PRINCIPLES
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Certain motor cortical cells fire less and less often as muscle force increases. That is, their activity is correlated negatively with force. However, like neurons with positive correlations (see Figure 38-12), these cells also facilitate their target muscles. They discharge only during tasks that require precise control of force and smooth changes in force. Thus their function may be to provide more precise descriptoring of motor units than would be afforded simply by inhibiting the so-called positive cortical neurons. This would be helpful, for example, in releasing delicate objects carefully.

In conclusion, the primary cortex has two levels of functional organization. First, a low-level control system, the CM cells, controls groups of muscles that can be brought together into task-specific combinations. Second, a higher-level control system encodes more global features of the movement. Practice and learning adjust the relation between these two levels of organization.

Each Premotor Area Contributes to Different Aspects of Motor Planning

Although the outputs of the premotor areas and the primary motor cortex overlap in the spinal cord, the inputs to the premotor areas are quite different from those to the primary motor cortex (see Figure 38-4). Moreover, damage to premotor areas causes more complex motor impairments than does damage to primary motor cortex. When a monkey with a large lesion of the premotor area is presented with food behind a transparent shield, it will reach directly for the food and bump into the shield. Unlike a normal animal it is unable to incorporate visuospatial information about the shield into the kinematic plan for moving its hand.

The idea that premotor areas are involved in planning movement has received crucial support during the past 20 years from physiological and imaging studies of humans and monkeys performing a variety of special tasks. In monkeys, distinct populations of cells are active in conjunction with ipsilateral movements, bilateral movements, or specific combinations of movements. Se-related and preparatory activity predominates, and cell activity is often associated primarily with specific tasks as we will see below.

Studies of the premotor areas have identified several basic features of the neural organization of motor preparation. First, movements that are initiated internally by the subject—such as the sequencing of finger movements when manipulating an object—involves primarily the supplementary motor area. Second, movements triggered by external sensory events involve primarily the lateral premotor areas. More specifically, separate populations of lateral premotor neurons map different arbitrary relationship between stimulus and response. The lateral dorsal premotor area is also concerned with delayed action (executed later on cue), whereas the lateral ventral premotor area is concerned with conforming the hand to the shape of objects.

Third, mental rehearsal of a movement—that is, the use of visual imagery to plan a movement—involves the same patterns of activity in the premotor and posterior parietal cortical areas as those that occur during performance of the movement. Psychophysical studies have shown that mental rehearsal of movement has a similar time course and closely simulates task performance. This observation helps explain the importance of mental rehearsal to athletes and skilled performers. Fourth, the motor and premotor neurons activated during a particular task are not the same over time but change progressively as performance becomes automatic.

The Supplementary and Preparatory Motor Areas Play an Important Role in Learning Sequences of Discrete Movements

Motor actions are often self-initiated without an environmental cue. Nearly a full second before a self-initiated voluntary movement begins, a characteristic negative shift in cortical potentials is seen in the electroencephalogram (EEG) record of medial premotor region, where the supplementary motor area is situated. This negative potential, referred to as the preparatory potential or Bereitschaft potential, signals the planning that occurs before movement is executed.

The region responsible for this negative potential was localized more precisely in a study comparing increases in regional cerebral blood flow (a measure of increases in neuronal activity) during simple, complex,
Figure 38-16 Whether an individual corticomotoneuronal (CM) cell is active depends on the motor task. The activity of a CM cell and the activity in its target muscles are not directly related. Cumulative histograms show the activity of a single neuron during a precision grip and a power grip. During the precision grip the neuron’s activity is the same whether overall force is light or heavy and the level of electromyographic (EMG) activity in the target muscle is similar for both forces. During the power grip there is almost no activity in the neuron despite a greater amount of EMG activity in the muscle. Thus, even if a given motor neuron is monosynaptically connected to a given CM cell, their firing patterns do not have to parallel each other because the multiplicity of connections to motor neurons allows task flexibility. (From Mjolby LM, Lemon RN. 1983. Corticospinal neurons with a special role in precision grip. Brain 106: 312–316.)

and imagined sequences of finger movements. Complex movement sequences require more planning than do simple repetitive movements. Imagining complex movements might require the same amount of planning as real movements. As expected, during forceful repetitive finger flexions against a spring-loaded movable cylinder, increases in regional cerebral blood flow were largely confined to the contralateral primary sensorimotor hand-control region. A complex sequence of finger movements was accompanied by regional cerebral blood flow increases within the supplementary motor area. Remarkably, when the complex sequence of finger movements was simply imagined, regional cerebral blood flow increased in an area anterior to the supplementary motor area on both sides (Figure 38-17). This area, the presupplementary motor area, provides the main input to the supplementary motor area and is discussed in detail below.

The specific role of the supplementary motor area in the internal representation of sequences of movements was examined in another experiment, in which recordings were made from neurons in the primary motor cortex, supplementary motor area, and lateral premotor areas of monkeys while the animals performed two variations of an instructed-delay task. In this type of task subjects are taught which movements to make and later given a cue telling them when to make the movements. The monkeys in this experiment were instructed to touch three panels in a specific sequence. In one variation the instruction was visual. Three panels were lit up in a sequence that the monkeys had to follow. In the other variation the monkeys were instructed to perform a previously memorized sequence. As expected, neurons in the primary motor cortex generally discharged before and during movements to the same degree for visually guided and memorized sequences. In contrast, many supplementary motor area neurons fired only before and during performance of a memorized sequence. The reverse was true for the lateral premotor neurons (Figure 38-18). In addition, a movement-related discharge of some supplementary motor area neurons is specific to a particular sequence of movements such as pushing followed by turning a handle. The cells do not fire in connection with other combinations of the same movements. Thus the supplementary motor area seems to be involved in preparing movement sequences from memory in the absence of visual cues.

The main cortical input to the supplementary motor area arises from the presupplementary motor area (see Figure 38-4). This region projects only to the supplementary motor area and has no clear somatotopy. Whereas the supplementary motor area is involved in setting the motor programs for learned sequences, the presupplementary motor area is thought to be involved in learning these sequences. For example, in one study the presupplementary motor area was preferentially activated while subjects learned a new sequence of button presses: the supplementary motor area became active only during the performance of the movements once they were learned. This motor learning likely involves a continuous interchange of information with the prefrontal cortex (area 46) and other areas of cortex.

When proficiency and skill are gained, the neural control of task performance can also shift from the supplementary motor area to the primary motor cortex. In one recent study with monkeys, movement activity in the supplementary motor area during the performance of a key-pressing task disappeared after 12 months of overttraining. Subsequently, an experimental lesion in the right primary motor cortex of these overtrained monkeys caused weakness in the left digits, thereby greatly compromising the monkeys’ ability to perform the task. After 21 days the monkeys recovered sufficiently to press the keys with the same skill as before they received the lesion. Twenty-two days after the monkeys received the lesion recordings from the supplementary motor area showed that neurons were again very active before movement. Much as extended practice influences the extent of
motor representation in the primary motor cortex, a shift in representation occurs in the supplementary motor cortex as a task goes from being novel to automatic. Conversely, recovery of function following damage to the primary motor cortex represents a new learning challenge in which the supplementary and perhaps pre-supplementary motor areas participate anew.

The Lateral Premotor Areas Contribute to the Selection of Action and to Sensorimotor Transformations

Selection of appropriate action can be the result of internal reflection, which may involve evocation of mental imagery. More often, however, actions are responses to visual or auditory cues. Such cues may signify that a particular action is required immediately (e.g., a red light telling us to stop) or that some type of situation is imminent in which action will be required (e.g., a yellow light signaling an imminent change to red). The ability to learn new, adaptive responses to particular environmental stimuli is crucial to effective and accurate movement.

We have seen that set-related activity occurs in the primary motor cortex and supplementary motor area before movement is executed. In the primary motor cortex, this activity represents specific parameters of a particular movement in the supplementary motor area it represents a specific order of responses. In the lateral premotor areas it represents how visual or other sensory stimuli are to be used to direct the movement. Characteristically, set-related activity in the premotor area persists during the entire interval between an anticipatory cue and the signal to move (Figure 38-19).

Set-related activity in the lateral dorsal premotor area is related predominantly to sensory stimuli that do not convey spatial cues to direct movement. For example, the stimulus could be a light in a location that is not

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Figure 38-18 Cell activity in the motor cortex depends on whether a sequence of movements is guided by visual cues or by prior training. Monkeys were required to press three buttons either in a sequence presented by lighting three panels in turn or in a pseudorandom order presented by a computer. After being instructed to perform the observed sequence or the trained sequence, there was a delay before the animal was given a signal to initiate the movement. Raster plots represent cell discharge before and during movement on 16 trials, and the histogram shows the summed activity over all trials. Data are aligned to the onset of the first key touch. The cell in the primary cortex fired whether the sequence performed was the one learned in prior training or the one used by lighted panels. The cell in the lateral premotor area fired only when the visually cued sequence was used, whereas the cell in the supplementary motor area fired only when the trained sequence was used. (From Musha and Fetsch 1991.)

Figure 38-19 A cell-related neuron in the dorsal premotor area becomes active while the monkey prepares to make a movement to the left. An instructive signal (illumination of one of four panels) tells the monkey which panel it will have to depress when a trigger signal (illumination of a nearby light-emitting diode) is presented. In the raster plots each dot on each line represents a kilo in the recorded neuron. Each line is one trial, and successive trials are aligned on the onset of the instructive signal. The delay between the instructive and trigger signals varied randomly among these values. In the raster plots and histograms the responses made with each delay time are grouped to show that the discharge of the neuron correlated with the instructive signal and lasts until the response is made after the trigger signal. (From Weinrich and Wise 1982.)

Figure 38-20 The visuomotor transformations required for reaching and grasping involve two different pathways from the primary visual cortex to the premotor areas.

Reaching. A path connects the parieto-occipital extrastriate area (PO) and the dorsal premotor area (PMd). Some of these connections reach PMd directly, and some relay via areas in the intraparietal sulcus: the medial dorsal parietal (MDP) and medial intraparietal (MIP) areas. This system is responsible for transforming visual information about the location of objects in extrapersonal space into the direction of a reaching movement.

Grasping. A path connects the dorsal extrastriate (ES) cortex and the ventral premotor area (PMv) via the anterior intraparietal area (AIP). This system is responsible for transforming visual information about the properties of objects, such as shape and size, into commands for effective grasping.
Figure 38-21 Individual neurons in the ventral premotor area fire during specific hand actions only.Raster plots and cumulative histograms show the discharge of a single neuron in the lateral ventral premotor area of a monkey during a precision grip and a power grip involving all the fingers. The cell is active during the precision grip by either arm but not during the power grip by either arm. Thus its activity is specific to the grip type employed by either hand. The fact that the neuron is active during movement of both arms excludes the possibility that this difference is due solely to the different patterns of contralateral activation required by the two grips. If this were the case, only contralateral activation would occur. (From Rizzolatti et al. 1995.)

Figure 38-22 An individual cell in the ventral premotor area is active whether the monkey performs a task or observes someone else perform the task. The fact that the same cell is active during action or observation suggests that it is involved in the abstract representation of the motor task.

A. Activity in the neuron as the monkey observes another monkey make a precision grip.
B. Activity in the same neuron as the monkey observes the human experimenter make the precision grip.
C. Activity in the same neuron as the monkey itself performs a precision grip. (From Rizzolatti et al. 1995.)

The monkeys were able to execute the required movements without impairment, none was able to learn the association between the background color and whether to push or pull.

Reaching and Grasping Are Mediated by Separate Parieto-Premotor Channels

Goal-directed movements require transformation of sensory representations of the environment into muscle-
control signals, a process termed sensorimotor transformation. Reaching, a goal-directed movement, requires that visual information about target location and the position of the upper limb be used to specify critical features of the upcoming arm movement. In addition, reaching is commonly coupled with grasping an object.

The parameters for reaching movement, notably direction and distance, depend on the location of the target relative to the body, shoulder, or hand. Grasping, in contrast, is governed mainly by the shape and dimensions of the object. Grasping involves first a separation of the fingers sufficient to enclose the object and then closure as the object is gripped between the pads. Separation of the fingers occurs during transport of the hand toward the object. The kinematics of grasping thus depend on the object itself and not on its location. Thus reaching and grasping are interesting behaviors to study in order to better understand the process of visuomotor transformation.

Anatomical evidence and single-cell recordings have shown that separate but parallel prefronto-pontocerebellar channell mediate visuomotor transformations required for reaching and grasping (Figure 36-20). During reaching, neurons in parietal area 5 code for direction of the movement but discharge later than dorsal premotor neurons to which they are connected. These neurons could monitor ongoing movements and improve the planning and execution of subsequent reaches by premotor areas.

During grasping, different neurons in the lateral ventral premotor area of monkeys fire in connection with different hand actions and object shapes. These neurons are active throughout reach, well before the fingers begin to grasp. Moreover, different cells fire during different patterns of hand shaping. Some neurons are active only when the action is a precision grip; others are active only when the action is a swiping movement to retrieve food; still others are active only if the action is a power grip (Figure 38-21A). The cells in the lateral ventral premotor area thus seem to direct motor acts that are guided by visual information about object shape received from the posterior parietal cortex. Another set of neurons discharges whether an object is grasped or bitten.

A single type of neuron has been discovered in the lateral ventral premotor area. Like others, these neurons discharge when the monkey performs a specific grasping movement, but they also discharge when the monkey reaches toward an object without touching it. The movement being made by the other monkey or even by the experimenter. These neurons have been called mirror neurons (Figure 38-22).

These different neurons all share the characteristic of encoding a vocabulary of goal-directed actions rather than how these behaviors will be executed.

The ventral premotor area receives its main input from neurons with similar task-related properties in the anterior intraparietal region, a region buried in the intraparietal sulcus. Recordings of these neurons were made while a monkey performed a series of tasks involving different switches and knobs. Cells fired selectively when particular switches were operated and also fired when the monkey visually fixed the same switch without grasping it. These cells may have a role in transforming the dimensions of an object in visual space into motor signals.

An Overall View

Our understanding of the functional organization of the motor areas of the cerebral cortices has undergone substantial change in recent years, as a new picture of the cortical control of movement has emerged. The primary motor cortex can no longer be seen as a simple motor map of the body in which adjacent muscles or joints are represented in adjacent cortical sites. Instead, individual muscles and joints are represented repeatedly in a complex mosaic that makes it possible for the cortex to organize combinations of movements suitable to specific tasks. Each muscle and joint is represented by columnar arrays of neurons whose axons branch and make connections with several functionally related motor nuclei. This branching is more modest for cells that control distal muscles, providing these muscles with more independent control.

In addition to terminating on spinal motor neurons, corticospinal neurons also terminate on interneurons in the spinal cord. These connections can gate reflex circuits, allowing voluntary movements to take advantage of spinal circuits, as these circuits can link local sensory input to output. Distinct populations of motor cortical neurons appear to have specialized roles in determining specific features of motor performance. The characteristics of these different populations and their distribution within the motor areas of cortex point to a hierarchical organization of movement. Thus motor cortex activity may change actively before and during movement. Neurons of the primary motor cortex differ from spinal motor neurons in that the former are less sensitive to electrical stimulation and show the most pronounced forms of muscle activation (eg. precision grip versus power grip), they encode a more restricted range of contractile force than do spinal motor neurons, and they are even more responsive to environmental factors. The kinematic details of movement are determined by population codes, the summed activity of entire populations of neurons.

In contrast to neurons in the primary motor cortex, movement-related neurons in the premotor areas may fire during movements that are related to specific goals and not others to encode a more global feature. Goal-related neurons, which are relatively rare in the primary motor cortex, are more common in premotor areas. These cells are active in the absence of any overt behavior, such as during a delay between task instructions and execution of the task. Some encode a response to be made after a delay; others encode a global sensorimotor transformation (eg. "always move to the right in the visual stimulus"). Thus, just as there is a hierarchy of spinal and supraspinal motor control, there is a hierarchy of neuronal representations of task features within the different cortical areas.

The planning and execution of voluntary movements relies on sensorimotor transformations in which representations of the external environment are integrated into movements. This integration is the product of premotor and primary motor areas operating in conjunction with sensory and association areas. We have seen an example of this in the communication between parietal and motor areas during visually guided reaching.

In contrast to reflex movements, voluntary movements are highly adaptable—they improve in speed and accuracy with repeated trials of practice. This adaptability may reflect an optimization process in which the minimal circuits needed to accomplish a behavior are selected, with training, selected from redundant sensorimotor connections. Such an optimization process could be responsible for the observed shift in the encoding of particular parameters of movement from one group of cells to another, or from one area of cortex to another, as proficiency develops.

A novel behavior initially requires processing in multiple motor and parietal areas as it is continuously monitored for errors and subsequently modified. As the behavior becomes more accurate, the need for sampling of the sensory inflow and updating of the motor program decreases and the need for the computational power of large networks lessens. For example, the pre-supplementary motor area is active during the learning of a novel behavior but becomes less active as learning progresses. After long periods of practice, when the behavior becomes automatic, activity in the supplementary motor area ceases.

References


Selected Readings


John Krakauer
Claude Ghez