Encoding in the Motor Cortex: Was Evarts Right After All? Focus on "Motor Cortex Neural Correlates of Output Kinematics and Kinetics During Isometric-Force and Arm-Reaching Tasks"

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Encoding in the Motor Cortex: Was Evarts Right After All? Focus on "Motor Cortex Neural Correlates of Output Kinematics and Kinetics During Isometric-Force and Arm-Reaching Tasks"

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The primary motor cortex is arguably the first cortical area to be functionally examined in the history of neuroscience. Beginning with the early electrical stimulation experiments by Fritsch and Hitzig (1960) in 1870 and then the first electrophysiological recordings in awake, behaving primates by Evarts in the 1960s (Evarts 1968), numerous experiments have been performed to try to understand what features of movement are encoded in the activity of motor cortical neurons. And yet, despite extensive experimental efforts recording and stimulating primarily from the arm area of motor cortex, it still remains controversial whether motor cortex encodes lower-level kinetic features such as the force/torque applied by the hand/joint (Cheney and Fetz 1980; Smith et al. 1975; Taira et al. 1996) or higher-level kinematic features such as position, velocity, and direction of the limb (Georgopoulos et al. 1982, 1984; Moran and Schwartz 1999; Paninski et al. 2004). Often using different behavioral paradigms, experimental data have supported both the "old" kinetic view as well as the "newer" kinematic view. In this issue of the *Journal of Neurophysiology* (p. 2353–2378), Sergio and colleagues present one of the first (if not the first) studies that directly compared motor cortical encoding under two very different behavioral conditions: an isometric force task and a movement task. By recording from single neurons in the *caudal* portion of motor cortex on the rostral bank of the central sulcus, the authors convincingly demonstrate the activity of this portion of motor cortex is sensitive to the kinetic aspects of movement under both tasks conditions.

In their study, the authors designed both isometric force and movement tasks such that they required comparable ranges of static and dynamic forces to be generated by the hand. In the isometric task, the monkey was required to move a cursor the position of which was directly related to the imposed isometric force of the hand from a center target to one of eight peripherally positioned targets. In the movement task, the monkey moved the cursor by moving the base of a relatively massive pendulum the position of which determined the cursor's position. Unlike the isometric force task, the motion of the cursor was directly related to the motion of the hand and only indirectly related to the forces imposed by the hand.

The most striking result of their study was that many single motor cortical neurons exhibited distinctly different temporal patterns of activity under the two behavioral tasks that reflected the kinetic differences of the force imposed by the hand. In the isometric task, neurons exhibited a large increase in tonic discharge beginning prior to force onset often with an initial phasic burst at the beginning of the tonic increase. This was evident in the neurons' preferred direction ($\text{PD}_{\text{isometric}}$) but not in the opposite direction in which the neurons exhibited a suppression of activity. In the "movement" task, however, the same neurons would often exhibit a triphasic pattern of activity reminiscent of similar activity patterns shown by muscles under certain movement conditions. In the neurons' preferred direction defined in the isometric task, they increased their activity phasically prior to the initial accelerative and force ramp-up phase followed by a decrease or pause in activity prior to the decelerative and force ramp-down phase. Finally, the neurons' again increased their activity once the cursor reached the target, and the hand force attained its final static level. In the opposite direction, the neurons often displayed a reciprocal pattern with a phasic increase prior to the decelerative and force ramp-down phase. This triphasic pattern of activity led to a dramatic change in the preferred direction ($\text{PD}_{\text{movement}}$) of the neurons. Prior to force onset as well as during the final target hold period, neurons' possessed a $\text{PD}_{\text{movement}}$ that closely matched $\text{PD}_{\text{isometric}}$. However, as the movement began and the decelerative phase of motion approached, the $\text{PD}_{\text{movement}}$ almost completely reversed its direction reflecting the phasic burst that occurred prior to the decelerative phase in the direction opposite to $\text{PD}_{\text{isometric}}$.

The second important result of this study was the vastly different neuronal population responses that occurred during the two behavioral conditions. By applying the population vector decoding method (Georgopoulos et al. 1986), the authors demonstrated that the population response reflected to a first approximation the forces imposed by the hand. Whereas in the isometric task the population vector pointed consistently in a direction close to that of the target, in the movement task, the population vector dynamically changed direction throughout the course of the movement to a particular target as did the hand force vector. On closer examination, however, the population vector exhibited systematic differences in its orientation with respect to the endpoint force direction. In the isometric force task, there was a bias in the population vector direction along the 0–180° axis for diagonally oriented targets. For certain target directions in the movement task, the population vector often dynamically shifted its direction in the opposite fashion from the dynamic shifts in hand force.

This study is significant because it provides strong evidence that motor cortical neurons in the rostral bank of the central sulcus are particularly sensitive to the kinetic features of the movement under two very different behavioral paradigms. However, the population analyses as well as some of the single-cell results clearly demonstrate that the patterns of motor cortical activity do not perfectly match the kinetics of movement. One possibility mentioned by the authors is that

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motor cortex may need to compensate for nonlinearities at the spinal motoneuron level as well as the low-pass filter characteristics of the muscles resulting in a nonlinear mapping between these neurons and the resulting forces at the hand. Nevertheless, this study seems to support the "older" view of motor cortical encoding that was first put forward by Evarts in the 1960s using single-joint movements but broadens its domain to include multijoint movements of the arm.

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