Population vectors and motor cortex: neural coding or epiphenomenon?

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A simple model suggests that activity in primary motor cortex may encode the activity of individual muscles and not higher-order features as previously suspected.

The primary motor cortex (M1) plays a pivotal role in controlling volitional movement, yet there is considerable debate as to how best to interpret neural activity in this brain region. The traditional approach, first introduced by Ed Evarts almost forty years ago, relates the activity of motor cortical neurons to variables such as movement or force at individual joints. A second approach, introduced by Apostolos Georgopoulos and colleagues in the early 1980s, is based mainly on studies in which monkeys make an arm movement to reach for a target; this approach relates M1 activity to the movement of the hand rather than of the individual joints (such as the shoulder and elbow) that contribute to the movement. Neurons in M1 are broadly tuned to the direction of hand movement[1], with each neuron having a preferred direction of movement for which its firing rate is maximal; Georgopoulos and colleagues showed[2] that a population vector constructed from the firing rates of many cortical neurons tends to point in the direction of the hand movement (see **Fig. 1** for theory). Subsequent work from various laboratories has used this hand-based framework to demonstrate impressive relationships between hand motion and neural activity, at both the single-cell and population levels.

These correlations have been interpreted as suggesting that the motor cortex controls higher-level features of hand movements, rather than the lower-level features related to the individual joints and muscles that bring about those movements. This interpretation has important implications not only for understanding M1 but also for the role of other parts of

the motor system that lie hierarchically above (dorsal premotor cortex) or below (spinal cord) the motor cortex. For example, if M1 represents hand movements using a population code, then the conversion of this relatively abstract representation into commands to the specific muscles would have to occur downstream, presumably in the spinal cord.

The article by Todorov[3] on page 391 of this issue challenges this view. The author's thesis—which seems certain to be controversial—is that many of the previously-described correlations between motor cortical activity and hand motion can be explained with a simple model in which the activity of cortical neurons encodes the activation of a group of muscles. This is not a radically new hypothesis to the field, nor is it a complete account of the motor cortex. The strength of Todorov's model, however, lies in its demonstration that so many observations from the previous literature can be accounted for by the complexity of the musculoskeletal system.

The relationship between arm muscle activity and hand motion is not trivial. Classical studies of muscle physiology have shown that the relationship between a muscle's activity (that is, the firing rate of its motor units) and its force output is strongly dependent on muscle velocity and length. Furthermore, the conversion of muscle force to hand motion depends on the geometry of the limb, its inertial properties and the presence of external loads. Todorov's model incorporates these various factors (albeit in a simplified form) in order to calculate the patterns of cortical activity that would be associated with various whole-limb motor tasks, assuming that cortical neurons encode muscle activation. One result of the model is that population vectors tend to point in the direction of movement, simply because of the balance that exists between

the various mechanical factors related to muscle and limb dynamics. The model also predicts that the direction of the population vector will no longer point in the direction of movement if one disturbs this natural balance. This prediction is supported by experiments[4] in which monkeys performed reaching movements while pulling against a mechanical load whose direction could vary. In this situation, the mechanical action of the load at the hand requires greater muscular torque (or muscle activity) at the joints when loads are applied in a lateral as compared to a sagittal direction. Todorov's model[3] predicts that population vectors will be skewed laterally under these conditions, and this is what was observed[4].

A more complex and surprising property of Todorov's model is its ability to account for differences in the relative timing of motor output and motor cortical
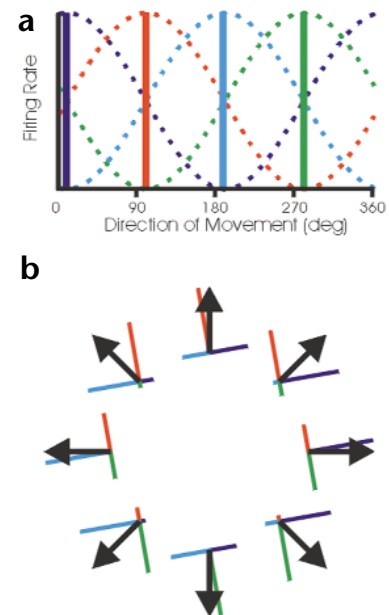
Fig. 1. The construction of a population vector from the firing rates of cells. (**a**) The activities of motor cortical neurons tend to be broadly tuned to the direction of movement (dashed lines). The solid vertical lines denote the preferred direction (PD) of each cell, the movement direction for which that cell is maximally active. (**b**) For each movement direction, the activity of each cell scales the length of a vector aligned with its PD, and the vector sum of all cells defines a population vector. It has been shown that this population vector will predict the direction of movement if three conditions are met. First, neural activity is broadly tuned to the direction of movement; second, the PDs of the cells are uniformly distributed in space; and third, there is no systematic relationship between a cell's discharge rate and its preferred direction[8,9].

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activity as defined by the population vector. When monkeys make circular arm movements (whose direction changes continuously), the direction of the hand was found to lag behind that of the population vector, with a time interval that varied with the degree of curvature[5]. For tight circles, the lag was about 100 ms, but for large circles the lag was only 30 ms. These results were interpreted as evidence that the motor cortex is involved in controlling movements with high curvature, but not movements that are more straight. Todorov's model, however, predicts the exact same time differences between the population vector and hand movement, even while assuming a fixed time lag between the firing of the cortical neurons and the activation of the muscles. This is because the interplay between the mechanical properties of the musculoskeletal system related to length, velocity and acceleration create a systematic temporal shift between population vector direction and hand motion. In other words, the mechanical complexity of the limb leads to complexity of the population vector.

Todorov's article also illustrates some of the pitfalls that can occur when statistical approaches are used to correlate neural activity with different movement parameters. Various investigators have used multiple regression techniques to look for parameters of hand movement that show correlations with neural activity. A common finding has been that many parameters show some correlation, but that the correlations are greatest for movement direction and smallest for acceleration[6]. Because acceleration is tightly linked to force (according to Newtonian mechanics), this finding has been interpreted as suggesting that force is not among the major parameters coded by M1. Todorov shows, however, that a muscle-based model predicts virtually the same results: high correlations with movement direction and low correlations with acceleration. The model also predicts that, because of the force-velocity relationship of muscle, neural activity should also correlate with hand velocity; this too has been observed experimentally[7]. Finally, Todorov illustrates how the methods used to analyze neural data can have considerable consequences for the observed correlations. Specifically, squaring the discharge rate of neurons in order to stabilize the variance (as is commonly done; see for instance ref. 6), causes a dramatic increase in the percentage of neurons that appear to represent movement direction (from

17% to 43% in Todorov's model). This implies that previous studies may have overestimated the representation of movement direction in M1; indeed, Todorov suggests that many of the previously described correlations may be epiphenomenal, given that similar correlations arise in his model even though movement direction is never specified directly.

The new model is not meant to capture all the nuances of motor cortical activity during movement, and it does not prove that motor cortical activity is devoid of all higher-level features of movement related to the hand. It does, however, demonstrate two important points. First, even the simplest model of motor cortical function, treating it as a generator of muscle activity patterns, can lead to unanticipated and complex correlates of hand motion due to the mechanical properties of the limb and its musculature. Second, given these complexities, the relationship between neural activity and limb movement is not easily determined. Therefore, before concluding that brain activity reflects complex representations of movement, the data must be scrutinized to ensure that the observed correlations are not merely a reflection of properties of the peripheral motor apparatus. Engineers have to understand the plant before they can figure out how to control it. Why should it be any different when examining biological control?

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