Journal Club

Editor's Note: These short reviews of a recent paper in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to mimic the journal clubs that exist in your own departments or institutions. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Different Roles of PMv and PMd during Object Lifting

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Review of Davare et al. (http://www.jneurosci.org/cgi/content/full/26/8/2260)

Introduction

The ventral premotor (PMv) and the dorsal premotor (PMd) areas are well placed to influence movements required for object lifting (Fig. 1). In the macaque monkey, these areas connect strongly with the hand area of primary motor cortex and project fibers directly to the spinal cord (Dum and Strick, 1991). PMv and the anterior intraparietal cortex transform the representation of the geometrical properties of an object to the motor commands required for grasping (Rizzolatti and Luppino, 2001). PMd receives information for the visual guidance of arm movement trajectories required to reach for an object (Rizzolatti et al., 1998) and also selects motor programs based on learned associations (Wise and Murray, 2000; Chouinard and Paus, 2006). Guiding the arm toward an object and the shaping of the hand for grasping are not enough to ensure proper manipulation of objects. To lift objects successfully, people must also apply forces that match their expected weight (Johansson and Westling, 1984).

In a recent study published in *The Journal of Neuroscience*, Davare et al. (2006) used transcranial magnetic stimulation (TMS) to examine further the role of PMv and PMd in the control of hand movements and in generating forces applied during object lifting, which the authors refer as the grip–lift task [Davare et al. (2006), their Fig. 1 (http://www.jneurosci.org/cgi/content/full/26/8/2260/F1)]. In one set of experiments, the authors applied trains of high-frequency repetitive TMS to disrupt neural processing in PMv or PMd in both hemispheres [Davare et al. (2006), their Fig. 2 (http://www.jneurosci.org/cgi/content/full/26/8/2260/F2)]. The trains lasted for 500 ms and were applied at the onset of a GO signal that instructed subjects to use precision grip to lift a manipulandum with their dominant right hand. They then performed another set of experiments in which they applied double-pulse TMS over the left PMv or left PMd at different time points during a given trial. This enabled them to infer subsequently the temporal contribution of PMv and PMd. The authors used electromyography to determine when different proximal and distal arm muscles were recruited and force transducers to measure the accuracy of grasping as well as grip and load forces applied during lifting.

The authors demonstrate that 500 ms trains of repetitive TMS applied over the left or right PMv disrupted proper positioning of the fingers on the manipulated object (or manipulandum). Electromyography revealed that subjects took a longer time to position their hand [Davare et al. (2006), their Fig. 3*A*,*B* (http://www.jneurosci.org/cgi/content/full/26/8/2260/F3)], and measurements acquired with the force transducers revealed that subjects placed their index and thumb fingers less accurately on the manipulandum [Davare et al. (2006), their Fig. 4 (http://www.jneurosci.org/cgi/content/full/26/8/2260/F4)]. These results confirm previous studies in the monkey that reveal a role for PMv in the shaping of the hand. The same effects also occurred only when double-pulse TMS was applied ~200 ms before the fingers actually touched the manipulandum [Davare et al. (2006), their Fig. 5 (http://www.jneurosci.org/cgi/content/full/26/8/2260/F5)]. This finding coincides with early neuronal responses observed in PMv of the monkey when an object is displayed (Murata et al., 1997). Together, these results demonstrate that PMv transforms the representation of the geometrical properties of an object to the motor commands required for grasping.

The authors also demonstrate that 500 ms trains of repetitive TMS applied over the left PMd disrupted the generation of proximal arm movements required for lifting. Electromyography revealed that subjects took a longer time to move the arm during the lifting phase [Davare et al. (2006), their Fig. 3*C* (http://www.jneurosci.org/cgi/content/full/26/8/2260/F3)], and measurements acquired with the force transducers revealed a longer delay between the time subjects began to apply grip forces and the time when they began to apply load forces [Davare et al. (2006), their Fig. 3*D* (http://www.jneurosci.org/cgi/content/full/26/8/2260/F3)]. Double-pulse TMS revealed that PMd involvement during object lifting occurred ~100 ms after that of PMv [Davare et al. (2006), their Fig. 5*B* (http://www.jneurosci.org/cgi/content/full/26/8/2260/F5)]. Thus, the authors provide

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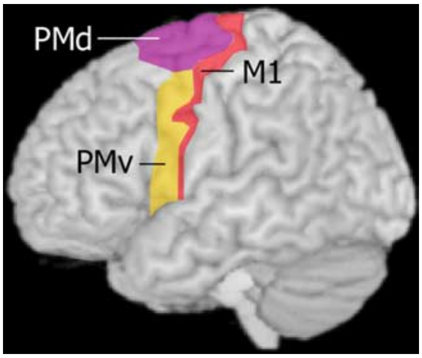

Figure 1. Areas PM and PMd of the human cerebral cortex. PMv encompasses the portion of the precentral gyrus that is ventral to the superior frontal sulcus, and PMd encompasses the portion of the precentral gyrus that is dorsal to the superior frontal sulcus as well as the posterior portion of the superior frontal gyrus on the lateral surface of the brain. Both areas are well placed to influence movements required for object lifting. In the macaque monkey, these areas connect strongly with the hand area of primary motor area (M1) and project fibers directly to the spinal cord.

compelling evidence for a dissociation between the role of PMv and PMd during object lifting in which PMv shapes the hand before lifting and PMd then initiates motor commands for lifting.

It is plausible that PMv and PMd fulfill their roles independently. Jackson and Shaw (2000) demonstrated that forces applied during object lifting change independently from the shaping of the hand. Why is this important? Take the case of two objects of the same size but different weights; for example, a phone book and a box of biscuits. The requirements to shape the hand for both objects are the same. Yet, people will apply greater forces for the heavier object such as the phone book compared with the lighter object such as the box of biscuits (Gordon et al., 1993). This is because we know from previous experience the relative weights of phone books and boxes of biscuits. In a different TMS study, Chouinard et al. (2005) demonstrated that PMd selects forces for object lifting based on previously learned associations between arbitrary color cues and a particular weight. This finding is consistent with the notion that PMd is critical for implementing associations between contextual cues and motor responses (Wise and Murray, 2000; Chouinard and Paus, 2006).

The study by Davare et al. (2006) constitutes the first use of TMS to identify movement parameters controlled by PMv during object lifting. Investigating the role of PMv using neuroimaging techniques has proven to be challenging. A number of neuroimaging studies have failed to demonstrate changes in PMv during object-related hand movements (for review, see Chouinard and Paus, 2006). In these studies, the lack of change in PMv might relate to the fact that PMv fulfills different roles in both object recognition and object manipulation. This in turn makes subtraction-based analyses commonly used in neuroimaging studies difficult to tease apart blood-oxygenation level-dependent or cerebral blood-flow responses related to the visual characteristics of objects and those related to their manipulation. In contrast, Davare et al. (2006) used TMS to more easily replicate primate studies implicating PMv in the shaping of the hand. More importantly, Davare et al. (2006) provide evidence for a dissociation between the role of PMv and PMd during object lifting in which PMv shapes the hand before lifting and PMd then initiates motor commands for lifting.

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