Journal Club

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Correcting and Adapting

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Review of Lee and van Donkelaar (<http://www.jneurosci.org/cgi/content/full/26/12/3330>)

Successful movement and interaction with our dynamic environment requires the ability to update motor plans based on our sensory input. However, feedback requires time and, as such, can play only a very limited role during rapid actions. Wolpert et al. (1995) demonstrated that to accommodate such situations, we maintain a representation of the expected sensory consequences of an ongoing action, and compare it with the actual outcome. Differences between observed and expected states lead to updated representations of the necessary action(s) to accomplish a desired outcome. This adaptable system is referred to as an “internal model,” and can be updated on a trial-by-trial basis. These models can accommodate changes both in our environment (e.g., displaced visual feedback) and within our motor system (e.g., muscle fatigue).

The neural regions where internal models are maintained and updated is an open question. In their recent report, Lee and van Donkelaar (2006) provide evidence that the human dorsal premotor cortex (PMd) plays a critical role in on-line correction and sensorimotor adaptation. They used prism adaptation to disrupt sensorimotor feedback, and measured pointing performance during preadaptation, training, and postadaptation periods. The preadaptation and postadaptation

phases included tests of visual adaptation (indicating when a moving visual target appeared “straight ahead”), proprioceptive adaptation (pointing “straight ahead” without visual feedback), and sensorimotor adaptation (pointing to a visual target without visual feedback). During the training phase, participants were asked to point to a visible target using visual feedback which, when present, was laterally displaced by the prisms 17°. Furthermore, in separate training sessions, they applied single-pulse transcranial magnetic stimulation (TMS) to the PMd either at the onset or termination of the movement.

Lee and van Donkelaar (2006) report that TMS at the onset of a movement disrupted both on-line error corrections and sensorimotor adaptation, whereas a pulse at termination had no effect [Lee and van Donkelaar, their Fig. 1B (<http://www.jneurosci.org/cgi/content/full/26/12/3330/FIG1>)]. Comparison of preadaptation and postadaptation performance on specialized tests revealed that sensorimotor adaptation could not be attributed to a remapping of the visuospatial environment, but rather, was attributable to adaptation of proprioceptive information [Lee and van Donkelaar, their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/26/12/3330/FIG2>)]. This onset-specific TMS effect was only observed when visual feedback was provided throughout the execution of a pointing movement to a visually presented target [Lee and van Donkelaar, their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/26/12/3330/FIG4>)]. Thus, on-line error correc-

tion signal of the PMd was critical to adaptation.

The PMd could have a direct or indirect role in adaptation: indirectly via its necessity for the on-line corrections that are required for sensorimotor adaptation, or directly by subserving both adaptation and correction.

A direct role for the PMd in sensorimotor adaptation is certainly plausible, but additional testing is necessary to determine the relative contribution of other regions. For example, interactions between PMd and the cerebellum may be critical to sensorimotor adaptation because trial-by-trial adaptation requires cerebellar processing (Martin et al., 1996). The results reported by Lee and van Donkelaar (2006) could reflect disrupted implementation or translation of critical cerebellar contributions to sensorimotor adaptation. If PMd played a direct role in sensorimotor adaptation, TMS should have impaired adaptation in the terminal vision condition, which best approximates the task used previously by Martin et al. (1996). This leaves open the possibility that the cerebellum is also critical to sensorimotor adaptation, and that PMd is only indirectly influencing this process when on-line visual information is available. In combination, these alternatives bring into question the generator role Lee and van Donkelaar (2006) assign to PMd.

Although Lee and van Donkelaar's (2006) experiments demonstrate a role for PMd in on-line visually based error correction for sensorimotor adaptation, sufficiency of its role is unclear because they did not apply TMS to other candidate

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regions. TMS to other neural regions might similarly alter on-line corrections for adaptation. Specifically, the cerebellum and anterior regions of the parietal lobe are known to play a critical role in on-line error corrections (Diedrichsen et al., 2005), and both project to PMd. Some evidence for the roles of these areas in on-line error correction comes from reports of impairments in individuals with cerebellar damage (Morton and Bastian, 2004) and in those undergoing TMS to the parietal cortex (Desmurget et al., 1999). Although Diedrichsen et al. (2005) did not specifically address the necessity of the anterior parietal cortex and the cerebellum in the generation of error signals before movement termination, they clearly demonstrated these regions play a critical role in error signal processing and adaptation. Using the methodological approach of Lee and van Donkelaar (2006), but including the applications of TMS to the regions of activation observed by Diedrichsen et al. (2005), could address whether PMd is sufficient for (i.e., the generator of) on-line error signals and its critical role in adaptation.

Lee and van Donkelaar (2006) propose

that PMd does not play a critical role in visual adaptation. However, no manipulation produced a measurable change in visual adaptation. Before arguing that PMd does not play a role in visual adaptation, validation of the visual adaptation measure is therefore warranted. If TMS to other areas involved in sensorimotor, visuomotor, or even visual attention caused visual adaptation to be disrupted, the test would be validated as an adequate measure of perceptual performance. Validation of the visual adaptation measure would exclude the possibility that PMd stimulation might impair visual adaptation. One could then make stronger inferences about necessary or sufficient regions for on-line correction generation or sensorimotor adaptation. Should TMS reveal similar performance disruption across multiple regions, exploring the timing of TMS relative to the onset of movement could elucidate which region serves as an error-correction signal generator. At present, it is difficult to dissociate the role of PMd from that of the cerebellum or regions of the parietal lobe in the generation or implementation of error-correction signals, and the influence of these signals on senso-

rimotor adaptation. Lee and van Donkelaar (2006) have nonetheless provided an important and compelling step in demonstrating the participation of PMd in the neural network underlying these mechanisms.

References

- Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST (1999) Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci* 2:563–567.
- Diedrichsen J, Hashambhoy Y, Rane T, Shadmehr R (2005) Neural correlates of reach errors. *J Neurosci* 25:9919–9931.
- Lee JH, van Donkelaar P (2006) The human dorsal premotor cortex generates on-line error corrections during sensorimotor adaptation. *J Neurosci* 26:3330–3334.
- Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT (1996) Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* 119:1183–1198.
- Morton SM, Bastian AJ (2004) Prism adaptation during walking generalizes to reaching and requires the cerebellum. *J Neurophysiol* 92:2497–2509.
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880–1882.