# News in Motor Cortical Physiology

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***Motor cortical activity relates to static motor parameters (isometric force, limb position) under static conditions but predominantly to dynamic parameters (change of force, limb velocity) under dynamic conditions. This dual relation conceptually unifies the role of motor cortex in the control of isometric force and movement.***

Twenty years ago, Thach (15) eloquently expressed the quest for elucidating the relations of motor structures to abstract motor parameters: "Theoretical requirements for the neural control of movement and posture, together with the motor deficits caused by ablation of the nervous system at different levels, have generated the theory that there are representations encoded in neural activity of abstract commands that govern volitional movement and posture, and that these commands sequentially descend from higher levels through adaptive stages to arrive at the muscles in a language appropriate for muscle control." These views are quite different from others for which the essence and the principle of neural control of movement is the single muscle or, at best, movement about a single joint. The idea of a direct specification and control of arm movement as a unit in extrapersonal space was introduced by Mountcastle and colleagues (11) in 1975 in the context of the role of posterior parietal cortex in motor control. Indeed, the seeds for the subsequent studies of the present author that led to the discovery of directional tuning (8) can be traced to his exposure to Mountcastle's parietal work (11).

*"...force is ... a vector possessing direction and magnitude...."*

If movement and isometric force are considered as whole units, then they can be described as vectors in space and defined fully by their direction and magnitude. Neuronal activity might then control them by suitably relating to these motor parameters. In what follows, I discuss recent advances in this topic.

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### Isometric force

The first motor parameter to be investigated rigorously was the force exerted (see Ref. 1 for review), which began with the pioneer work of Evarts. Since Evarts's original study (4) in 1969 on the relations of motor cortical cell activity and postural fixation, almost all studies dealing with isometric force were focused on the intensity of static force. However, force is by definition a vector possessing direction and magnitude, and commonly the force exerted by the hand can be directed in any of the three dimensions of space. Until 1995, the neural coding of force had been investigated under conditions that restricted the dimensionality of the force vector to simply a scalar (e.g., force magnitude in a fixed direction; see Ref. 1 for review) or a pure two-dimensional (2-D) direction of constant magnitude (9). Not surprisingly, motor cortical cell activity was found to relate somehow to both parameters, namely, magnitude and direction of force. In 1995, Taira et al. (14) described these relations for the most general case of three-dimensional (3-D) isometric force vector. Force direction varied in three dimensions, and its intensity ranged from 0.255 to 4.89 N. Data were analyzed from two monkeys ($n$ = 188 cells) using stepwise multiple linear regression to determine the relations of single-cell activity to the direction of force and its magnitude. In 154/188 (81.9%) cells, the regression model was statistically significant. In 121/154 (78.6%) cells, the direction but not the magnitude of force had a statistically significant effect on cell activity; in 11/154 (7.1%) cells, only the magnitude effect was significant; and in 22/154 (14.3%) cells, both the direction and magnitude effects were significant. The same

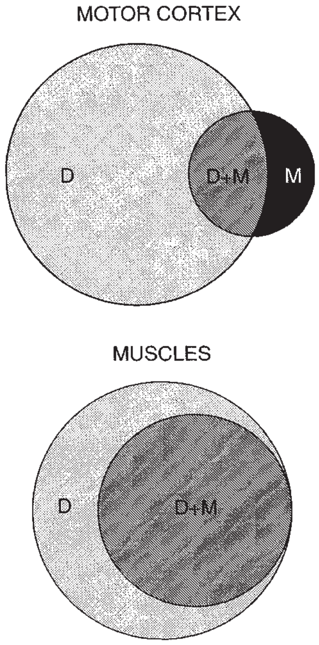

**FIGURE 1.** Venn diagrams illustrating the relative proportions of motor cortical cells and proximal arm muscles that showed significant relations to the direction of 3-dimensional static isometric force (D), its magnitude (M), or both (D + M). None of the muscles studied (see text) related to force magnitude alone. Data are from Ref. 14.

analysis was used to assess the effect of the direction and magnitude of force on the electromyographic (EMG) activity of nine muscles of the arm and shoulder girdle (anterior deltoid, posterior deltoid, upper trapezius, lower trapezius, supraspinatus, infraspinatus, pectoralis, biceps, and triceps). For all of the muscles studied the regression model was statistically significant. In 4/9 (44.4%) muscles, only the direction effect was significant, whereas in the remaining 5/9 (55.6%) muscles, both the direction and magnitude were significant. No muscle studied showed a significant effect of force magnitude alone. These differences in the frequency of occurrence of direction and magnitude effects between cells and muscles were statistically significant ($P < 0.005$, $\chi^2$-test). These relations are illustrated in Fig. 1 in the form of Venn diagrams. The combined direction-plus-magnitude effect was 3.9 times more prevalent in the muscles than in the cells studied, whereas the pure direction effect was 1.8 times more prevalent in the cells than in the muscles studied. The fact that all muscles showed a directional force effect emphasizes the point that the action of proximal muscles is exerted on a hand-held object through the linked skeleton of the arm by which the tension developed by a muscle on its attachments is translated to a 3-D directed force at the hand.

These findings underscore the fundamental importance of the direction of force in space and indicate that the specification of the magnitude of 3-D force is embedded within the directional signal. It is noteworthy that only a very small proportion (7.1%) of cells showed a relation to the magnitude of force in the absence of a directional effect. This shows that the tremendous emphasis placed during the past 30-odd years on the magnitude of force as the major determinant of motor cortical cell activity was unwarranted and was apparently due to the restriction of the experimental design to the study of force within a single directional dimension.

A different issue concerns whether cells related to force magnitude belong to a special class, such as those projecting to the spinal cord or, more specifically, to those making presumed monosynaptic connections with motoneurons ("corticomotoneuronal" cells), as assessed by the spike-triggered averaging technique. Ashe (1) has thoroughly reviewed the evidence from several studies that investigated the relations between the magnitude of static force and identified (e.g., pyramidal tract neurons, corticomotoneurons, corticostriatal neurons) or nonidentified motor cortical cells. It seems that similar qualitative and quantitative relations hold for all these different classes of neurons, which means that the relation to force is not a privilege of a particular neuronal class. Finally, it is interesting to note that even within the specific class of corticomotoneuronal cells, both positive and negative slopes of cell activity against force have been observed (10).

*"...the exertion of static force is not uncommon...."*

Although the exertion of static force is not uncommon, as, for example, when we hold a book against gravity, the production of a change in force is almost universally present in all actions, for it precedes the beginning of the movement. Study of force change under conditions of limb motion is hampered by several factors that cannot be easily controlled experimentally (e.g., interaction forces). An experimentally "clean" case is provided by the exertion of an isometric force pulse, that is, by the production of a rapid change in force in the absence of limb motion. Such a paradigm, which allows the study of the relation of neural activity to pure dynamic force change, was employed recently (6). The following experimental arrangement allowed the dissociation between dynamic and static components of the force exerted. Monkeys produced pure force pulses on an isometric handle in the presence of a constant force bias so that the net force (i.e., the vector sum of the monkey's force and the bias force) was in a visually specified direction. The net force developed over time had to stay in the specified direction and to increase in magnitude to exceed a required intensity threshold. Now consider the case in which the directions of the net and bias forces differ, by being, for example, orthogonal. For the task to be performed successfully under these conditions, the animal's force has to change continuously in direction and magnitude, so that, at any moment during force development, the vector sum of this force and the bias force is in the visually specified direction. Thus this experimental arrangement effectively dissociated the animal's force vector, the direction of which changed continuously in a trial, from the net force vector, the direction of which remained invariant. Eight net force directions and eight bias force directions were employed. Recordings of neuronal activity in the motor cortex revealed that the activity of single cells was directionally tuned in the absence of bias force and that this tuning remained invariant when the same net forces were produced in the presence of different directions of bias force. These results show that, during the generation of the force pulse, cell activity does not relate to the direction of the animal's force per se but to its dynamic component.

## Movement

Until 1982, almost all studies of the relations of motor cortical cell activity to limb movements stayed within the framework of single-joint movements, beginning with the pioneering work of Evarts (4). This may have reflected an underlying theoretical assumption concerning the way by which the brain specifies and controls movement, namely, that single cells control motions around single joints. This attitude in interpreting data from a single-joint perspective was best exemplified in the study by Murphy and colleagues (12), who recorded single-cell activity in the motor cortex while monkeys made free reaching movements to visual targets in 3-D space. First, the title of the paper ["Precentral unit activity correlated with angular components of a compound arm movement" (Ref. 12)] reveals the attitude of those times: reaching is reexpressed as a "compound movement," that is, as a movement composed of single-joint submovements. Of course, this description is correct, but it prevented the analysis of the data obtained at the level of the reaching movement itself as reference. Not surprisingly, the results obtained with this single-joint reference analysis looked baffling. First, no simple relation was observed between single cell activity and the EMG, even when the muscle from which the EMG was recorded was activated by intracortical microstimulation. Second, single cells related to motion about the shoulder or elbow joints behaved similarly in the task, although the motions produced about these joints could be quite different. Third, the discharge of shoulder-related cells seemed to vary systematically with the movement trajectory. These results indicated that the relations between single-cell activity in the motor cortex and components (joint rotation, EMG activity) of reaching are complex, that is, when viewed within the conceptual framework of the reaching movement as an aggregate of single-joint movements. The picture is different when the neural data are analyzed with respect to the whole of the reaching movement itself as a reference.

*"Cell activity was directionally tuned. . . ."*

In the same year, 1982, we (8) published the results of a study in which data were obtained in a similar experimental framework, namely, single-cell recordings in the motor cortex while monkeys made 2-D reaching movements to visual targets on a plane. The fundamental difference between these two studies was, in a sense, a philosophical one, for we analyzed the neural activity within the context of the reaching movement itself, namely, within a model in which the direction of the movement in space was the fundamental explanatory factor and not motions about individual joints. Thus the whole arm movement in space was considered as the important parameter. Remarkably, the variation in cell activity with respect to the direction of movement in space was found to be very orderly indeed (8). Cell activity was directionally tuned, in the sense that cell activity was highest for movements in a certain direction (the cell's "preferred direction") and decreased gradually with movements made farther and farther away from the preferred direction. Mathematically, the form of this functional relation was captured by a cosine tuning function that was later shown to hold for free reaching movements in 3-D space as well. The directional coding above was complemented recently by studies of the neural coding of the amplitude of movement (5). Two points from this study are noteworthy. First, the variation in cell activity with respect to the amplitude of movement is observed mostly during the movement time, in contrast to the directional effect, which is observed during the reaction time. This suggests that the motor cortex participates in the planning of the direction of movement, but it may only be receiving a feedback from the periphery regarding movement amplitude. The second important finding of this study was that the preferred direction remained practically invariant for movements of different amplitudes. This finding indicates that the coding of direction and amplitude at the level of the motor cortex are independent processes.

All of the studies discussed above were performed using discrete, pointing movements. In an important extension, Schwartz (13) studied motor cortical cell activity during continuous tracing movements in 2-D and 3-D space. These studies confirmed the importance of the direction of movement for cell activity, but they also revealed a relation to the speed of the movement, which is equivalent to the instantaneous movement amplitude, i.e., the amplitude of movement for a short, constant time interval (e.g., 10 or 20 ms). Interestingly, this relation could be manifested only above a threshold speed, which suggests a nonlinear relation. A relation to movement velocity was also documented for discrete, planar movements by performing a multiple linear regression of the instantaneous frequency of discharge against the time-shifted position, velocity and acceleration of the movement, and a constant, visually instructed direction (3). The best relations were found when neural activity was shifted such that it preceded movement parameters by ~100 ms (median value). The most important explanatory variables were *1*) the visually instructed direction and *2*) hand velocity, whereas hand acceleration had the weakest effect. Because this analysis was performed on the whole movement, the results above are likely to reflect both feedforward as well as feedback signals from the moving limb. Therefore, it is interesting to note that the relations between motor cortical single cell activity and movement are dominated by the directional specification and the kinematic parameter of velocity, whereas the parameter most closely related to force, i.e., acceleration, had only a minor effect.

*"A relation to movement velocity was also documented. . . ."*

## Coding of motor parameters: static and dynamic

Although movement is produced by a change in force, the latter can be studied best in isolation, i.e., as isometric force in the absence of movement. Under these conditions, as discussed above, motor cortical cell activity is related to the static force vector, when a constant force is exerted, or its dynamic component, when the force is changing (6). During pointing movements, force is changing, but the situation is complicated, compared with the isometric case, by the fact that a moving mass now comes into play and a variety of peripheral receptors from muscles and skin are activated. Therefore, the general cases of isometric force and movement should be treated separately as two only partially overlapping cases that differ in qualitative as well as quantitative ways. Accordingly, results obtained in one case can only be extrapolated cautiously and only to a limited degree to the other case. This is important to realize, for frequently sweeping, and superficially reductionist, statements are made such as "motor cortex controls force" because it is assumed that force is the most fundamental motor variable and that, therefore, motor cortex must relate to just this "primary" variable. Of course, the truth of the matter is that movement is more than "change in force" and should be taken into account with its own peculiarities, the most obvious of which is that a mass is moving; for example, the same change in force can produce very different effects depending on the mass acted upon. Finally, it is also important to realize that this is not an "either or" situation in the sense that the fact that motor cortex relates to the change in force does not preclude that it may also relate to a change of limb position as well, i.e., to limb velocity when the limb is moving. In fact, what seems to be a unifying principle is that, for both isometric force and movement, during static conditions motor cortical cell activity relates to static force (14) or static limb position (7), whereas during dynamic conditions motor cortical cell activity relates to dynamic aspects of force (6) or movement (i.e., velocity) (3, 13). In fact, when examined within the isometric force domain, static and dynamic processes seem to be processed differently and without overlap by motor cortical cells (2). Thus motor cortex can be viewed as participating in both static and dynamic processes in a similar qualitative way for both isometric force and movement. Remarkably, these relations are deeply rooted in the spatial domain, for motor cortical cell activity clearly relates to the spatial vector of force or movement, both in the static and the dynamic domain.

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