Trends in Neurosciences

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.

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.

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

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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]

[a] Abbreviations: 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