

## Preparing for Speed. Focus on “Preparatory Activity in Premotor and Motor Cortex Reflects the Speed of the Upcoming Reach”

Paul Cisek

Département de Physiologie, Université de Montréal, Montreal, Quebec, Canada

It is generally accepted that movements can be prepared before their execution, but what preparation entails is not precisely understood. Some computational models suggest that preparation involves the optimization of a “desired trajectory” that describes the movement in its entirety, prior to onset, and is then read-out during overt performance (e.g., Flash and Hogan 1985; Tanaka et al. 2006; Uno et al. 1989). At the other extreme, some models suggest that preparation only describes some simple aspects of the movement and that the details unfold on-line (e.g., Bullock and Grossberg 1988; Feldman 1974; Shadmehr and Wise 2005). In the context of these theoretical proposals, it is interesting to ask: what aspects of an intended movement can be prepared ahead of movement onset?

A large number of neurophysiological studies have addressed this question by examining the activity of cells in the reach system during an *instructed delay period*, between presentation of information specifying a reaching movement and the “go” signal instructing its onset. These studies have consistently found that neural activity during the delay period accurately predicts the intended direction of movement (Alexander and Crutcher 1990; Kalaska and Crammond 1995; Kurata 1993; Wise 1985). Delay-period activity has also been shown to correlate with movement extent (Fu et al. 1993; Messier and Kalaska 2000; Riehle and Requin 1989) as well as hand-path curvature (Hocherman and Wise 1991). Correlation with nonspatial aspects of the movement, however, has not often been reported. In particular, can the motor system preplan the speed of the upcoming movement?

In this issue of *Journal of Neurophysiology* (p. 3130–3146), Churchland, Santhanam, and Shenoy address this question directly through a simple and elegant experiment. In their study, monkeys were trained to make delayed “center-out” reaching movements with different directions and distances at either a slow speed or a fast speed, depending on a visual instruction. Importantly, the information about movement metrics and speed was provided 400–800 ms before the go signal, and it is activity during this delay period that is of most interest. Neural recordings were made in the caudal portion of the dorsal premotor cortex (PMd) and the rostral part of primary motor cortex (M1). These regions project to the spinal cord (He et al. 1993) and have long been implicated in preparation and execution of visually guided reaching movements (Wise 1985). In addition to the well-known directional tuning of delay period activity, 78% of cells showed some influence of movement distance, in agreement with previous studies (Fu et al. 1993; Messier and Kalaska 2000).

The main novel finding of this study is that neural activity in dorsal premotor and primary motor cortex, even during the

delay period, is also influenced by the instructed speed of the movement. Ninety-four percent of cells showed some influence of speed with 61% of them preferring fast movements and 39% preferring slow ones. This is not merely due to the natural tendency to move faster toward further targets because even for a given direction and extent of movement, the tonic firing rate during the delay period was influenced by instructed speed. The authors performed a number of careful analyses to show quite convincingly that speed sensitivity was not simply a consequence of distance sensitivity, movement trajectory, or oculomotor behavior.

As Churchland et al. point out, the presence of speed modulation does not imply that PMd and M1 explicitly encode speed per se. These cells may instead be sensitive to one or more of the many movement-related variables which co-vary with speed, such as movement duration, task difficulty, muscle force, interaction torques, expended effort, etc. This possibility is consistent with another very interesting finding reported by these authors: that the preferred direction (PD) of cells was not the same across the different speed conditions. Thirty-two percent of cells exhibited significant PD rotations between speed conditions, and the mean rotation across all cells was 39°. This is much larger than the 15° rotation expected on the basis of sampling error. In other words, the directional tuning function of PMd and M1 cells is not invariant across speed conditions.

One way to interpret this lack of tuning invariance is from the perspective of the different biomechanical demands of moving at different speeds. Even if the spatial trajectory is the same, at higher speeds interaction torques are more significant, deceleration requires more active braking, and the force produced by contracting muscles is reduced. One can therefore expect muscles to be recruited differently as speed increases, necessitating different patterns of descending control signals. Indeed, the PDs of muscles recorded by Churchland et al. also changed significantly across speed conditions, with a mean PD rotation of 65°. This suggests that the PD rotations exhibited by cortical cells may be taking these biomechanical factors into account so as to produce the proper balance of muscular contraction demanded by the given intended combination of direction, speed, and distance. In general, what appears as a varying directional tuning in the Euclidean space of the task may be invariant in some native coordinate system (e.g., joint torques) that takes biomechanics into account (Ajemian et al. 2000).

Nevertheless, there are some reasons to question whether such biomechanical concerns can fully explain what occurs in cortex during the delay period. Although sensitivity to dynam-

Address for reprint requests and other correspondence: P. Cisek, Ph.D., Dept. de Physiologie, Université de Montréal, C.P. 6128 Succursale Centre-ville, Montréal, QC, H3C 3J7 Canada (E-mail: paul.cisek@umontreal.ca).

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ics has been shown for neurons in the regions studied by Churchland et al. (Riehle et al. 1994; Xiao et al. 2006), even during a delay period, other studies have suggested that these neurons do not strongly care about the details of movement execution. For example, an important study by Shen and Alexander (1997a,b) found that the delay-period directional tuning functions of a large majority of cells in PMd and M1 were related to the motion of an on-screen cursor *regardless* of the arm movement required to produce that motion. Other studies have shown that PMd cells, at least during the delay period, are similarly tuned regardless of whether the movement is made with the contralateral or ipsilateral arm (Cisek et al. 2003; Hoshi and Tanji 2000). In other words, delay-period activity appears most concerned with the motion of a controlled object and not with the movement of the arm that controls it (Cisek 2005). But if that's the case, then why should these cells encode movement variables such as direction in a manner that changes with speed?

Perhaps part of the reason, suggest Churchland et al., is that "encoding" is not what these cells are doing. After all, the role of the motor system is to produce movement, not to describe it, and the patterns of neural activity which implement action may not necessarily be constrained to represent movement variables in any particular reference frame (Fetz 1992). With the large number of cells that exist in cortex, the motor system is incredibly redundant. To produce any given pattern of activities descending to the muscles one could use a nearly infinite number of patterns of neural activation. This means that individual cells do not have to explicitly encode the variables relevant for task success (be they direction, speed, etc.) as long as the population as a whole specifies those variables appropriately. Indeed, "intermediate" reference frames are commonly found throughout the mammalian cortex and may possess valuable computational properties (Pouget et al. 2002). The study of Churchland et al. shows that even in such a seemingly simple task as reaching at different speeds, the neural representations employed by the brain may not be as simple as we neuroscientists might wish.

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