywords: motor learning; sensory plasticity; arm movements; proprioception; speech motor control; auditory perception.

Introduction

To what extent is plasticity in motor and sensory systems linked? Neuroplasticity in sensory and motor systems is central to the development of

the human motor system and, likewise, to skill acquisition in the adult nervous system. Here, we summarize two studies in which we have examined the hypothesis that motor learning, which is associated with plastic changes to motor areas of the brain, leads to changes in sensory perception. We have investigated motor learning in the context of reaching movements and in speech motor control. We have examined the

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extent to which motor learning modifies somatosensory perception and the perception of speech. Our findings suggest that plasticity in motor systems does not occur in isolation, but it results in changes to sensory systems as well.

Our studies examine sensorimotor learning in both an arm movement task and a speech task. It is known that there are functional connections linking brain areas involved in the sensory and motor components of these tasks. There are known ipsilateral corticocortical projections linking somatosensory cortex with motor areas of the brain (Darian-Smith et al., 1993; Jones et al., 1978). Activity in somatosensory cortex varies systematically with movement (Ageranioti-Bélanger and Chapman, 1992; Chapman and Ageranioti-Bélanger, 1991; Cohen et al., 1994; Prud'homme and Kalaska, 1994; Prud'homme et al., 1994; Soso and Fetz, 1980), and the sensory signals arising from movement can result in changes to somatosensory receptive fields (Jenkins et al., 1990; Recanzone et al., 1992a,b; Xerri et al., 1999). Likewise, auditory processing recruits activity in motor areas of the brain (Chen et al., 2008; Pulvermüller et al., 2006), and auditory and somatosensory inputs converge within auditory cortex (Foxe et al., 2002; Fu et al., 2003; Kayser et al., 2005; Shore and Zhou, 2006). In addition, there are a number of pieces of evidence suggesting perceptual changes related to somatosensory input, movement, and learning. These include proprioceptive changes following visuomotor adaptation in reaching movements and in manual tracking (Cressman and Henriques, 2009, 2010; Cressman et al. 2010; Malfait et al., 2008; Simani et al., 2007; van Beers et al., 2002) and visual and proprioceptive changes following force field learning (Brown et al., 2007; Haith et al., 2008). They also include changes to auditory perception that are caused by somatosensory input (Ito et al., 2009; Jousmäki and Hari, 1998; Murray et al., 2005; Schürmann et al., 2004). These studies thus suggest that via the links between motor, somatosensory, and auditory areas of the brain, an effect of motor learning on perception may be likely.

Below, we describe a study involving human arm movement that tests the idea that sensory function is modified by motor learning. Specifically, we show that learning to correct for forces that are applied to the limb by a robot results in durable changes to the sensed position of the limb. We report a second study in which we test the hypothesis that speech motor learning, and in particular the somatosensory inputs associated with learning, affect the classification of speech sounds. In both studies, we observe perceptual changes following learning. These findings suggest that motor learning affects not only the motor system but also involves changes to sensory areas of the brain.

The effect of motor learning on somatosensory perception of the upper limb

Subjects made movements to a target in a standard force field learning procedure. In this task, subjects make reaching movements to a visual target while holding the handle of a robotic device that is programmed to apply forces to the subject's hand (Fig. 1a). Studies employing this technique have been used to document learning and plasticity in motor systems (Gribble and Scott, 2002; Shadmehr and Holcomb, 1997; Shadmehr and Mussa-Ivaldi, 1994). Figure 1b shows the experimental sequence. We interleaved blocks of trials in which we estimated the sensed position of the limb (shown in gray) with blocks of force field learning trials. We tested sensory perception twice before and once after force field learning. We also tested for the persistence of changes in sensory perception after the effects of motor learning were eliminated using washout trials.

We obtained estimates of the sensed position of the limb using an iterative procedure known as PEST (parameter estimation by sequential testing; Taylor and Creelman, 1967). The PEST procedure was done in the absence of vision. On each movement in the testing sequence, the limb was displaced laterally using a force channel (Fig. 1c). At

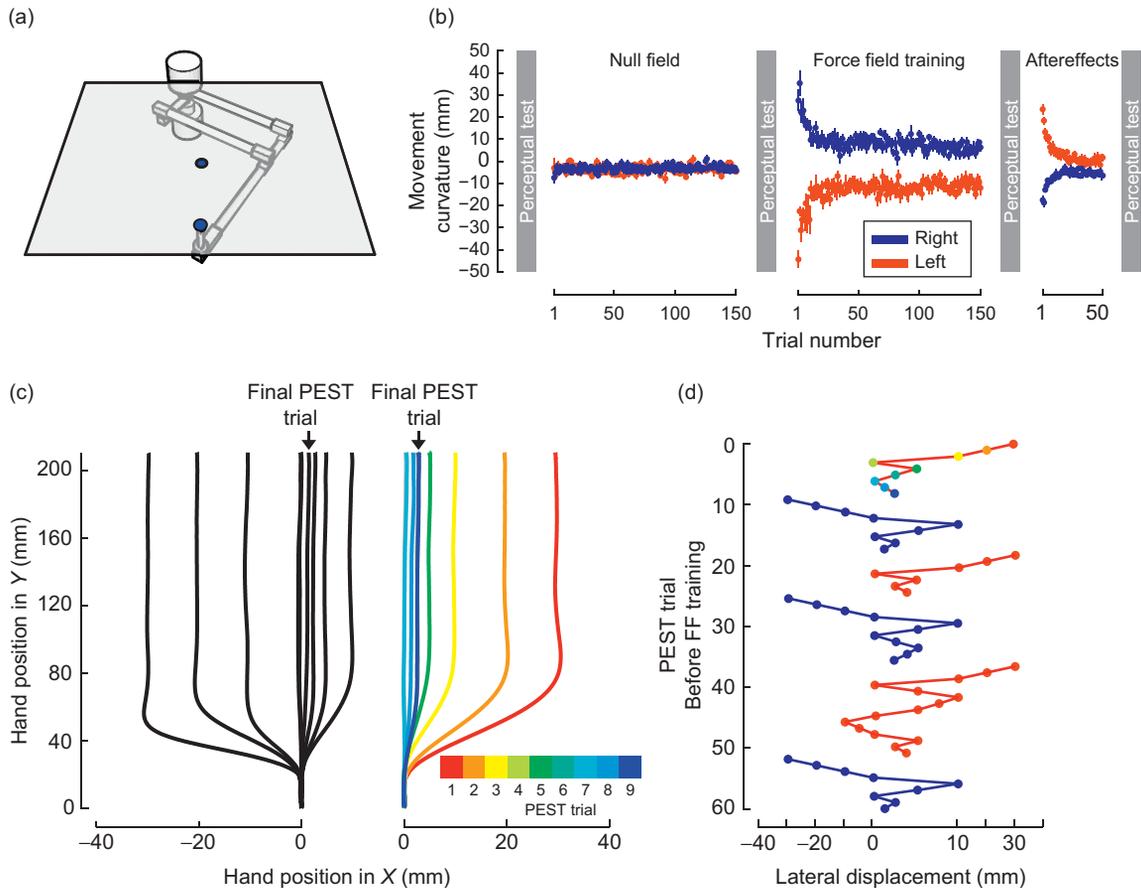


Fig. 1. Force field learning and the perception of limb position. (a) Subjects held the handle of a robotic device, when making movements to targets and during perceptual testing. The robot was capable of applying forces to the hand. Targets were presented on a horizontal screen that occluded vision of the hand, arm, and robot. (b) Subjects learn to compensate for velocity-dependent mechanical loads that displace the limb to the right or the left. Perceptual tests (gray bars) of the sensed limb position are interleaved with force field training. Average movement curvature (\pm SE) is shown throughout training. (c) An iterative procedure known as PEST estimates the perceptual boundary between left and right. A computer-generated force channel laterally displaced the limb, and subjects are required to indicate whether the limb has been deflected to the right. Individual PEST runs starting from left and right, respectively, are shown. The sequence is indicated by the shading of the PEST trials beginning at the right. (d) A sequence of six PEST runs (starting from the top) with the horizontal axis showing the lateral position of the hand and the PEST trial number on the vertical. The shaded sequence of trials shown at the top is the same as is shown on the right side of (c). PEST runs alternately start from the right and the left and end on a similar estimate of the perceptual boundary. Note that the horizontal axis highlights lateral hand positions between 0 and 10 mm.

the end of each movement the subject gave a “yes” or “no” response indicating whether the limb had been deflected to the right. Over the course of several trials, the magnitude of the deflection was modified based on the subject's responses in order

to determine the perceptual boundary between left and right. Figure 1b shows a sequence of PEST trials for a representative subject, prior to force field learning. The left panel shows a PEST sequence that began with a leftward deflection;

the right panel shows a sequence for the same subject beginning from the right. [Figure 1d](#) shows a sequence of six PEST runs. Each run converges on a stable estimate of the perceptual boundary between left and right.

In the motor learning phase of the experiment, subjects made movements in a clockwise or counterclockwise force field applied by a robot arm ([Fig. 1a](#)), whose actions were to push the hand to the right or to the left. Performance over the course of training was quantified by computing the maximum perpendicular distance (PD) from a straight line joining movement start and end. [Figure 1b](#) shows movement curvature (PD values), averaged over subjects, for each phase of the experiment. Under null conditions, subjects move straight to the target. Upon the introduction of the force field, movements are deflected laterally but over the course of training they straighten to near null field levels. The reduction in curvature from the initial 10 movements to the final 10 movements was reliable for both force field directions. Curvature on initial aftereffect movements is opposite to the curvature on initial force field movements reflecting the adjustment to motor commands needed to produce straight movements in the presence of load. Curvature at the end of the washout trials differs from initial null field trials; movements remain curved in a direction opposite to that of the applied force.

On a per-subject basis, we quantified perceptual performance by fitting a logistic function to the set of lateral limb positions and the associated binary responses that were obtained over successive PEST runs. For example, the sequence of PEST trials shown in [Fig. 1d](#) would lead to a single psychometric function relating limb position to the perceptual response. For visualization purposes, [Fig. 2a](#) shows binned response probabilities, averaged across subjects, and psychometric functions fit to the means for the rightward and leftward force fields. Separate curves are shown for estimates obtained before and after learning. The psychometric curve, and hence the perceptual boundary between left and right

shifts in a direction opposite to the applied load. If the force field acts to the right ([Fig. 2a](#), right panel), the probability of responding that the hand was pushed to the right increases following training. This means that following force field learning, the subject feels as if the hand is located farther to the right.

[Figure 2b](#) shows the position of the perceptual boundary in each of the four test sessions. The perceptual boundary was computed as the 50% point on the psychometric curve. For each subject separately, we computed the shift in the perceptual boundary as a difference between the final null condition estimate and the estimate following force field training. We computed the persistence of the shift as the difference between the final null condition estimate and the estimate following aftereffect trials. The shifts are shown in [Fig. 2c](#). It can be seen that immediately after force field training there was a shift in the sensed position of the limb that was reliably different than zero. The shift decreased following washout but remained different than zero. The magnitude of the shift was no different for both force field directions. Thus, the sensed position of the limb changes following force field learning, and the shift persists even after the kinematic effects of learning have been washed out.

In a control study, we examined the persistence of the perceptual change. Subjects were tested in a procedure that was identical to the main experiment, but it included an additional perceptual test 24 h following learning. The results are shown in [Fig. 2c](#). It can be seen that the force field led to a reliable shift in the perceptual boundary that was no different across the three estimates. Thus, periods of force field learning lasting ~ 10 min result in shifts in the perceptual boundary that persist for at least 24 h.

We conducted a second control experiment to determine the extent to which the observed perceptual changes are tied to motor learning. We used methods that were identical to those in the main experiment, except that the force field learning phase was replaced with a task that did

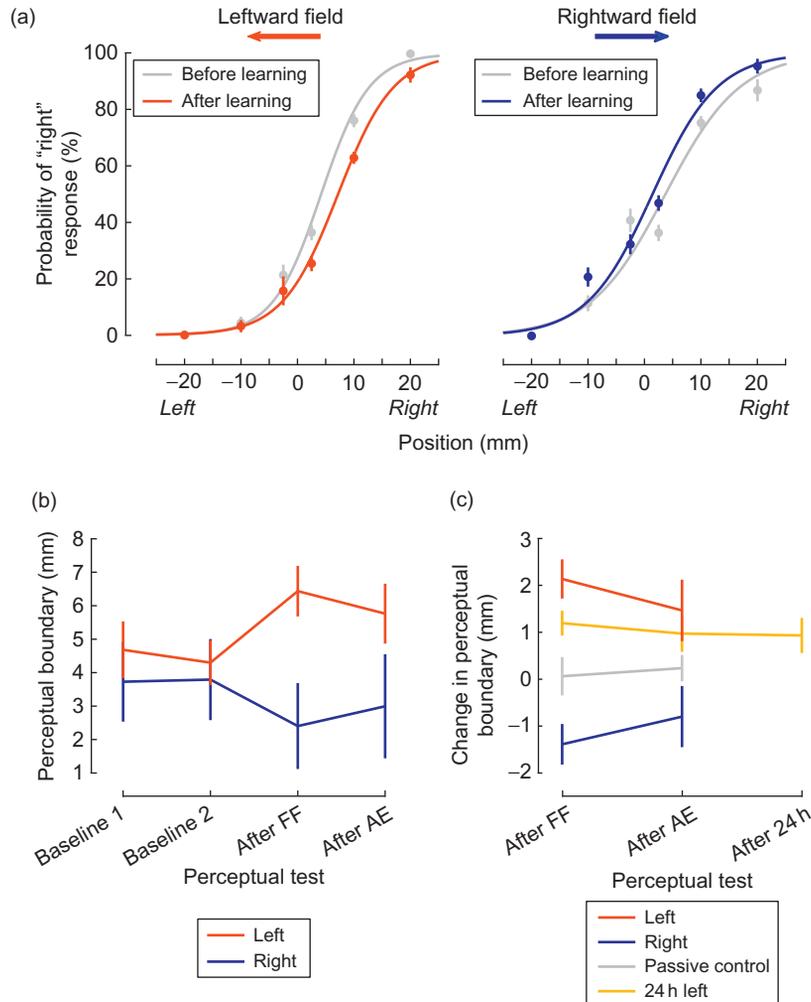


Fig. 2. The perceptual boundary shifts in a direction opposite to the applied force following motor learning. (a) Binned response probabilities averaged over subjects (\pm SE) before (light gray) and after (black or dark gray) learning. Fitted psychometric functions reflect the perceptual classification for each force field direction. (b) Mean perceptual boundary between left and right (\pm SE) for baseline estimates (baseline 1 and baseline 2), estimates following force field learning (after FF), and estimates following aftereffect trials (after AE). The sensed position of the limb changes following learning, and the change persists following aftereffect trials. (c) The direction of the perceptual shift depends on the force field (left vs. right). The perceptual shift persists for at least 24 h (24 h left). A perceptual shift is not observed when the robot passively moves the hand through the same sequence of positions and velocities as in the left condition such that subjects do not experience motor learning (passive control).

not involve motor learning. In the null field and aftereffect phases of the experiment, subjects moved actively. The force field learning phase was replaced with a passive task in which subjects

held the robot handle as it reproduced the movements of subjects in the leftward force field condition of the main experiment. Under position-servo control, the robot produced this series of

movements and the subject's arm was moved along the mean trajectory for each movement in the training sequence. Thus, subjects experienced a series of movements with the same kinematics as those in main experiment, but importantly they did not experience motor learning.

The upper panel of Fig. 3 shows the mean movement curvature (PD) for subjects tested in the passive control experiment and for subjects tested in the original experiment. The lower panel shows the average difference between PD in the passive control condition and PD in the original leftward force field. The lower panel of Fig. 3 shows that in the null phase, movement kinematics were well matched when subjects in both conditions made active movements. In the force field phase of the experiment, the near-zero values indicate that subjects in the passive control experiment experienced kinematics that closely

matched the mean trajectory in the original experiment. The nonzero values at the start of the aftereffect phase indicate that in the main experiment, training in the force field resulted in aftereffects and hence motor learning that was greater than following training in the passive control experiment.

Figure 2c shows measures of perceptual change for subjects trained in the original experiment, as well as for subjects trained in the passive control. Perceptual shifts depended on whether or not subjects experienced motor learning. As described above, subjects in the original experiment who learned the leftward force field showed perceptual shifts that were reliably different than zero both immediately after learning and after washout trials. In contrast, subjects tested in the passive control experiment showed shifts that did not differ from zero at either time point.

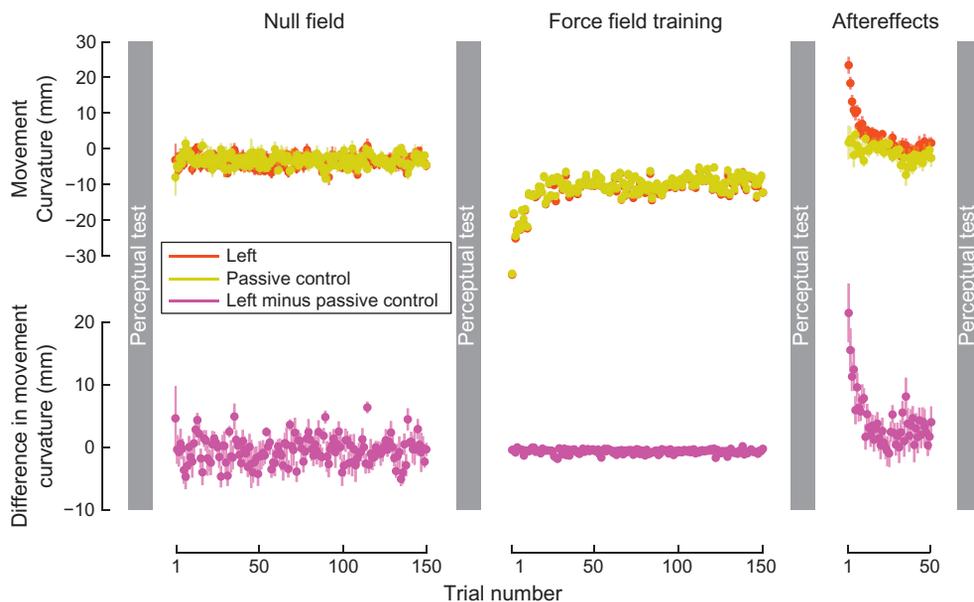


Fig. 3. The perceptual shift depends on motor learning. In a control experiment, subjects experience the same trajectories as individuals that display motor learning. Subjects move actively in the null and aftereffect phases of the study. In the force field training phase, the robot moves the arm to replicate the average movement path of subjects that learned the leftward force field. The top panel shows mean movement curvature (\pm SE) for subjects in the original leftward condition (black) and the passive control condition (light gray). The bottom panel gives the difference between active and passive movements (dark gray). Movement aftereffects are not observed in the passive condition (light gray) indicating there is no motor learning.

The effect of speech motor learning on the perception of speech sounds

In order to evaluate the idea that speech motor learning affects auditory perception, we trained healthy adults in a force field learning task (Lackner and Dizio, 1994; Shadmehr and Mussa-Ivaldi, 1994) in which a robotic device applied a mechanical load to the jaw as subjects repeated aloud test utterances that were chosen randomly from a set of four possibilities (*bad*, *had*, *mad*, *sad*; Fig. 4). The mechanical load was velocity-dependent and acted to displace the jaw in a protrusion direction, altering somatosensory but not auditory feedback. Perception of speech sounds was assessed before and after force field training.

In the perceptual tests, the subject had to identify whether an auditory stimulus chosen at random from a synthesized eight step spectral continuum sounded more like the word *head* or *had* (Fig. 4). A psychometric function was fitted to the data and gave the probability of identifying the word as *had*. We focused on whether motor learning led to changes to perceptual performance.

Sensorimotor learning was evaluated using a composite measure of movement curvature. Curvature was assessed on a per-subject basis, in null condition trials, at the start and at the end of learning. Statistically reliable adaptation was observed in 17 of the 23 subjects. This is typical of studies of speech motor learning in which about a third of all subjects fail to adapt (Nasir

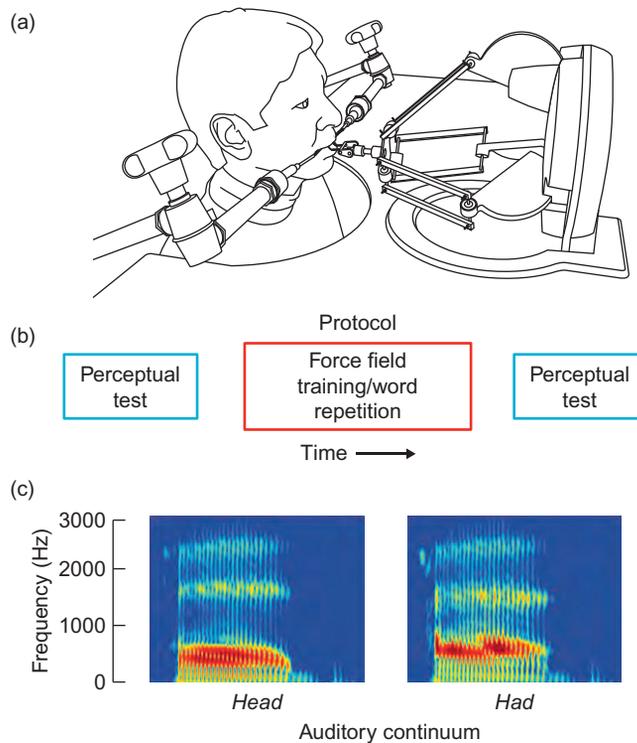


Fig. 4. Experimental set-up, protocol, and auditory test stimuli for the speech experiment. (a) A velocity-dependent load was delivered to the jaw by a robotic device. (b) Subjects completed an auditory identification task before and after motor learning. Control subjects repeated the same set of utterances but were not attached to the robot. (c) During perceptual testing, subjects indicated whether a given auditory test stimulus sounded more like *head* or *had*.

and Ostry, 2006, 2008; Purcell and Munhall, 2006; Tremblay et al., 2003). Figure 5a shows a representative sagittal plane view of jaw trajectories during speech for a subject that adapted to the load. Movements are straight in the absence of load; the jaw is displaced in a protrusion direction when the load is first applied; curvature decreases with training. Figure 5b shows movement curvature measures for the same subject, for individual trials, over the course of the entire experiment.

As shown in Fig. 5a, movement curvature was low in the null condition, increased with the introduction of load and then progressively decreased with training. The auditory psychometric function for this subject shifted to the right following training (Fig. 5c). This indicates that words sounded more like *head* after learning.

Figure 6a shows perceptual psychometric functions for adapted subjects before and after force field training. A rightward shift following

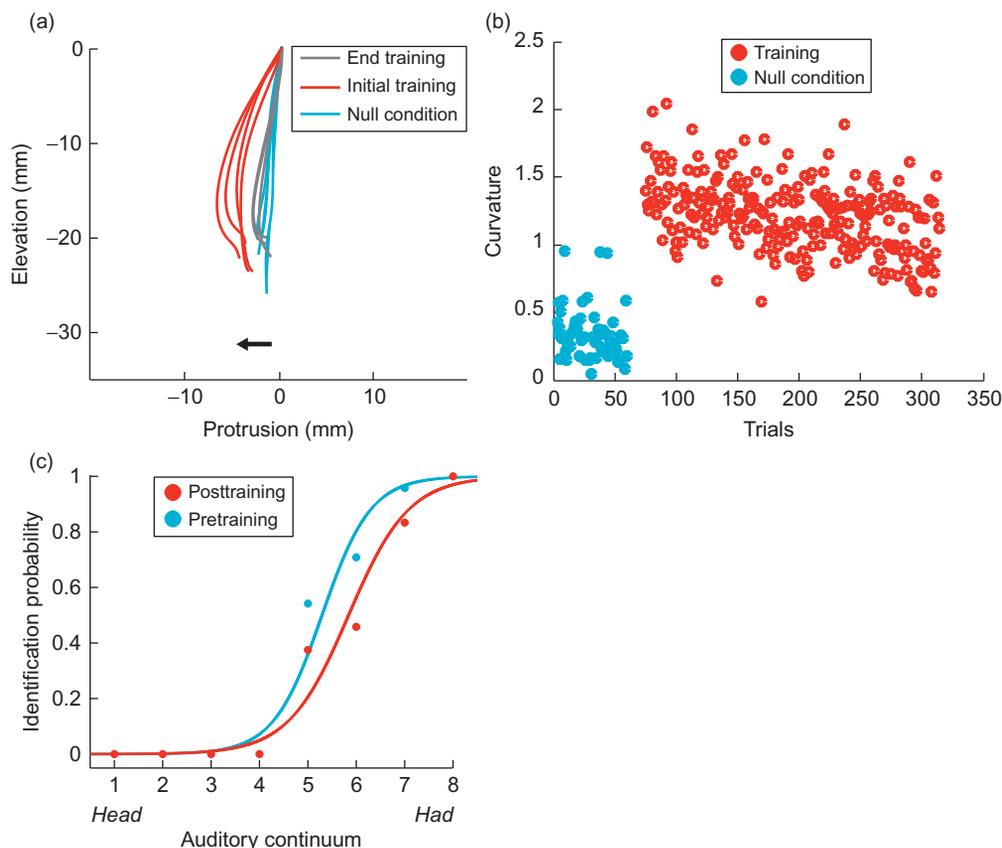


Fig. 5. Speech motor learning and changes in speech perception. (a) Sagittal view of jaw movement paths for a representative subject who adapted to the load. Movements were straight in the absence of load (light gray). The jaw was deflected in the protrusion direction when the load was introduced (black). Curvature decreased with training (dark gray). (b) Scatter plot showing movement curvature over the course of training for the same subject as in (a). The vertical axis shows movement curvature; the horizontal axis gives trial number. Curvature is low on null trials (light gray) increases when the load is introduced and decreases over the course of training (black). (c) The psychometric function depicting identification probability for *had* before (light gray) and after (black) training. A perceptual shift toward *head* was observed following learning.

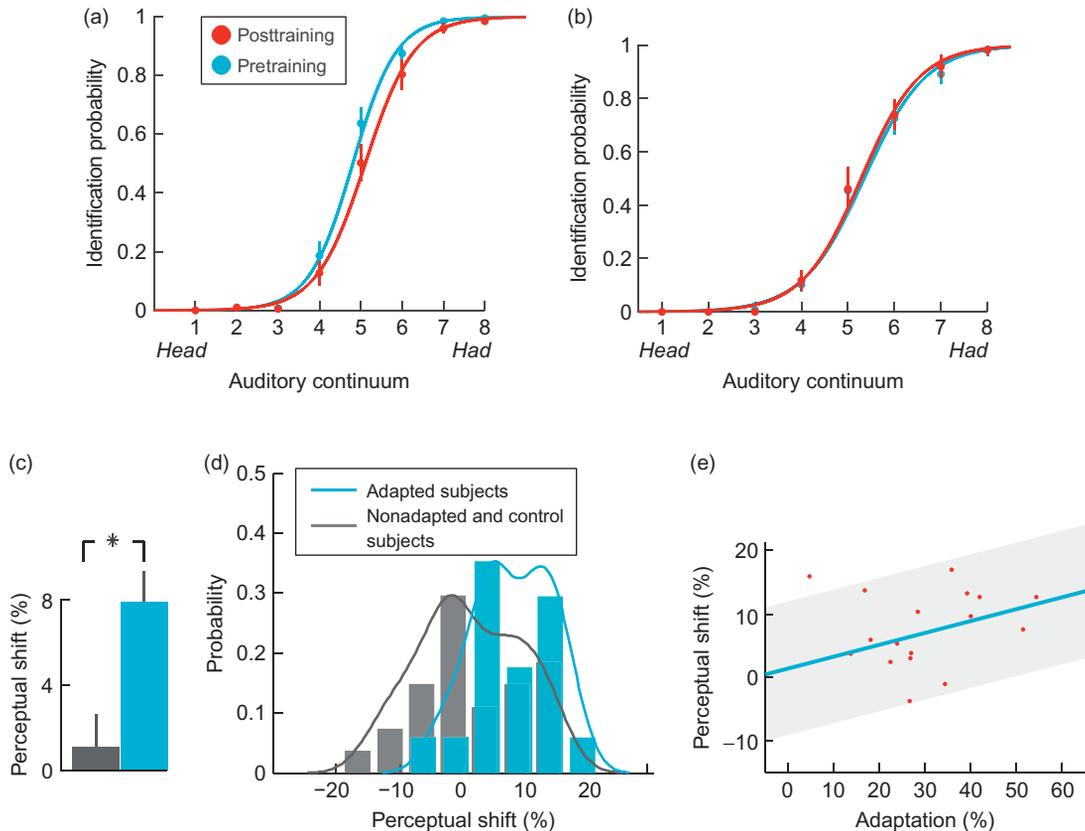


Fig. 6. Perception of speech sounds changes following speech motor learning. (a) The average psychometric functions for adapted subjects reveal a perceptual shift to the right following training (light gray: pretraining, black: posttraining). (b) There is no perceptual shift for nonadapted and control subjects. (c) The perceptual shift for adapted subjects (black) was reliably greater than the shift observed in nonadapted and control subjects (light gray), which was not different than zero. (d) Histograms showing the perceptual change for adapted (black) and nonadapted/control subjects (light gray). (e) The perceptual shift was correlated with adaptation. Subjects that showed greater adaptation also had greater perceptual shifts.

training is evident. A measure of probability, that was used to assess perceptual change, was obtained by summing each subject's response probabilities for individual stimulus items and dividing the total by a baseline measure that was obtained before learning. The change in identification probability from before to after training was used to gauge the perceptual shift. In 15 of the 17 subjects that adapted to the force field, we found a rightward shift in the psychometric function following training. This rightward

perceptual shift means that after force field learning the auditory stimuli are more likely to be classified as *head*. In effect, the perceptual space assigned to *head* increased with motor learning. The remaining six subjects who failed to adapt did not show any consistent pattern in their perceptual shifts.

We evaluated the possibility that the perceptual shift might be due to factors other than motor learning by testing a group of control subjects who completed the entire experiment without

force field training. This control study included the entire sequence of several hundred speech movements. For control subjects, the perceptual shift, computed in the same manner as for the experimental subjects, was not different than zero (Fig. 6c). Moreover, we found that perceptual shifts obtained for the nonadapted subjects in the main experiment did not differ from the shifts obtained from control subjects. Figure 6b shows the psychometric functions averaged over non-adapted and control subjects combined, before and after word repetition (or force field training for the nonadapted subjects). No difference can be seen in the psychometric functions of the subjects that did not experience motor learning.

Statistical tests were conducted on the perceptual probability scores before and after training. The analysis compared the scores of adapted subjects with those of control subjects and nonadapted subjects combined. The test thus compared the perceptual performance of subjects that successfully learned the motor task with those that did not. For adapted subjects, we found that identification scores were significantly different after training than before. For subjects that did not show motor learning, the difference in the two perceptual tests was nonsignificant. Thus, speech motor learning in a force field environment modifies perception of speech sounds. Word repetition alone cannot explain the observed perceptual effects.

In order to characterize further the pattern of perceptual shifts, we obtained histograms giving the distribution of shifts for both the adapted and the combined nonadapted and control groups (Fig. 6d). The histogram for the adapted group is to the right of the histogram for the nonadapted subjects. We also examined the possibility that subjects that showed greater learning would also show a greater perceptual shift. We calculated an index of learning for each adapted subject by computing the reduction in curvature over the course of training divided by the curvature due to the introduction of load. A value of 1.0 indicates complete adaptation. Computed in this

fashion, adaptation ranged from 0.05 to 0.55 and when averaged across subjects and test words, it was 0.29 ± 0.03 (mean \pm SE). Figure 6e shows the relationship between the amount of adaptation and the associated perceptual shift. We found that adapted subjects showed a small, but significant, correlation of 0.53 between the extent of adaptation and the measured perceptual shift.

We assessed the possibility that there are changes in auditory input over the course of force field training that might contribute to motor learning and also to the observed perceptual shift. Acoustical effects related to the application of load and learning were evaluated by computing the first and second formant frequencies of the vowel /æ/ immediately following the initial consonant in each of the test utterances. A statistical analysis found no reliable differences in either formant frequency over the course of the experiment. This suggests that there were no changes in auditory input over the course of adaptation.

Discussion

In the limb movement study, we showed that motor learning results in changes in the sensed position of the limb. The passive control experiment reveals that changes in somatosensory perception depend on motor learning. The perceptual change is robust, in that it persists for periods lasting at least 24 h.

In the absence of movement, sensory experience results in a selective expansion of the specific regions of somatosensory cortex that are associated with the sensory exposure, and it also results in changes in the size of sensory receptive fields that reflect the characteristics of the adaptation (Recanzone et al., 1992a,b). Changes to receptive field size in somatosensory cortex are observed when sensory training is combined with motor tasks that require precise contact with a rotating disk (Jenkins et al., 1990) or finger and forearm movements to remove food from a narrow well (Xerri et al., 1999). In these latter cases,

it is not clear whether it is the sensory experience, the motor experience, or both factors in combination that leads to changes in the sensory system. This issue is clarified by the findings summarized here. Changes in sensory perception depend on active movement and learning. Control subjects who experienced the same movements but did not experience motor learning showed no perceptual change. This points to a central role of motor learning in somatosensory plasticity.

The idea that sensory perception depends on both sensory and motor systems has been proposed by other researchers (Feldman, 2009; Haith et al., 2008). One possibility is that the central contribution to position sense involves motor commands that are adjusted by adaptation (see Feldman, 2009, for a recent review of central and afferent contributions to position sense). In effect, sensory signals from receptors are measured in a motoric reference frame that can be modified by learning. Another possibility is that the learning recalibrates both sensory and motor processes. Haith et al. propose that changes in performance that are observed in the context of learning depend on changes to both motor and sensory function that are driven by error (Haith et al., 2008).

In a second study, we found that the perceptual classification of speech sounds was modified by speech motor learning. There was a systematic change such that following learning, speech sounds on a continuum ranging from *head* to *had* were more frequently classified as *head*. Moreover, the perceptual shift varied with learning; the perceptual change was greater in subjects that showed greater adaptation during learning. The perceptual shift was not observed in subjects who failed to adapt to the forces applied by the robot, nor was it observed in control subjects who repeated the same words but did not undergo force field learning. This suggests a link between motor learning and the perceptual change. The findings thus indicate that speech learning modifies not only the motor system but also the perception of speech sounds.

The sensory basis of the auditory perceptual effect was somatosensory in nature. Force field training modified the motion path of the jaw and hence somatosensory feedback, but it did not affect the acoustical patterns of speech at any point during training. Hence, there was no change in auditory information that might result in perceptual modification. Thus the sensory basis of both the motor learning and the perceptual recalibration is presumably somatosensory but not auditory. This conclusion is supported by the observation that adaptation to mechanical load occurs when subjects perform the speech production task silently, indicating that it is not dependent upon explicit acoustical feedback (Tremblay et al., 2003). It is also supported by the finding that profoundly deaf adults who are tested with their assistive hearing devices turned off can still adapt to mechanical loads applied during speech (Nasir and Ostry, 2008).

The perceptual shift we observed is in the same direction as in previous studies of perceptual adaptation (Cooper and Lauritsen, 1974; Cooper et al., 1976). Cooper and colleagues observed that after listening to repetitions of a particular consonant–vowel stimulus, the probability that subjects would report hearing this same stimulus in subsequent perceptual testing was reduced. The effect reported here is similar to that observed by Cooper, but there are important differences suggesting the effects are different in origin. We found no perceptual shift in non-adapted subjects who repeatedly said or heard a given test stimulus. Moreover, control subjects also repeated and listened to the same set of utterances but did not show a reliable perceptual change. Both of these facts are consistent with the idea that motor learning, but not repeated experience with the speech stimuli, is the source of the perceptual change.

Influences of somatosensory input on auditory perception have been documented previously. There is somatosensory input to the cochlear nucleus, and there are known bidirectional interactions between auditory and somatosensory

cortex (Foxye et al., 2002; Fu et al., 2003; Jousmäki and Hari, 1998; Kayser et al., 2005; Murray et al., 2005; Schürmann et al., 2006; Shore and Zhou, 2006). In addition, there are reports that somatosensory inputs affect auditory perceptual function in cases involving speech (Gillmeister and Eimer, 2007; Ito et al., 2009; Schürmann et al., 2004). The present example of somatosensory–auditory interaction is intriguing because subjects receive somatosensory input when producing speech but not when perceiving speech sounds produced by others. Indeed, the involvement of somatosensory information in the perceptual processing of speech would be consistent with the idea that speech perception is mediated by the mechanisms of speech production (Hickok and Poeppel, 2000; Libermann and Mattingly, 1985). This view is supported by other studies demonstrating that electromyographic responses evoked by transcranial magnetic stimulation (TMS) to primary motor cortex are facilitated by watching speech movements and listening to speech sounds (Fadiga et al., 2002; Watkins et al., 2003), and that speech perception is affected by repetitive TMS to premotor cortex (Meister et al., 2007). However, the perceptual effects described here may well occur differently, resulting from the direct effects of somatosensory input on auditory cortex (Hackett et al., 2007).

In summary, in both of the studies described above, we have found that motor learning leads to changes in perceptual function. In both cases, the perceptual change was grounded in motor learning; sensory experience on its own was not sufficient for changes in perception. These findings suggest that plasticity in sensory and motor systems is linked, and that changes in each system may not occur in isolation.

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