

Review

Sensory Plasticity in Human Motor Learning

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There is accumulating evidence from behavioral, neurophysiological, and neuroimaging studies that the acquisition of motor skills involves both perceptual and motor learning. Perceptual learning alters movements, motor learning, and motor networks of the brain. Motor learning changes perceptual function and the sensory circuits of the brain. Here, we review studies of both human limb movement and speech that indicate that plasticity in sensory and motor systems is reciprocally linked. Taken together, this points to an approach to motor learning in which perceptual learning and sensory plasticity have a fundamental role.

Perceptual Change and Human Motor Learning

There has been recent interest in the idea that perceptual and motor learning do not occur in isolation but rather that motor learning changes sensory systems and sensory networks in the brain and, likewise, that perceptual learning changes movements and the motor areas of the brain. In this review, we present evidence in support of both of these ideas, drawing on examples from human arm movement and speech motor learning. We suggest that perceptual learning is an integral part of motor learning and contributes in several ways. Perceptual learning results in changes to motor networks in the brain and, in this way, participates directly in motor learning. Perceptual learning is also associated with plasticity in sensory systems that is dependent on both afferent inputs from the periphery and on corticocortical projections from motor areas. We propose that perceptual learning, and associated changes to sensory systems, have a fundamental role in human motor learning and that, in this context, the two generally occur together.

Neuroanatomical Basis for Reciprocal Plasticity in Sensory and Motor Networks

The efferent and afferent pathways linking the spinal cord with sensorimotor cortex and cerebellum are well known (reviewed in [1–3]). There are also extensive neuroanatomical connections between cortical motor and somatosensory areas that could drive plasticity in either direction, on the basis of use or experience. The connections extend from those between primary motor and somatosensory cortices to more distant connections linking premotor and prefrontal cortex with second somatosensory (SII) and parietal cortex (Table 1).

Somatosensory receptive fields are present in primary motor cortex and dorsal and ventral premotor cortices [4,5] and there are both visual and auditory receptive fields in ventral premotor cortex [6,7]. Neurons in ventral premotor cortex, SMA, and even ventrolateral prefrontal cortex are involved in perceptual decision-making [8,9]. Accordingly, one would expect that plasticity in the frontal motor networks should occur in conjunction with sensory processing, in particular, from the extended and systematic nature of inputs related to perceptual learning.

Motor Learning Results in Changes to Sensory Function

In work on human arm movement, both somatosensory and visual perceptual changes have been observed to accompany sensorimotor adaptation (Box 1). The changes are obtained in the

Trends

Sensorimotor adaptation results in changes to sensory systems and sensory networks in the brain.

Perceptual learning modifies sensory systems and directly alters the motor networks of the brain.

Perceptual changes associated with sensorimotor adaptation are durable and occur in parallel with motor learning.

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Table 1. Anatomical Connections between Somatosensory Cortex and Frontal Motor Areas^a

	Source/Origin	Target	Refs
Core sensorimotor network	Frontal motor areas:	Somatosensory cortex:	
	M1	1	[68]
	M1, PMC	2	[69]
	SMA, CMA	3a	[70]
	PMC	PV	[71]
	M1, SMA	3a (marmosets)	[72]
	M1	3b (squirrel monkeys)	[73]
	Somatosensory cortex:	Frontal motor areas:	
	1, 2, 3a, 5	M1	[70,74]
	1	M1, SMA	[75]
	2	SMA, PMC	[75]
	3a, 3b, 1, 2, SII, PV	M1 (squirrel monkeys)	[76]
	3a, 1, 2, SII, PV, 5	PMV (owl monkeys)	[77]
Extended network	Parietal cortex:	Frontal cortex:	
	PF, PFG, SII	PMV, 46v	[78,79]
	PE	PMD, SMA	[80]

^aAbbreviations: CMA, cingulate motor area; M1, primary motor cortex; PMC, premotor cortex; PF, PFG, SII, second somatosensory cortex; PE, PMV, ventral premotor cortex; PMD, dorsal premotor cortex; SMA, supplementary motor area; Data are for macaques unless otherwise indicated.

context of **force-field learning** (see [Glossary](#)) [10–13], **visuomotor adaptation** [14–16], and **prismatic adaptation** [17–22]. In each, there are systematic shifts in the somatosensory **perceptual boundary** (the felt position of the limb) and these occur over the same time period as adaptation [13]. There are also changes in visual motion processing in relation to force-field learning and prism adaptation [20–23] and changes to auditory localization following visuomotor adaptation [24]. The magnitude of the perceptual change ranges from approximately 20% to as much as 50% of the observed change in movement associated with adaptation. This is true even for force-field learning if average rather than maximum movement deviation is used as a behavioral measure of learning. The somatosensory shifts are in the direction of the perturbation. Thus, if the limb is deflected to the right, the sensed position of the limb likewise shifts rightward.

The perceptual change that occurs in conjunction with adaptation is durable. In studies to date, the magnitude of perceptual change is little altered in the period from immediately following training to 24 h later [11,25]. In work with prisms, it was shown that initial changes in sensed limb position initially decreased and then recovered and were present up to 7 days later [26]. The other notable features are that subjects that showed greater motor adaptation likewise showed greater perceptual change [11] and, similarly, larger experimental perturbations resulted in larger perceptual changes [27].

The perceptual alteration that is observed in these studies is primarily in the perceptual boundary rather than in **perceptual acuity**. In functional terms, the perceptual boundary shift seems to be central to the phenomenon. For example, in visuomotor adaptation, the altered visual input creates a sensory mismatch between visual and somatosensory information. The resulting somatosensory perceptual shift is in the direction of the external perturbation and would seem to be required to keep the senses in register. This same notion has been advanced to explain both

Glossary

Adaptation to altered auditory feedback: participants read words aloud that are presented on a computer screen. The acoustical speech signal is altered in real time and played back to the participant through headphones. As in other adaptation procedures, participants learn to shift their vocal output in a direction opposite to the applied acoustical shift. As in visuomotor adaptation, participants tolerate proprioceptive error, in this case, to have their speech sound correct.

Force-field learning: predictable mechanical loads are applied to the arm during movement or to the jaw in speech, in both cases typically using a robotic device. The perturbations initially alter the movement path, which gradually returns to normal as subjects learn to counteract the load. A negative after-effect (movement in the opposite direction) occurs when the perturbation is removed. The after-effect provides a measure of the compensation learned by subjects to produce straight movement in the presence of load.

Perceptual acuity: perceptual classification data are used to estimate acuity, using a measure of the slope of the psychometric function about its midpoint.

Perceptual boundary: in these studies, subjects typically make binary judgments to classify perceptual stimuli. For somatosensory judgments, limb position is systematically varied. For auditory judgments, participants classify sounds. In vision, the stimulus position is varied. The set of actual positions and participant's judgments are fit with psychometric function. The 50% point serves as an estimate of the perceptual boundary.

Prismatic adaptation: the earliest motor adaptation studies were done using prisms. Prisms shift the entire visual scene rather than just a single point (as in visuomotor adaptation). The compensatory pattern is similar to that in visuomotor adaptation. Prism adaptation is associated with both visual and proprioceptive perceptual change.

Visuomotor adaptation: predictable displacements of a visual target are applied during reaching movement, typically by changing the mapping between the position of the hand and

Box 1. Motor Learning and Sensorimotor Adaptation

The studies reviewed here primarily involve adaptation to experimentally imposed perturbations. The main examples come from the literature on force-field learning, which involves the introduction of novel force loads, visuomotor, and prism adaptation in which the correspondence between vision and proprioception is manipulated and adaptation to altered auditory feedback in speech. The subject is required to move to a target, perturbations are delivered, and the resulting movement error is corrected by changes to motor commands. Although termed 'adaptation', these manipulations typically result in changes to behaviors and brain networks that are normally associated with learning. Adaptation is generally distinguished from motor learning in that adaptation is associated with corrections that occur when perturbations are delivered to well-learned motor behaviors. The corrections or compensation bring the behavior back towards its unperturbed form. By contrast, learning is not dependent on perturbation and results in persistent changes to brain and behavior. The studies reviewed here have many of the features of learning. The correction, similar to the original learning, is often incomplete and the changes to movement are durable in the sense that, when subjects are retested after considerable delay, there are substantial savings, both in the rate of re-adaptation and in changes to perceptual systems. Moreover, adaptation results in changes to both motor and sensory networks of the brain, a finding that would not be expected if adaptation acted simply to return the system to its unperturbed state.

the position of a cursor on a display screen. The pattern during adaptation is similar to that seen in force-field learning, namely, an initial error in the direction of the perturbation is gradually corrected over a series of subsequent movements. A negative after-effect follows the removal of the perturbation. In visuomotor adaptation, participants tolerate proprioceptive error so that movements appear visually correct.

somatosensory and visual changes in prism adaptation, although, in this case, the visual and proprioceptive shifts are in opposite directions ([17–19]; reviewed in [28]). It is noteworthy that, in force-field adaptation studies, which are normally conducted without introducing a mismatch between visual feedback and limb position, adaptation is nevertheless accompanied by systematic changes to somatosensory function and somatosensory brain areas.

There have been two recent studies in which perceptual acuity rather than the perceptual boundary was found to change with learning. These are notable because neither is an adaptation study. In one report [29], subjects learned to make movements in a restricted part of the workspace. This resulted in changes in proprioceptive acuity that were spatially localized. Improvements in somatosensory acuity were likewise observed when movement training was paired with reinforcement [30].

Several studies have presented data that speak to the robustness of the perceptual adaptation result. In particular, in visuomotor adaptation, the perceptual change is observed regardless of whether visual feedback of the hand is rotated or translated [15]. It likewise occurs and is approximately similar in magnitude when perceptual testing involves either active or passive movement. Finally, it occurs regardless of whether the perturbation is introduced abruptly [11,31] or gradually [15].

The pattern of generalization for perceptual change is similar to that observed for motor learning. Thus, for example, in recent work on visuomotor adaptation, there was no evidence of intermanual transfer of proprioceptive recalibration [32]. Limited interlimb generalization has been previously reported for force-field learning [33]. However, others have reported small amounts of interlimb transfer following force-field adaptation. In a more recent study, generalization of proprioceptive recalibration to positions nearer, but not further, than the training target was reported [34], which is likewise consistent with work on force-field learning [35].

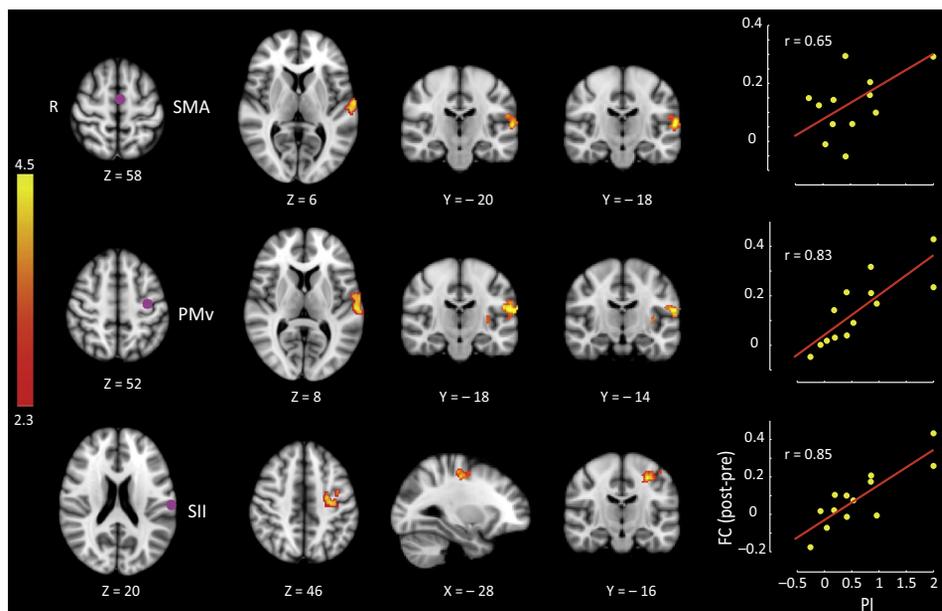
Perceptual shifts are similarly observed in association with speech motor **adaptation to altered auditory feedback** and altered somatosensory feedback. Auditory perceptual shifts have been reported following adaptation to altered vowel sounds [36]. It was shown that the perceptual change is related to the sounds that subjects have to produce to compensate for the acoustical perturbation rather than what the subjects hear as a perturbed utterance. Auditory perceptual change in speech is also observed in the context of adaptation to altered somatosensory feedback, even in cases where there is no measurable auditory perturbation [37]. In one further study of the effects of adaptation to altered auditory feedback on speech perception, auditory perturbation of consonant sounds resulted in a perceptual boundary shift in the identification of consonants that was in a direction opposite to the applied perturbation [38]. That is, if the

auditory perturbation made a consonant sequence sound more like 'sh' than 's', subjects were more likely, following adaptation, to classify subsequent sounds on this continuum as sounding 'sh'-like.

Motor Learning Results in Changes to Sensory Areas of the Brain

There is a range of electrophysiological evidence indicating that sensory processing changes with motor learning. Changes to activity in orofacial somatosensory cortex were observed in conjunction with orofacial motor learning [39]. In this study, monkeys were trained in a novel tongue protrusion task. Rapid and long-lasting changes to M1 and S1 were observed in parallel. In both cases, there were increases in the proportion of task-modulated neurons, and reductions across trials in firing rate variability. In humans, there are also electrophysiological data showing sensory change following learning. In particular, there are changes to somatosensory evoked potentials following force-field learning [40], following learning an arm muscle timing task [41] and a repetitive typing task [42].

There are likewise neuroimaging data showing changes in functional connectivity following force-field adaptation in networks related to both perceptual change and motor learning [12]. Changes in resting-state networks that are related to the perceptual changes that occur in conjunction with force-field adaptation can be seen in patterns of altered functional connectivity between second somatosensory cortex, supplementary motor area, and ventral premotor cortex (Figure 1). The results are noteworthy in that these same areas have been implicated in tasks involving the transient storage of somatosensory information and somatosensory decision-making [8,9]. Other examples of changes to sensory systems in conjunction with motor learning come from tasks involving sequence learning and from long-duration training tasks. In particular, daily practice of a sequential movement task involving



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Figure 1. Motor Learning Increases Functional Connectivity in Sensory Networks in the Brain. Each row shows a seed region (left) and those clusters of voxels whose correlation with the seed regions are strengthened in proportion to the perceptual change produced by motor learning (PI). The scatter plots show that subjects who show greater perceptual change (PI) likewise show greater changes in connectivity between each specific seed and the clusters shown to the right. It is seen that motor learning results in increases connectivity in proportion to perceptual change in a network comprising second somatosensory cortex (SII), ventral premotor cortex (PMV), and supplementary motor area (SMA).

the fingers and thumb of the left hand resulted in clusters of activity in postcentral gyrus and supramarginal gyrus that were related to learning [43]. Jugglers were found to have increases in gray matter in V5/MT following extended periods of practice [44,45] and musicians showed greater gray matter concentration in right planum temporale (auditory cortex) compared with nonmusicians [46]. A somewhat different pattern was seen in prism adaptation, where the main changes in activity during adaptation were in parietal multisensory areas and cerebellum [47].

Taken together, the studies summarized above indicate that motor adaptation involves concurrent and durable changes to motor, visual, and somatosensory systems. In neuroimaging studies, sensorimotor adaptation also results in changes in connectivity in sensory networks of the brain. In adaptation studies, the changes appear to keep sensory and motor systems in register, whereas more limited results from studies focused on skill acquisition suggest that, in some cases, improvements are focused on acuity rather than on alignment. We expect that future studies will reveal further instances of perceptual change in the context of motor learning, each matched to the specific role of the sensory system in the acquired motor behavior. While the relative contribution to sensory plasticity of corticocortical and afferent factors is unresolved, the evidence to date is consistent with the conclusion that perceptual learning and motor adaptation are part and parcel of human motor skill learning.

Source of Sensory Effects in Motor Learning: Are They Efferent or Afferent?

What causes sensory change during motor learning? Is it due to motor outflow, sensory inflow, or the two in combination? There is an extensive literature documenting sensory plasticity produced by manipulating afferent input alone. For example, there is reorganization of somatosensory cortex following digit amputation in raccoons and monkeys [48,49] and following peripheral nerve stimulation in adult cats [50]. There are changes to primary auditory cortex following frequency discrimination training in adult monkeys [51], and human cortical plasticity in primary and second somatosensory cortex has been shown using fMRI following somatosensory stimulation applied passively to the fingertip [41].

There is also evidence that plasticity in the sensorimotor network arises from corticocortical connections. Evidence in sensory systems was obtained in work on crossmodal plasticity in which the loss of input to one sensory modality resulted in cortical reorganization in other sensory systems. For example, in response to somatosensory stimulation, individuals with early loss of vision showed significant activation in early visual areas that was not seen when the same stimulation was applied in sighted control subjects [52]. Concordantly, stimulation of visual cortex in early blind subjects using TMS disrupted tactile perception, but this disruption did not occur in sighted controls [53]. In animal studies, crossmodal reorganization in the posterior auditory field of deaf cats resulted in enhanced visual localization of peripheral stimuli [54]. Evidence for plasticity induced in motor areas was reported in recent studies in which mice learned to discriminate textures using facial whiskers. It was found that the fraction of whisker touch-activated neurons in M1, which receive projections from S1 neurons, increased over the course of training and the increase persisted during post-training recordings [55].

In studies that have attempted to distinguish sensory changes associated with motor learning that are due to afferent input, from changes related to the efferent outflow, the results are mixed. In one study, the magnitude of perceptual recalibration and motor adaptation was similar when the hand was moved passively during the training phase, rather than actively [56]. However, in another, no perceptual change was observed following passive control experiments in which limb kinematics were matched to those that occurred during learning, but in the absence of voluntary movement [11]. In experiments on speech motor learning, it appears that sensory change is dominated by motor outflow. Specifically, perceptual change was associated with the

sounds the subject produced rather than what the subject heard during adaptation to altered auditory feedback [36].

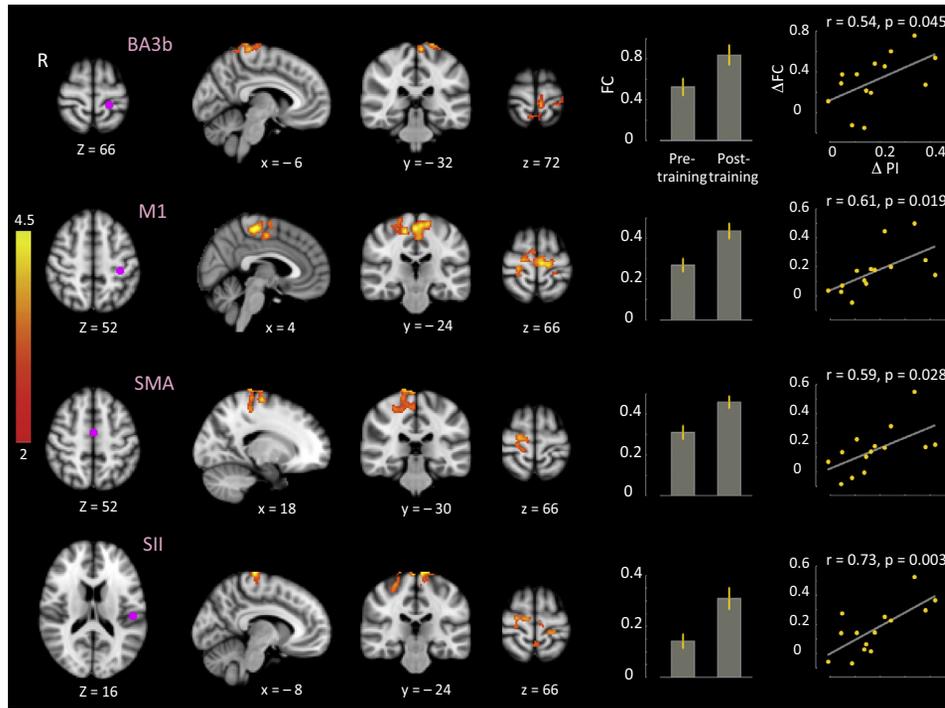
One potential account of sensory change that occurs in conjunction with learning is that it is a by-product of efference copy during voluntary movement. This is certainly a possibility. Somatosensory evoked potentials (SEPs) are reduced in conjunction with finger and limb movement [57–59]. However, these changes are transient and occur on a timescale that is much shorter than the sensory and perceptual changes observed in association with motor learning. Similarly, an SEP reduction occurs early in visuomotor learning but dissipates quickly, such that SEPs are back to baseline levels well before the end of training [60]. Efference copy might well contribute to perceptual changes in the early stages of learning, but sensory and perceptual change persists long after the end of any ongoing motor signals (and associated efference copy).

Several lines of evidence suggest that somatosensory change is not an epiphenomenon but is tied to the motor system. Circumstantial evidence is that movements follow new perceptual boundaries [11]. A more direct test involves manipulating the somatosensory system (e.g., the auditory system in speech) and observing systematic changes in motor behaviour and learning (as in [61–63]). In studies of force-field and visuomotor adaptation, and in adaptation to altered auditory feedback during speech, correlations were often observed between the magnitude of adaptation and the associated perceptual change [11,15]. In other studies, while changes were observed in both sensory and motor function, there was no indication that the magnitudes of adaptation were correlated [27,36]. It has been suggested that the latter constitutes evidence that the adaptation processes involved are independent, although they occur simultaneously [27].

Perceptual Learning Changes Movement and the Motor Areas of the Brain

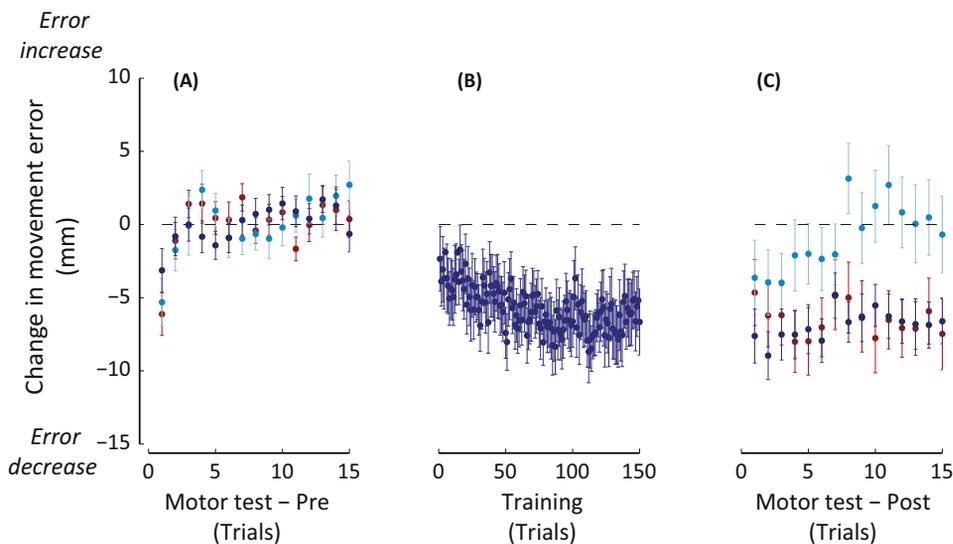
The preceding sections focused on the idea that motor learning drives sensory plasticity and changes perceptual systems. In this section, we consider evidence that the relation is reciprocal, that is, perceptual learning produces changes in motor function and motor areas of the brain. Indeed, perceptual learning, particularly in the somatosensory system, may well have an essential role in motor learning, particularly in the initial stages of learning, when the somatosensory targets of movement are frequently unknown. In situations such as learning the feel of a good tennis serve or learning to speak a foreign language, perceptual and motor learning occur together. Studies that have attempted to separate perceptual from motor learning provide the possibility of better assessing the relative balance of these factors in the broader undertaking of motor learning.

There is a substantial literature documenting benefits to movement that originate in sensory systems. The focus of much of this work is on plasticity in sensory systems, which is due to stimulation or sensory loss and subsequent changes to movement that occur as a result (reviewed in [64]). There is also evidence involving human limb movement showing that somatosensory training acts directly on the motor system and improves motor learning, increases motor cortex excitability [as reflected in changes to motor evoked potentials (MEPs)], and increases activity in frontal motor areas during passive movement. Thus, for example, it has been shown that passive limb movement paired with visual input improved the learning of complex hand trajectories [29]. It has also been shown that perceptual training involving somatosensory discrimination with feedback resulted in changes to motor learning in a task requiring rapid thumb abduction and changes to MEPs in vibrated hand muscles [65]. Similarly, passive wrist movement over a 28-day period resulted in increases in activity in primary motor cortex and supplementary motor area in response to passive movement conducted in the MRI scanner [66]. Finally, it has been demonstrated that proprioceptive stimulation resulting from passive movement of the wrist led to increases in the evoked response to a constant cortical stimulus produced using TMS [67].



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Figure 2. Somatosensory Perceptual Learning Strengthens Functional Connectivity in Motor Networks in the Brain. It is seen that perceptual learning results in changes in connectivity that strengthens networks in primary motor cortex (M1), primary somatosensory cortex (S1), supplementary motor area (SMA), and dorsal premotor cortex. Layout as in Figure 1.



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Figure 3. Passive Movement Paired with Reinforcement (Red Circles) Results in Improvements in Movement Following Training as Great as Those Obtained for Subjects who Train with Active Movement and Receive the Same Reinforcement (Dark-Blue Circles). The benefits of passive movement without reinforcement (light-blue circles) are transient. (A) Baseline movements in the absence of feedback. The broken line shows baseline performance before training. (B) Training movements produced by subjects in the active reinforcement condition. Subjects in the other two groups experience the same movements passively (produced under position servocontrol by a robot arm). (C) Movements following training, also in the absence of feedback or vision of the arm.

When passive somatosensory training is paired with reinforcement, changes are observed in perceptual function, movement, and in motor networks of the brain. In these studies, participants hold the handle of a robot that moves the arm along one of several trajectories. The participant is required to indicate the direction of limb displacement. Binary feedback regarding the accuracy of judgment is provided. Perceptual training conducted in this fashion results in improvements in perceptual acuity and to changes in judgments regarding the position of the limb. It also produces improvements in the rate and extent of subsequent force-field adaptation, which persist for at least a day [61]. This same perceptual training procedure, involving passive movement paired with reinforcement, alters functional connectivity in both sensory and motor networks of the brain. Reliable changes in connectivity related to perceptual learning are observed in the links between supplementary motor area (SMA) and M1, dorsal premotor cortex (PMd) and cerebellar cortex, and also bilaterally in M1 [62] (Figure 2).

Recent work using a similar procedure [30] (Figure 3) suggests that somatosensory inputs drive the initial stages of human motor learning. In these studies, participants make movements to uncertain target locations in the absence of either visual feedback or vision of the limb. When a movement successfully lands within an unseen target zone, binary reinforcement is provided. Subjects who trained using active movement showed improvements to movement accuracy that persisted for at least 1 week. Participants in a matched passive condition that had their arm moved along the same trajectories and received the same reinforcement as subjects in the active movement condition, showed just as great a benefit to subsequent movement as subjects that trained actively, and, similar to active subjects, the benefits persisted at the 1-week retest. Participants that experienced the same passive movements, but in the absence of feedback or reinforcement, showed little benefit from the perceptual training.

Concluding Remarks

Changes to both sensory and motor systems are observed in the context of sensorimotor adaptation and motor skill acquisition. Perceptual changes occur in each of the widely studied motor adaptation tasks: (force-field learning, visuomotor, and prism adaptation) and they also occur in adaptation to altered auditory feedback in speech. Perceptual change occurs concurrently with motor adaptation, it is durable and is often correlated in magnitude with behavioral measures of motor adaptation. In neuroimaging studies, changes to sensory networks in the brain are seen in conjunction with sensorimotor adaptation. When perceptual learning is directly manipulated, it results in systematic changes to motor adaptation and also alters motor networks of the brain. Indeed, in some cases, skill acquisition is substantially driven by somatosensory inflow. These observations are consistent with the idea that perceptual learning and sensory plasticity are fundamental to sensorimotor adaptation and motor skill acquisition. If we are to improve models of skill acquisition or develop new therapeutic interventions, we need a better understanding of how skill acquisition is determined by plasticity in both sensory and motor systems (see Outstanding Questions).

Acknowledgments

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Outstanding Questions

What is the balance between motor and sensory learning in human motor skill acquisition? Changes to sensory networks are observed in adaptation tasks, but this may underestimate the role of sensory plasticity in motor skill acquisition. Adaptation tasks involve well-defined sensory targets and well-learned sensorimotor maps. Somatosensory factors seem to have a larger role early in learning when sensory targets are unknown [30].

What causes sensory change during motor learning? Is it due to motor outflow, sensory inflow, or the two in combination? Existing studies point to effects in both directions. Attempts to directly address this question in the same study have been equivocal.

What is the relation between the sensory changes that are observed in adaptation studies and demonstrations that perceptual learning changes motor networks in the brain? The question is whether these demonstrations reflect two sides of the same coin or simply different phenomena.

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