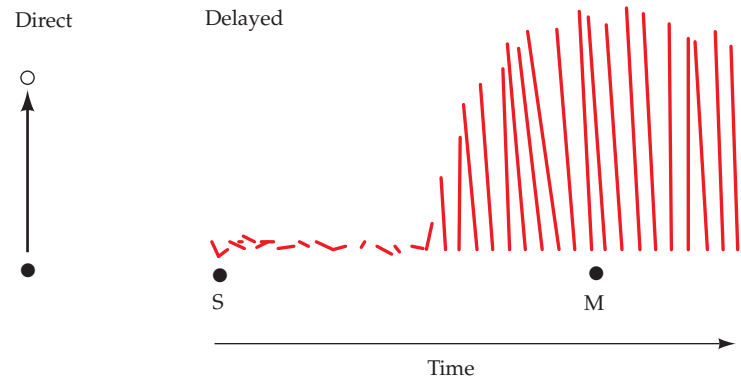


Figure 5.11 Population vectors in the primary motor cortex Each line indicates the direction and amplitude of an arm movement decoded from the activity of a population of neurons recorded in the primary motor cortex. The time of the trials proceeds from bottom to top; S indicates the cue for movement, and M indicates the onset of movement. Movement in direct response to a cue results in immediate generation of a population vector specifying the movement. Delayed movement evokes a population vector specifying the movement hundreds of milliseconds before movement onset. (After Georgopoulos et al. 1986.)



amplitude, whereas stimulation at nearby sites evokes saccades with slightly different vectors. Thus, the superior colliculus contains a topographical map of eye movements, much like the topographical maps of skeletal movements in the primary motor cortex (see Figure 5.7A).

Each superior colliculus neuron is thought to vote for its range of movements, with the weight of the vote cast determined by how strongly the neuron fired. The weighted votes would then be averaged across the population to arrive at the vector for the desired movement. To test this idea, small portions of the map of eye movements in the superior colliculus were reversibly inactivated in monkeys trained to look toward visual targets for fruit juice rewards. Following inactivation, eye movements were systematically biased away from the inactivated portion of the collicular map, as would be expected if movements were specified by the weighted average of the activity of all the neurons in the superior colliculus (Figure 5.10B). This experiment provided the first functional support for the notion that the brain achieves precise movements by averaging together the activation of large populations of coarsely tuned neurons.

The idea that precise movements are encoded by averaging the activity of many coarsely tuned neurons has been extended to the primary motor cortex. Neurons in the primary motor cortex are broadly tuned to generate a range of movement directions and amplitudes, firing strongly for some movements but weakly or not at all for others. A vector representing the weighted average of activity across the population of neurons in the motor cortex as a function of time (Figure 5.11) specifies the impending movement well in advance of any activity in the muscles. This observation supports the idea that the primary motor cortex encodes intended movements by the vector average of activity across the active neuronal population.

Planning Movements

Although many movements are more or less automatic in response to a sensory stimulus, other actions are planned in advance and their initiation held off until the circumstances are appropriate for their execution. For example, when monkeys are cued to reach toward a target but are forced to delay initiation of the reach, neurons in the primary motor cortex become active before the movement is initiated. Anticipatory activation of neurons during arm movement planning has been observed in a number of premotor areas as well, including the premotor, supplementary motor, dorsolateral prefrontal, and parietal cortices.

In the case of visual orienting movements, such activity is seen in the frontal and supplementary eye fields, and in the dorsolateral prefrontal and lateral parietal cortices. Planning-related activity in premotor areas typically persists when movement cues are removed and ceases when monkeys are cued to stop

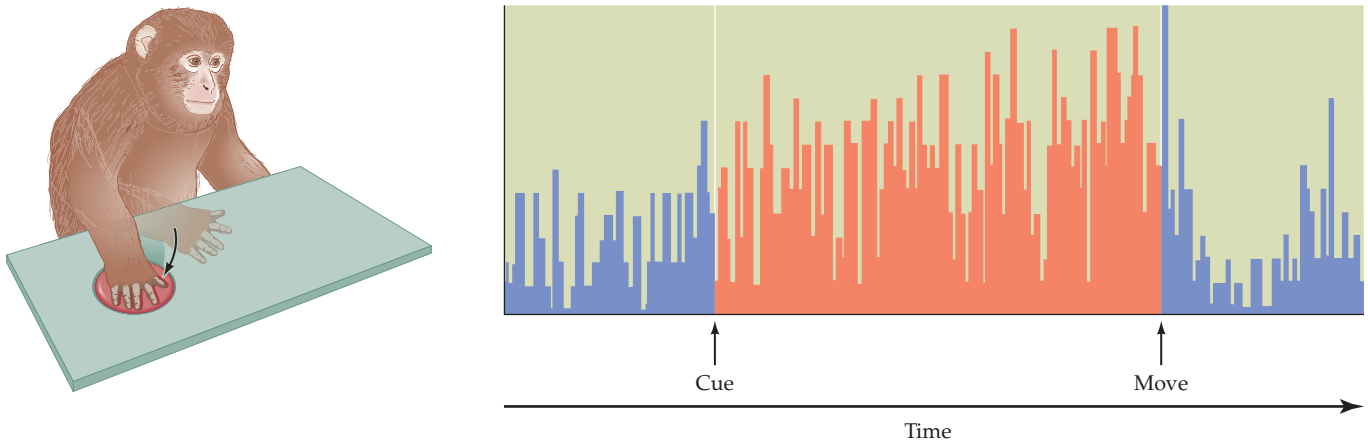


Figure 5.12 Evidence of anticipatory activity as a correlate of movement intention in the premotor cortex The histogram shows neuronal firing as a function of time in a monkey cued to reach toward a target after a delay (red). Neuronal activity continues from the cue until the movement, suggesting a neural correlate of the intention to reach toward the target.

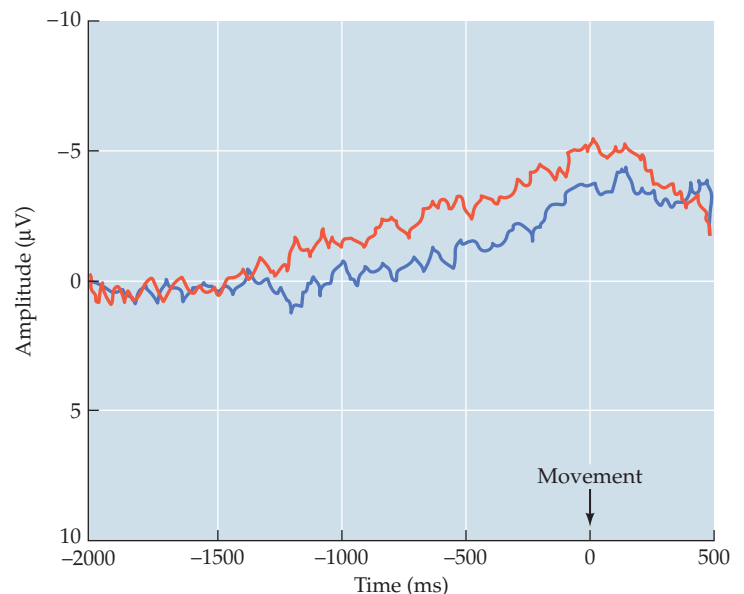
planning the movement, thus suggesting a role in intention (**Figure 5.12**). One indication of the functional role of these premotor areas is that planning-related neuronal activity typically begins even earlier in these areas than in the primary motor cortex (or the superior colliculus for saccades).

These observations support the idea that motor areas are hierarchically organized, with premotor areas providing more abstract planning information related to behavioral goals, which is then translated into the intention to perform specific movements in the primary motor cortex (and the superior colliculus for visual orienting movements). Thus, higher motor areas appear to serve a functional role in specifying the motor program discussed earlier. Motor intention signals in the primary motor cortex are then translated by downstream local circuits in the brainstem and spinal cord into neural activity that specifies the patterns of muscle contraction necessary to accomplish the intended movements.

Scalp recordings from humans (see Chapter 2) have tended to confirm this hierarchical organization of movement planning. When subjects are asked to voluntarily generate a movement—for example, lifting a finger at a time of their choosing—EEG recordings from medial frontal electrodes show a pronounced negative wave that begins up to several seconds in advance of the actual movement. This **readiness potential** initially begins bilaterally over premotor areas, but later it becomes enhanced over the primary motor cortex contralateral to the finger movement (**Figure 5.13**). Neuroimaging studies have identified the readiness potential with activation in premotor areas, particularly the supplementary motor areas. Interestingly, when premotor areas are damaged along with the primary motor cortex, patients are unaware of (or even deny) their inability to move—a phenomenon known as **anosognosia**, meaning “loss of awareness.” This clinical observation provides additional evidence that the premotor cortex is the source of motor planning and intentional awareness.

Figure 5.13 Readiness potential

These EEG recordings were taken from scalp electrodes over premotor and supplementary motor cortices in human subjects asked to voluntarily move a finger. EEG amplitude when subjects attend to their own movement (blue) increases several seconds in advance of the actual movement. EEG amplitude when subjects attend to the urge to move—the readiness potential (red)—is enhanced relative to the movement potential. Readiness potentials begin later in the contralateral primary motor cortex, consistent with a hierarchical progression of motor intention. (After Eagleman 2004.)



The readiness potential also provides a means of further exploring the role of awareness in motor planning. In a famous but controversial study conducted several decades ago by physiologist Benjamin Libet, subjects were asked to produce an uncued voluntary movement and then estimate (from a clock display) the time at which they became aware of the intention to move. EEG recordings indicated, not surprisingly, that estimates of the intention to move preceded the movement itself by about 200 milliseconds. However, readiness potentials over premotor areas clearly preceded subjects' awareness of when they intended to move. Although these results have a number of possible confounding factors, the study implies that conscious awareness actually follows the intention to move rather than preceding and thus causing it.

Selecting goals for action

At any given moment, several competing or alternative behavioral goals might be options for motor planning. For example, on approaching a stoplight that just turned yellow, a driver might either slow to stop, or accelerate to get through the intersection before the light turns red. The neural processes responsible for selecting a course of action to reach a goal (e.g., getting to the destination faster) and generating the relevant movement have come under increasing scrutiny as researchers have realized the importance of cognitive contexts for motor behaviors. Most such studies have focused on the processes that link sensory information to motor output.

Early electrophysiological studies in monkeys demonstrated that neurons in a variety of premotor areas where planning-related activity occurs respond to sensory cues used to guide movements. Moreover, these responses to sensory cues can be enhanced or diminished if the stimulus is made more or less likely to be the target of a movement. Subsequent work showed that such sensory-motor linkage is graded by the quality of information guiding the movement integrated over time. For instance, neurophysiologists William Newsome and Michael Shadlen provided evidence that neuronal responses in a number of premotor areas involved in saccadic eye movements are systematically related to the weight of sensory evidence favoring a particular movement. In these experiments, monkeys were trained to judge the net direction of motion in a field of moving dots and report this evaluation by shifting their gaze to a specific target if they judged the motion to be in one direction and a different target if they saw motion in the opposite direction (**Figure 5.14A**). Newsome and Shadlen systematically manipulated the quality of the evidence favoring responses to each target by changing the fraction of dots moving coherently in one direction or another. When about 50 percent of the dots moved in one direction, monkeys were nearly always correct in their responses; their performance fell to chance levels, however, when less than 5 percent of the dots moved coherently.

The responses of neurons in the posterior parietal cortex, frontal eye fields, supplementary eye fields, dorsolateral prefrontal cortex, and even superior colliculus were all found to be modulated by the strength of the motion stimulus favoring a particular eye movement response (**Figure 5.14B**). When monkeys were permitted to move their eyes as soon as they had made a decision, the speed with which neuronal activity in the parietal cortex increased matched the speed of the monkeys' eye movement responses. Similar graded responses as a function of stimulus quality have been reported in the higher-order somatosensory cortex and premotor areas in monkeys trained to report the frequency of vibration applied to the forearm by pushing a button.

Taken together, these studies imply that neurons in a number of premotor areas specify movements in a graded manner as sensory evidence is accumulated. This hypothesis was tested directly by applying microstimulation to

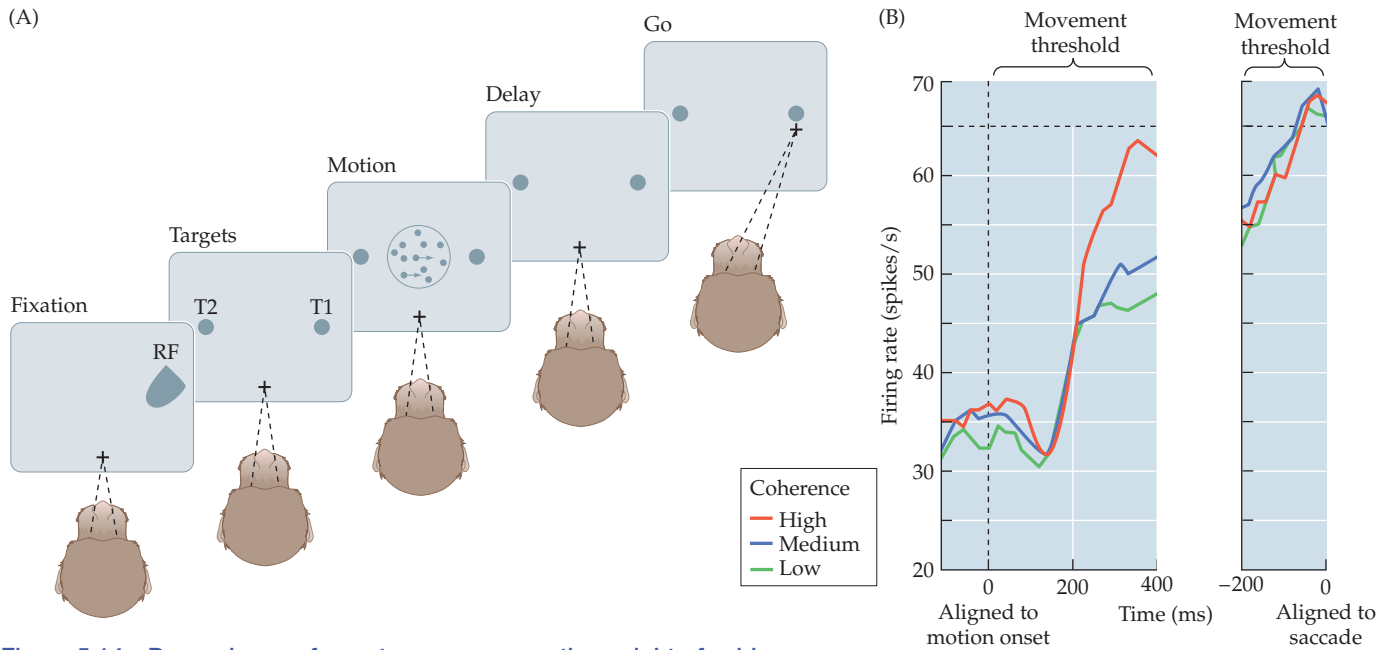


Figure 5.14 Dependence of a motor response on the weight of evidence (A) Monkeys performed a visual discrimination task in which, by moving their eyes, they reported the direction of motion in a field of randomly moving dots. One target was in the response field (RF) of a neuron in the posterior parietal cortex; the other was in the opposite visual field. (B) The firing rate of neurons in posterior parietal cortex increased when monkeys viewed dots moving toward the target in the RF. The rate of increase over time was directly proportional to motion coherence, or the weight of evidence favoring an eye movement to the RF target. The relation between firing rate and motion coherence reflects the integration of motion over time. (After Roitman and Shadlen 2002.)

the frontal eye fields while monkeys performed the dot discrimination task illustrated in Figure 5.14A. Stimulation in this area evoked saccadic eye movements at short latencies, but the endpoints of the movements were systematically biased by the pattern of motion the monkeys saw (Figure 5.15A). Moreover, the amount of bias gradually increased as monkeys viewed the motion longer, as well as when the fraction of coherently moving dots was gradually increased (Figure 5.15B). When the locations of the movement targets were not revealed

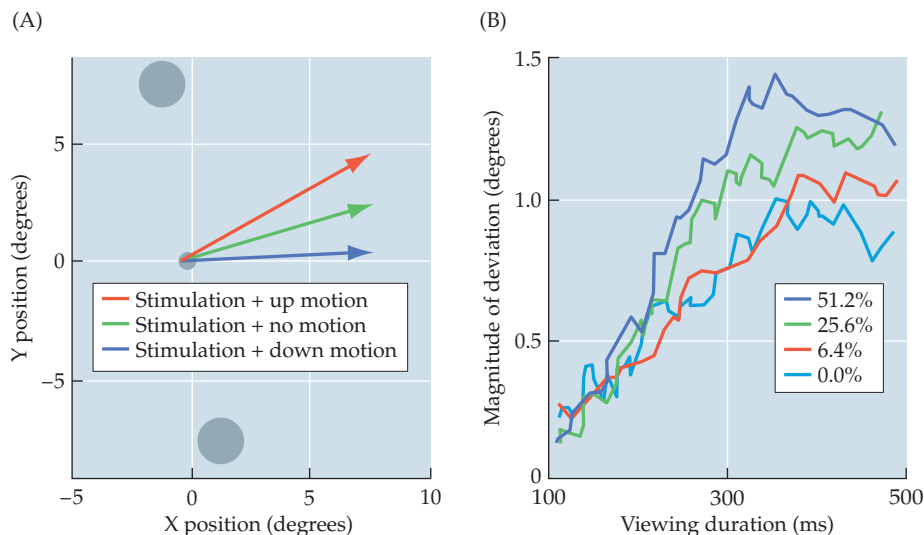


Figure 5.15 Graded conversion of sensory percepts into action (A) Monkeys were trained to fixate centrally while observing motion stimuli that were moving either up or down, or that had no net motion. Microstimulation of the frontal eye fields evoked eye movements that were systematically biased by the direction of viewed motion, thus indicating that ongoing motor planning in this area is influenced by gradually accumulating motion information. (B) The magnitude of the deviation in stimulation-induced eye movements depended on both motion coherence of the stimuli and viewing duration. With higher motion coherence, the rate of deviation in eye position as a function of time increased, implying that the integration of sensory evidence over time favors a particular motor response. Each curve represents a particular percentage of dots moving coherently. (After Gold and Shadlen 2000.)

in advance of the dot stimulus, however, dot motion had very little effect on stimulation-evoked saccades.

All told, a variety of observations support the conclusion that motor preparation is a dynamic, competitive process linking sensory information to the intention to move, and that such processing entails the graded activation of neurons in a variety of higher-order premotor cortical (and subcortical) areas.

Motivational control of goal selection

Although sensory stimulation often indicates which movement should be produced (e.g., the response to the yellow light in the driving example described in the previous section), people must often select a goal primarily on the basis of additional, far more complex stimuli, as well as stored information about the likely state of the environment (in the yellow-light example, the factors indicating the relative need to get to the destination quickly that influence the significance of the stimulus). Indeed, when monkeys performed the moving-dot task illustrated in Figure 5.14, they reported their judgments not because of the stimulus per se, but because if they responded, they would receive squirts of fruit juice—highly desirable treats.

Although behavior is typically directed toward acquiring rewards and avoiding punishments, very little is understood about the mechanisms that guide the motor system to select goals that satisfy such biological motivations. This question was tackled directly in a series of studies by neurobiologists Paul Glimcher and Michael Platt designed to understand how internal motivations shape the responses of neurons in the posterior parietal cortex (Figure 5.16). They trained monkeys to choose between looking at two visually identical lights and then, across a series of trials, systematically varied either the probability or the amount of fruit juice reinforcement the monkeys received for looking at one light versus the other. Platt and Glimcher found that neurons in the posterior parietal cortex were sensitive to the **reward value** of shifting gaze to a particular target, which depended on both the probability and the magnitude of the juice reward associated with that target.

Neurons in a number of premotor areas, including the dorsolateral prefrontal cortex, supplementary eye fields, frontal eye fields, and posterior cingulate cortex have also been found to be sensitive to movement value. Further, fMRI studies of people choosing between movements of different value have found similar scaling of activation by movement value. In one study, scientists asked

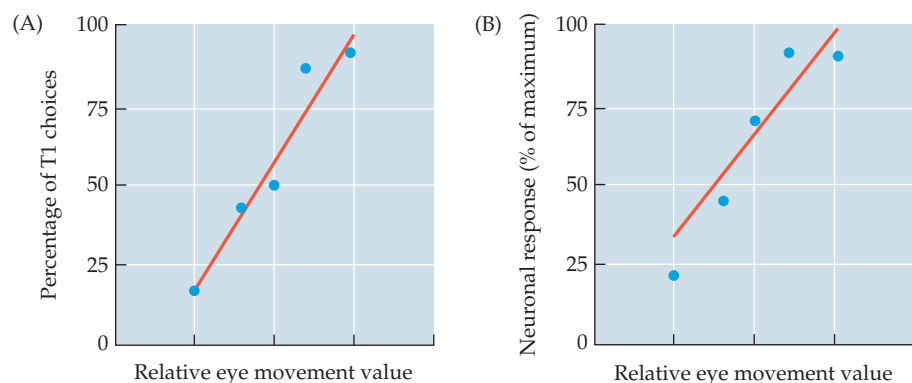
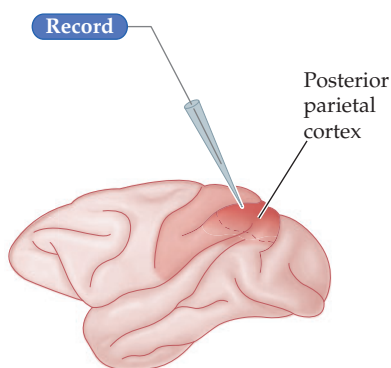


Figure 5.16 The sensitivity of premotor neurons to movement values (A) Monkeys choose to spend time looking at a particular target in direct proportion to the relative reward value of that action. (B) Neurons in the posterior parietal cortex respond in direct proportion to the relative reward value associated with an eye movement. (After Platt and Glimcher 1999.)

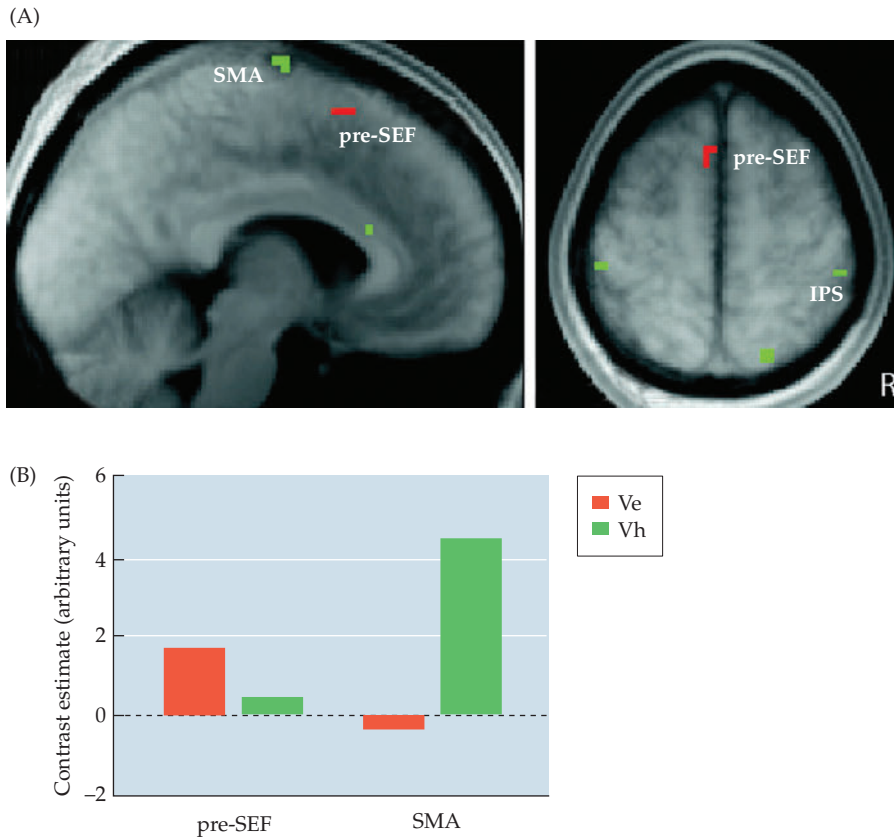


Figure 5.17 Action value signals in the human brain (A) Region of the supplementary motor area (SMA) showing correlations with action values for hand movement (Vh; green) and a region of presupplementary eye field (pre-SEF) showing correlations with action values for eye movements (Ve; red). IPS, intraparietal sulcus. (B) Average sizes of the effects of eye movement value (red) and hand movement value (green) extracted from the SEF and SMA. The effects shown here were calculated from trials independent of those used to functionally identify the region of interest. Note that only Ve (but not Vh) modulates the signal in the pre-SEF, and that activity in the SMA shows the opposite pattern. (After Wunderlich et al. 2009.)

people to choose between an eye movement and a hand movement, each of which varied in value across trials. As expected, people generally tended to choose the more valuable option. Importantly, activity in the supplementary eye field (Figure 5.17) tended to vary with the value of the eye movement, whereas activity in the supplementary motor area tended to vary with the value of the hand movement, paralleling the findings from single-neuron recording studies done in monkeys. Together, these studies suggest that selecting a movement goal involves scaling neuronal responses associated with each possible movement by that movement's value, thereby biasing the motor system to produce a movement that best satisfies biological motivations such as acquiring rewards or avoiding punishments.

Sequential Movements and the Supplementary Motor Area

The discussion so far has focused on the selection and planning of a *single* movement. Clearly, however, the behavioral repertoire of humans and other animals normally consists of *sequences* of movements that together constitute meaningful behaviors that satisfy specific goals. Not surprisingly, regions of the frontal cortex are specialized to support the production of movement sequences. As a rule, the **supplementary motor area**, or **SMA** (also called area 6) is crucial for generating movements in the absence of explicit sensory cues, and the premotor cortex is especially important for the production of cued movements. When the SMA is ablated, monkeys can no longer perform well-learned movements and must instead rely on external cues to tell them which movement should be performed. The reverse is true for lesions of the premotor cortex, which selectively disrupt visually guided movements but do not affect