

voluntary control is the *pyramidal tract*, which originates in cortical layer V in a number of precentral and parietal areas. The pyramidal tract contains axons that terminate in brain stem motor structures (the *corticobulbar tract*) and axons that project down to the spinal cord (*corticospinal tract*). Precentral areas include not only M1 but also SMA, PMd, PMv, and the cingulate motor areas (Figure 34–3). Descending fibers from S-I and parietal areas, including PE and PFG, also travel in the pyramidal tract. The pre-SMA and pre-PMd do not send axons directly to the spinal cord; instead, their descending outputs reach the spinal cord indirectly through projections to other subcortical structures.

Most corticospinal tract axons originating in one hemisphere cross to the other side of the midline (decussate) at the pyramid in the caudal medulla, and from there project to the spinal cord itself, forming the lateral corticospinal tract. A small portion does not decussate and forms the ventral corticospinal tract. Many corticospinal axons in primates, and virtually all corticospinal axons in other mammals, terminate only on spinal interneurons and exert their influence on voluntary movement indirectly through spinal interneuronal and reflex pathways. In monkeys, all corticospinal axons from premotor cortical areas and many from M1 terminate on interneurons in the spinal intermediate zone, whereas postcentral and parietal areas target interneurons in the dorsal horn. The terminal endings of a sizeable portion of the corticospinal axons arising from M1 in primates, but not other mammals, arborize at their targets and synapse directly on spinal alpha motor neurons that in turn innervate muscles; these M1 neurons with direct monosynaptic projections to spinal motor neurons are called *corticomotoneuronal cells*.

Any voluntary arm movement can have destabilizing effects on the rest of the body due to mechanical interactions between body segments. Thus, control of voluntary arm movements requires coordination with neural circuits responsible for the control of posture and balance. This is mediated by descending projections from cortical motor areas to the reticular formation, which in turn project to the spinal cord via the reticulospinal tract (Chapters 33 and 36).

Imposing a Delay Period Before the Onset of Movement Isolates the Neural Activity Associated With Planning From That Associated With Executing the Action

Voluntary movement requires the intervention of a number of neural processes between the arrival of salient sensory inputs and the initiation of an appropriate motor response. With the development in the 1960s of

single-cell recording in the cerebral cortex of awake animals, tasks that experimentally manipulate different attributes of movements have been used to study every cortical area involved in the control of arm and hand movements to try to identify neural correlates of the presumed control processes in each area.

In “reaction-time” tasks, animals make a prespecified response when they detect a particular stimulus, such as reaching to a target when it appears (Figure 34–4A). The stimulus informs the animal both what movement to make and when to make it. However, reaction times in such tasks are typically short, often less than 300 ms, and most or all putative planning stages leading up to the initiation of the movement are accomplished within that brief time. This makes it very difficult to discern what kinds of information are represented in the activity of the neurons at each given moment and thus to what processes they are contributing (Figure 34–4B).

However, a critical feature of voluntary behavior is that movement initiation is not obligatory the instant an intention to act is formed. This volitional control over the timing of movement has been exploited by so-called “instructed-delay” motor tasks (Figure 34–4A), in which an instructional cue informs the animal about specific aspects of an impending movement such as the location of a target, but the animal must withhold the response until a delayed stimulus signals when to make the movement. This protocol allows researchers to dissociate in time the neural processes associated with the early stages of planning the intended act from those that are directly coupled in real time to the initiation and control of the movement.

As expected, neurons in all the movement-related cortical areas discharge prior to and during movement execution in reaction-time tasks (Figure 34–4B), and their activity correlates systematically with different properties of movements, such as their direction, velocity, spatial trajectory, and causal forces and muscle activity. Critically, however, many neurons in the same areas also signal information about an intended motor act during an instructed-delay period long before its initiation (Figure 34–4B). Thus, even though planning and execution are distinct serial stages in voluntary motor control, they are not implemented by distinct neural populations in different cortical areas. Moreover, even a well-trained monkey will occasionally make the wrong movement in response to an instructional cue. In those trials, the activity during the delay period generally predicts the erroneous motor response that the monkey will eventually make. This is compelling evidence that the activity is a neural correlate of the monkey’s motor intentions, not a passive sensory response to the instructional cues.

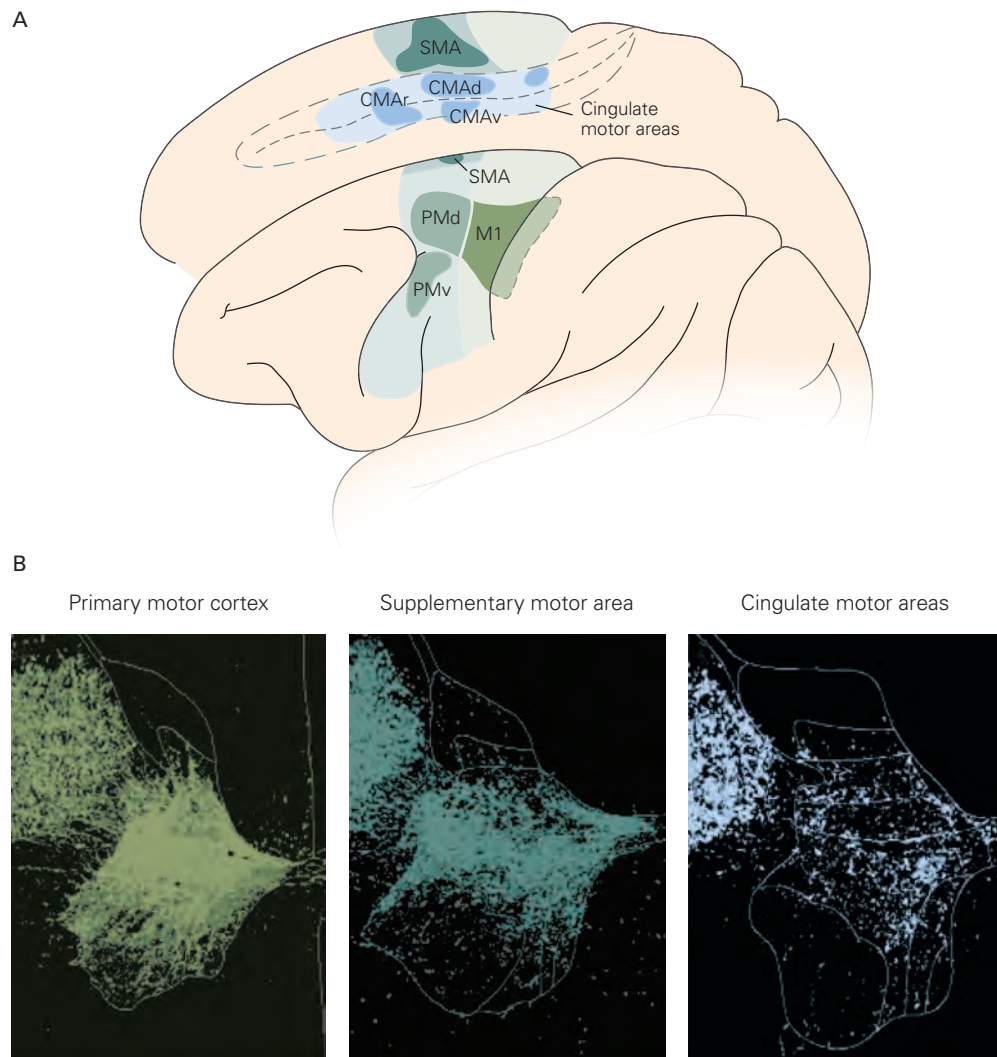


Figure 34-3 Cortical origins of the corticospinal tract. (Reproduced, with permission, from Dum and Strick 2002. Copyright © 2002 Elsevier Science Inc.)

A. Corticospinal neurons that modulate muscle activity in the contralateral arm and hand originate in the parts of the primary motor cortex (**M1**) motor map and many subdivisions of the premotor cortex (**PMd**, **PMv**, **SMA**) that are related to arm and hand movements (indicated by the darker zones). The axons from these areas project into the spinal cord cervical enlargement (see part **B**). Corticospinal fibers projecting to the leg, trunk, and other somatotopic parts of the brain stem and spinal motor system originate in the other parts of the motor and premotor cortex, indicated by the lighter zones. (Abbreviations: **CMAv**, dorsal cingulate motor area; **CMAr**, rostral cingulate motor area; **M1**, primary motor cortex; **PMd**, dorsal premotor cortex; **PMv**, ventral premotor cortex; **SMA**, supplementary motor area.)

B. Transverse sections of the spinal cord at the level of the cervical enlargement in monkeys after injection of the anterograde tracer horseradish peroxidase into different arm-related cortical motor regions to label the distribution of corticospinal axons arising from each cortical region. The corticospinal axons from the primary motor cortex (*left*), supplementary motor area (*middle*), and cingulate motor areas (*right*) all terminate on interneuronal networks in the intermediate laminae (V–VIII) of the spinal cord. Only the primary motor cortex contains corticospinal neurons (corticomotoneuronal cells) whose axons terminate directly on spinal motor neurons in the most ventral and lateral part of the spinal ventral horn (Rexed's lamina IX). Rexed's laminae I to IX of the dorsal and ventral horns are shown in faint outline in each section. The dense cluster of labeled axons adjacent to the dorsal horn (*upper left*) in each section are corticospinal axons descending in the dorsolateral funiculus, before entering the spinal intermediate and ventral laminae.

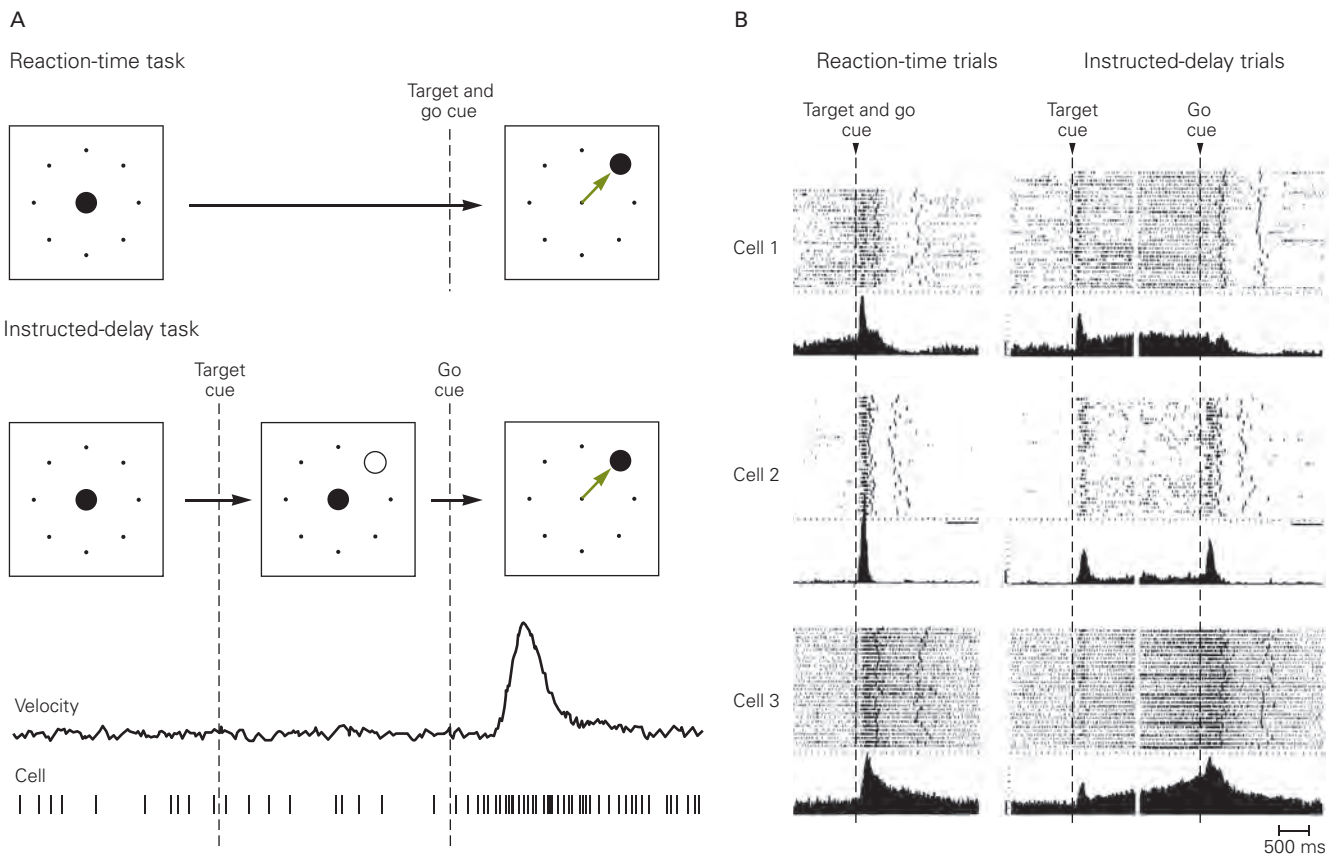


Figure 34-4 Neural processes related to movement planning and movement execution can be dissociated in time. (Reproduced, with permission, from Crammond and Kalaska 2000.)

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 neural 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 go cue given. 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 neural correlates of the planning stage.

B. Movement planning and execution are not completely segregated at the level of single neurons or neural 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 in each raster row represent action potentials, and the two thicker ticks show the onset and end of movement. 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, activity in many premotor cells shows directionally tuned changes 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.

Parietal Cortex Provides Information About the World and the Body for State Estimation to Plan and Execute Motor Actions

Sensory information is essential for selecting appropriate and effective actions. Before drinking from a cup, the brain uses visual input to identify which object is the cup, where it is located relative to the body, and its physical properties such as size, shape, and handle orientation.

In addition, information about the current posture and motion of the arm and hand is provided by integrating proprioceptive signals from the limb with efference copies of motor commands (Chapter 30). Finally, cutaneous signals are critical when interacting manually with objects, such as grasping and lifting the cup.

Several lines of evidence implicate the parietal cortex as a key brain region in sensory processing for motor action. The parietal lobe, especially PE, PEip, and MIP,

receives strong somatic sensory inputs about body posture and movement from S-I. Several parietal regions along and within the IPS are major components of the dorsal visual pathway, which processes visuospatial information about objects that guides arm and hand movements while reaching to, grasping, and manipulating them. The parietal lobe is also reciprocally interconnected with precentral cortical motor areas to provide the precentral cortex with signals for the sensory guidance of movement and to receive efference copies of motor commands from those same precentral areas. Finally, human subjects with lesions of the posterior parietal cortex often demonstrate specific impairments in using sensory information to guide motor action (Box 34–1).

The Parietal Cortex Links Sensory Information to Motor Actions

We experience the space that surrounds us as a single unified environment within which objects have specific locations relative to each other and to ourselves. Classical neurology suggested that the parietal lobe constructed a unified multimodal neural representation of the world by integration of inputs from different sensory modalities. This single map of space was assumed to provide all the information necessary both for spatial perception and for the sensory guidance of movement, and so was shared by the different motor

circuits that controlled different parts of the body, such as the eyes, arm, and hand.

However, the idea that the parietal cortex contains a single topographically organized representation of space is incorrect. Instead, the posterior parietal cortex contains several distinct functional areas that work in parallel and receive different combinations of sensory and motor inputs related to the guidance of movement of different effectors, such as the eyes, arm, and hand. Neurons in these areas are often multimodal, with both visual and somatic sensory receptive fields, and also discharge preferentially prior to and during movements of a specific effector. Each functional area is connected to frontal motor regions involved in control of the same effectors. Finally, each region is not topographically organized in the familiar sense of a faithful point-to-point representation of surrounding space, but rather comprises a complex mixture of neurons with different sensory inputs that may contribute to the multisensory integration required to guide motor actions with the environment.

Body Position and Motion Are Represented in Several Areas of Posterior Parietal Cortex

The S-I and adjacent superior parietal cortex regions PE, MIP, and PEip are a major source of proprioceptive and tactile sensory information about the position and motion of body parts. Neurons in S-I areas 1 and 2

Box 34–1 Lesion Studies of Posterior Parietal Cortex Lead to Deficits in the Use of Sensory Information to Guide Action

Naturally occurring or experimentally induced lesions have long been used to infer the roles of different neural structures. However, the effects of lesions must always be interpreted with caution. It is often incorrect to conclude that the function perturbed by an insult to a part of the motor system resides uniquely in the damaged structure or that the injured neurons explicitly perform that function. Furthermore, the adverse effects of lesions can be masked or altered by compensatory mechanisms in remaining, intact structures. Nevertheless, lesion experiments have been fundamental in differentiating the functional roles of brain regions.

Behavioral studies by Goodale, Milner, Rossetti, and others on patients with parietal cortical damage have led to the conclusion that a primary function of the parietal lobe is to extract sensory information about the external world and one's own body for the planning and guidance of movements. Such studies have shown that patients with

lesions of certain parts of the parietal lobe suffer specific deficits in the ability to direct their arm and hand accurately to the spatial location of objects and to shape the orientation and grip aperture of the hand prior to grasping it.

They have also shown a particularly severe deficit in the ability to make rapid adjustments to their ongoing reach and grasping actions in response to unexpected changes in the location or orientation of the target object. This visual guidance of action is provided by visual signals that are routed through the dorsal visual stream and may operate in parallel with and independently of perceptual processes evoked by the visual inputs that are routed simultaneously through the ventral visual stream in the temporal lobe. For instance, whereas our visual perception of the size and orientation of objects can be deceived by certain perceptual illusions, the motor system often behaves as if it is not fooled and makes accurate movements.

typically respond to tactile input from a limited part of the contralateral body or to movements of one or a few adjacent joints in specific directions.

In contrast, many PE and MIP neurons discharge during passive and active movements of multiple joints. Some cells also respond during combined movements of multiple body parts, including bilateral movements of both arms. Many PE and MIP neurons also have large tactile receptive fields whose responses are modulated by context during limb movement or posture. For instance, a neuron with a tactile receptive field that covers the entire glabrous (palmar) surface of the hand may only respond to physical contact with an object when the hand is close to the body and not when it touches the object with the arm fully extended.

These findings indicate that while area 1 and 2 neurons encode the positions and movements of specific body parts, superior parietal neurons 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 neural “body schema” that provides information on where the arm is located with respect to the body and how different arm segments are positioned and moving with respect to one another. This body schema is critical for selecting how to attain behavioral goals and for ongoing control of movement.

For instance, a key requirement for efficient reaching is knowledge of where the arm is before and during the reach. Monkeys with experimental lesions in Brodmann’s area 2 and the adjacent superior parietal lobule (area 5 or PE) show deficits in reaching to and manipulating objects under proprioceptive and tactile guidance without vision. Human patients with similar lesions show the same deficit, without the spatial neglect that is a common consequence of more lateral lesions in the inferior parietal lobe.

Spatial Goals Are Represented in Several Areas of Posterior Parietal Cortex

Functional areas within the IPS are strongly implicated in the processing of spatial, especially visual, information relevant to action. Each of these areas has unique ways of representing objects and spatial goals relative to the body and contributes to controlling motor actions of different parts of the body. For instance, many neurons in the lateral intraparietal area (LIP) receive visual input from extrastriate cortical areas. Their receptive fields are fixed in retinal coordinates and shift to new spatial locations whenever the monkey changes its direction of gaze. Neural responses also often increase when the animal attends to a stimulus within the receptive field even without looking

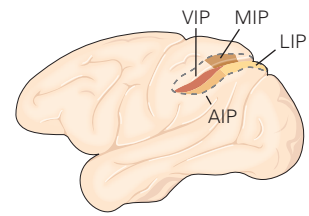
at it, and they often discharge prior to a saccade that is directed toward a visual stimulus in their receptive field (Figure 34–5A; and see Chapter 35).

Several parietal regions are preferentially implicated in the control of arm and hand movements. For instance, the most medial regions of the superior parietal cortex, areas V6A and PEc, receive input from extrastriate visual areas V2 and V3. Many V6A and PEc neurons have visual receptive fields in retinal coordinates, but their activity is also frequently modulated by the direction of gaze, the current arm posture, and the direction of reaching movements.

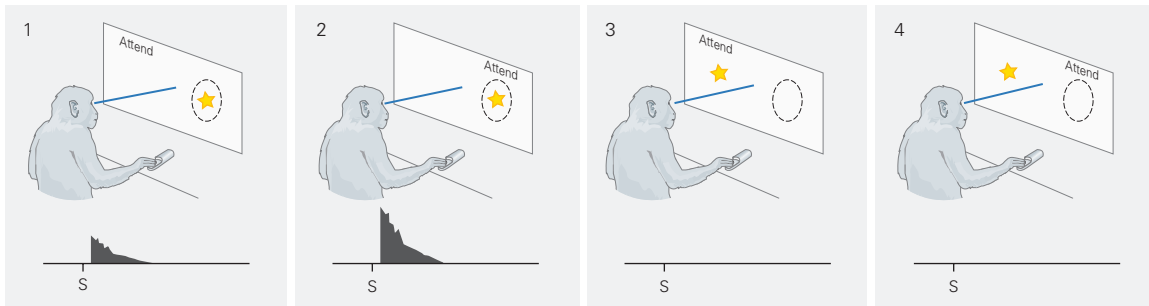
The ventral intraparietal area (VIP) in the fundus of the IPS receives inputs from two components of the dorsal visual stream, the medial temporal cortex and medial superior temporal cortex, which are involved in the analysis of optic flow and visual motion. Many VIP neurons respond to visual stimuli and somatosensory stimuli with receptive fields on the face or head and, in some cases, on the arm or trunk. Neural activity is in head-centered coordinates, as somatosensory and visual information remains in register even if the eyes move to fixate different spatial locations (Figure 34–5B). Some VIP 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. These neurons may allow the monkeys to link the location and motion of objects in their immediate peripersonal space with different parts of their body.

Another area of parietal cortex related to reaching is the parietal reach region (PRR). The PRR likely corresponds to the medial intraparietal cortex (MIP) and adjacent arm-control parts of the superior and inferior parietal cortex. The activity of many PRR neurons varies with the location of reach targets relative to the hand. However, this signal is not fixed to the current location of the hand or target but rather on the current direction of gaze (Figure 34–5C). Each time the monkey looks in a different direction, the reach-related activity of PRR neurons changes, even if the location of the target and hand and the required reach trajectory do not change. In contrast, the reach-related activity of many neurons in areas PE and PEip is less related to gaze and more strongly related to the current hand position and arm posture. PE and PEip neurons thus provide a more stable signal about the location of the reach target relative to the current position of the hand compared to PRR.

Finally, neurons in the anterior intraparietal area (AIP) are primarily implicated in object grasping and manipulation by movements of the hand. Many AIP neurons are preferentially active while reaching for



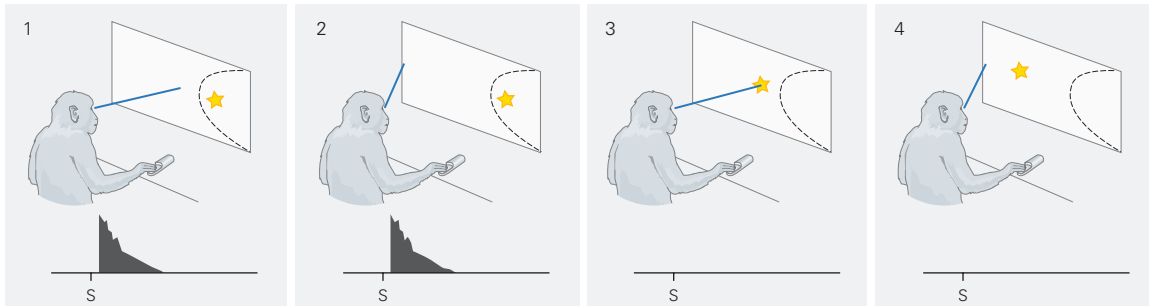
A Lateral intraparietal area (LIP)



Receptive field characteristics

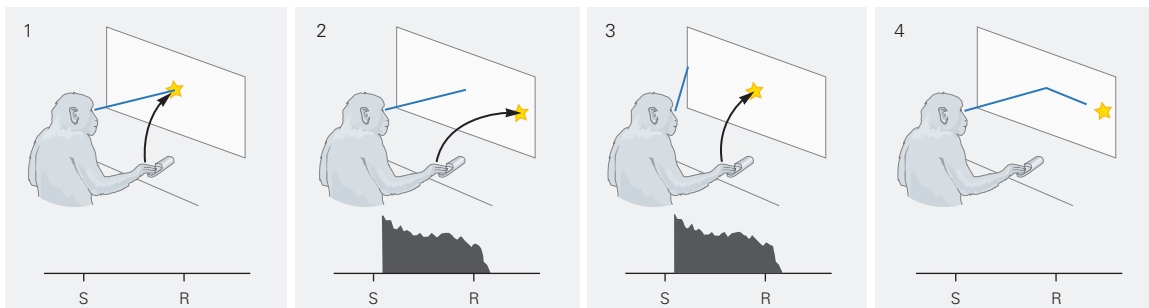
Retina-centered, attention sensitive

B Ventral intraparietal area (VIP)



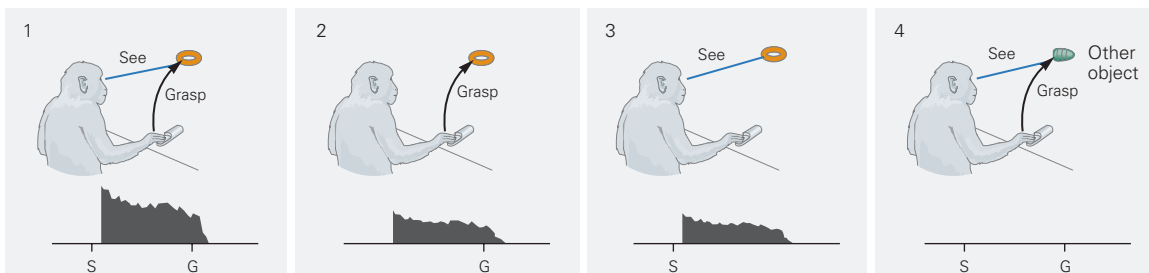
Head-centered

C Medial intraparietal area (MIP)



Retina-centered direction of reach; preparation to reach

D Anterior intraparietal area (AIP)



Retina-centered, object-specific viewing, grasping

and grasping objects of particular shapes, sizes, and spatial orientations, and often even while viewing those objects before grasping them (Figure 34–5D). There is a broad range of neural response properties, from neurons that respond almost exclusively to visual input about the objects but not to the grasping actions to neurons that discharge only during the hand movements themselves even in the dark. This suggests that the AIP contains neural circuits that begin to transform visual information about the physical properties of an object that are relevant to how it could be handled—what James Gibson has called the object's *affordances*—into appropriate hand actions (Chapter 56).

A fascinating discovery about the parietal cortex is that the receptive fields of neurons can be altered by individual experience, such as tool use. Monkeys were trained to retrieve food pellets that were out of normal reach of the arm and hand by using a rake-shaped tool. Many VIP neurons normally respond to visual objects when they are either located near the current position of the hand or anywhere within reach with the arm. After training, their visual receptive fields transiently expand to incorporate the tool when the monkey grasps it, as if the distal end of the tool had become a functional extension of the monkey's own hand and arm (Figure 34–6).

Internally Generated Feedback May Influence Parietal Cortex Activity

The delays involved in the transmission of visual and somatic feedback about arm movements from the periphery to cortical circuits can lead to oscillations

or even instabilities in real-time sensorimotor control. One theoretical solution to this problem is to use a forward internal model to make predictive estimates of body motion based on internal efference copies of outgoing motor commands as well as from slower peripheral feedback signals (Chapter 30).

Several lines of evidence suggest that parietal cortex circuits, along with the cerebellum (Chapter 37), may implement a similar solution. Many reach-related neurons in PE, MIP, and PRR are active not only in response to passive sensory inputs but also before the onset of movement and during the instructed-delay period of delayed-reaching tasks. These responses suggest that these neurons process centrally generated signals about motor intentions prior to movement onset. This premovement activity is often interpreted as evidence that the parietal cortex generates feedforward signals that contribute to the early planning of movements. However, an alternate interpretation is that the premovement activity is driven by an efference copy of the motor command for the intended movement that is transmitted into the parietal cortex via its reciprocal connections with precentral motor areas. This combination of peripheral sensory inputs and central efference copies could permit some parietal reach-related circuits to compute a continuously updated estimate of the current state of the arm and its position relative to the behavioral goal. This estimate could be used to make rapid corrections for errors in ongoing arm movements.

Whether the parietal circuits are primarily involved in the formation of a subject's motor intentions or in

Figure 34–5 (Opposite) Neurons in the parietal cortex of the monkey are selective for the location of objects in the visual field relative to particular parts of the body. Each histogram represents the firing rate of a representative neuron as a function of time following presentation of a stimulus. In each diagram, the line emanating from the eyes indicates where the monkey is looking.

A. Neurons in the lateral intraparietal area have *retina-centered* receptive fields. The strength of the visual response depends on whether the monkey is paying attention to the stimulus (**S**). The neuron fires when a light is flashed inside its receptive field (**dotted circle**) (**1**). The response is more robust if the monkey is instructed to attend to the location of the stimulus (**2**). The neuron does not fire if the stimulus is presented outside the receptive field, regardless of where attention is directed (**3**, **4**).

B. In the ventral intraparietal area, some neurons have *head-centered* receptive fields. This is determined by keeping the head in a fixed position while the monkey is instructed to shift its gaze to various locations. This neuron fires when a light appears to the right of the midline of the head (**1**, **2**). It does not fire when the light appears at another location relative to the head, such as the midline or to the left. (**3**, **4**). The critical

contrast is between situations **1** and **4**. The retinal location of the light is the same in both (slightly to the right of the fixation point), yet the neuron fires in **1**, when the stimulus is to the right of the head, but not in **4**, when the stimulus is to the left of the head.

C. In the medial intraparietal area, neurons are selective for the retina-centered direction of the reach (**R**) and fire when the monkey is preparing to reach for a visual target. This neuron fires when the monkey reaches for a target to the right of where he is looking (**2**, **3**). It does not fire when he reaches for a target at which he is looking (**1**) or when he moves only his eyes to the target at the right (**4**). The physical direction of the reach is not a factor in the neuron's firing: It is the same in **1** and **3**, and yet, the neuron fires only in **3**.

D. In the anterior intraparietal area, neurons are selective for objects of particular shapes and fire when the monkey is looking at or preparing to grasp (**G**) an object. This neuron fires when the monkey is viewing a ring (**3**) or making a memory-guided reach to it in the dark (**2**). It fires especially strongly when the monkey is grasping the ring under visual guidance (**1**). It does not fire during viewing or grasping of other objects (**4**).

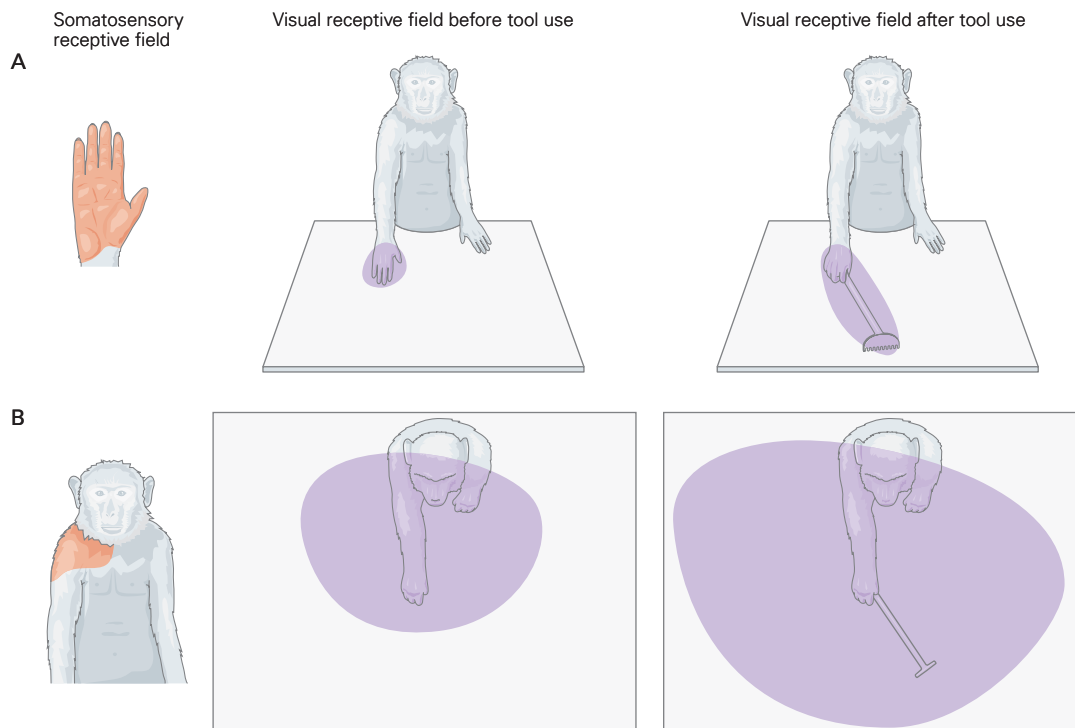


Figure 34-6 Some neurons in the parietal cortex of the monkey have receptive fields that dynamically expand once a tool is grasped. (Adapted from Maravita and Iriki, 2004. Copyright © 2003 Published by Elsevier Ltd.)

A. The orange area on the hand (*left*) indicates the somatosensory receptive field for a neuron. The purple area (*middle*) indicates the neuron's visual receptive field (vRF) region around the hand. The vRF is anchored to the hand and changes spatial location whenever the monkey moves its arm. The vRF expands

when the monkey grasps a rake after it has learned how to use the rake to reach for objects in the workspace (*right*).

B. A single neuron that has a shoulder-centered bimodal somatosensory (orange) and visual (purple) receptive field is illustrated. The vRF for this neuron (*middle*) is larger than the one shown in part A, possibly reflecting the potential workspace related to whole-arm function. The vRF also expands to incorporate the extended workspace permitted by use of a rake (*right*).

state estimation will depend on the origin of its pre-movement activity. If it is mainly generated within the parietal cortex itself, this will strongly implicate the parietal cortex in the planning of intended movements. In contrast, if it is primarily driven by an efference copy relayed from precentral motor areas, this would strongly implicate the parietal circuits in state estimation, including predicting how the arm should move in response to the motor command.

Premotor Cortex Supports Motor Selection and Planning

As outlined at the beginning of this chapter, a decision to act in a particular way in a given situation is shaped by many factors, including sensory information about objects, events, and opportunities for action from the

environment, body position and motion, internal motivational states, prior experiences, reward preferences, and learned arbitrary rules and strategies linking sensory inputs to motor actions. There can be many reasons why you want to drink some coffee, and that desire can be fulfilled by actions ranging from simply reaching out to your full coffee cup to making coffee at home or going to a café.

Frontal premotor cortical regions just rostral to M1 play an important role in early movement planning or task-selection processes. Many neurons in those areas, such as the PMd neurons shown in Figure 34-4, generate activity during instructed-delay tasks that reflect the motor intentions of the monkey and even the factors that influenced those action choices. The different premotor cortical regions are presumed to make different but overlapping contributions to motor selection and planning. For instance, the lateral premotor