

## Shared internal models between feedforward and feedback control

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An influential idea in sensorimotor neuroscience is that the nervous system relies on a set of internal predictions (i.e., an internal model) to generate feedforward (i.e., voluntary) motor commands that account for delayed and noisy sensory feedback, and that can adapt to new altered environments.<sup>1</sup> This idea has recently been extended to a class of rapid feedback responses (i.e., long-latency stretch reflexes) that are partially mediated by neural structures that contribute to voluntary motor control, and which have to deal with the same factors.<sup>2,3</sup> In this current opinion article, we present some evidence that feedforward motor commands and these fast feedback responses share an internal model for motor control.

A classic method to study internal models during upper-limb movements involves having participants reach towards visually presented targets in the presence of an external force field. In the absence of the force field, participants easily perform straight movements to a target. However, upon the introduction of the force field, movements are initially deviated, as participants try to perform the same straight reach to the target. Participants gradually learn the dynamics of the novel force environment and return to straight reaches by modifying their motor commands predictively to compensate for the force field.<sup>1</sup> A similar approach has been used to test whether such learning also influences fast feedback responses to mechanical perturbations applied to the arm. After learning, when a perturbation is delivered just prior to entering the force field, fast feedback responses are increased, similar to the increase observed in muscle activity after learning to reach in the force field.<sup>4</sup> These results support the notion that motor learning during reaching transfers to feedback responses.

We recently took another approach to this question by leveraging intersegmental arm dynamics. Specifically, the fact that torques applied at one joint produces movement at multiple joints.<sup>3</sup> Previous work has demonstrated that when generating single-joint elbow movements and when responding to mechanical perturbations that create pure elbow motion with a robotic exoskeleton, the nervous system makes use of an internal model of the arm's dynamics. This allows generating predictive shoulder muscle activity and robust shoulder feedback responses to counter the underlying torques that arise at the shoulder

joint because of forearm rotation about the elbow joint.<sup>2,3</sup> One way of determining how the nervous system accounts for arm dynamics is by altering the normal mapping between joint torques and joint motion. When we did this experiment, we found that generating pure elbow movements with the shoulder joint fixed (i.e., altered arm dynamics) causes people to reduce shoulder muscle activity during reaching and that such learning transfers to feedback responses, even though these feedback responses were never directly trained.<sup>5</sup> This learning and transfer are appropriate and efficient because fixing the shoulder joint eliminates the interaction torques that arise at the shoulder when the forearm rotates and thus removes the need to recruit shoulder muscles. Such transfer from feedforward motor commands to feedback responses is thought to take place because of their shared neural circuits at the level of the spinal cord, brainstem, and cortex.<sup>6</sup>

The presence of shared neural resources also predicts the transfer from feedback responses to feedforward motor commands. To answer this question, we used two approaches to elicit learning in feedback responses without engaging associated voluntary responses following perturbations: 1) we applied very short mechanical perturbations and 2) we instructed participants to not respond to them in the course of learning shoulder fixation.<sup>7</sup> We found that fixing the shoulder joint leads to a reduction in shoulder feedback responses (i.e., learning arm dynamics) with a minimal engagement of voluntary motor responses in the learning process. Moreover, we found that this reduction in feedback responses transfers to feedforward motor commands during elbow reaching, even though participants never practiced reaching with the shoulder fixed. These results support the notion of a bidirectional transfer of motor learning between feedforward and feedback control.

An important avenue of future research is determining the extent of such bidirectional motor learning and transfer between feedforward and feedback control at the behavioral and neurophysiological levels. At the behavioral level, it is important to find out whether the nervous system shares internal models for a range of motor tasks or whether the shared internal models are restricted to some specific situations, such as after learning altered force-fields or visuomotor environments. At the neurophysiological level, there are neural nodes that are particularly engaged during both feedforward generation of motor commands and feedback responses.<sup>8,9</sup> Future work should focus on examining neural activity in these nodes, as a means of determining which of them provides the neural substrate for shared internal models.<sup>10</sup>

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