

## 38

**Voluntary Movement: The Parietal and Premotor Cortex**[Voluntary Movement Expresses an Intention to Act](#)[Voluntary Movement Requires Sensory Information About the World and the Body](#)[Reaching for an Object Requires Sensory Information About the Object's Location in Space](#)[Space Is Represented in Several Cortical Areas with Different Sensory and Motor Properties](#)[The Inferior Parietal and Ventral Premotor Cortex Contain Representations of Peripersonal Space](#)[The Superior Parietal Cortex Uses Sensory Information to Guide Arm Movements Toward Objects in Peripersonal Space](#)[Premotor and Primary Motor Cortex Formulate More Specific Motor Plans About Intended Reaching Movements](#)[Grasping an Object Requires Sensory Information About Its Physical Properties](#)[Neurons in the Inferior Parietal Cortex Associate the Physical Properties of an Object with Specific Motor Acts](#)[The Activity of Neurons of the Inferior Parietal Cortex Is Influenced by the Purpose of an Action](#)[The Activity of Neurons in the Ventral Premotor Cortex Correlates with Motor Acts](#)[The Primary Motor Cortex Transforms a Grasping Action Plan into Appropriate Finger Movements](#)[The Supplementary Motor Complex Plays a Crucial Role in Selecting and Executing Appropriate Voluntary Actions](#)[The Cortical Motor System Is Involved in Planning Action](#)[Cortical Motor Areas Apply the Rules That Govern Behavior](#)[The Premotor Cortex Contributes to Perceptual Decisions That Guide Motor Behavior](#)[The Premotor Cortex Is Involved in Learning Motor Skills](#)[Cortical Motor Areas Contribute to Understanding the Observed Actions of Others](#)[The Relationship between Motor Acts, the Sense of Volition, and Free Will Is Uncertain](#)[An Overall View](#)

IN THIS CHAPTER WE DESCRIBE HOW the cerebral cortex uses sensory information about the external world in deciding on which actions to take and how to organize voluntary movements to accomplish those actions. Studies over the past 25 years have shown that the cortical motor system is not an unthinking, passive circuit controlled by more intelligent parts of the brain. Instead, it is intimately involved in the many interrelated neural processes required to choose a plan of action, including processes that appear to be more perceptual and cognitive than motor in nature. The motor system also contributes to cognitive processes that appear unrelated to motor control, such as understanding the actions of others and the potential outcomes of observed events.

**Voluntary Movement Expresses an Intention to Act**

Voluntary behavior is the physical expression of an intention to act on the environment to achieve a goal. Let us say you want a cup of coffee. There may be many reasons why: You may wish to enjoy the stimulating effect of caffeine or may simply be thirsty. Whatever its origin, your behavioral goal is established by your motivational state but is fulfilled by voluntary motor behavior. The motor system has to transform your intention into action.

How you achieve your goal depends on the circumstances in which you find yourself. If the cup of coffee is already prepared and sitting in front of you, you can simply reach out, grasp the cup, and bring it to your lips.

Often, however, the situation is more complex. The coffee might not be ready, or you might not have any coffee at home. In this case, to satisfy your craving for coffee you must organize and perform a complex series of actions to fulfill your goal of drinking coffee. You may go out to buy the coffee and return home, or you may go to a café, order a coffee, and drink it there. Alternatively, if it is too late in the evening or if the weather is inclement, you may alter your goal, such as drinking tea instead of coffee.

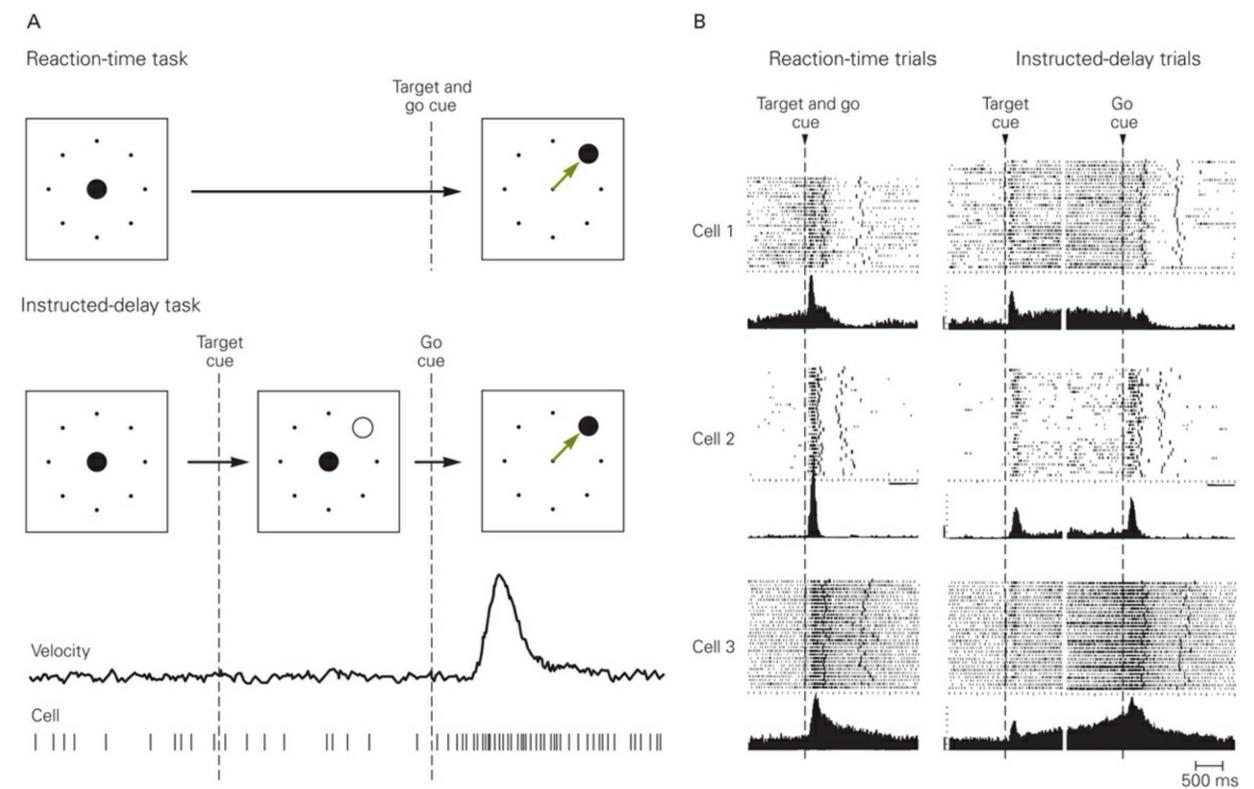
Each of these different voluntary behaviors is an action that serves an intermediate goal. However, only the entire series of actions can achieve your ultimate goal. The capacity to maintain a behavioral goal during a series of actions, and to develop alternative behavioral strategies and action sequences to fulfill the goal, are hallmarks of voluntary behavior. The pre-frontal cortex located rostral to the motor areas plays a critical role in the organization of voluntary behavior. Here we focus on the neuronal mechanisms in the parietal and premotor cortex that mediate voluntary behaviors.

Voluntary behavior often involves physical interaction with objects in the external world. This requires the brain to convert sensory inputs about the state of the world and the individual's internal state into motor commands. As described in [Chapter 33](#), the transformation involves a sequence of neural operations in many cortical and subcortical areas. No single area is responsible for all the steps between intention and action, or indeed for any one particular operation. This distributed organization is characteristic of all aspects of the neural control of voluntary behavior.

Another important feature of voluntary behavior is that once an intention is formed, action can be delayed or not performed at all. One is not irrevocably compelled to act on an intention the moment it is formed. A reflex, by contrast, is evoked immediately by a stimulus. Without self-control over whether, how, and when to act, behavior would be driven by the moment—impulsive, compulsive, and even antisocial. These considerations suggest that the motor system operates in at least two stages: movement planning and execution. Planning involves deciding what action or series of actions to perform to fulfill an intention, whereas execution orchestrates actual movement.

Studies of nearly every cortical area involved in arm movement have attempted to identify the neural pathways specific to planning or execu-

tion. This is often done by imposing a delay between the instruction about what movement to make and the cue to execute it. These studies show that none of the cortical areas contains a homogeneous population of neurons dedicated only to planning or execution. Instead, a broad range of neuronal function is evident in each area. Some neurons respond only during the planning phase of the task, whereas others discharge during the execution phase. Still others show activity changes during both stages ([Figure 38-1](#)).



**Figure 38-1** Neural processes related to movement planning and movement execution can be dissociated in time. (Reproduced, with permission, from Crammond and Kalaska 2000.)

**A.** In a *reaction-time task* a sensory cue instructs the subject both where to move (target cue) and when to move (go cue). All neuronal operations required to plan and initiate the execution of the movement are performed in the brief time between the appearance of the cue and the onset of movement. In an *instructed-delay task* an initial cue tells the subject where to move and only later is the cue given to start movement. The knowledge provided by the first cue permits the subject to plan the upcoming movement. Any changes in activity that occur after

the first cue but before the second are presumed to be neuronal correlates of the planning stage.

**B.** Movement planning and execution are not completely segregated at the level of single neurons or neuronal populations in a given cortical area. Raster plots and cumulative histograms show the responses of three premotor cortex neurons to movements in each cell's preferred direction during reaction-time trials and instructed-delay trials. In the raster plots each row represents activity in a single trial. The thin ticks represent action potentials, and the two thicker ticks show the time of movement onset and end. In reaction-time trials the monkey does not know in which direction to move until the target appears. In contrast, in instructed-delay trials an initial cue informs the monkey where the target lies well in advance of the appearance of a second signal to initiate the movement. During the delay period many premotor cells show directionally tuned changes in activity that signal the direction of the impending delayed movement. The activity in cell 1 appears to be strictly related to the planning phase of the task, for there is no execution-related activity after the go signal in the instructed-delay task. The other two cells show different degrees of activity related to both planning and execution.

The major difference between cortical areas is whether the predominant neural activity is correlated with planning or execution. Whereas many primary motor cortex neurons discharge mainly during execution, premotor and parietal cortices contain more neurons that are strongly activated during the planning stage.

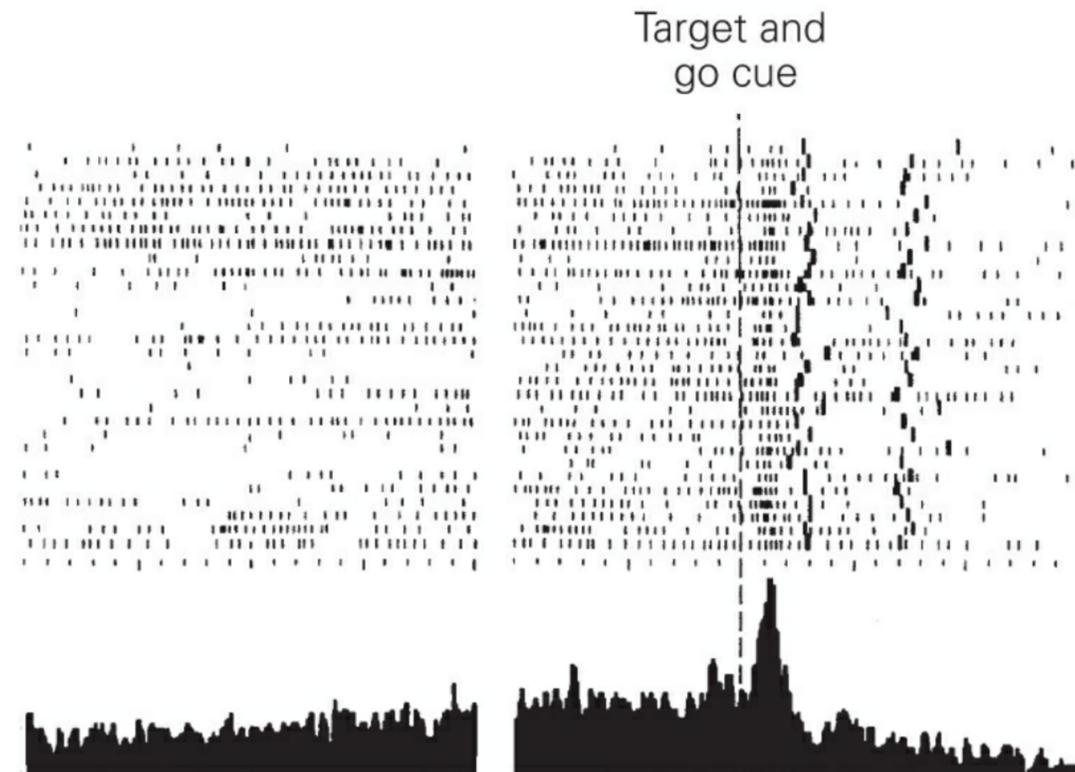
Neural activity during the planning stage also provides information about the intended act. The activity of single neurons and populations during the delay period of reach-to-grasp tasks conveys such information as the location of the target, the direction of arm movement, and the configuration of the hand required to grasp an object. This activity even encodes information about higher-order aspects of the action, such as its goal and expected reward value.

Even when a well-trained monkey makes the wrong movement in response to an instruction, the neural activity during the delay period before movement onset generally predicts the erroneous response. This is compelling evidence that the activity is a neural correlate of the intended

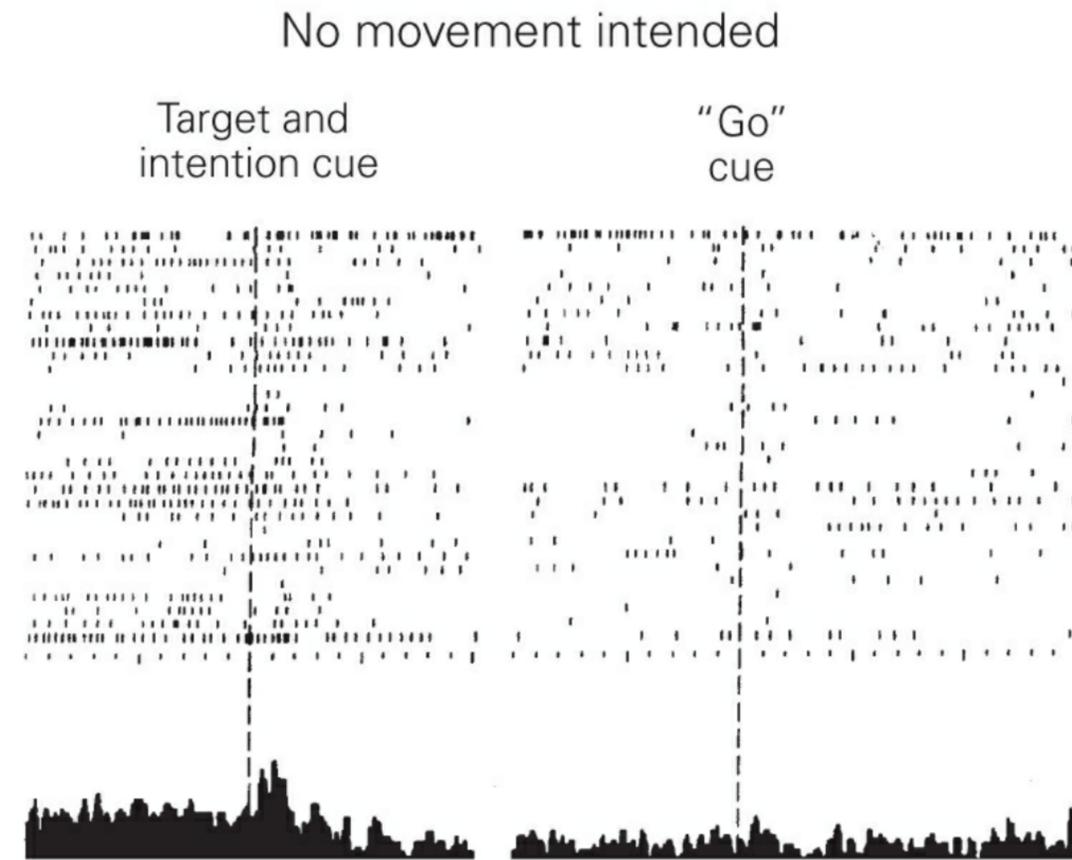
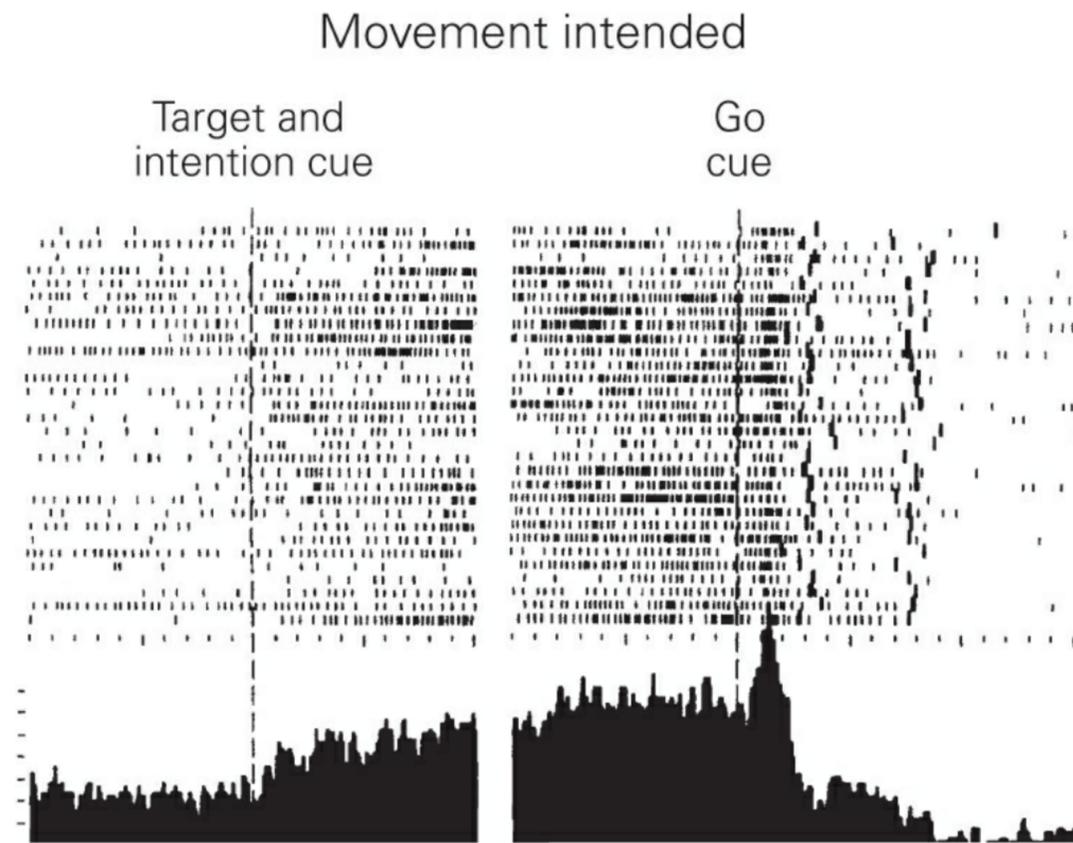
motor act, not a passive sensory response to the stimulus that instructed it.

Further evidence of motor planning in the cortex comes from comparing the neural activity in a monkey when it has been instructed to make a reaching movement and when it has been instructed to withhold reaching. Many neurons in the premotor cortex generate directionally tuned activity during the delay period when the monkey is instructed to move, but not when it is instructed to refrain from moving. This differential activity represents an unequivocal signal about the monkey's intention either to reach in different directions or not to move in response to an instructional cue seconds before the action is executed ([Figure 38–2](#)).

### A Reaction-time task



**B** Instructed-delay task



**Figure 38–2** Decisions about response choices are evident in the activity of premotor cortex neurons. (Reproduced, with permission, from Crammond and Kalaska 2000.)

**A.** In a reaction-time task (reaching) a cell exhibits gradually increasing, nondirectional, tonic firing while waiting for the appearance of a target. When the target appears (**go cue**) the cell generates a directionally tuned response.

**B.** In an instructed-delay task, when a monkey is shown the target and instructed to move once the go cue appears, the cell generates a strong, directionally tuned signal for the duration of the delay period before the go cue. When the monkey is shown the target but is instructed not to move when the go cue appears, the cell’s activity decreases.

These studies demonstrate that activity in several movement-related cortical areas signals information about the nature of an intended motor act well before execution of the act. Many neurons in the same cortical areas also discharge during movement execution, implicating those areas in the control of movement. Given this close anatomical proximity of

planning- and execution-related activity, even at the level of individual neurons, a major unresolved question is why planning-related neural activity does not immediately initiate the movement. There must exist a mechanism that either prevents movement execution during the delayed planning stage or permits the start of movement at a later time (see [Box 38-2](#)).

## **Voluntary Movement Requires Sensory Information About the World and the Body**

Let us return to the action of getting a cup of coffee. The deceptively simple action of drinking from a cup represents not a single motor act but a series of motor acts, each with a specific goal: reaching for the cup, grasping, lifting, holding, and bringing the cup to the mouth. The sequence of acts must be coordinated so that the arm and hand can interact physically with the cup in an efficient manner to achieve the desired goal.

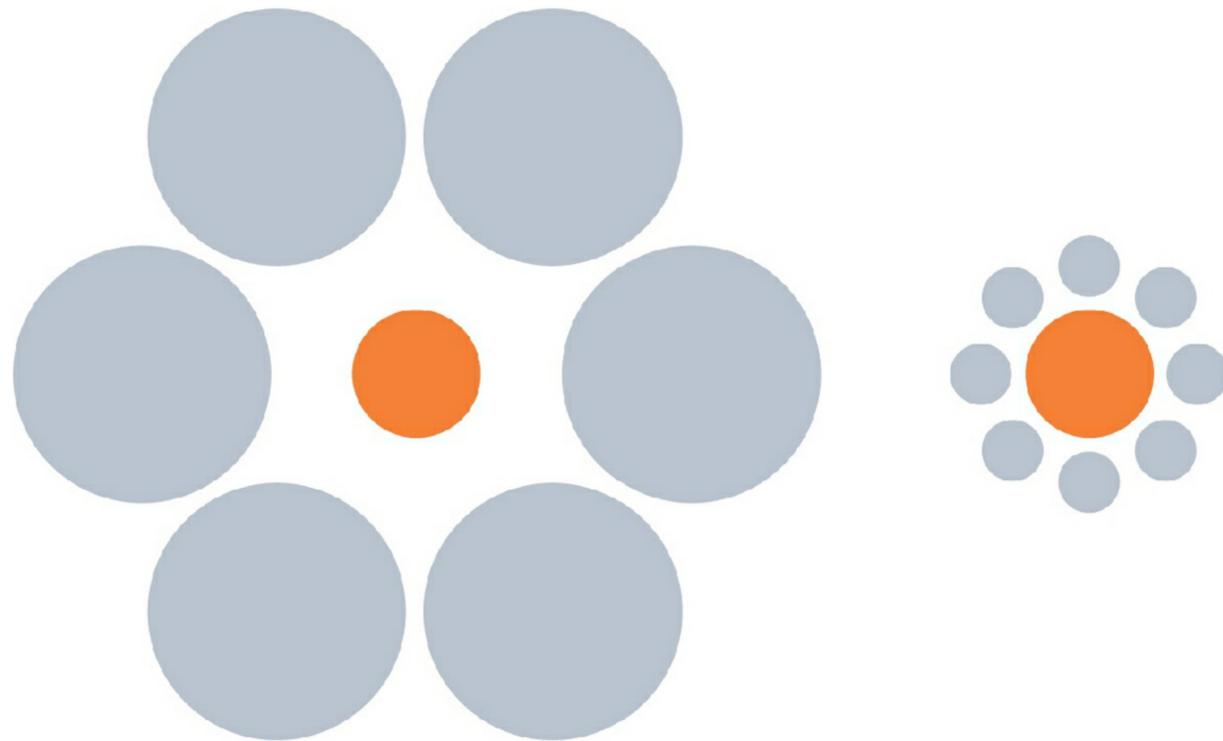
To reach out and grasp the cup the motor system must solve two basic problems. First, it has to localize the cup in space and transform this location into a reaching movement of the arm to bring the hand to the cup. Second, it must encode the physical properties of the cup, such as its size and shape, and transform them into a particular grip. One might suppose that reaching and grasping are conducted sequentially. However, recordings of hand and arm kinematics show that this is not so: The two acts occur largely simultaneously. As the arm reaches toward the cup, the hand starts to rotate and open to match the size, shape, and orientation of the target. The hand and fingers then begin to close even before the hand contacts the cup. Furthermore, although the two processes occur in parallel, they can influence each other. Both the velocity and acceleration of grasping and reaching, for example, can depend on the location, distance, orientation, size, and shape of the object to be lifted.

Along with information about the target object the motor system requires information about the current status of the arm, including its posture and motion and the position of the hand relative to the target. The various brain operations required to plan and guide arm movements are implemented in part by interconnected populations of neurons in the primary motor cortex, premotor cortex, and parietal cortex.

The parietal lobe is the principal target of the dorsal visual stream. It has long been implicated in a variety of functions such as the perception of the spatial structure of the world and the control of directed attention. As a result, the dorsal visual stream is often called the “where” pathway to distinguish it from the “what” pathway, the ventral visual stream that projects from the primary visual cortex into the temporal lobe and is involved in the recognition of objects.

Pioneering neurophysiological studies of the parietal lobe in active monkeys conducted independently by Vernon Mountcastle and Juhani Hyvärinen and their colleagues in the 1970s showed that many parietal neurons also discharge during eye, arm, or hand movements when an animal attentively explores and interacts with its environment. One striking property that both groups observed is that the discharge of many parietal neurons is highly dependent on the goal of the behavior. Neurons discharge strongly when a monkey reaches to grasp an object, searches for an object in a box, or manipulates an object with its hand, but are much less active when the monkey makes other arm and hand movements.

More recently, behavioral studies by Mel Goodale and David Milner and their collaborators have led to an important and still controversial hypothesis about the role of the dorsal visual stream. They propose that a primary function of the parietal lobe is to extract sensory information about the external world and one’s own body that is useful for the planning and guidance of movements. This sensory guidance of action may operate in parallel with and independently of perceptual processes evoked by the same sensory inputs. For instance, whereas our perception of the size and orientation of objects can be deceived by certain visual illusions, the motor system often behaves as if it is not fooled and makes accurate movements ([Figure 38-3](#)). As a result, the dorsal visual stream is also called the “how” pathway (see [Chapter 18](#)).



**Figure 38–3** The visual information that serves object perception and movement may be processed in distinct, parallel pathways. In the Ebbinghaus illusion two orange disks of identical diameter appear to be of different size because one is surrounded by large disks and the other by small disks. Mel Goodale and collaborators reported that when subjects were asked to indicate the size of the central disks with their thumb and index finger, the separation between finger and thumb was significantly larger for the disk on the right. However, when subjects reached out to grasp the identical disks surrounded by larger or smaller disks, their thumb-finger separation was nearly the same in both cases. This and similar evidence suggests that visual pathways to the parietal lobe are distinct from those that support object perception and that the parietal inputs are not solely the output of the perceptual pathways.

This does not mean, however, that the parietal lobe has no role in spatial perception or attention. On the contrary, we now recognize that its contributions to spatial perception, attention, and sensorimotor transformations are intimately intertwined. This interconnectedness of function is clear in an examination of how different parts of the parietal lobe and associated precentral motor areas contribute to the planning and execution of the reach-to-grasp action required to drink a cup of coffee.

## Reaching for an Object Requires Sensory Information About the Object's Location in Space

Although we describe the neural processes underlying reach and grasp separately, the two actions are usually coordinated. Coordination is achieved through reciprocal axonal connections between reach- and grasp-related populations both within the same cortical areas and between different areas and through populations of neurons that discharge in connection with components of both reach and grasp.

## Space Is Represented in Several Cortical Areas with Different Sensory and Motor Properties

The planning of a reaching movement is usually defined as the neural process by which the location of an object in space is translated into an arm movement that brings the hand into contact with the object. Our intuitive conception of space as a single continuous expanse—one that extends in all directions and within which objects have locations relative to one another and to ourselves—has long influenced neuroscience.

According to classical neurology the neural counterpart of the space that we experience is a single map in the parietal lobe constructed by inputs from different sensory modalities. This unified, multimodal neural replica of the world is assumed to provide all the information necessary for acting on an object and is shared by the different motor circuits that control the eyes, arm, hand, and other effectors.

An alternative view is that there are many maps each related to a different motor effector and adapted to its specific needs. These spatial representations are created when the individual interacts with its environment, defining a series of motor relations determined by the properties of a particular effector. For example, a rodent has a locomotion map in the hippocampus and adjacent entorhinal cortex representing the animal's current location and direction of motion. This alternative hypothesis suggests that our intuitive sense of space arises at least in part from our motor interactions with the world.

Evidence collected in recent years clearly does not support the notion

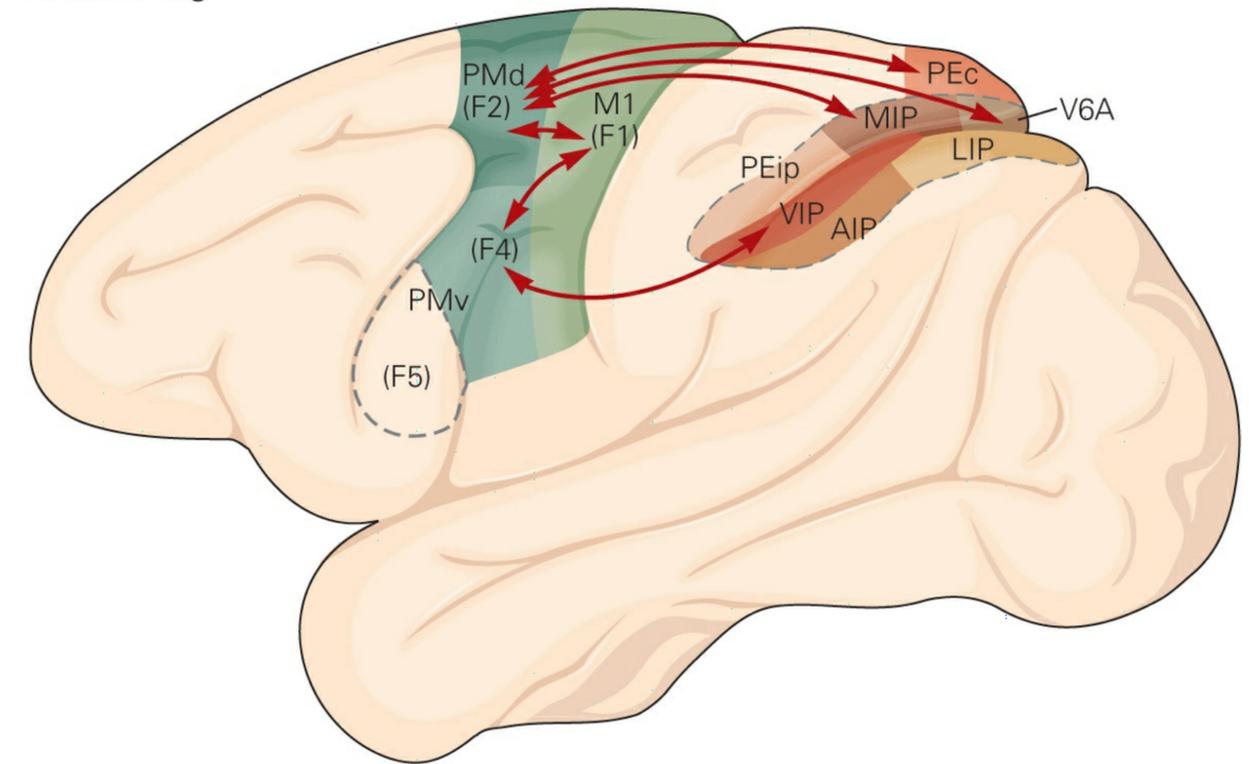
of a single topographically organized representation of space in the parietal cortex. First, the parietal cortex is organized as a series of areas working in parallel. Second, *near space* or *peripersonal space*, the space within our reach, is encoded in areas different from those that represent *far space*, the space beyond our reach. Third, the functional properties of the neurons in parietal and frontal areas of cortex involved in spatial coding vary depending on the body part controlled, such as the eyes versus the arm.

These findings support the idea there are many spatial maps, some located in the parietal cortex and others in the frontal cortex, whose properties are tuned to the motor requirements of different effectors. Moreover, the spatial maps in each cortical area are not maps in the usual sense of a faithful point-to-point representation of surrounding space, but rather dynamic maps that may expand or shrink according to the motor requirements necessary to interact with a given stationary or moving object.

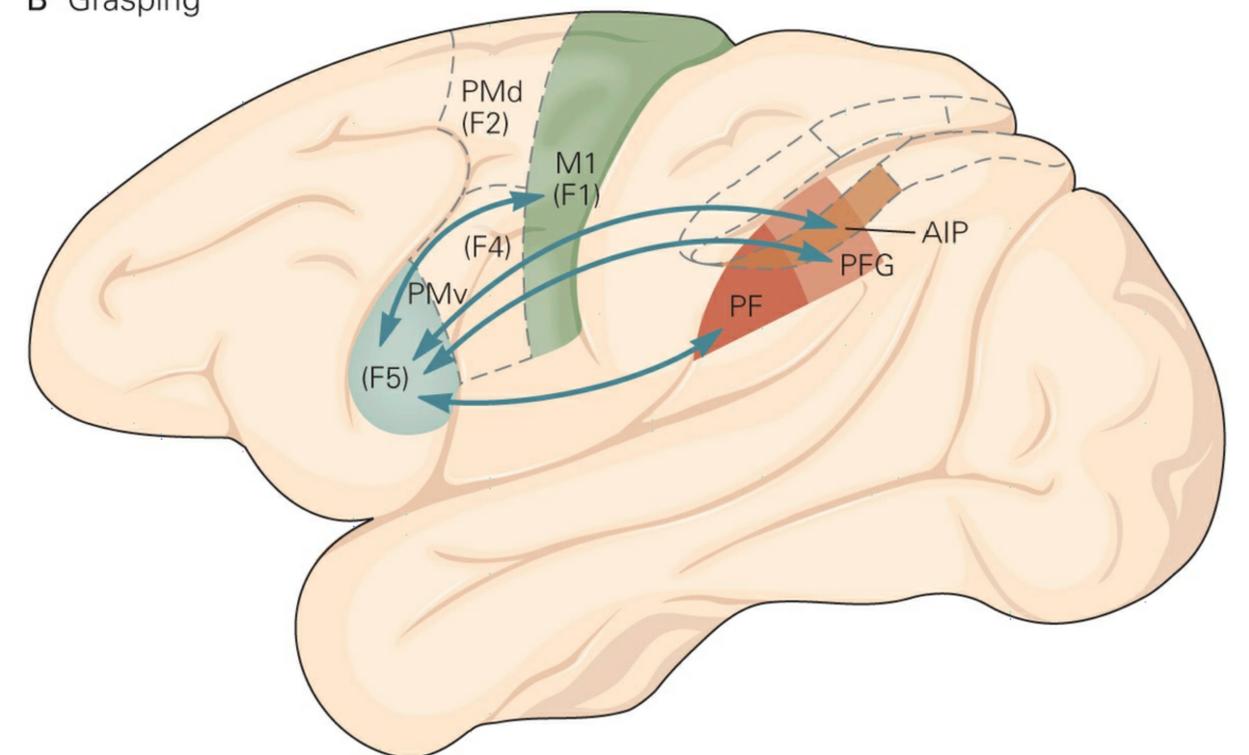
### The Inferior Parietal and Ventral Premotor Cortex Contain Representations of Peripersonal Space

In monkeys several areas in the inferior parietal cortex and interconnected parts of the premotor cortex contain representations of peripersonal space. One such area, the ventral intraparietal area, is located in the fundus of the intraparietal sulcus (Figure 38-4A). It receives visual projections from components of the dorsal visual stream, including areas MST (medial superior temporal cortex) and MT (medial temporal cortex), that are involved in the analysis of optic flow and visual motion.

A Reaching



B Grasping



**Figure 38–4** Separate parietofrontal pathways are involved in the visuo-motor transformations for reaching and grasping.

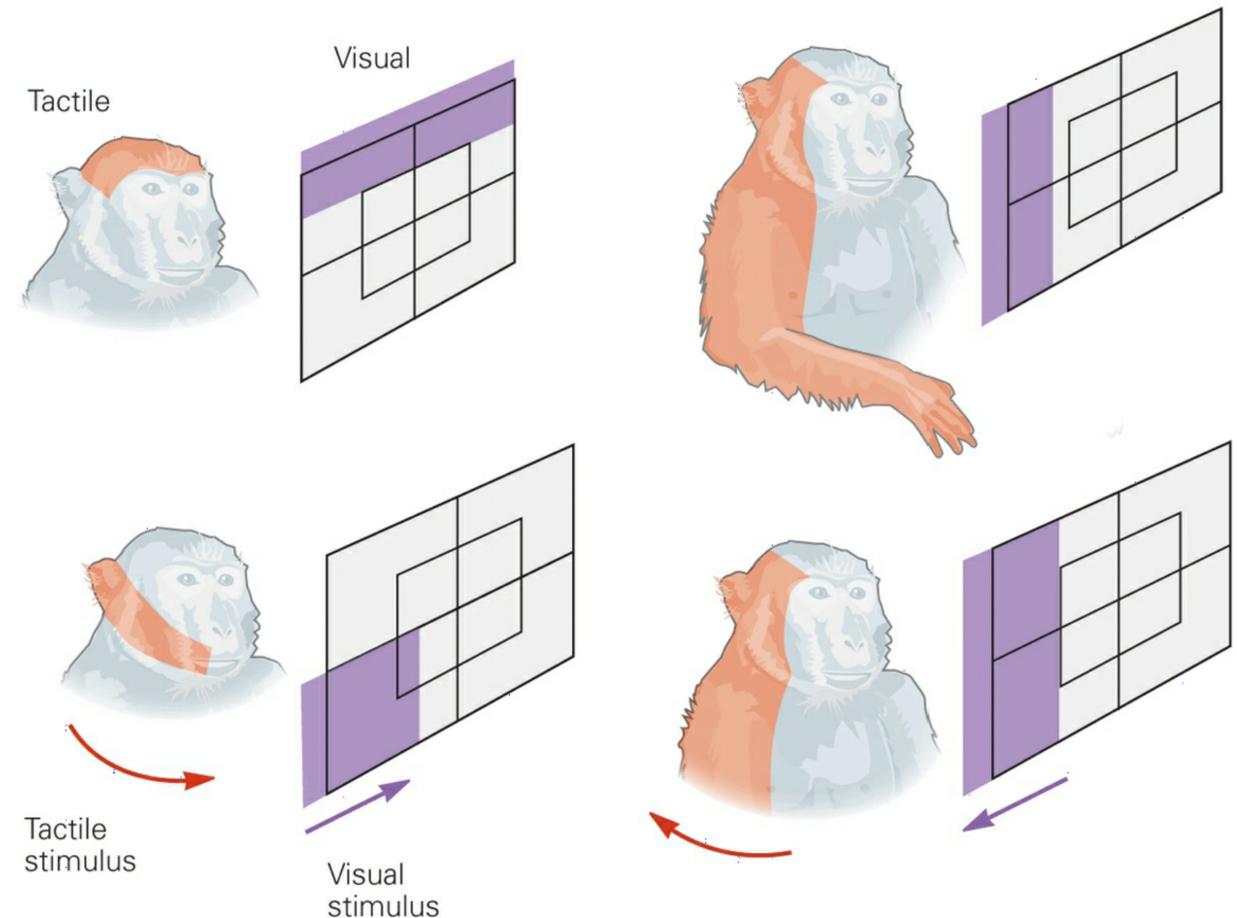
**A.** The visuomotor transformation necessary for reaching is mediated by the parietofrontal network shown here. The areas located within the intraparietal sulcus are shown in an unfolded view of the sulcus. Two serial pathways are involved in the organization of reaching movements. The *ventral stream* has its principal nodes in the ventral intraparietal area (**VIP**) and area F4 of the ventral premotor cortex, whereas the *dorsal stream* has synaptic relays in the superior parietal lobe (**MIP**, **V6A**) and the dorsal premotor cortex (**gPMd**), which includes area F2. (Parietal areas include **AIP**, anterior intraparietal area; **LIP**, lateral intraparietal area; and **V6A**, the parietal portion of the parieto-occipital area.) PEc and PEip are parietal areas according to the nomenclature of von Economo. Somatosensory areas 1, 2, and 3 and area PE, which provide somatosensory input to M1 (**F1**), are not shown in the figure. Precentral areas include F5, a subdivision of PMv, the ventral premotor cortex, and the primary motor cortex (**M1**, **F1**).

**B.** The visuomotor transformation necessary for grasping is mediated by the parietofrontal network shown here. The AIP and PFG areas are concerned mostly with hand movements, whereas area PF is concerned with mouth movements. PF and PFG are parietal areas according to the nomenclature of von Economo. Area F5 in PMv is concerned with both hand and mouth motor acts. Some grasping neurons have been found in F2, the ventral part of PMd. Area M1 (or F1) contains a large sector that controls the fingers, hand, and wrist (see [Figure 37–2A](#)). Other abbreviations are explained in part A.

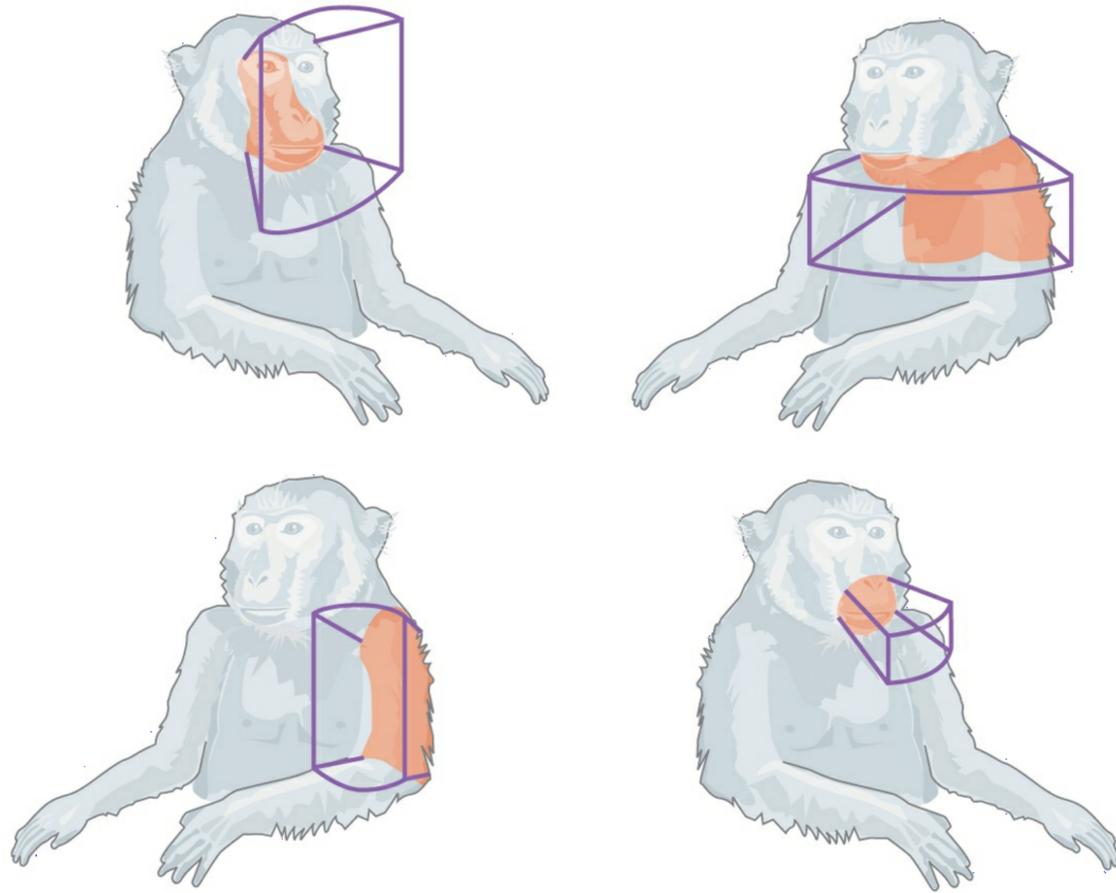
Some ventral intraparietal neurons respond only to visual stimuli and respond preferentially either to expanding (looming) or contracting (receding) stimuli or to stimuli moving in the horizontal or vertical plane. Others have polymodal receptive fields within which inputs from different sensory modalities lie in spatial register ([Figure 38–5A](#)). These neurons respond to tactile stimuli, most often near the mouth or on the face but also on the arm or trunk, as well as to visual stimuli located immediately adjacent to the tactile receptive field. Some even respond to auditory stimuli in the same spatial location. Certain polymodal neurons

respond to both visual and tactile stimuli moving in the same direction whereas others are strongly activated by visual stimuli that move toward their tactile receptive field but only if the path of motion will eventually intersect the tactile receptive field.

**A** Receptive fields of neurons in ventral intraparietal cortex (VIP)



B Receptive fields of neurons in the ventral premotor cortex (F4)



**Figure 38–5** Some neurons in the parietal and premotor cortex respond to both tactile and visual stimuli within receptive fields that are spatially in register.

**A.** Some neurons in the ventral intraparietal cortex have tactile and visual receptive fields that are aligned in a congruent manner. **Orange** areas on the monkey represent tactile receptive fields; **purple** areas on the screen in front of the monkey's face and centered on its nose represent visual receptive fields. Many of the neurons also share directional preferences for movement of tactile and visual stimuli (**arrows**). (Reproduced, with permission, from Duhamel, Colby, and Goldberg 1998.)

**B.** Neurons in ventral premotor cortex area F4 respond to either tactile or visual stimulation. **Orange** areas are tactile receptive fields; **purple lines** indicate the three-dimensional receptive fields within which visual stimuli activate the neuron. (Reproduced, with permission, from

Fogassi et al. 1996.)

Ventral intraparietal neurons appear to represent an early stage in the construction of a peripersonal spatial map that is more fully expressed in a caudal part of the ventral premotor cortex, area F4, with which it is strongly interconnected. Virtually all neurons in area F4 respond to somatosensory inputs, especially tactile stimuli. The tactile receptive fields are located primarily on the face, neck, arms, and hands. Half of the neurons also respond to visual stimuli and a few to auditory stimuli.

As with ventral intraparietal neurons, the modality-specific receptive fields in area F4 lie in register ([Figure 38–5B](#)). This suggests that the visual receptive fields are not defined by the location of the visual stimulus on the retina, as in most neurons in the visual cortex, but are anchored to specific parts of the individual's body. One striking feature of such a poly-modal neuron, especially in the ventral premotor cortex, is that its visual receptive field remains aligned with the tactile receptive field when the monkey looks in different directions, but moves with the tactile receptive field to a different part of peripersonal space when the monkey moves the corresponding part of its body.

Nevertheless, area F4 is a motor area and its neurons also discharge in association with movements, most often of the arm, wrist, neck, and face. The neurons in this area control movements of the head and arm toward different parts of the body, or toward objects close to the body, to permit the animal to grasp them with its mouth or hand. Some neurons discharge during the entire action of bringing the hand to the mouth and opening the mouth to ingest food, as well as during arm reaching and associated neck- and trunk-orienting movements. Activity in other neurons is correlated not only with reaching but also with other behaviors such as the avoidance of threatening stimuli. The sensory representation of peripersonal space in area F4 contributes to the planning and execution of those behaviors.

### The Superior Parietal Cortex Uses Sensory Information to Guide Arm Movements Toward Objects in Peripersonal Space

A key requirement for efficient reaching is knowledge of where the arm is

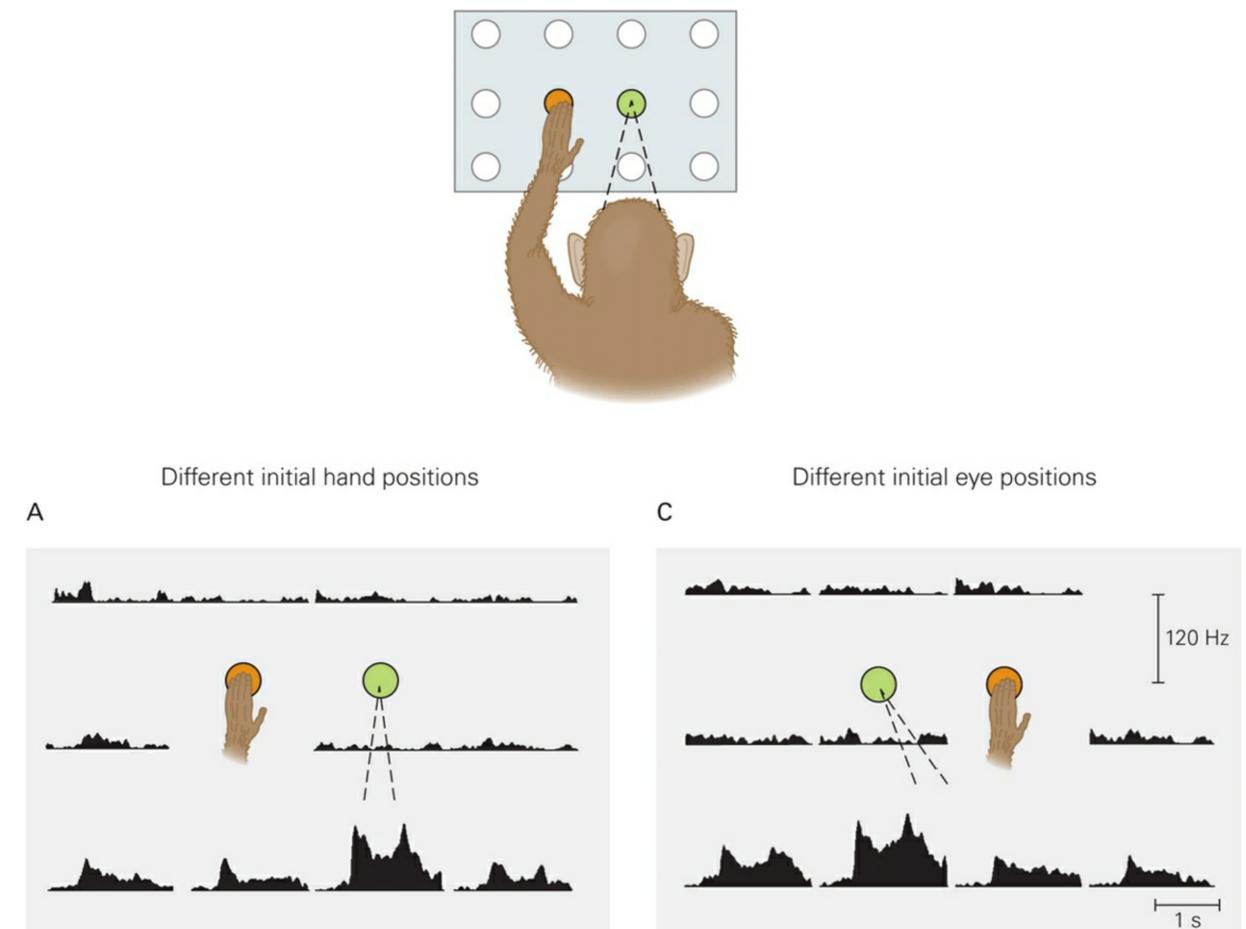
before and during the action. Lesion studies suggest that this information is represented in Brodmann's area 2, the primary somatosensory area (S-I), and in the superior parietal lobule. Patients with lesions of these regions are unable to reach toward objects efficiently, even though they do not have the deficits of spatial perception, such as spatial neglect, that are typical of lesions in the inferior parietal lobe (see [Chapter 19](#)).

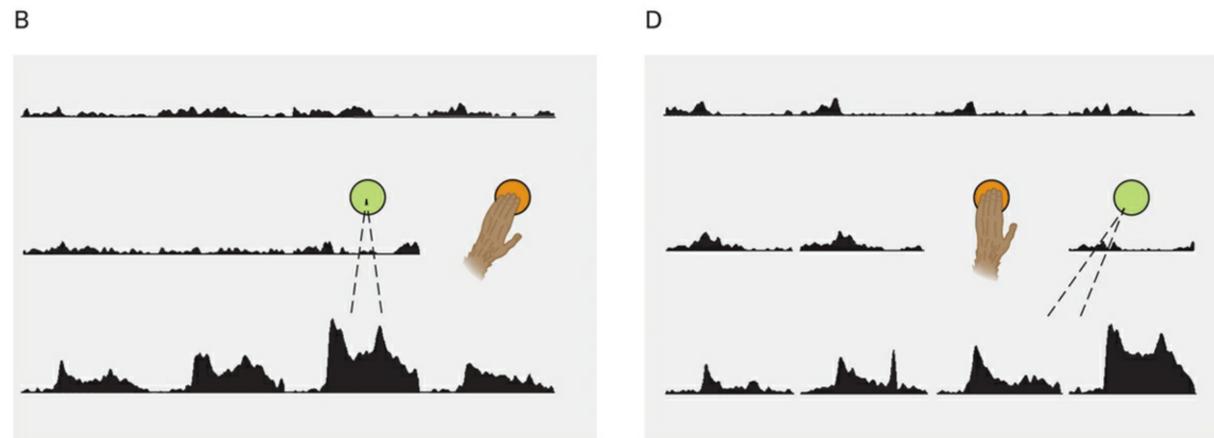
Although single-neuron studies confirm the role of these areas in providing information about arm location, there are clear functional differences between the two areas. Neurons in area 2 usually respond to tactile input from a limited part of the body or to movements of a single joint or a few adjacent joints in specific directions and most commonly on the contralateral side of the body. In contrast, many neurons in the superior parietal lobule discharge during combined movements of multiple joints, the assumption of specific postures, or movements of the limbs and the body. Some cells also respond during combined movements of the arms and hind limbs or bilateral movements of both arms.

These findings indicate that, unlike neurons in area 2 that encode the positions and movements of specific parts of the body, neurons in the superior parietal lobe integrate information on the positions of individual joints as well as the positions of limb segments with respect to the body. This integration creates a body schema that provides information on where the arm is located with respect to the body and how the different arm segments are positioned with respect to one another. This schema provides fundamental information for the proprioceptive guidance of arm movements.

More posterior and medial sectors of the superior parietal cortex also receive input from areas V2 and V3 of the extrastriate visual cortex. Important nodes in this network include areas V6A and PEc and an area of parietal cortex involved in reaching described by Richard Andersen and colleagues and which most likely corresponds to the medial intraparietal area (MIP) and nearby parts of the superior and inferior parietal cortex (see [Figure 38-4A](#)). In these areas the spatial representation for reaching is not based on body-centered coordinates. For example, neurons in V6A and PEc often signal the retinal location of possible targets for reaching, but their activity is also strongly modulated by complex combinations of inputs related to the direction of gaze and the current arm posture and hand position.

Andersen and his associates propose that the reach-related region of parietal cortex is particularly important for specifying the goal or target of reaching but not how the action should be performed. The activity of many neurons in this area varies with the location of the target relative to the hand. Remarkably, however, this motor error signal is not centered on the current location of the hand or target but rather on the current direction of gaze. Each time the monkey looks in a different direction the reach-related activity in the neurons changes ([Figure 38-6](#)). In contrast, the reach-related activity of many neurons in area PEip is less gaze-centered and more related to the current hand position and arm posture.





**Figure 38–6** Neurons in the parietal reach area encode target location in eye-centered coordinates. An upright board contains an array of pushbuttons. The four panels show the possible behavioral conditions at the beginning of a trial. The initial hand position and point of visual fixation are indicated by the **green** and **orange buttons**, respectively. Histograms of activity in a single neuron are arranged to correspond to the locations of the buttons on the board that serve as the target of a reaching movement from the start position in different trials. The firing pattern of this neuron does not vary with changes in initial limb position (A, B), but shifts with a change in the initial direction of gaze (C, D). The neuron thus signals the target location relative to the current direction of gaze, independent of the direction of arm movement required to reach the target. (Modified, with permission, from Andersen and Buneo 2002.)

Another important property of neurons in the parietal reach region is that they respond not only to passive sensory inputs but also before the onset of movements and during the planning period of delayed-reaching tasks. This behavior indicates that these neurons receive centrally generated signals about motor intentions prior to movement onset, likely through their reciprocal connections with precentral motor areas. Recent theoretical and experimental findings suggest that this combination of peripheral sensory and central motor inputs permits the parietal reach region to integrate sensory input with efference copies of outgoing motor commands to compute a continuously updated estimate of the current arm state and a prediction about how the arm will respond to the motor command. This forward internal model of the arm could be used to make rapid corrections for errors in ongoing arm movements and to acquire

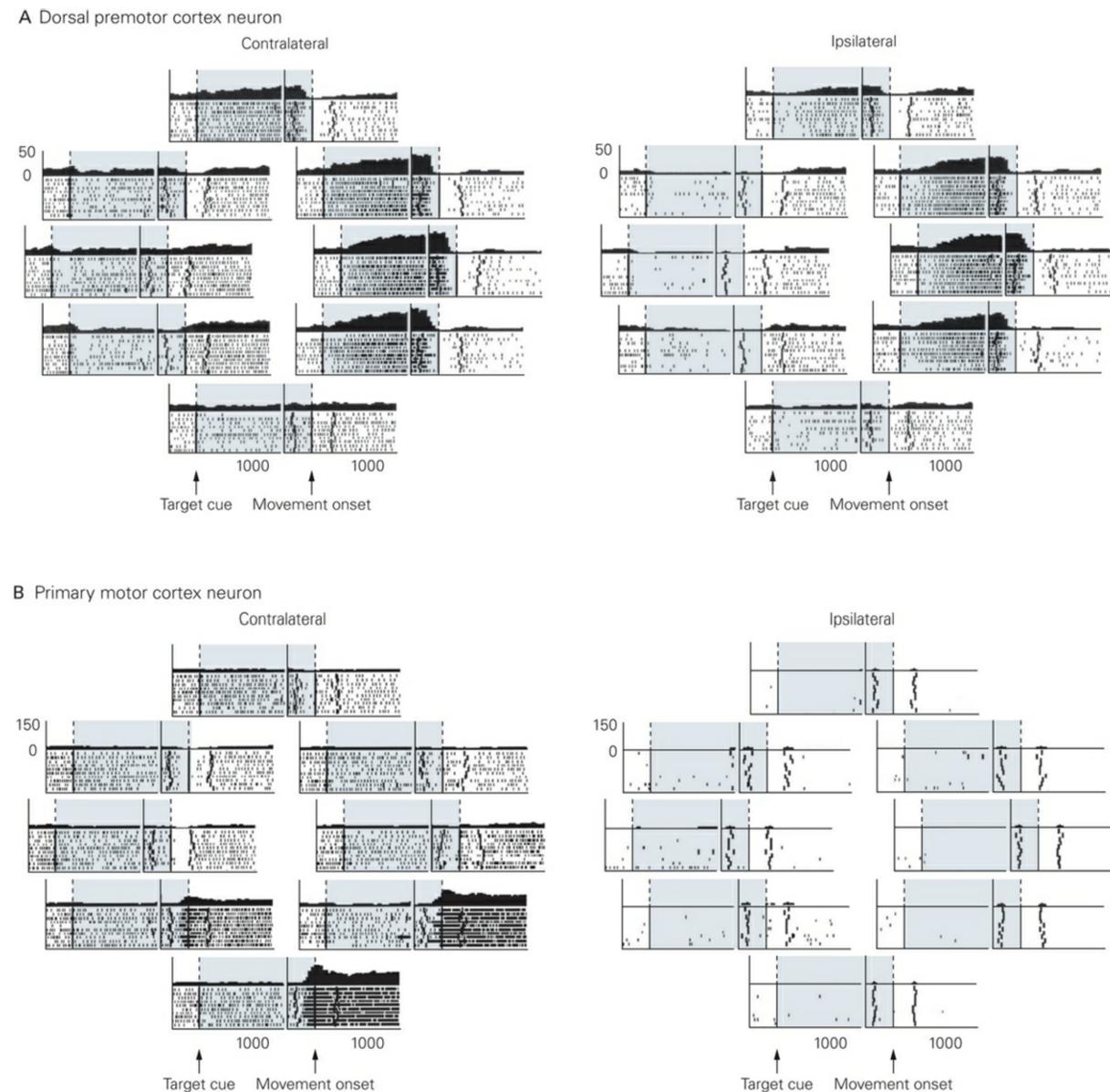
motor skills.

The functional properties of areas in the superior parietal cortex concerned with reaching suggest an intriguing explanation of the clinical phenomenon of *optic ataxia*. Patients with a lesion of the superior parietal cortex have difficulty with visually guided arm movements toward an object. Making errors in the frontal or sagittal plane, the arm gropes for the target until it encounters the object almost by chance. The deficit is severe when the target is in the peripheral part of the visual field, less when the target lies in the parafoveal region, and negligible when the patient fixates the target. The symptoms of optic ataxia may result from failure of the neural circuits that convert sensory information about targets and the arm into motor plans or from failure of the circuits that contribute to a predictive forward model of the arm's current state.

### Premotor and Primary Motor Cortex Formulate More Specific Motor Plans About Intended Reaching Movements

The reach-related areas of the parietal cortex are reciprocally connected to several precentral motor areas, including the primary motor cortex, dorsal and ventral premotor cortex, and supplementary motor area. Neurons in all of these areas contribute to sensorimotor transformations that provide increasingly detailed information about the desired spatial kinematics and causal mechanical details of the movements.

For example, the reach-related neurons in the dorsal premotor cortex are much less strongly influenced by the direction of gaze than are neurons in the parietal reach area. Instead they are driven by the direction of the intended reaching movements during the planning period of delayed-reaching tasks and during the reaching movement itself. Furthermore, during the planning period many dorsal premotor neurons signal the direction of movement to the target whether the left or right arm is used to reach for the target ([Figure 38–7](#)). This finding suggests that the premotor neurons represent the appropriate extrinsic spatial kinematics of the reaching movement independent of the arm that will perform it. In contrast, the activity of most reach-related neurons in the primary motor cortex is related to movement of the contralateral arm.



**Figure 38–7** Reaching movement is represented differently in the pre-motor and primary motor cortex during planning and execution of the movement. (Modified, with permission, from Cisek, Crammond, and Kalaska 2003.)

**A.** Activity of a dorsal premotor cortex neuron in a monkey during an instructed-delay reaching task. The animal is trained to reach for targets in eight directions from a central starting position using either arm. During testing one arm is contralateral and one arm is ipsilateral to the recording site. During the planning period—the time between the presentation of the target cue and the delayed onset of movement

—the neuron is directionally tuned with a preference for rightward movements.

The directional tuning is identical whether the left or right arm is used. The neuron is relatively inactive during movement execution. In each raster plot the left vertical line indicates presentation of the target cue, and the right vertical line indicates the onset of arm movement. The thick ticks to the left and right of the movement-onset line in each trial indicate, respectively, presentation of the go cue and the end of movement.

**B.** Activity of a primary motor cortex neuron during the same task as in part A. The neuron is strongly active and directionally tuned toward the lower targets when the contralateral arm is used but only during the execution phase. It is essentially inactive when the ipsilateral arm is used.

In other studies a monkey was trained to make arm movements to move a cursor on a computer monitor. In some trials the motions of the arm and cursor were collinear. In other trials they were decoupled in one of three ways: by rotating the cursor motion at a 90 degree angle to the arm movement, applying a mirror-image transformation, or requiring the monkey to make elliptical motions of its arm to draw a circle with the cursor. Some neurons, especially in the primary motor cortex, signaled the motions of the arm in both the collinear and decoupled conditions. Other neurons concentrated in the dorsal and ventral premotor cortex signaled the desired motions of the cursor under the different visuomotor conditions.

**Box 38–1 The Cortical Motor System Does Not Solve Newtonian Equations**

Understanding the cortical mechanisms underlying the planning and execution of reaching movements requires insight into how single neurons and neuronal populations encode different properties of intended movements and how they transform that information into motor commands.

For many years the study of the cerebral cortical mechanisms of motor control has been guided by terminology and concepts bor-

rowed from physics, engineering, and control theory. Many studies have therefore sought and found statistical correlations between the activity of neurons in movement-related cortical areas and such movement-related parameters as target location, the velocities of hand displacement and reach trajectory, motor output force, and joint torque.

It is unlikely, however, that the motor system controls movements by encoding them in the familiar but arbitrary terms of Newtonian mechanics or by solving equations derived from the Newtonian laws of motion. Even though neural responses are consistent with a sequence of sensorimotor transformations, it is improbable that neural circuits explicitly solve the trigonometric and algebraic equations that define those transformations.

The cortical mechanisms for the planning and control of reaching movements are not based on the formalisms and first principles of physics, mechanics, and mathematics. They are determined by the stream of signals provided by peripheral sensors, by the force-generating properties of muscles, by the emergent dynamic mechanical properties of the arm, and by the properties of the spinal motor circuitry that converts the descending motor commands into muscle activity and movements.

These findings indicate that premotor cortex neurons can generate an abstract representation of the goal of the motor output, in this case the motion of the cursor that the monkey was moving, independent of the arm movements that control the cursor's motion. Other neurons in the premotor and primary motor cortex translate that abstract representation into signals about what the arm must do to produce the desired cursor movements.

Although these results suggest that the motor system initially plans reaching movements in extrinsic spatial coordinates, we move by contracting muscles. Many neurophysiological studies have therefore sought the neural correlates of the transformation of a desired spatiotemporal movement pattern into its causal forces and muscle activity. The consensus is that the primary motor cortex plays an important role in that transformation (see [Chapter 37](#)). However, the final motor command for the

muscle-activity patterns required to execute the desired reaching movement is probably generated by spinal motor circuits.

In summary, neurophysiological studies have provided support for the general hypothesis that reaching movements involve neuronal processes that implement a sequence of transformations between sensory input and motor output. These processes occur in a dynamic, distributed network of cortical areas rather than in a strictly serial pathway. There are no abrupt transitions of cellular properties between cortical areas; instead there is a progression. Neural correlates of each putative transformation can be seen in both parietal and precentral areas, whose true nature and functions are still not fully known (Box 38–1).

## Grasping an Object Requires Sensory Information About Its Physical Properties

At the same time as neural populations in several areas of the parietal and precentral cortex are controlling the reaching movement to bring your hand into proximity with a coffee cup, neural populations in several other overlapping and adjacent parietal and precentral areas are preparing the hand to grasp and lift the cup. These areas include the anterior intraparietal area (AIP) and area PFG of the rostral inferior parietal cortex, the ventral premotor cortex, and the large central core of the arm's motor map in the primary motor cortex (see [Figure 38–4B](#)).

We have seen how the planning and control of the reaching movement involves a sequence of sensorimotor transformations that convert input about the spatial location of the coffee cup into a motor command to move the hand to the cup. The sensorimotor transformation involved in grasping the coffee cup is somewhat different. The sensorimotor system for the hand must possess a mechanism that can match the configuration of the hand and fingers and the grip forces exerted by the fingers to the physical properties of the cup. These include properties that you can see, such as the size, shape, and spatial orientation of the coffee cup. They can also include physical properties that have been learned through experience, such as the cup's expected weight and fragility and whether it contains hot or cold liquid. All of these factors influence how you use your hand to grasp and lift the cup.

To help understand how visual information about an object is transformed into specific movements to grasp and manipulate it, we shall speak of the *affordances* of an object, a concept introduced by James Gibson. When we observe an object our visual system automatically identifies the parts of it that allow for efficient manipulation of it. Those parts are not necessarily the features that permit recognition of the object, but rather those that afford specific opportunities for action. For example, the handle, body, and top of the coffee cup afford opportunities to grasp it. Any one affordance may be more appropriate in particular circumstances. If the cup is hot, for example, you will likely prefer to use the handle. If the handle is large, you may be able to insert all four fingers into it, but if it is small you may be able to use only one or two. If the coffee is not too hot, you may just as likely grasp the cup by its body or top.

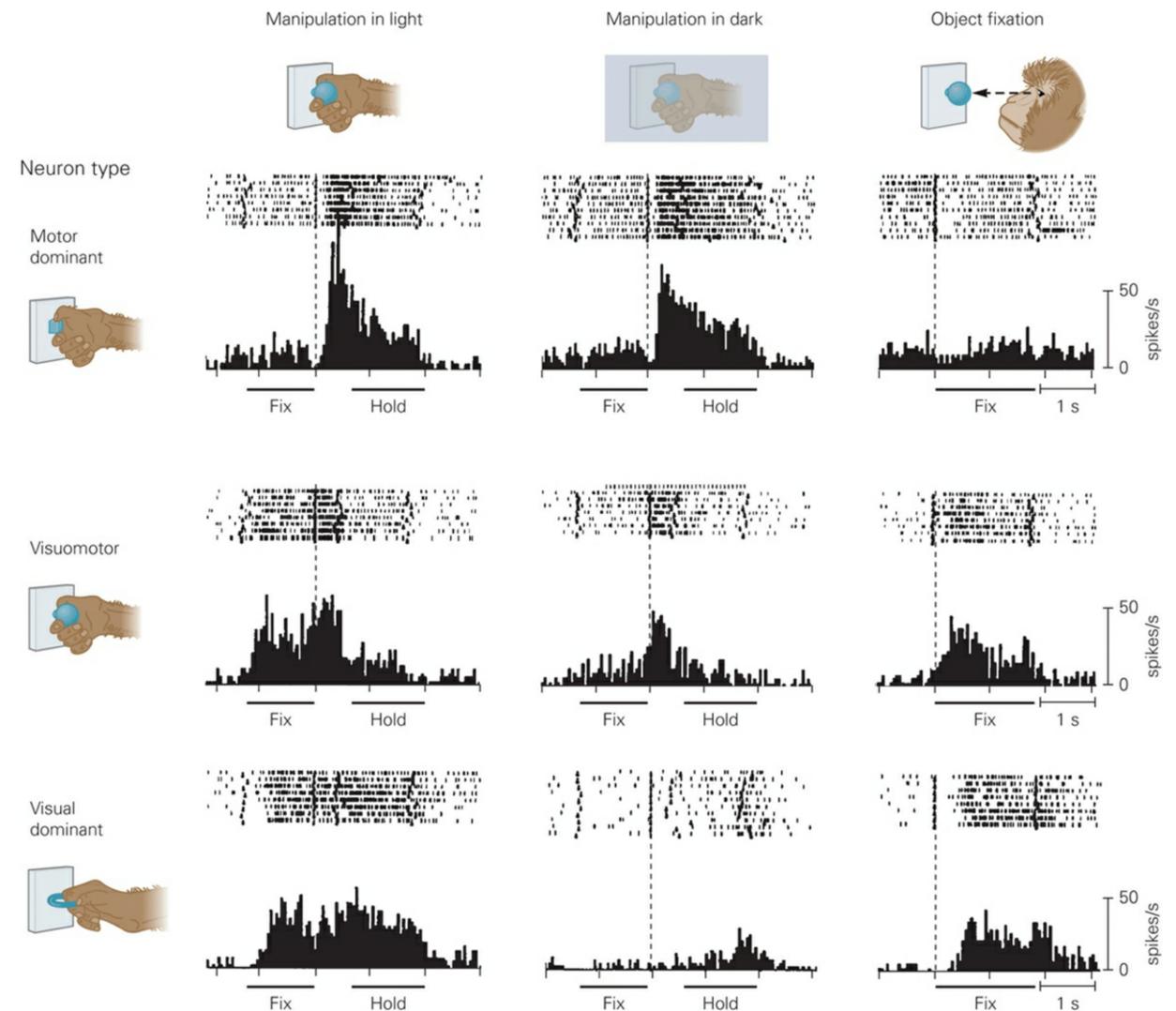
### Neurons in the Inferior Parietal Cortex Associate the Physical Properties of an Object with Specific Motor Acts

Beside being involved in the representation of space and the sensory guidance of reaching movements, the dorsal visual stream also provides the inferior parietal cortex with the visual information necessary for coding object affordances. The cortical processes that extract the affordances of observed objects and associate them with specific actions begin in the lateral and rostral part of the inferior parietal cortex, especially in the AIP and PFG areas (see [Figure 38-4B](#)).

The functional properties of neurons in AIP of the monkey have been investigated by Hideo Sakata and co-workers. They recorded the responses of neurons under three conditions: grasping objects in the light when they can be seen or in the dark when they cannot be seen, and merely observing the objects. The experiments showed that the neurons fall into three major categories: visually dominant, visuomotor, and motor-dominant neurons. Together these three classes of neurons contribute to neural operations that use visual input to encode the affordances of observed objects and associate them with appropriate motor acts.

*Visual-dominant neurons* discharge when the monkey fixates an object or grasps it in the light, but not when the monkey grasps an object in

the dark ([Figure 38-8](#)). In contrast, *motor-dominant neurons* are active during grasping both in the light and in darkness. They are not active, however, during object fixation, indicating that they signal primarily the motor act of grasping, independent of visual input. Many visual-dominant and motor-dominant neurons respond selectively to objects of particular shapes such as spheres, rings, and flat disks, each of which requires a different type of grip.



**Figure 38-8** The three major categories of neurons in the anterior intraparietal area. A monkey sits in front of a dark box housing six distinct objects that are presented one at a time in a random order. Neural activity is tested during three behaviors: manipulation of the object in light, manipulation in the dark, and object fixation. The protocol for the manipulation in light begins with a red spot of light projected onto the object. The

monkey fixates the spot of light and presses a lever that turns on a light inside the box that illuminates the object. After the monkey has held the lever for 1.0–1.2 s, the light changes to green, cuing the monkey to release the lever and grasp the object.

In the records shown here trials are aligned at the end of the visual fixation period and beginning of the reach-to-grasp period. The protocol for manipulation in the dark is similar except that all trials after the first are executed in darkness. In the object fixation protocol the green light cues the monkey to fixate the red spot of light and press the lever to illuminate the object; the animal then releases the lever but does not grasp the object. Trials are aligned at the beginning of the fixation period. The activity of different anterior intraparietal neurons shows differing degrees of dependence on the visual and motor components of this task. (Modified, with permission, from Murata et al. 2000.)

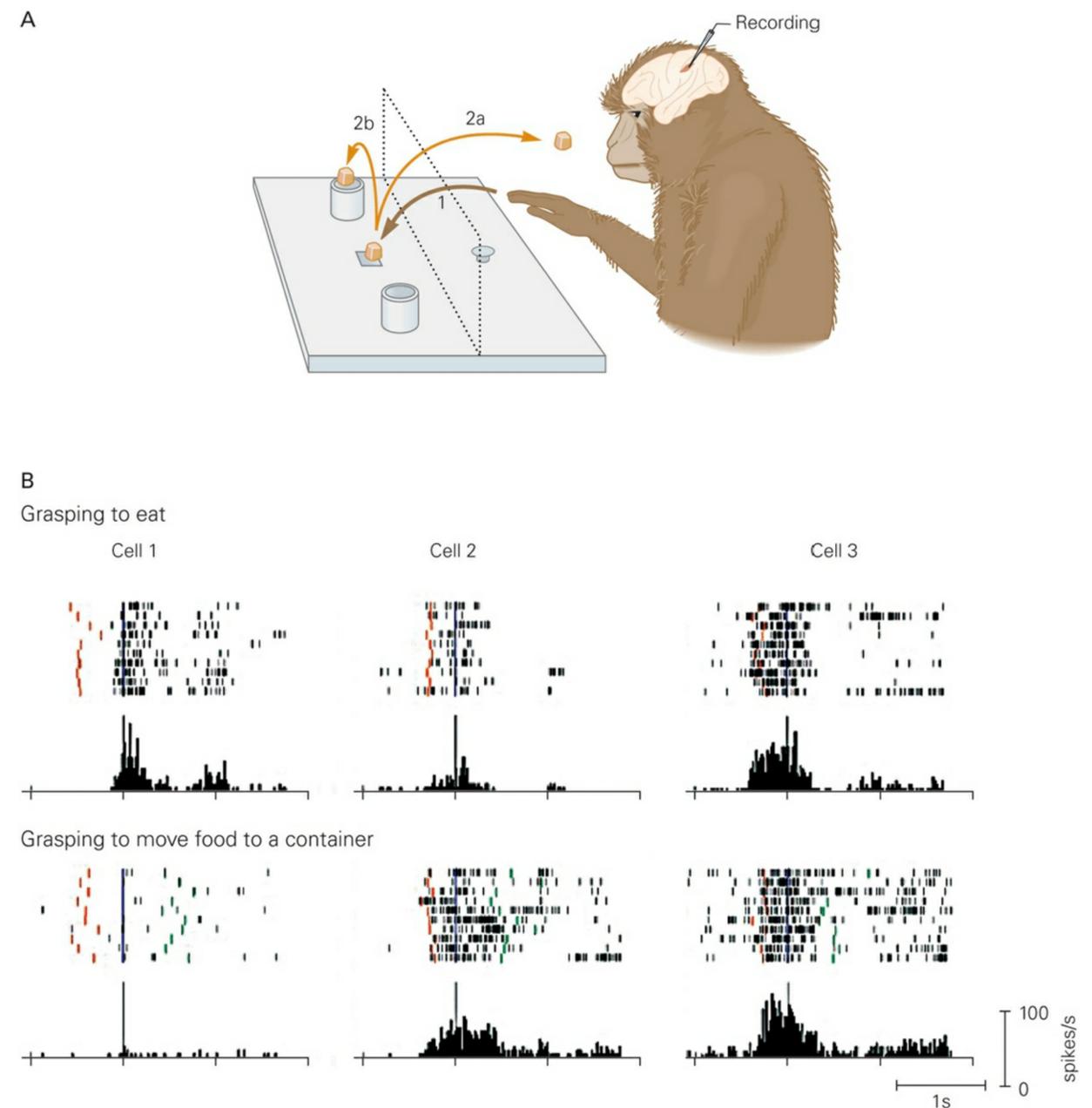
*Visuomotor neurons* discharge when the monkey grasps objects, whether in the dark or in the light, but also during visual fixation. Individual visuomotor neurons additionally respond preferentially to shape: A neuron that becomes active when the monkey looks at a small disk also discharges when the monkey grasps the disk, but not when it grasps a sphere. This specificity to the shape of viewed objects indicates that these neurons link the affordances of an object to particular motor actions.

### The Activity of Neurons of the Inferior Parietal Cortex Is Influenced by the Purpose of an Action

We often perform similar motor acts for different purposes. We pick up a coffee cup to drink from it or to wash it. The motor act of grasping is the same, but the objective is different.

As already noted, Mountcastle and Hyvärinen reported that the activation of many parietal neurons depends on the goal of the act being performed. More recently, Leonardo Fogassi and co-workers compared the firing patterns of grasp-related inferior parietal neurons under two conditions. In one the monkey grasped a piece of food and brought it to its mouth; in the other it placed the food into a container. The activity of many of the neurons varied with the task. Some were strongly active when the monkey picked up food to bring it to the mouth, but only weakly

excited when it picked up food to put it into a container. Others showed the opposite response (Figure 38–9). Factors such as grasping force, kinematics of reaching movements, and type of stimulus could not account for the context-specific activation of the neurons.



**Figure 38–9** The activity of functionally distinct parietal motor neurons varies with the purpose of a grasping action. (Modified, with permission, from Fogassi et al. 2005.)

**A.** Apparatus and protocol for the experiment. A monkey is trained to press a button (start position) and reach and grasp a piece of food

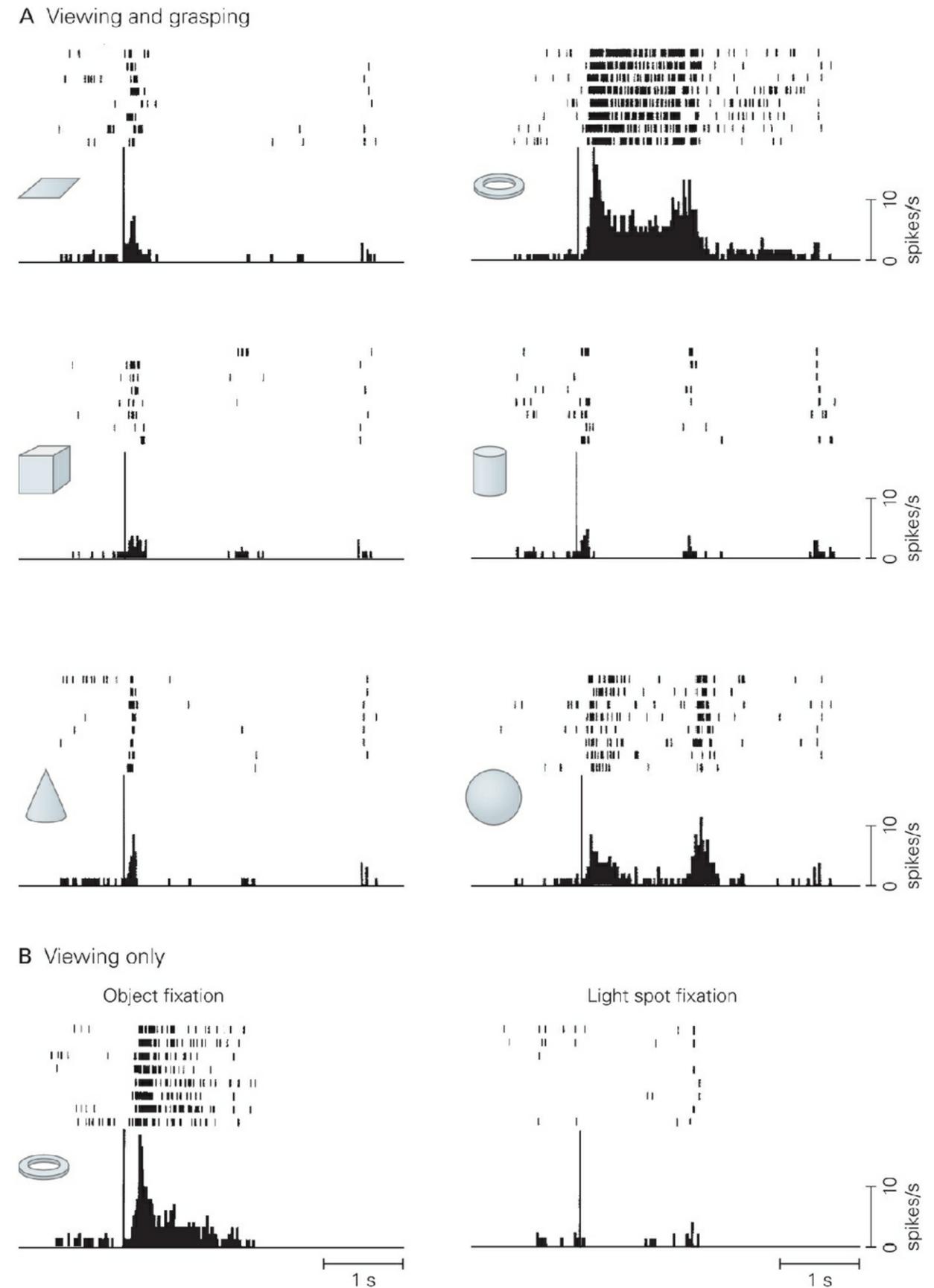
(1) either to bring it to the mouth (2a) or to place it into a container (2b). In the first condition the monkey eats the food brought to the mouth, whereas in the second it receives a food reward after the correct response.

**B.** Activity of three neurons in the inferior parietal cortex during the two actions. Cell 1 discharges more strongly when the monkey grasps the food to eat it than when it grasps the food simply to move it. The behavior of cell 2 is the opposite. Cell 3 shows no difference between the two actions. Raster plots and histograms are aligned with the moment when the monkey touches the object to be grasped. **Orange tics** indicate when the monkey releases its hand from the button at the starting position; **green tics** indicate when the hand touches the container.

### The Activity of Neurons in the Ventral Premotor Cortex Correlates with Motor Acts

The rostral part of the ventral premotor cortex, often called area F5, is reciprocally connected with the anterior intraparietal area, the rostral part of the inferior parietal cortex, and the secondary somatosensory area. Functional mapping of area F5 based on electrical stimulation shows that this area contains representations of hand and mouth movements that overlap considerably.

Recording studies in monkeys indicate that the response properties of F5 neurons are elaborations of the properties of neurons in the parietal regions that project into area F5. Unlike the anterior intraparietal area, however, F5 contains few or no visually dominant neurons. Murata and colleagues found that many neurons in area F5 discharge exclusively during the execution of certain motor acts, both in the light and in the dark. About 20% of the neurons, called *canonical neurons*, also respond to the sight of three-dimensional objects. They thus discharge whether the animal grasps an object or simply observes it and they show a preference for a particular type of grip ([Figure 38–10](#)).



**Figure 38–10** A canonical neuron in the ventral premotor cortex (area F5) of a monkey. (Reproduced, with permission, from Murata et al. 1997.)

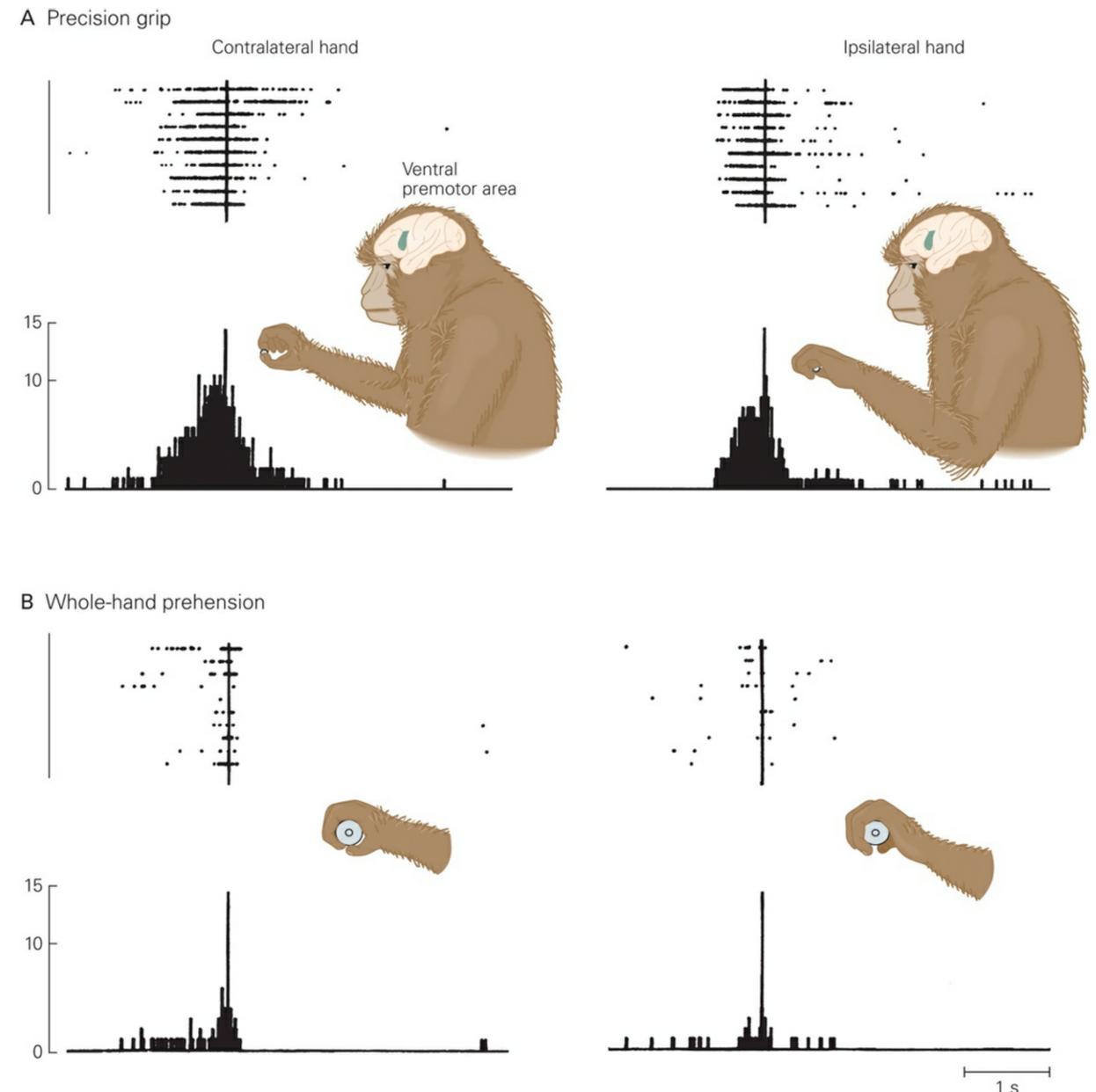
**A.** The neuron’s responses to viewing and grasping of six objects vary with the shape of the objects. The cell is more strongly activated by a ring-shaped object than by other shapes.

**B.** The neuron responds when the animal fixates a ring-shaped object but not when the animal fixates a light spot. Raster plots and histograms are aligned (vertical bar) with the moment when the object becomes visible.

The signal from a canonical neuron is identical whether the monkey observes or grasps an object. Thus when the cell is activated by the sight of an object, its activity signifies how to interact with the object. The activation of a canonical neuron does not automatically lead to overt action, for inhibitory control is exerted by other neural circuits. Only when that inhibition is released does the internal representation become an overt action.

Another fundamental property of area F5 neurons is that their discharge correlates with the goal of a motor act and not with the individual movements forming it. Thus many neurons in F5 discharge when grasping is executed with effectors as different as the right hand, the left hand, and even the mouth. Conversely, an area F5 neuron may be active when an index finger is flexed to grasp an object but not when the animal flexes the same finger to scratch itself. This property of grasp-related neurons in area F5 resembles that of many reach-related neurons in the dorsal premotor cortex.

Based on these properties, Giacomo Rizzolatti and co-workers subdivided F5 neurons into several functional classes that discharge preferentially during certain stereotypical hand actions, such as grasping, holding, tearing, or manipulating objects. In each of these classes many neurons discharge only if the monkey uses a specific type of grip, such as precision grip, whole-hand prehension, or finger prehension (Figure 38–11). Precision grip is the type most represented. Moreover, individual F5 neurons may discharge selectively at particular stages of one type of prehension. Some discharge throughout the entire action, others during the opening of the fingers, and still others during finger closure.



**Figure 38–11** Some individual neurons in the ventral premotor cortex (area F5) of a monkey discharge selectively during one type of grasping. This neuron discharges vigorously during precision grip with either the right or the left hand but barely at all during whole-hand prehension with either hand. Raster plots and histograms are aligned (vertical line) with the moment the monkey touches the food (A) or grasps the handle (B). (Reproduced, with permission, from Rizzolatti et al. 1988.)

The view that the organization of area F5 is based on a repertory of motor acts has important implications. First, the existence of neurons that encode a limited range of specific motor acts is consistent with and

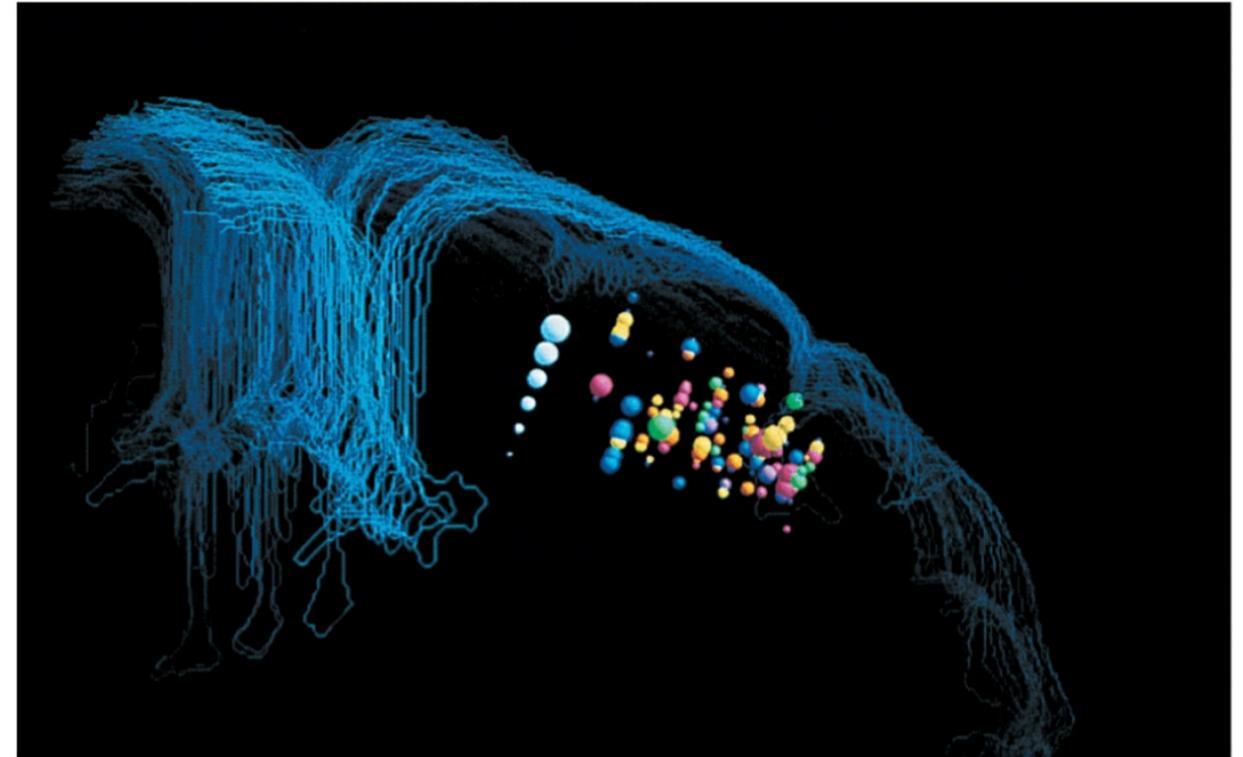
may account for the fact that we repeatedly interact with a particular object in a specific way. There exists in principle a very large number of possible ways to grasp an object, but we typically use only a few of them. We almost never use the fourth and fifth fingers to lift a cup of coffee, for example. The organization of area F5 allows the object affordances extracted by the anterior intraparietal area to be associated with appropriate motor actions. As we shall see later, this organization may also underlie the ability to recognize the goals of actions performed by others.

### **The Primary Motor Cortex Transforms a Grasping Action Plan into Appropriate Finger Movements**

The ventral premotor cortex, including areas F4 and F5, projects to the hand and arm fields of the primary motor cortex. The primary motor cortex contains the largest and most detailed representation of finger and hand movements of all cortical motor areas (see [Chapter 37](#)).

Although some hand-related neurons in the primary motor cortex discharge in relation to the goal of a motor act rather than to specific movements, many others are active during finger or wrist movements across a broad range of grasping motions and object manipulation as well as during other activities. The grasp-selective input from premotor areas could facilitate the recruitment and organization of a set of neurons distributed across the motor map that controls a particular grasping action and matches it to an object's shape ([Figure 38-12](#)).

A



B



**Figure 38–12** Neurons that control the movement of individual fingers are distributed throughout the hand-control area of the primary motor cortex. (Reproduced, with permission, from Schieber and Hibbard 1993.)

A. A view of the frontal pole of the monkey's cerebral cortex shows the interhemispheric fissure and lateral convexity. The colored spheres represent the locations of single neurons in the hand-control region of the primary motor cortex from which recordings were made.

B. The same data at a higher magnification. Neurons that discharge preferentially during isolated movements of individual digits and the wrist are represented by different colors. As shown by the scale at the left, the diameter of a sphere indicates a neuron's change in firing frequency (spikes per second). Neurons that are most active for a particular digit or for the wrist are not grouped together but instead are distributed throughout the hand-control area of the primary motor cortex.

During grasping, hand muscles must exert gripping forces perpendicu-

lar to the surface of the object to secure it between the fingers without slippage and to overcome the load forces imposed by gravity. Many neurons in the primary motor cortex are very sensitive to sensory feedback from somatic receptors in the hand that signal deformations of the skin perpendicular to the skin's surface. These cells are ideally organized to provide feedback control of grip and load forces during grasping and manipulation of an object.

In summary, when you look at your cup of coffee, neurons in the inferior parietal cortex, especially in the anterior intraparietal area, begin signaling the cup's affordances. These affordances are linked with specific grip representations in the parietal cortex and in the ventral premotor cortex. This activity is not sufficient to initiate grasping. Other areas controlling the initiation of action must also become active to allow the action represented in area F5 to be executed. When this occurs F5 neurons activate primary motor cortex neurons that control independent finger movements and spinal motor neurons and interneurons involved in hand opening and closing. Finally, as your hand touches the cup's handle, sensory feedback provides the somatosensory information necessary for forming and maintaining a stable grip.

This picture of grip generation is very schematic. It does not take into consideration the activity of reciprocal connections from the primary motor cortex to premotor areas and from there to the associated parietal areas. Even more important, we have focused exclusively on the cortical mechanisms responsible for action generation, leaving aside the important contributions of the cerebellum and basal ganglia (see [Chapters 42](#) and [43](#)).

## The Supplementary Motor Complex Plays a Crucial Role in Selecting and Executing Appropriate Voluntary Actions

Classical electrical-stimulation studies of motor regions of the cortex showed that the medial wall of the frontal cortex contains a map of contralateral body movements (see [Chapter 37](#)). This region was initially called the supplementary motor area. Today there is agreement that this region contains two areas that have distinct cytoarchitectonic character-

istics, connections, and functional properties: a more caudal supplementary motor area (SMA) proper and a more rostral presupplementary motor area (pre-SMA), which we will collectively call the supplementary motor complex (SMC).

The motor map in SMA covers the entire contralateral body but is not as detailed as the motor map in the primary motor cortex. Neurons in SMA require strong stimulus currents to evoke movements, which are often complex actions such as postural adjustments or stepping and climbing and can involve both sides of the body. Such movements are rarely evoked by stimulation of the primary motor cortex. In humans stimulation of the SMC below the threshold for movement initiation sometimes evokes an urge to move. Lesions of the SMC do not result in paralysis but do produce problems initiating or suppressing movement (Box 38–2).

The results of stimulation and lesion studies of the SMC indicate that motor centers outside of the primary motor cortex have a role in motor control. Further support for this idea emerged from studies of humans using evoked potentials. Recordings of slow cortical potentials from motor areas during the execution of self-generated movements showed that a slow potential arises in the frontal cortex 0.8 s to 1.0 s before the onset of movement. This signal, named the *readiness potential*, has its peak in the medial part of the precentral motor region over the SMC. Because it occurs well before movement, the readiness potential provides evidence that this region is involved in forming the intention to move, not just in movement execution.

Neurons in both the SMA and pre-SMA discharge before and during voluntary movements. There is a gradient in response properties across each area. Recent studies have indicated that much of the higher-order control of motor behavior originally attributed to SMA proper actually reflects the contribution of the pre-SMA. Unlike neurons in the primary motor cortex, the activity of most SMA neurons is less tightly coupled to particular actions of a specific part of the body and instead appears to be associated with more complex, coordinated motor acts of the hand, arm, head, or trunk.

**Box 38–2 Neurological Disorders Affect the Initiation and**

**Suppression of Voluntary Behavior**

Lesions of the supplementary motor area, presupplementary motor area, and pre-frontal areas connected with them produce deficiencies in the initiation and release of movements.

Initiation deficits manifest themselves as loss of self-initiated arm movements, even though the patient can move when adequately prompted. This deficit can involve contralesional parts of the body (*akinesia*) and speech (*mutism*).

Release phenomena, in contrast, include a large variety of behaviors that patients cannot suppress when inappropriate. These include compulsive grasping of a stimulus when the hand touches it (*forced grasping*), irrepressible reaching and searching movements aimed at an object that has been presented visually (*groping movement*), and impulsive arm and hand movements to grab nearby objects and even people without conscious awareness of the intention to do so (*alien- or anarchic-hand syndromes*).

Particularly interesting is the syndrome known as *utilization behavior*, in which a patient compulsively grabs objects and uses them without consideration of need or the social situation. Examples are picking up and putting on multiple pairs of glasses or reaching for and eating food even when the individual is not hungry or when the food is clearly part of someone else's meal.

These deficits in the initiation and suppression of actions may represent opposite facets of the same functional role for the supplementary motor area and especially the presupplementary motor area in the conditional control of voluntary behavior.

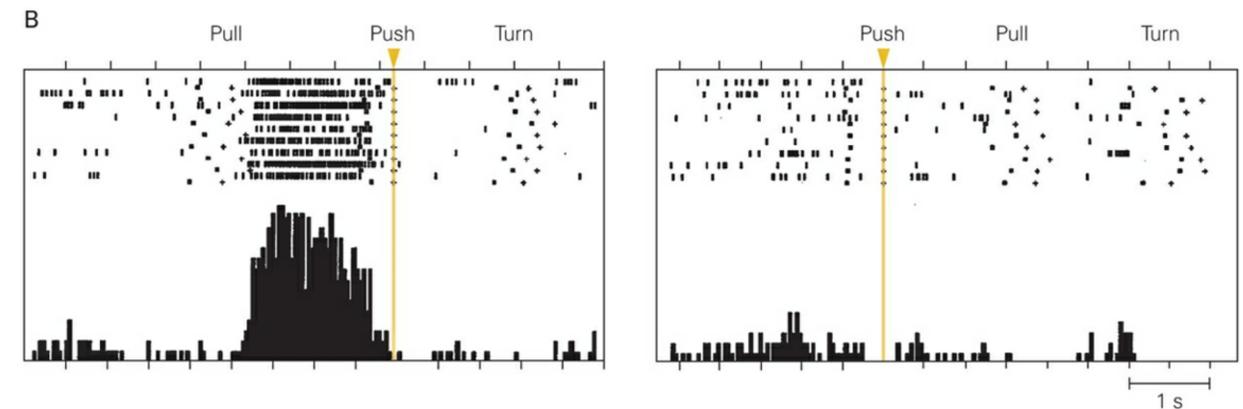
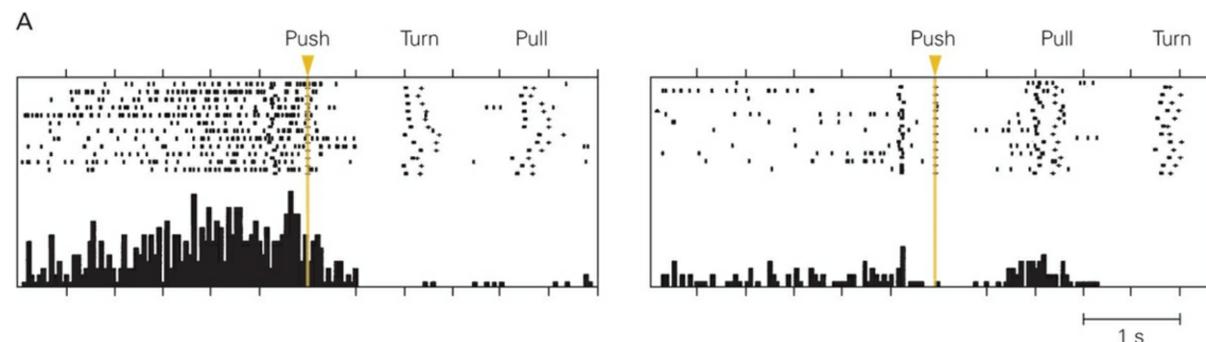
In contrast, pre-SMA neurons often begin to discharge long before movement onset, are less tightly coupled to the execution of movements, and show an even more context-dependent relation to impending movements. For example, when tested in the same conditions used to study reach- and grasp-related activity in the parietal and ventral premotor cortex, the activity of pre-SMA neurons is less coupled to distinct actions of the hand or arm than neurons in the other regions, but is instead related to the overall act of reaching to grasp and manipulate objects.

Some pre-SMA neurons begin to discharge when a graspable object ap-

pears anywhere in the monkey's field of view and increase firing as the object moves within reach. Others are initially inhibited when the object appears but begin to discharge as soon as it moves within reach. Some neurons discharge during the actual reach-to-grasp movement, whereas others are inhibited. Although the patterns of response may vary, what remains constant is that changes in firing rate depend on whether an object can or cannot be acted upon. The pre-SMA may therefore contain a system that controls the execution of motor acts that are encoded in more lateral parietal-precentral circuits.

Many different roles in voluntary behavior have been attributed to the SMC, and its contribution remains controversial. One popular hypothesis was that the SMC is concerned with self-generated or internally guided behavior, whereas the dorsal and ventral premotor cortex primarily controls externally guided behavior. However, recent single-neuron studies do not support that functional dichotomy.

The SMC has been implicated in the organization and execution of movement sequences. Tanji and co-workers showed that some SMC neurons discharge before the performance of a particular sequence of three movements but not before a different sequence of the same movements (Figure 38–13). Other neurons discharge when a particular movement occurs in a specific position in a sequence or when a particular pair of consecutive movements occurs regardless of their order. Some SMC neurons encode the position of a movement in a sequence independently of the nature of the act or of how many movements remain to be executed before a reward is delivered.



**Figure 38–13** Some neurons in the supplementary motor complex encode a specific sequence of motor acts. (Modified, with permission, from Tanji 2001.)

**A.** A neuron discharges selectively during the waiting period before the first movement of the memorized sequence push-turn-pull (left panel). The cell remains relatively silent, however, when the sequence is push-pull-turn (right panel), even though the first movement in both sequences is the same. Triangles at the top of each raster plot indicate the start of the first movement.

**B.** Records of a neuron whose activity increases selectively during the interval between completion of one motor act, a pull, and the initiation of another act, a push. The cell is not active when a push is the first movement in the sequence, or when pull is followed by turn.

Still other studies have suggested that the SMC is primarily concerned with the acquisition of certain motor skills and less with their performance. Finally, the SMC has been implicated in the so-called *executive control* of behavior, such as the operations that are required to switch between different actions, plans, and strategies. For example, some SMC neurons discharge strongly when a subject receives a sensory cue instructing it to change movement targets or to suppress a previously intended movement.

These seemingly disparate behaviors may reflect a more general role of the SMC in *contextual control* of voluntary behavior. Contextual control is concerned with selecting and executing actions deemed appropriate on the basis of different combinations of internal and external cues as well as withholding inappropriate actions. Such control also situates a particular

action in a goal-directed sequence or in a specific environmental and social context.

## The Cortical Motor System Is Involved in Planning Action

So far we have focused on the role of cortical motor areas in the sensorimotor transformations required to reach for and grasp an object. However, voluntary behavior is not always directed specifically at objects or shaped by their physical properties. It is often determined by long-term goals and social conventions and may involve choosing from among alternative actions.

Furthermore, like the supplementary motor complex, many cortical areas implicated in the sensorimotor control of reaching and grasping also contribute to the choice of action. Neurons in these areas are involved not only in choosing particular actions but even in setting and applying the rules on which those choices are based.

## Cortical Motor Areas Apply the Rules That Govern Behavior

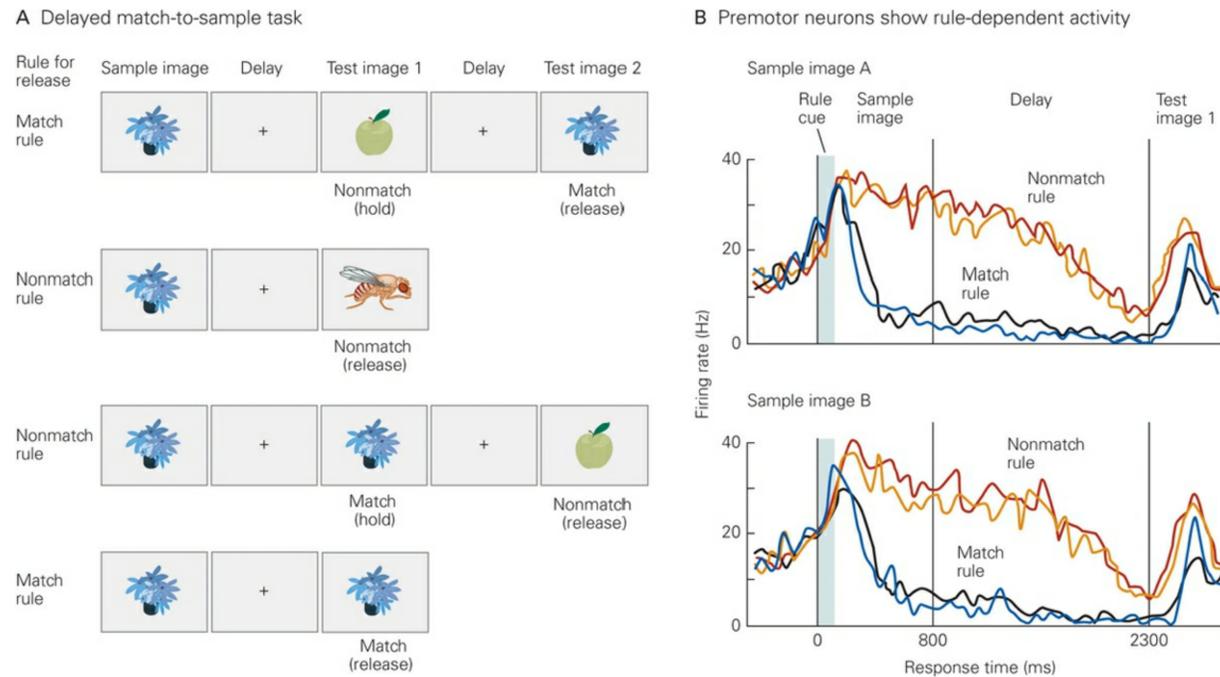
Behavior is often guided by rules that link specific symbolic cues to particular actions. When driving your car you must perform different actions depending on whether a traffic light is green, yellow, or red. In monkeys that have learned to associate arbitrary cues with specific movements, many cells in the motor and premotor cortices respond selectively to specific cues.

This activity is dependent on the nature of the selection rule. In monkeys that have been trained to choose between several possible movements based on a spatial rule (an icon's location) or a semantic rule (an icon's designated meaning), many neurons in both pre-frontal and premotor cortices are more active when the animal chooses a movement using one rule but not the other. This strong correlation of neuronal responses with the selection rule shows that both pre-frontal and premotor cortices use concrete rules to interpret behaviorally salient sensory inputs

and associate them with appropriate actions. Such neuronal activity is related not to the identity of the sensory input or the chosen action but to the association between them.

Cortical motor areas are involved in the implementation of even very abstract rules. Jonathan Wallis and Earl Miller trained monkeys to decide whether to make a particular hand movement (a *go/no-go decision*). In each trial the monkey first had to make a perceptual decision whether the two images were the same or different. In some trials the animal was required to move its hand if the images were identical and to refrain from movement if they differed; in other trials the rule was reversed (a *match/nonmatch decision*) after viewing sequential pairs of complex images. The animal therefore had to make two decisions, one perceptual and the other behavioral, neither of which had any a priori significance.

Neural populations in both the pre-frontal and dorsal premotor cortices generated activity that correlated with either the perceptual or the behavioral decision ([Figure 38–14](#)). Neuronal correlates of the perceptual decision were more prominent in the pre-frontal cortex, whereas correlates of the behavioral decision were stronger in the dorsal premotor cortex. Most strikingly, however, activity correlated with the perceptual choice was stronger and occurred earlier in the dorsal premotor cortex than in the pre-frontal cortex. These results suggest that the dorsal premotor cortex has a major role in applying rules that govern the appropriateness of a behavior and in making decisions about movement according to the prevailing rules.



**Figure 38–14** Premotor cortex neurons choose particular voluntary behaviors based on decisional rules. (Reproduced, with permission, from Wallis and Miller 2003.)

**A.** A monkey must make a decision about whether to release a lever or keep holding it based on two prior decisions: a perceptual choice, whether a test image is the same as or different from a sample image presented earlier, and a behavioral choice, whether the current rule is to release the lever when the test image is the same as the sample (match rule) or when it is different (nonmatch rule). The monkey is informed of the behavioral rule that applies in each trial by a rule cue, such as an auditory tone or juice drops, which is presented for 100 ms at the same time as the onset of the sample image.

**B.** A neuron in the dorsal premotor cortex has a higher discharge rate whenever the nonmatch rule is in effect during the delay between the presentation of the first and second images. The top and bottom sets of responses were recorded from the same cell in trials with different sample images, indicating that the rule-dependent activity is not altered by changing the images. Nor, as shown by the pairs of differently colored histograms associated with each rule, does activity depend on the type of rule cue (auditory tone or juice drops). Other dorsal premotor cortex cells (not shown) respond preferentially to the match rule over the non-

match rule. The differential activity of the neuron up to presentation of the test image reflects the nature of the rule that will guide the animal's motor response to the test image, not the physical nature of the visual stimuli or the motor response.

## The Premotor Cortex Contributes to Perceptual Decisions That Guide Motor Behavior

An elegant series of studies by Ranulfo Romo and his colleagues provides further evidence that cortical motor areas contain not only representations of the sensory information that guides voluntary movements but also the neuronal operations necessary to act on perceptual decisions. Although intuitively it may seem that perceptual processes are completely outside the domain of motor control, Romo's results indicate otherwise.

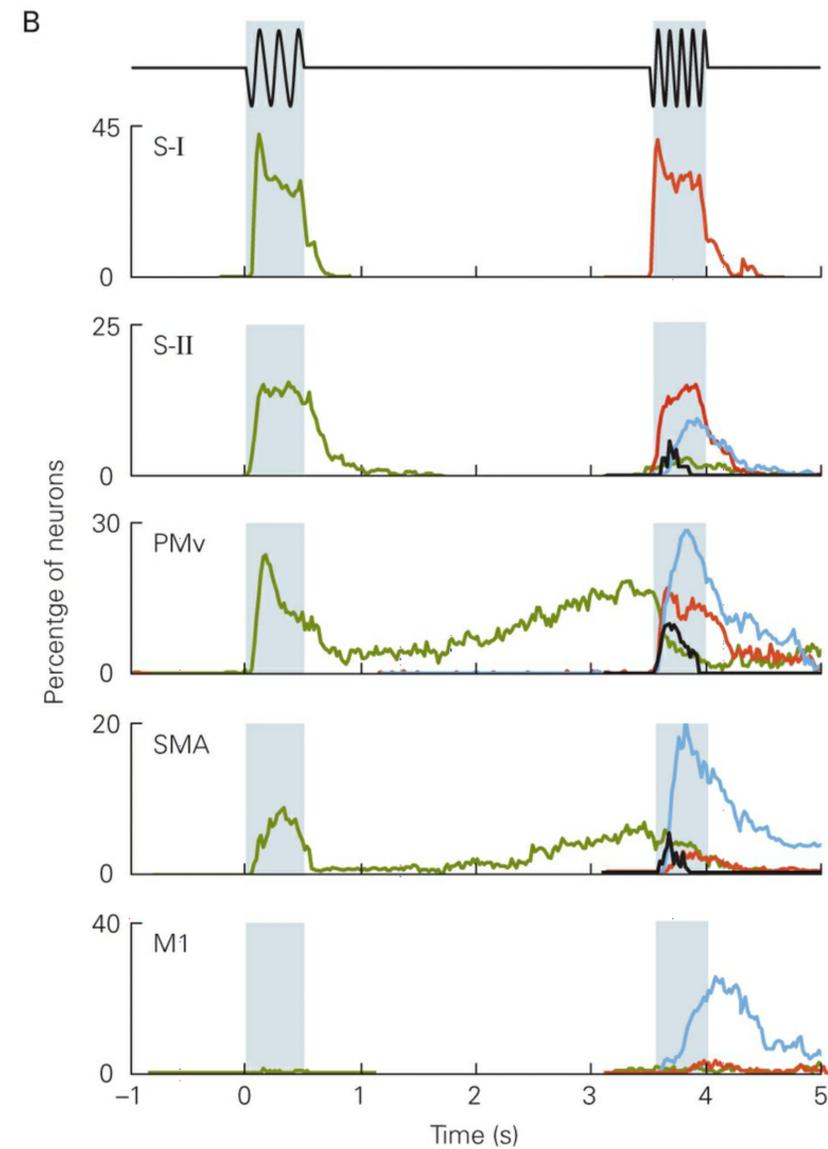
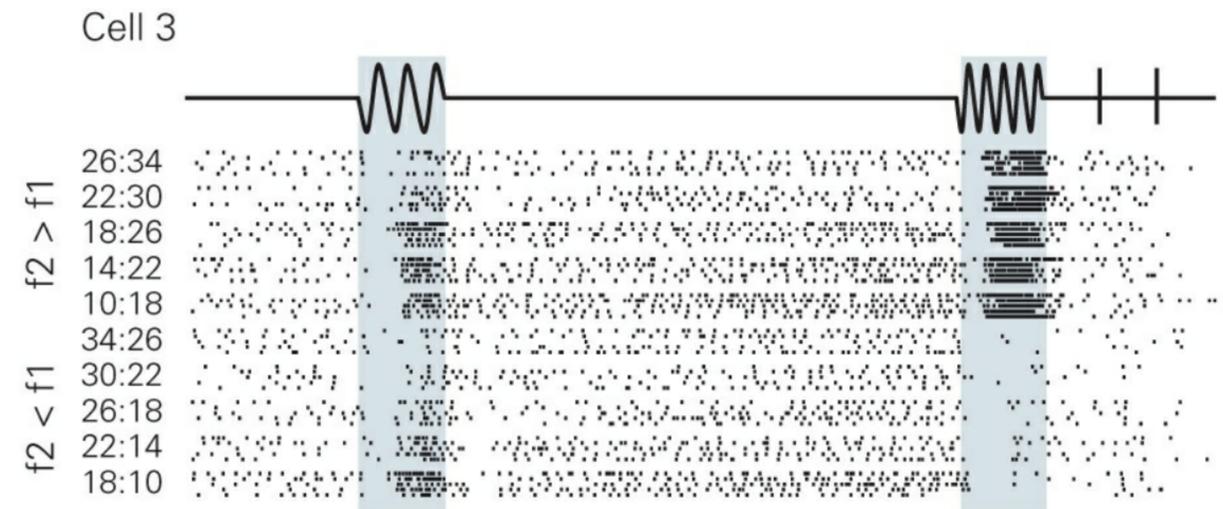
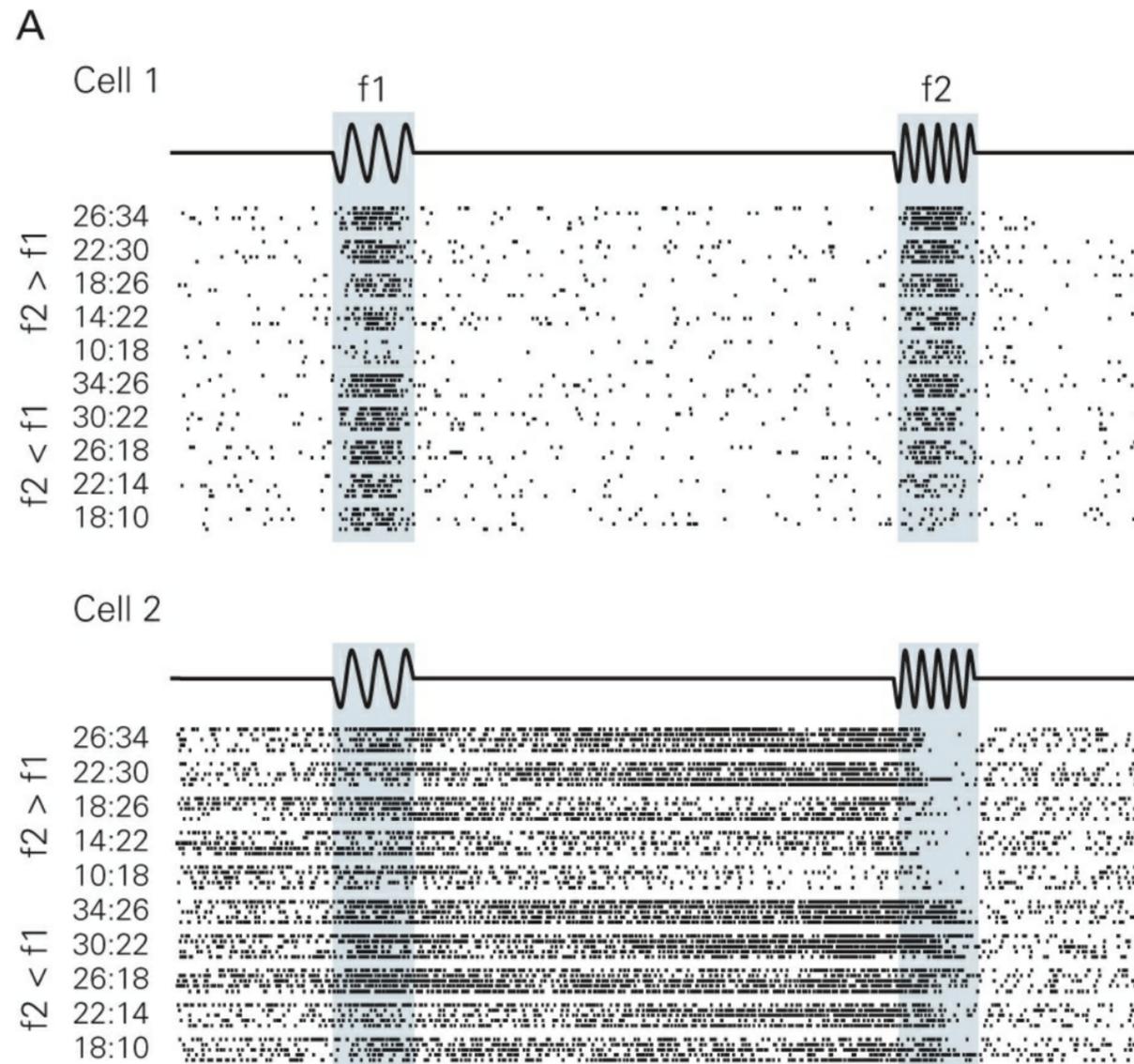
A monkey was trained to discriminate the difference in frequency between two brief vibratory stimuli applied to one finger and separated in time by a few seconds. The animal had to decide whether the frequency of the second stimulus was higher or lower than the first and to report the perceptual decision by making one of two movements with the other hand.

The decision-making process in this task can be conceived as a chain of neural operations: encode the first stimulus frequency ( $f_1$ ) when it is presented; maintain a representation of  $f_1$  in working memory during the interval between the two stimuli; encode the second stimulus frequency ( $f_2$ ) when it is presented; compare  $f_2$  to the memory trace of  $f_1$ ; decide whether the frequency of  $f_2$  is higher or lower than that of  $f_1$ ; and, finally, use that decision to choose the appropriate movement of the other hand. Everything prior to the last step would appear to fall entirely within the domain of sensory processing.

While the monkeys performed the task, neurons in the primary (S-I) and secondary (S-II) somatosensory cortices encoded the frequencies of the stimuli as they were presented. During the interval between  $f_1$  and  $f_2$  there was no sustained activity in S-I representing the memorized  $f_1$  and only a transient representation in S-II that vanished before  $f_2$  was presented.

Strikingly, however, many neurons in the pre-frontal cortex, supple-

mentary motor complex, and ventral premotor cortex encoded the  $f_1$  and  $f_2$  frequencies. Furthermore, some of the pre-frontal and premotor neurons that encoded the frequency of  $f_1$  sustained their activity during the delay period between  $f_1$  and  $f_2$  (Figure 38-15). Most remarkably, many neurons in those areas, especially the ventral premotor cortex, encoded the *difference* in frequency between  $f_2$  and  $f_1$  independently of their actual frequencies. This centrally generated signal is appropriate to mediate the perceptual discrimination that determined the corresponding motor response. Neurons that encoded the  $f_2-f_1$  difference were absent in S-I and were far more common in the supplementary motor complex and ventral premotor cortex than in S-II.



**Figure 38–15** The ventral premotor cortex contains the operations required to choose a motor response based on sensory information. (Modified, with permission, from Romo, Hernandez, and Zainos 2004.)

**A.** These records of three neurons in the ventral premotor cortex of a monkey were made while the animal performed a task in which it had to decide whether the second of two vibration stimuli ( $f_1$  and  $f_2$ , applied to the index finger of one hand) was of higher or lower frequency than the first. The choice was signaled by pushing one of two buttons with the nonstimulated hand. The frequencies of  $f_1$  and  $f_2$  are indicated by the numbers on the left of each set of raster plots. Cell 1 encoded the frequencies of both  $f_1$  and  $f_2$  while the stimuli were being presented but was not active at any other time. This response profile resembles that of many neurons in the primary somatosensory cortex. Cell 2 encoded the frequency of  $f_1$  and sustained its response during the delay period. During the presentation of  $f_2$  the neuron's response was enhanced when  $f_1$  exceeded  $f_2$  and suppressed when  $f_2$  exceeded  $f_1$ . Cell 3 responded to  $f_1$  during stimulation and was weakly active during the delay period. However, during exposure to  $f_2$  the cell's activity explicitly signaled the difference  $f_2 - f_1$  independently of the specific frequencies  $f_1$  and  $f_2$ .

**B.** The histograms show the percentage of neurons in different cortical areas whose activity correlated at each instant with different parameters during the tactile discrimination task. **Green** shows the correlation with  $f_1$ , **red** the correlation with  $f_2$ , **black** the interaction between  $f_1$  and  $f_2$ , and **blue** the correlation with the difference between  $f_2 - f_1$ . (**S-I**, primary somatosensory cortex; **S-II**, secondary somatosensory cortex; **PMv**, ventral premotor cortex; **SMA**, supplementary motor area; **M1**, primary motor cortex.)

The premotor cortex activity that encodes, stores, and compares  $f_1$  and  $f_2$  does not necessarily contribute to the sensations evoked by the tactile stimuli. Nevertheless, these experiments show dramatically that premotor cortex contains prominent representations of selected sensory information and the neuronal operations required to make a perceptual decision prior to choosing a motor action.

## The Premotor Cortex Is Involved in Learning Motor Skills

The premotor cortex has been implicated in the acquisition of new motor skills. Steven Wise and his colleagues recorded from neurons in the dorsal premotor cortex of a monkey while the animal learned a rule for associating unfamiliar visual cues with different directions of movement. Although an experienced monkey's choices were initially random, the animal could learn the rules within a few dozen trials.

Even though the monkey made an arm movement in response to each cue, many dorsal premotor neurons were only weakly active during the early, guessing phase of learning. Their activity gradually increased as the animal learned which cue signaled which movement. Other neurons showed a reciprocal decline in activity as the rules were acquired. These changes in activity reflected not only the movement choices but also the knowledge of the rule linking cues with actions.

These findings demonstrate that different cortical areas are involved in the acquisition of new motor skills and the recall of well-practiced skills. The role of cortical areas can change as new skills become motor habits that presumably require less attention, monitoring of performance, and feedback control.

## Cortical Motor Areas Contribute to Understanding the Observed Actions of Others

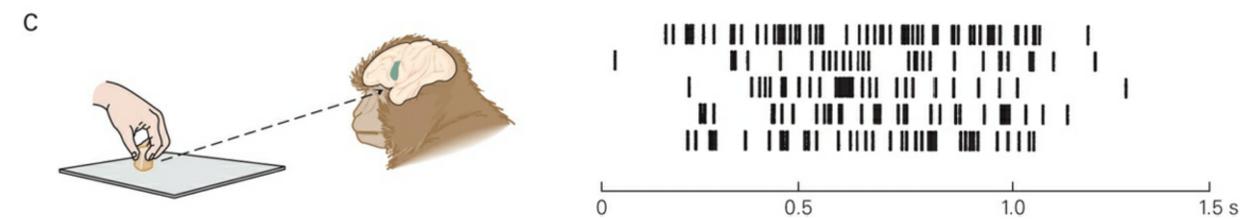
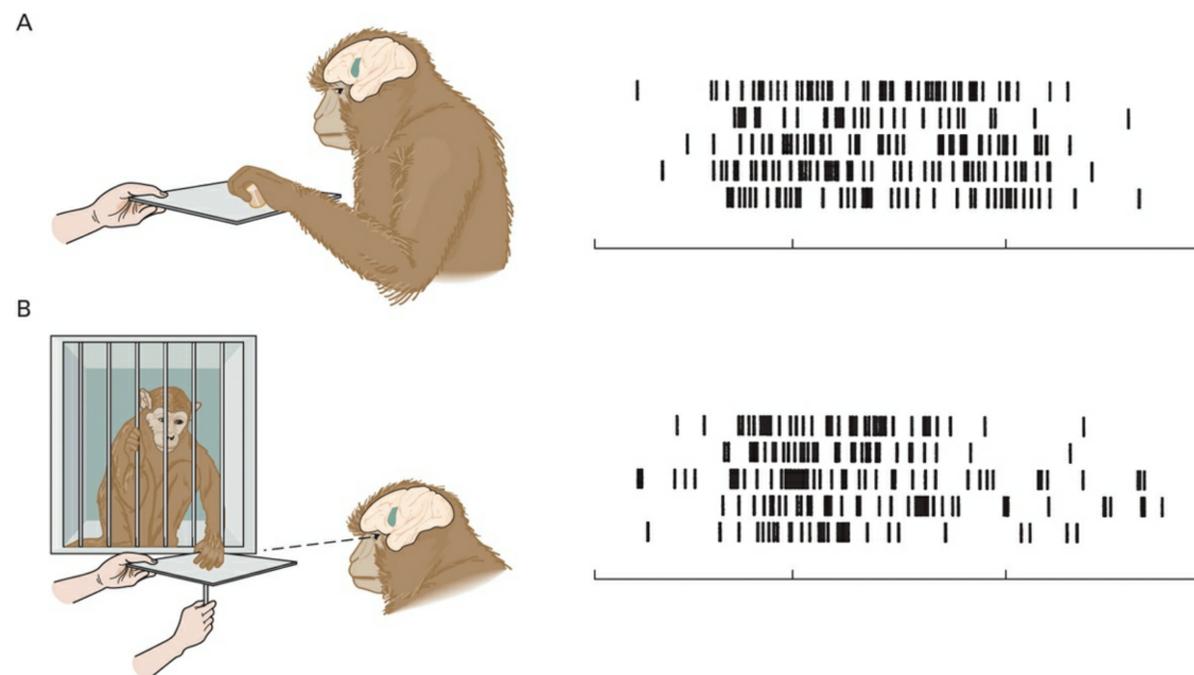
Premotor and parietal areas may be active when no overt action is intended, such as when an individual is asked to imagine performing a certain motor act or when he observes someone else performing an action.

The first condition, termed *motor imagery*, has been demonstrated in humans by functional brain imaging. When an individual follows the instruction "imagine yourself performing a specific action," the premotor and parietal cortex and even the primary motor cortices become active even though no overt act occurs. If the instruction is "imagine observing yourself performing an action as in a picture and not as an acting individual," the motor system is only weakly activated and activation of visual centers prevails. Motor imagery is interpreted by the brain as preparation

to act disassociated from motor execution.

The second condition in which cortical motor circuits are activated is when an individual observes another individual performing motor acts that belong to his own motor repertory. The control of behavior and social interaction depends greatly on the ability to recognize and understand what others are doing and why they are doing it. Such understanding could of course come from visual analysis of the stimuli and subsequent inferential reasoning. An alternative interpretation of actions done by others is the *direct matching hypothesis*, according to which observation of the actions of others activates the motor circuits responsible for similar motor actions by the observer. This empathetic activation of motor circuits would provide a link between the observed actions and the observer's stored knowledge of the nature, motives, and consequences of his own corresponding actions.

Compelling evidence in support of the direct-matching hypothesis was provided when Rizzolatti and colleagues discovered a remarkable population of neurons in area F5 of the ventral premotor cortex. These so-called *mirror neurons* discharge both when the monkey performs a motor act and when it observes a similar act performed by another monkey or by the experimenter (Figure 38-16).



**Figure 38-16** A mirror neuron in the ventral premotor cortex (area F5). (Reproduced, with permission, from Rizzolatti et al. 1996.)

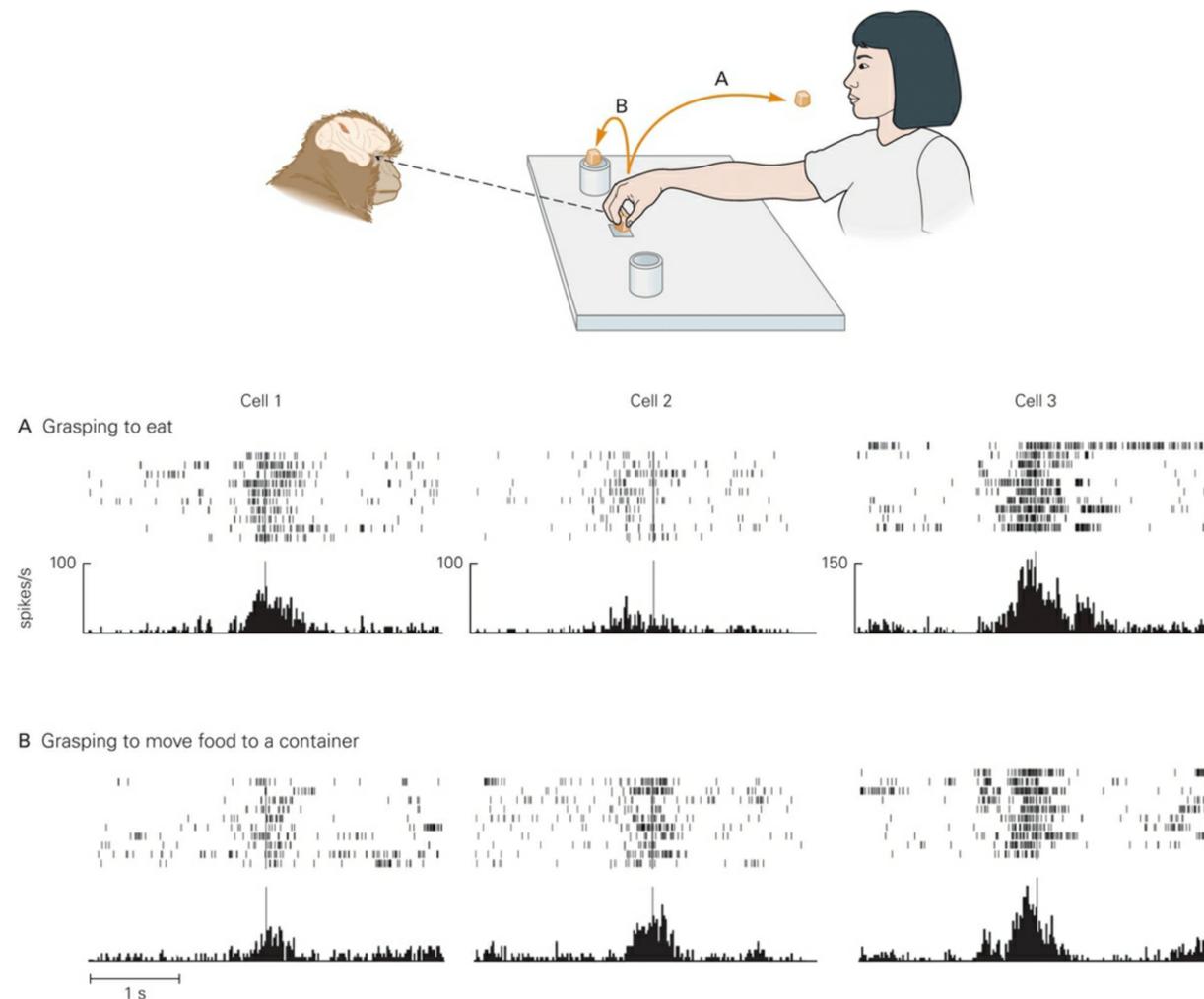
- A.** The neuron is active when the monkey grasps an object.
- B.** The same neuron is also excited when the monkey observes another monkey grasping the object.
- C.** The neuron is similarly activated when the monkey observes the human experimenter grasping the object.

Mirror neurons do not respond when a monkey simply observes an object or when it observes mimed arm and hand actions without a target object. Because each of us understands the causes and outcomes of our own motor acts, the direct-matching hypothesis proposes that the activity of mirror neurons during observation of the actions of others provides a mechanism of transforming complex visual inputs into a high-level understanding of the observed actions.

Other experiments with monkeys have provided further evidence that mirror neurons become active whenever an individual recognizes and understands the motor acts of others. For example, a noisy action such as ripping paper or cracking open a peanut can be recognized from its sound without direct visual observation. Many area F5 mirror neurons respond to such sounds in the absence of visual input. Some F5 neurons selectively discharge when the monkey observes the act of grasping an object with the hand. When the target object is obscured by a screen, some of those mirror neurons discharge as the hand approaches the hidden object and continue to respond while the hand is behind the screen. If the monkey is first shown that there is no object behind the screen, however, those same neurons remain silent when the hand disappears behind the screen. This result suggests that mirror neurons generate an internal representation of the action even when it is not visible.

Although area F5 receives no direct input from visual areas, the ros-

tral intraparietal cortex that projects to it receives visual input from the superior temporal sulcus, a region that encodes high-level visual information but is devoid of motor signals. Some neurons in the rostral intraparietal lobule have properties similar to F5 mirror neurons. They discharge more strongly when the monkey observes motor acts that have a particular goal, for example grasping food to eat it but not simply to move it (Figure 38–17). This type of coding indicates that when the monkey understands the intention behind an observed action, it is able to predict the next motor action.



**Figure 38–17** Mirror neurons in the inferior parietal cortex of a monkey are activated when the monkey observes a motor act. A monkey observes the experimenter perform the same grasping action to bring food to the mouth (A) or to place it into a container (B). Cell 1 discharges more strongly when the monkey observes the experimenter grasp the food to eat it, whereas cell 2 discharges more briskly when the monkey observes

the experimenter grasp the food to put it into another container. Cell 3 shows no difference in activity between the two conditions. Raster plots and histograms are aligned with the instant when the experimenter touches the food to be grasped. (Modified, with permission, from Fogassi et al. 2005.)

Neurophysiological and brain-imaging studies show that humans too are endowed with the mirror mechanism, matching observed actions with actions encoded in their motor system. This mechanism is located in various areas including the rostral inferior parietal lobule, intraparietal sulcus, ventral premotor cortex, and the posterior sector of the inferior frontal gyrus. Recent studies suggest that defects in the human mirror-neuron system contribute to some of the symptoms of autism. Whereas the motor system of a normally developing child is activated when he observes another person performing an action, this activation is lacking in children with autism. As a result, autistic children may lack the neuronal mechanism that normally mediates direct, experiential understanding of the intentions of others. Autistic children who are able to understand the behavior of others are thought to use cognitive inferential processes to compensate for the lack of a functional mirror-neuron system.

The involvement of cortical motor circuits in understanding and predicting the outcomes of observed events may not be limited to the mirror-neuron mechanism in the parietal and ventral premotor cortex. Recent experiments have revealed similar processes in the dorsal premotor cortex. Cisek and Kalaska found many neurons in the dorsal premotor cortex that showed directionally tuned activity when a monkey used visual cues to select the correct target for arm and cursor movements from among eight possibilities. The animal watched the cues and cursor motions on a monitor; the cursor was moved by an unseen party. The monkey received a juice reward when the cursor approached the correct target but not if the cursor moved in the wrong direction. The monkey began to lick the reward tube shortly after the cursor started to move in the correct direction but long before the juice was actually delivered. When the cursor moved in the wrong direction, however, the monkey quickly removed its mouth from the tube. This behavior showed that the monkey correctly interpreted what it saw and predicted the consequences.

Remarkably, activity in the majority of dorsal premotor neurons was strikingly similar whether the monkey used visual cues to plan and make

arm movements or simply observed and predicted the outcome. Those neurons stopped responding during observation if no reward was delivered after correct trials or if the animal became sated and was no longer interested in receiving rewards. This showed that the neurons were not simply responding to the sensory inputs, but instead were processing the observed sensory events to predict their ultimate outcome for the subject, namely the likelihood of a free reward.

## The Relationship between Motor Acts, the Sense of Volition, and Free Will Is Uncertain

At the beginning of the previous chapter we stated that voluntary behavior is willful: An action is considered voluntary if it is intentionally initiated by the actor following a decision to act, including a rejection of the alternative of doing nothing. This concept is a fundamental tenet of our legal system: A person is subject to criminal prosecution or civil liability for his actions if he performs them voluntarily and with full knowledge of their implications.

The subjective experience associated with a voluntary movement is different from that evoked when the movement is passively imposed; it includes a sense of ownership of the action. Our everyday experience also leaves us with the sense that our voluntary behavior is under conscious control and that intention precedes action. However, many skilled voluntary movements can be performed with minimal levels of conscious attention; we can, for example, ride a bicycle or drive a car while simultaneously engaged in conversation.

The relationship between behavior, intention, sense of volition, and free will has long been the subject of intense debate in philosophy and psychology. Some investigators propose that, contrary to our everyday impression, our subjective experience that intention and volition are mental processes that precede action is in fact a post hoc construct of the brain. According to this hypothesis, whenever the brain detects a temporal correlation between a motor command and subsequent sensory events, including feedback from the moving limb, it retrospectively infers that the motor command caused those events and therefore that the action was intended and that the individual was the causal agent.

Benjamin Libet and his colleagues explored this issue in the early 1980s by examining electroencephalographic activity during a self-paced movement task. They asked subjects to make a hand movement at a time of their choosing and then to use a clock-like visual time scale to report when they first became aware of his or her intention to move. Their surprising finding was that the subjects reported that they first recognized the intention to move only about 200 ms before the onset of muscle activity, as much as a second after the onset of the readiness potential, a bilateral signal arising in the frontal cortex and associated with the volitional preparation for movement. Libet concluded that neural processes leading to the initiation of a voluntary movement begin long before the subject reports any awareness of the intention to move and thus that consciousness and free will have little role in the early processes related to the control of voluntary behavior.

Libet's findings have been corroborated by other studies that show that the timing of the awareness of intention is better correlated with the onset of a later electroencephalographic event, the *lateralized readiness potential*, recorded over the motor cortex contralateral to the active limb about 200 ms before movement. The lateralized readiness potential is generally assumed to reflect the end of the decision making process and the onset of the formation of the motor command in the motor cortex.

Although the issue remains controversial, the consensus from these studies is that conscious awareness that one is about to perform a voluntary action is temporally coupled to neural activity in the brain areas associated with the planning and control of the movements. The sense that one is the causal agent of an impending action and that the action is an act of free will may be linked to neural activity in movement-related areas of the brain, rather than activity in separate, higher-order cortical areas that supposedly instruct motor areas what to do.

## An Overall View

Not long ago the motor system was viewed as a passive apparatus used by more "intelligent" parts of the brain to implement their plans. Experimental results in recent years have required a profound reevaluation of the role of the motor system in the totality of brain function.

Theoretical and behavioral investigations suggest that the control of motor behavior involves a sequence of neuronal operations that select, plan, and execute a movement. Neurophysiological studies identify those operations in populations of neurons in the parietal, premotor, prefrontal, and primary motor regions of the cerebral cortex. Neurons do not encode motor acts in terms of conventional coordinate systems and motor parameters derived from first principles of physics and engineering. Instead their activity reflects empirical solutions shaped by evolution.

Functions are distributed throughout the cortical motor system without a fixed serial order. A given neuronal operation is spread across multiple cortical areas and related operations occur in parallel in several areas. The particular distribution of activity across this network varies from moment to moment as a function of changing combinations of information and neuronal operations required to learn, plan, and execute the desired behavior in different situations.

Perception, cognition, and action have traditionally been considered distinct and serially ordered functions: An individual perceives the world, reflects on the resultant internal image of the world, and finally acts. This perspective relegates the motor system to the role of a passive apparatus that implements the decisions made by cleverer parts of the brain. Contemporary research indicates that perception, cognition, and action are neither functionally independent nor anatomically segregated. Neural correlates of the decision-making operations involved in voluntary behavior are distributed across cortical areas responsible for the motor control of the effectors that implement those decisions. No single area is responsible for general decisions about action that are then relayed to appropriate output systems for execution.

The complex behavior of higher primates is often regarded as a consequence of the development of sophisticated and adaptive perceptual and cognitive systems. This point of view may invert the evolutionary relationship. The most sophisticated cognitive processes have no inherent survival value without the means to translate them into action. The evolution of increasingly complex motor interactions with the world may have provided the evolutionary driving force that led to the development of more sophisticated perceptual and cognitive capacities to serve the

needs of action.

Giacomo Rizzolatti

John F. Kalaska

## Selected Readings

- Andersen RA, Buneo CA. 2002. Intentional maps in posterior parietal cortex. *Ann Rev Neurosci* 25:189–220.
- Buneo CA, Andersen RA. 2006. The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia* 44:2594–2606.
- Cisek P, Kalaska JF. 2010. Neural mechanisms for interacting with a world full of action choices. *Annu Rev Neurosci* 33:269–298.
- Colby CL, Duhamel JR. 1996. Spatial representations for action in parietal cortex. *Cogn Brain Res* 5:105–115.
- Colby CL, Goldberg ME. 1999. Space and attention in parietal cortex. *Annu Rev Neurosci* 22:319–349.
- Fabbri-Destro M, Rizzolatti G. 2008. Mirror neurons and mirror systems in monkeys and humans. *Physiology* 23: 171–179.
- Gibson JJ. 1979. *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.
- Haggard P. 2009. Human volition: towards a neuroscience of will. *Nat Rev Neurosci* 9:934–946.
- Hyvärinen J. 1982. Posterior parietal lobe of the primate brain. *Physiol Rev* 62:1060–1129.
- Jeannerod M. 1988. *The Neural and Behavioral Organisation of Goal-Directed Movements*. Oxford: Clarendon Press.
- Jeannerod M, Arbib MA, Rizzolatti G, Sakata H. 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci* 18:314–320.
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C. 1975. Posterior parietal association cortex of the monkey: command functions

- for operations with extra-personal space. *J Neurophysiol* 38:871–908.
- Nachev P, Kennard C, Husain M. 2008. Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci* 9:856–869.
- Rizzolatti G, Luppino G. 2001. The cortical motor system. *Neuron* 31:889–901.
- Rizzolatti G, Sinigaglia C. 2010. The functional role of the of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11:264–274.
- Tanji J. 2001. Sequential organization of multiple movements: Involvement of cortical motor areas. *Ann Rev Neurosci* 24:631–651.
- motor cortex: activity in the delay period and effect on pre-movement activity. *J Neurophysiol* 84:986–1005.
- Cui H, Andersen RA. 2007. Posterior parietal cortex encodes autonomously selected motor plans. *Neuron* 56:552–559.
- Deecke L, Kornhuber HH. 1969. Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Exp Brain Res* 7:158–168.
- Duhamel JR, Bremmer F, BenHamed S, Graf W. 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389:845–848.
- Duhamel JR, Colby CL, Goldberg ME. 1998. Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J Neurophysiol* 79:126–136.
- Fattori P, Kutz DF, Breveglieri R, Marzocchi N, Galletti C. 2005. Spatial tuning of reaching activity in the medial parieto-occipital cortex (area V6A) of macaque monkey. *Eur J Neurosci* 22:956–972.
- Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. 2005. Parietal lobe: from action organization to intention understanding. *Science* 308:662–667.
- Fogassi L, Gallese V, Fadiga L, Luppino G, Matelli M, Rizzolatti G. 1996. Coding of peripersonal space in inferior premotor cortex (area F4). *J Neurophysiol* 76:141–157.
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G. 1996. Action recognition in the premotor cortex. *Brain* 119:593–609
- Graziano MSA, Yap GS, Gross CG. 1994. Coding of visual space by premotor neurons. *Science* 266:1054–1057.
- Hikosaka O, Sakai K, Nakahara H, Lu X, Miyachi S, Nakamura K, Rand MK. 1999. Neural mechanisms for learning of sequential procedures. In: MS Gazzaniga (ed). *The New Cognitive Neurosciences*, pp. 553–572. Cambridge, MA: MIT Press.
- Hoshi E, Tanji J. 2006. Differential involvement of neurons in the dorsal and ventral premotor cortex during processing of visual signals for action planning. *J Neurophysiol* 95: 3596–3616.
- Hoshi E, Tanji J. 2004. Differential roles of neuronal activity in the

## References

- Ajemian R, Green A, Bullock D, Sergio L, Kalaska J, Grossberg S. 2008. Assessing the function of motor cortex: single-neuron models of how neural response is modulated by limb biomechanics. *Neuron* 58:414–28.
- Buch ER, Brasted PJ, Wise SP. 2006. Comparison of population activity in dorsal premotor cortex and putamen during the learning of arbitrary visuomotor mappings. *Exp Brain Res* 169:69–84.
- Cattaneo L, Fabbri-Destro M, Boria S, Pieraccini C, Monti A, Cossu G, Rizzolatti G. 2007. Impairment of actions chains in autism and its possible role in intention understanding. *Proc Natl Acad Sci USA* 104:17825–17830.
- Cisek P, Crammond DJ, Kalaska JF. 2003 Neural activity in primary motor and dorsal premotor cortex in reaching tasks with the contralateral versus ipsilateral arm. *J Neurophysiol* 89:922–942.
- Cisek P, Kalaska JF. 2005. Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45:801–814.
- Cisek P, Kalaska JF. 2004. Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature* 431:993–996.
- Crammond DJ, Kalaska JF. 2000. Prior information in motor and pre-

- supplementary and presupplementary motor areas: from information retrieval to motor planning and execution. *J Neurophysiol* 92:3482–3499.
- Jeannerod M, Arbib MA, Rizzolatti G, Sakata H. 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci* 18:314–320.
- Jeannerod M, Decety J. 1995. Mental motor imagery: a window into the representational stages of action. *Curr Opin Neurobiol* 5:727–732.
- Takei S, Hoffman DS, Strick PL. 2001. Direction of action is represented in the ventral premotor cortex. *Nat Neurosci* 4:1020–1025.
- Kalaska JF, Crammond DJ. 1995. Deciding not to go: neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cereb Cortex* 5:410–428.
- Libet B. 2004. *Mind Time: The Temporal Factor in Consciousness*. Cambridge, MA: Harvard Univ Press.
- Luppino G, Matelli M, Camarda RM, Gallese V, Rizzolatti G. 1991. Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: an intra-cortical microstimulation study in the macaque monkey. *J Comp Neurol* 311:463–482.
- Massion J. 1992. Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38:35–56.
- Mitz AR, Godschalk M, Wise SP. 1991. Learning-dependent neuronal activity in the premotor cortex: activity during the acquisition of conditional motor associations. *J Neurosci* 11:1855–1872.
- Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G. 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. *J Neurophysiol* 78:2226–30.
- Murata A, Gallese V, Luppino G, Kaseda M, Sakata H. 2000. Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J Neurophysiol* 83:2580–2601.
- Nakayama Y, Yamagata T, Tanji J, Hoshi E. 2008. Transformation of a virtual action plan into a motor plan in the premotor cortex. *J Neurosci* 28:10287–10297.
- Ochia T, Muchiaki H, Tanji J. 2005. Involvement of the ventral premotor cortex in controlling image motion of the hand during performance of a target-capturing task. *Cereb Cortex* 15:929–937.
- Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movement. *Exp Brain Res* 71:491–507.
- Rizzolatti G, Gentilucci M, Camarda RM, Gallese V, Luppino G, Matelli M, Fogassi L. 1990. Neurons related to reaching-grasping arm movements in the rostral part of area 6 (area 6ab). *Exp Brain Res* 82:337–350.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L. 1996. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3:131–141.
- Romo R, Hernández A, Zainos A. 2004. Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron* 41:165–173.
- Sakata H, Taira M, Murata A, Mine S. 1995. Neural mechanism of visual guidance of hand action in the parietal cortex of the monkey. *Cereb Cortex* 5:429–438.
- Schieber MH, Hibbard LS. 1993. How somatotopic is the motor cortex hand area? *Science* 261:489–492.
- Wallis JD, Miller EK. 2003. From rule to response: neuronal processes in the premotor and pre-frontal cortex. *J Neurophysiol* 90:1790–1806.
- Yamagata T, Nakayama Y, Tanji J, Hoshi E. 2009. Processing of visual signals for direct specification of motor targets and for conceptual representation of action targets in the dorsal and ventral premotor cortex. *J Neurophysiol* 102:3280–3294.