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The Motor Cortex and the Coding of Force

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The relation of cellular activity in the motor cortex to the direction of two-dimensional isometric force was investigated under dynamic conditions in monkeys. A task was designed so that three force variables were dissociated: the force exerted by the subject, the net force, and the change in force. Recordings of neuronal activity in the motor cortex revealed that the activity of single cells was directionally tuned and that this tuning was invariant across different directions of a bias force. Cell activity was not related to the direction of force exerted by the subject, which changed drastically as the bias force changed. In contrast, the direction of net force, the direction of force change, and the visually instructed direction all remained quite invariant and congruent and could be the directional variables, alone or in combination, to which cell activity might relate.

One problem in motor physiology concerns the relation between cell activity in the motor cortex and the force exerted by a subject. This problem has been studied extensively under static conditions—that is, when a constant isometric force is exerted. In this case, the rate of motor cortical cell discharge varies with the magnitude (*1–3*) and direction (*4*) of the force exerted. In contrast, the relation of motor cortical cell activity to force under dynamic conditions—that is, when the force changes—has not been studied adequately; for example, such studies have been restricted to one dimension (*1, 2, 5, 6*) or have been complicated by concomitant movement (*7*). In general, cell activity relates to the change in force (*2, 5*), although in several studies that involved movement, forces were not measured (*4, 8*).

We use the term "static force" (*9*) to refer to postural control and "dynamic force" to refer to changing force patterns. The usual experimental situation is a combination of a changing force in the presence of a constant bias force (for example, gravity). In this case, the desired outcome depends not only on the force exerted by the subject but also on the force bias: the crucial variable is the net force acting on the object, which is the vector sum of the force exerted by the subject and the force bias. We assume that the force exerted by the subject consists of a dynamic and a static component. Therefore

$$\text{Net force} = \text{subject force} + \text{force bias} \quad (1)$$

$$= \text{dynamic force} + \text{static force} + \text{force bias} \quad (2)$$

We assume that static force compensates for and is therefore equal and opposite to force bias, so that net force = dynamic force; we use these terms interchangeably. Finally, we define the change in force as the difference between successive force vectors at times t and $t + 1$:

$$\text{Force change} = \text{net force } (t + 1) - \text{net force } (t) \quad (3)$$

or, given Eq. 1,

$$\text{Force change} = \text{subject force } (t + 1) - \text{subject force } (t) \quad (4)$$

Therefore, the change in force is the same for both the net force and the force exerted by the subject. These forces change in time when a net force pulse is produced in a specified direction and in the presence of a constant force bias (Fig. 1). The various forces are dissociated, especially dynamic force and the force exerted by the subject; the time course of the change in force is similar to that of dynamic force. We used these dissociations to examine the relation of motor cortical activity to these different forces under isometric conditions and to determine which one is specified by the motor cortex.

For this purpose, we trained a monkey to grasp an isometric handle (*10*) with its hand pronated and to exert force pulses so that the net force was in eight visually specified directions. These directions were indicated by a target on a display placed 45 cm in front of the animal, and a force feedback cursor displayed the net force on the handle. A steady deflection of the force feedback cursor was used to produce a constant bias force. In the task, the visual target first appeared in the center of the

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display, and the monkey had to exert a force on the handle to align the net force–feedback cursor to the target cursor. After a 1-s period, the target jumped from the center to one of eight peripheral locations (every 45°) on a circle with a 100-g force radius, and the monkey was required to produce a force pulse so that the net force–feedback cursor would move in the direction (±22.5°) of the target; the animal was rewarded when this cursor moved past the target, which corresponded to a net force >100 g. The force pulses were produced in the presence of a constant force bias in eight directions; in addition, the same force pulses were produced in the absence of a force bias (*11*).

The activity of 132 cells was recorded in the arm area of the motor cortex during performance of this task (*12*). The activity of 74 of 132 (56.1%) cells during the

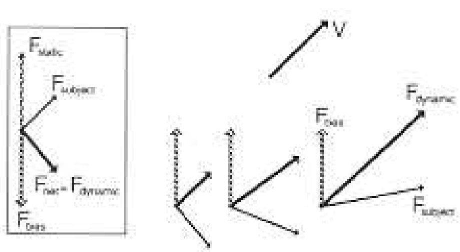

Fig. 1. (Left) Forces defined in the text: the force bias ($\mathbf{F}_{bias}$), the force exerted by the subject ($\mathbf{F}_{subject}$), the static force ($\mathbf{F}_{static}$), the dynamic force ($\mathbf{F}_{dynamic}$), and the net force ($\mathbf{F}_{net}$). (Right) Time-varying changes in these forces when $\mathbf{F}_{dynamic}$ increases in magnitude and is in the visually instructed direction **V** (arbitrary data). Bold letters indicate vectors. Hatched vectors indicate $\mathbf{F}_{bias}$, broken vector indicates $\mathbf{F}_{static}$.

reaction and force production time was directionally tuned (*13*); this tuning was preserved across the force biases used (Fig. 2). This finding suggests that the cell activity varies with the dynamic force or the change in force but not with the force exerted by the subject; unlike the first two forces, the force exerted by the subject changed drastically according to the force bias (Fig. 3). In contrast to cell activity, the electromyographic (EMG) activity of muscles active in the task changed appreciably with the force bias (*14*).

The relation of neuronal activity to the various forces was confirmed with the neuronal population vector (*15*), which can be calculated as a time-varying signal (*16, 17*) and, therefore, can be compared to the time-varying dynamic force, to the force exerted by the subject, and to the change in force (*18*). The population vector was related to the dynamic force or to the change in force but not to the force exerted by the subject (Fig. 4) (*19*). Another example is illustrated in a different form (cover). In this case, the force bias was in the direction of the pink line. Successive samples (every 10 ms) of the average force exerted by the subject are shown by the blue lines. The red, green, and yellow lines indicate the dynamic force, the population vector, and their overlap, respectively, over time. The dynamic force was dissociated from the force exerted by the subject, and the population vectors were related to the former and not to the latter.

We focused on multidimensional force as the motor output produced by the arm and chose an isometric task because the analysis of forces in multidimensional reaching movements is complicated by the presence of interactional forces (*20*). We sought to dissociate the dynamic force, the force exerted by the subject, and the change in force. For that purpose, we used a task that required the production of force pulses in the presence of constant bias forces in various directions; such bias forces have been used before (*4*). We also used "open loop" force pulses without a stopping requirement in order to study the initiation of a motor output without constraints on the accuracy of the magnitude of force to be exerted and without interference by static processes related to the maintenance of steady force at different levels.

Our data show that the activity of motor cortical cells was tuned with respect to the direction of two-dimensional isometric force pulses and that this directional tuning was similar across force biases in different directions, as observed previously in a movement study (*4*). Thus, single-cell activity did not relate to the force exerted by the subject, which changed under these conditions. In contrast, the direction of dynamic force, the change in force, and the visually instructed direction all remained invariant and congruent across different force biases and could be, alone or in combination, the directional variables to which cell activity is related.

This directional tuning has been documented in both isometric and movement (*4, 15, 21*) conditions. In the case of movement conditions, it was proposed (*4*) that this invariance reflects a relation to the direction of movement irrespective of externally applied loads—that is, a relation to kinematic (movement) planning as contrasted with kinetic (force) implementation (*22*). On the basis of this distinction and the relative insensitivity of cell activity in parietal area 5 to static bias forces, Kalaska and co-workers (*23*) hypothesized that movement planning is hierarchically organized, with area 5 of the parietal cortex providing the kinematic plan and the motor cortex participating in both kinematic and kinetic aspects of movement. Although these ideas may be applied to movements, they cannot be properly applied to isometric forces because for these forces there is no motion and, therefore, strictly speaking, no kinematics: in this sense, the isometric case is all kinetics (that is, force-related).

The mechanical conditions for the generation of the directed motor output are also very different in movement and isometric conditions—that is, when a mass to be accelerated is present (movement) or absent (isometric force). The presence, then, of directional tuning in both movement and isometric force conditions suggests that the common underlying factor for motor cortical activity may relate to an abstract

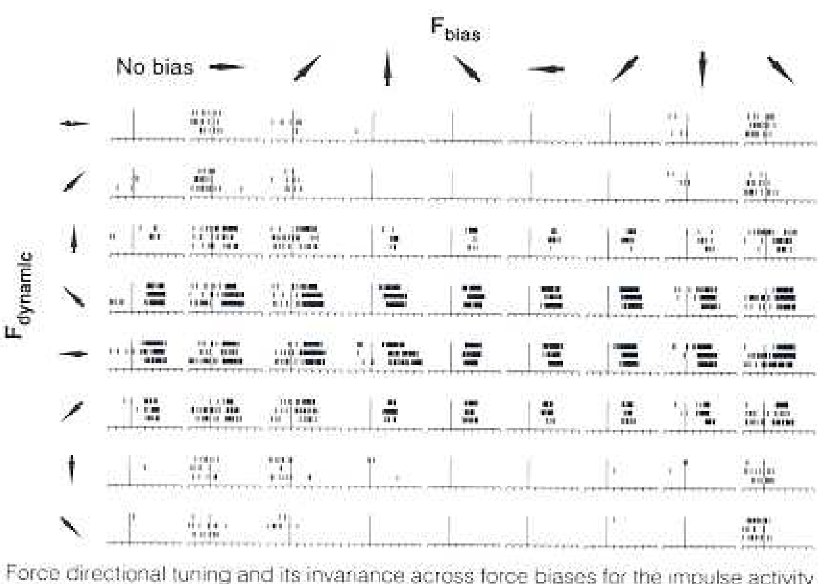

Fig. 2. Force directional tuning and its invariance across force biases for the impulse activity (three repetitions) of one motor cortical cell. The directions of the dynamic force and the force bias are shown in the rows and columns, respectively, including the case of no force bias (first column). Rasters are aligned to the onset of the peripheral stimulus (time zero); the time scale is 100 ms per division.

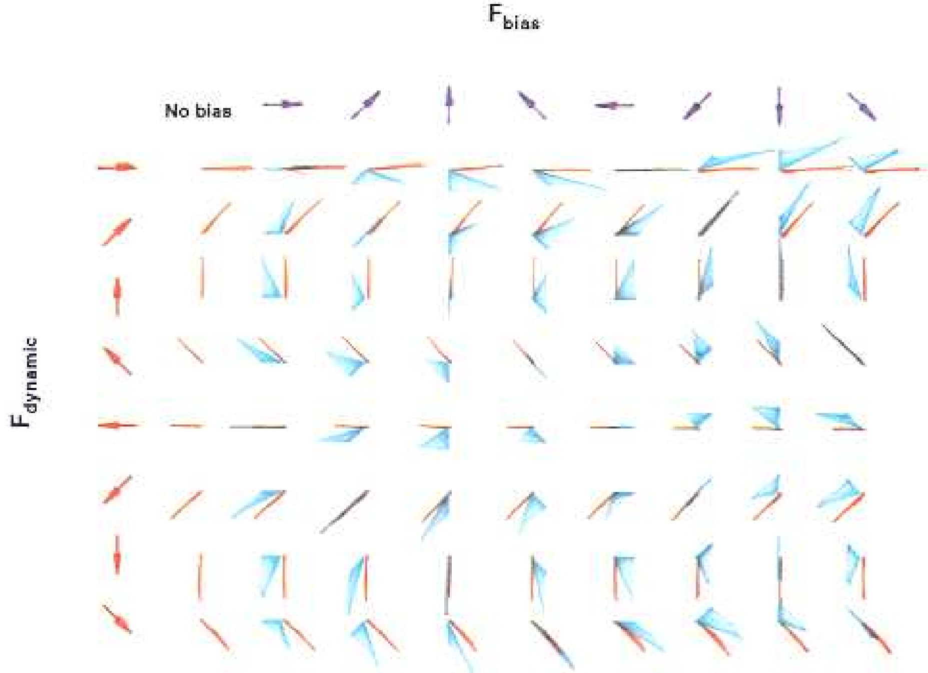

Fig. 3. Time-varying dynamic forces (red) and forces exerted by the subject (blue) in the presence of bias forces (purple) in various directions. Forces are averages of 10-ms samples from all trials during which tuned cells were recorded. In the no bias case (first column), the dynamic force and the force exerted by the subject were the same. Conventions are as in Fig. 2.

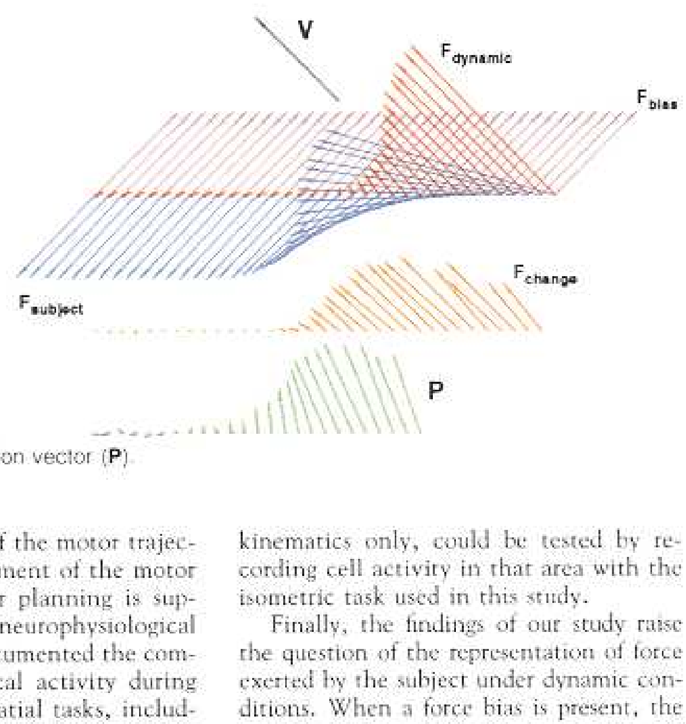

Fig. 4. The neuronal population vector points in the direction of the dynamic force or the change in force but not in the direction of the total force exerted by the subject. All vectors illustrated are time-varying (every 10 ms) for a particular force bias and instructed visual direction. The length of the change in force is six times that of the other force vectors. Red, $\mathbf{F}_{dynamic}$; blue, $\mathbf{F}_{subject}$; orange, $\mathbf{F}_{change}$; purple, $\mathbf{F}_{bias}$; and green, population vector (**P**).

spatial representation of the motor trajectory (*24*). The involvement of the motor cortex in spatial motor planning is supported by the results of neurophysiological studies, which have documented the complexity of motor cortical activity during performance of visuospatial tasks, including directional transformations and trajectory planning (*17, 25*). Moreover, the idea that spatial planning for movement and isometric force involves a common process is supported by the results of psychophysical studies that show similar constraints in both movement and isometric force trajectories (*26*). The possible participation of parietal area 5 in this more general spatial process, rather than in kinematics only, could be tested by recording cell activity in that area with the isometric task used in this study.

Finally, the findings of our study raise the question of the representation of force exerted by the subject under dynamic conditions. When a force bias is present, the force exerted by the subject is made up of both dynamic and static components (Fig. 1) and could be represented at the level of motoneuronal pools by the convergence of dynamic (*27*) and static (postural) (*28*) inputs from separate supraspinal structures and spinal interneuronal systems (*29*); this convergence would provide an ongoing integrated signal to the motoneuronal pools. Indeed, such an integration of postural and dynamic factors was suggested by a recent analysis of EMG activity (*30*).

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11. Altogether, nine force bias conditions were used: in one, the force bias was 0, and in the remaining eight conditions the force bias was 45 g and was in the directions shown (Fig. 2); thus, 72 combinations (classes) were used (nine bias conditions × eight visually instructed net force directions), and three repetitions of each were presented in a randomized block design.
12. The electrical signs of cell activity were recorded extracellularly with a seven-microelectrode recording system [V. B. Mountcastle, H. J. Reitboeck, G. F. Poggio, M. A. Steinmetz, *J. Neurosci. Methods* **36**, 77 (1991)] interfaced to a personal computer with a GHova Systems TB21EVR laboratory event recorder. The implantation of a recording chamber was performed aseptically under general pentobarbital anesthesia (28 mg per kilogram of body weight).
13. The preferred direction of force was calculated for each cell in the zero-bias condition. The steady-state cell activity during the static hold period before the onset of the target was directionally tuned in 63 of 74 (86.3%) of cells. In general, the preferred directions in the two cases were similar. These results agree with those obtained by others in a two-dimensional movement task (*4*).
14. The EMG activity of eight muscles of the arm was recorded during the task with multistranded stainless steel wires placed inside the muscles. The muscles studied included the anterior deltoid, posterior deltoid, trapezius, pectoralis major, triceps, biceps, forearm extensors, and forearm flexors. The task was accomplished mainly by the activation of proximal muscles that were differentially activated for different directions of dynamic force in the zero-bias condition. The EMG activity was influenced by the force bias and it reflected the force exerted by the subject. The effect of the force bias on EMG activity after the onset of the target was evaluated quantitatively as follows. For each muscle, we noted the direction of dynamic force for which EMG activity was maximum in the zero-bias condition and assessed the modulation of EMG activity for that direction of dynamic force across the nine force bias conditions by calculating the ratio of maximum to minimum activity observed in these nine conditions. The mean (± SD) ratio was 12.7 ± 8.64, which indicates a

modulation of more than 12 times. In contrast, the average (± SD) modulation for cells, calculated in the same way, was 2.52 ± 1.72. Thus, the effect of the bias force was more than ten times greater on the EMG activity than on the cell activity. This difference was statistically significant ($P < 0.0001$, t test).

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18. The population vector was computed every 10 ms with the cell-preferred directions determined in the zero-bias condition. For the calculation of the population vector, peristimulus time histograms (10-ms binwidth) were computed for each cell and each of the 72 combinations (classes) used with counts of fractional intervals as a measure of the intensity of cell discharge. A square root transformation was applied to these counts to stabilize the variance [G. W. Snedecor and W. G. Cochran, *Statistical Methods* (Iowa State Univ. Press, Ames, ed. 7, 1980), pp. 288–290]. For a given time bin, each cell made a vectorial contribution in the direction of the cell's preferred direction and of magnitude equal to the ongoing, binned cell activity. The population vector **P** for the j^{th} class and k^{th} time bin is

$$\mathbf{P}_{j,k} = \sum_{i}^{74} w_{i,j,k}\mathbf{C}_i$$

where $\mathbf{C}_i$ is the preferred direction of the i^{th} cell and $w_{i,j,k}$ is a weighting function such that

$$w_{i,j,k} = (d_{i,j,k})$$

where $d_{i,j,k}$ is the square root–transformed discharge rate of the i^{th} cell for the j^{th} class and the k^{th} time bin. In the present case, the control rate was not subtracted in order to minimize the assumptions of this analysis.
19. This was confirmed by the results of a root-mean-square (rms) analysis as follows. The population and force vectors were normalized with respect to their maximum and were aligned to the onset of their first change, and the rms of the differences between the population vector, the dynamic force, the force exerted by the subject, and the change in force was computed in the time series after target onset: the smaller the rms, the less different were the vectors in the paired series. The rms of the difference between either the population vector and dynamic force (*rms* = 42.25, normalized units) or the population vector and the change in force (*rms* = 34.95) was less than the rms of the difference between the population vector and the force exerted by the subject (*rms* = 68.96).
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COVER

Computer visualization of the relation of neuronal activity in the motor cortex of a monkey to the forces exerted during hand movement. The neuronal population vector (green) predicts the dynamic force (red) but not the total force exerted by the monkey (purple) in the presence of a constant bias force (pink). See page 1692. Vectors are successive 10-millisecond samples; yellow lines indicate overlapping green and red lines. [Computer graphics: Masato Taira and Apostolos Georgopoulos. Photography: Roger Paul. Production: Medical Media Service, Minneapolis VAMC]