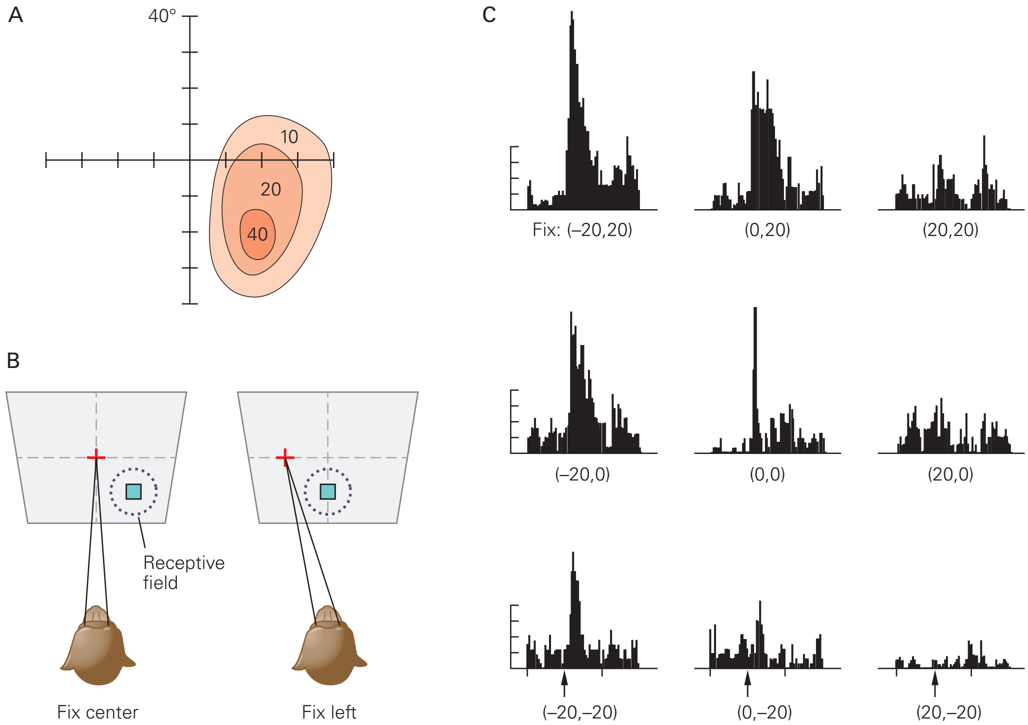

Figure 25–6 The position of the eye in the orbit affects the responses of parietal visual neurons with retinotopic receptive fields.

A. Receptive field relative to the fovea. Contour plot indicates spike rates for different spatial locations. Numbers are spikes per second for each contour at the maximum position.

B. The receptive field moves in space with the eye. On the left the monkey is fixating the center of the screen. On the right the same monkey is fixating 20° to the left of center. For the recordings in C, the stimulus (**blue square**) is always presented in the center of the receptive field.

C. Responses to a stimulus at the optimum location in the receptive field change as a function of the position of the eye in the orbit, from a maximum when the monkey fixates a point at –20°,20° to a minimum when the monkey fixates a point at 20°,–20°. **Arrows** indicate onset of stimulus flash. Trial duration, 1.5 sec; ordinate, 25 spikes/division. (Adapted, with permission, from Andersen, Essick, and Siegel 1985. Copyright © 1985 AAAS.)

exists that the brain calculates the spatial location of an object that appeared before an eye movement using two mechanisms: a corollary discharge that is rapid and a proprioceptive signal that is slow but can be more accurate than the corollary discharge. The proprioceptive signal can also be used to calibrate the corollary discharge.

Visual Scrutiny Is Driven by Attention and Arousal Circuits

In the 19th century, William James described attention as "the taking possession by the mind in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. It implies withdrawal from some things in order to deal effectively with others." James went on to describe two different kinds of attention: "It is either passive, reflex, non-voluntary, effortless or active and voluntary. In passive immediate sensorial attention the stimulus is a sense-impression, either very intense, voluminous, or sudden … big things, bright things, moving things … blood."

Your attention to this page as you read it is an example of voluntary attention. If a bright light suddenly flashed, your attention would probably be pulled away involuntarily from the page. Large changes in the visual scene that occur outside the focus of attention are often missed until the subject directs attention to them, a phenomenon referred to as change blindness (Figure 25–8).

Voluntary attention is closely linked to saccadic eye movements because the fovea has a much denser array of cones than the peripheral retina (Chapter 17) and moving the fovea to an attended object permits a finer-grain analysis than is possible with peripheral vision. Attention that selects a point in space, whether or not it is accompanied by a saccade, is called spatial attention. Searching for a specific kind of object, for

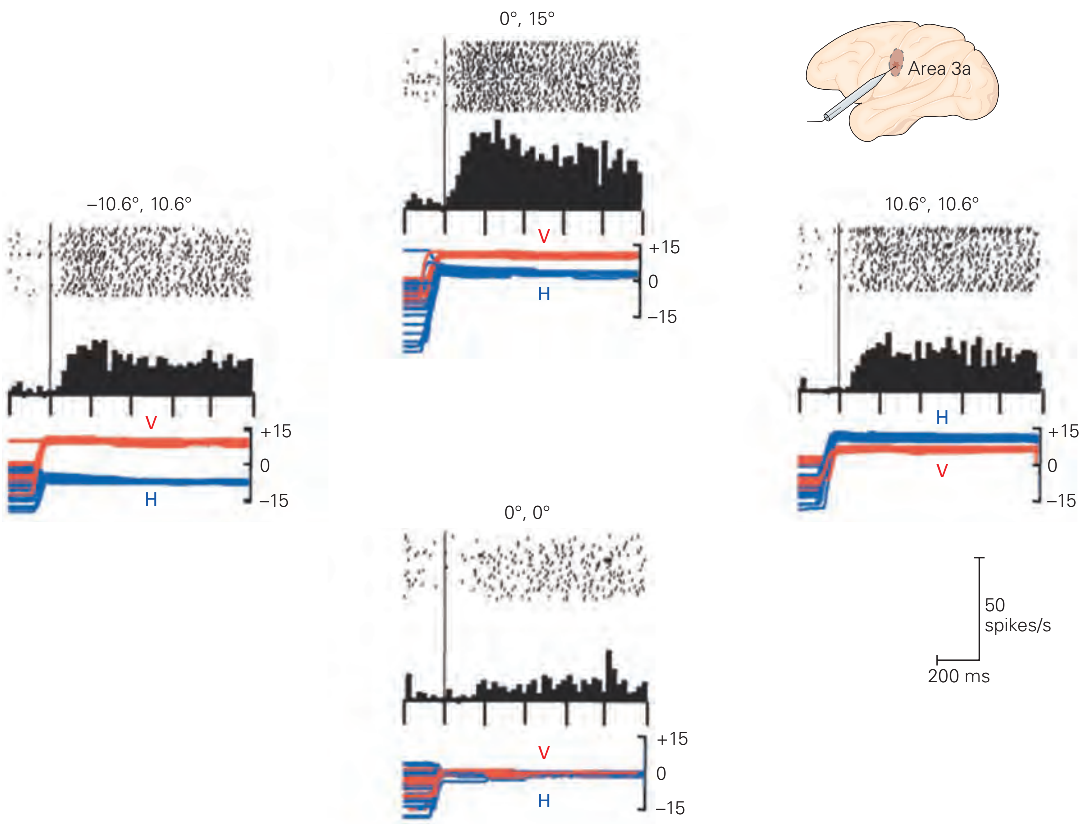

Figure 25–7 Eye position neuron in somatosensory cortex area 3a. Each panel shows horizontal (H) and vertical (V) eye position and the activity of the neuron after the monkey made a saccade to the eye position indicated above each raster. The neuron responds much more briskly when the eye is at 0°,15° than when it is at 0°,0°. (Reproduced, with permission, from Wang et al. 2007.)

example a red O among red and green Qs, involves a second kind of attention, feature attention: In your search, you ignore the green letters and attend only to the red ones.

Attention, both voluntary and involuntary, shortens reaction time and makes visual perception more sensitive. This increased sensitivity includes the abilities to detect objects at a lower contrast and ignore distracters close to an attended object. The abrupt appearance of a behaviorally irrelevant cue, such as a light flash, reduces the reaction time to a test stimulus presented 300 ms later in the same place. Conversely, when the cue appears away from the test stimulus, the reaction time is increased. The light flash draws involuntary attention to its location, thus accelerating the visual response to the test stimulus. Similarly, when a subject plans a saccade to a particular part of the visual field, the contrast threshold at which any object there can be detected is improved 50% by a cue.

Clinical studies have long implicated the parietal lobe in visual attention. Patients with lesions of the right parietal lobe have normal visual fields. When their visual perception is studied with a single stimulus in an uncomplicated visual environment, their responses are normal. However, when presented with a more complicated visual environment, with objects in the left and right visual hemifields, these patients tend to report less of what lies in the left hemifield (contralateral to their lesion) than in the right hemifield (ipsilateral to their lesion). This deficit, known as *neglect* (Chapter 59), arises because attention is focused on the visual hemifield ipsilateral to the lesion. Even when patients are presented with only two stimuli, one in each hemifield, they report seeing only the stimulus in the ipsilateral hemifield. When attention is focused on one stimulus in the affected hemifield and a second stimulus is presented in the unaffected hemifield, patients do not have the ability to shift attention to the new stimulus, even though the sensory pathway from the eye to the striate and prestriate cortex is intact.

This neglect of the contralateral visual hemifield extends to the neglect of the contralateral half of

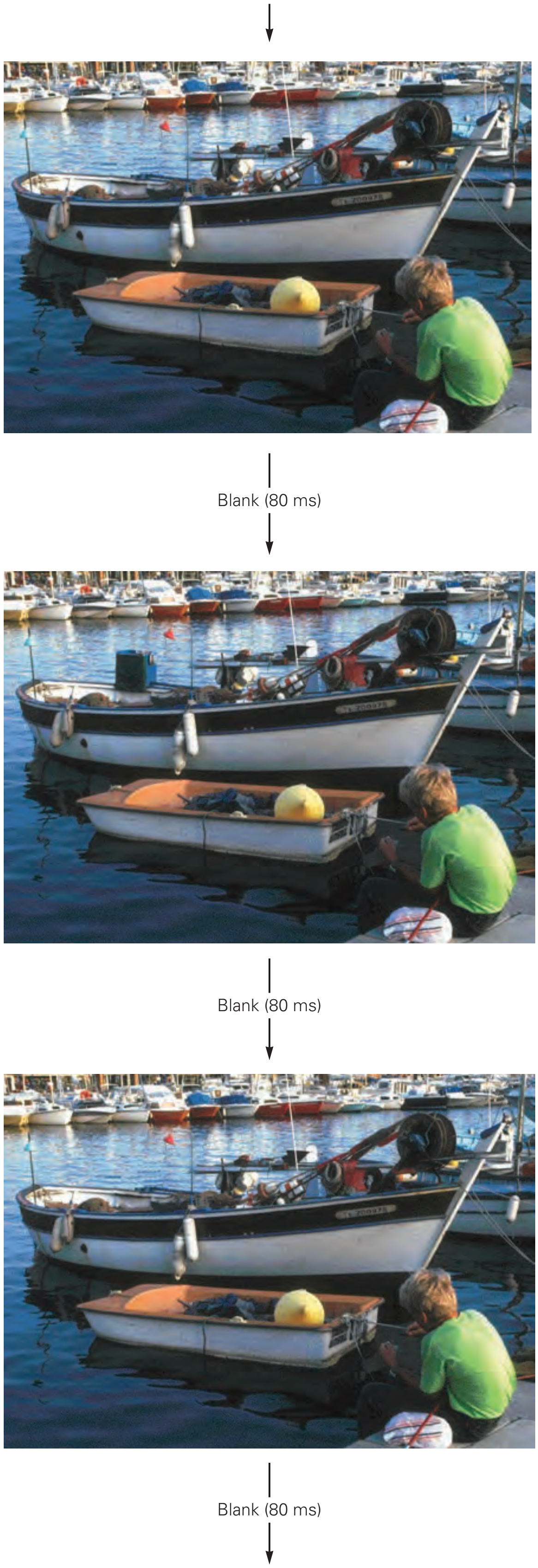

Figure 25–8 Change blindness. In a test for change blindness, one picture is presented followed by a blank screen for 80 ms, followed by the second picture, another blank screen, and a repeat of the cycle (*left*). The subject is asked to report what changed in the scene. Although there is a substantial difference between the two pictures, it takes multiple repetitions for most observers to detect the difference. (Reproduced, with permission, from Ronald Rensink.)

individual objects (Figure 25–9). Patients with right parietal lobe deficits often have difficulty reproducing drawings. When asked to draw a clock, for example, they may force all of the numbers into the right side of the clock's face, or when asked to bisect a line, they may place the midline well to the right of the line's actual center.

The process of attentional selection is evident at the level of single parietal neurons in the monkey. The responses of neurons in the lateral intraparietal area to a visual stimulus depend not only on the physical properties of the stimulus but also on its importance

Figure 25–9 Drawing of a candlestick by a patient with a lesion of the right parietal lobe. The patient neglects the left side of the candlestick, drawing only its right half. (Reproduced, with permission, from Halligan and Marshall 2001. Copyright © 2001 Academic Press.)

to the monkey. Thus, the responses to a behaviorally irrelevant stimulus are much smaller than for any event that evokes attention, such as the abrupt onset of a visual stimulus in the receptive field or the planning of a saccade to the receptive field of the neuron.

Although neurons in the lateral intraparietal area collectively represent the entire visual hemifield, the neurons active at any one moment represent only the important objects in the hemifield, a priority map of the visual field. The lateral intraparietal area acts as a summing junction for a number of different signals: saccade planning, abrupt stimulus onset, and the cognitive aspects of a searched-for feature.

The absolute value of the neuronal response evoked by an object does not by itself determine whether that animal is attending to that object. When a monkey plans a saccade to a stimulus in the visual field, attention is on the goal of the saccade, and the activity evoked by the saccade plan lies at the peak of the priority map. However, if a bright light appears elsewhere in the visual field, attention is involuntarily drawn to the bright light, which evokes more neuronal activity than does the saccade plan. Thus, the locus of attention can be identified only by examining the entire priority map and choosing its peak; it cannot be identified by monitoring activity at any one point alone (Box 25–1).

Box 25–1 The Priority Map in Parietal Cortex

Neurons in the lateral intraparietal area of the monkey represent only those objects of potential importance to the monkey, a priority map of the visual field. This selectivity for objects of behavioral importance can be demonstrated by recording from neurons in a monkey while the animal makes eye movements across a stable array of objects.

Stable objects in the visual world are rarely the objects of attention. In the lateral intraparietal area, as in most other visual centers of the brain, neuronal receptive fields are retinotopic; that is, they are defined relative to the center of gaze. As a monkey scans the visual field, fixed objects enter and leave the receptive fields of neurons with every eye movement without disrupting the monkey's attention (Figure 25–10).

The abrupt appearance of a visual stimulus involuntarily evokes attention. When a task-irrelevant light flashes in the receptive field of a lateral intraparietal

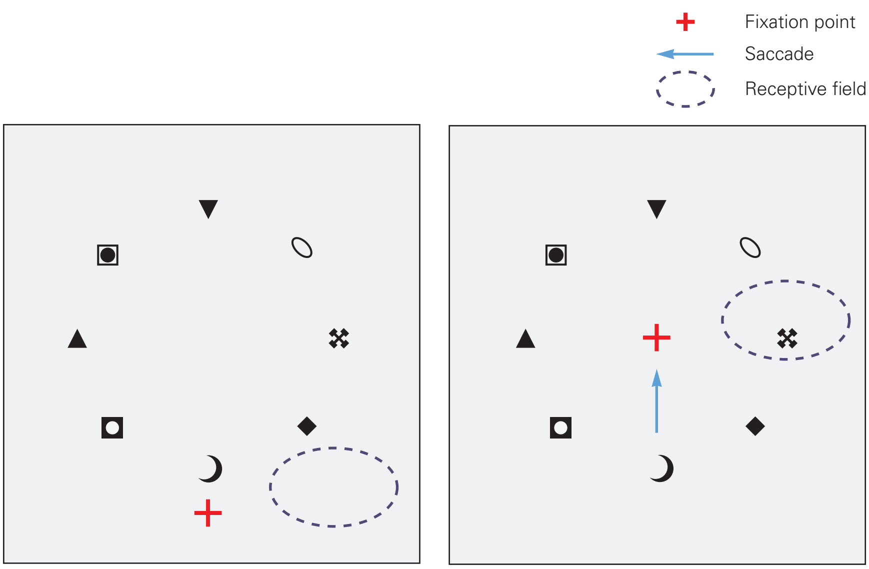

Figure 25–10 Exploring a stable array of objects. The monkey views a screen with a number of objects that remain in place throughout the experiment. The monkey's gaze can be positioned so that none of the objects are included in the receptive field of a neuron (*left*), or the monkey can make a saccade that brings one of the objects into the receptive field (*right*). (Reproduced, with permission, from Kusunoki, Gottlieb, and Goldberg 2000.)

(*continued*)

The Parietal Cortex Provides Visual Information to the Motor System

Vision interacts with the supplementary and premotor cortices to prepare the motor system for action. For example, when you pick up a pencil, your fingers are separated from your thumb by the width of the pencil; when you pick up a drink, your fingers are separated from your thumb by the width of the glass. The visual system helps to adjust the grip width before your hand arrives at the object. Similarly, when you insert a letter into a mail slot, your hand is aligned to place the letter in the slot. If the slot is tilted, your hand tilts to match.

Patients with lesions of the parietal cortex cannot adjust their grip width or wrist angle using visual information alone, even though they can verbally describe the size of the object or the orientation of the slot. Conversely, patients with intact parietal lobes and deficits in the ventral stream cannot describe the size of an object or its orientation but can adjust their grip width and orient their hands as well as normal subjects can. Neurons in parietal cortex are a critical source of information needed to manipulate or move objects.

Box 25–1 The Priority Map in Parietal Cortex (continued)

neuron, that cell responds briskly (Figure 25–11A). In contrast, a stable, task-irrelevant stimulus evokes little response when eye movement brings it into the neuron's receptive field (Figure 25–11B).

It is possible that the saccade that brings the stable object into the receptive field suppresses the visual response. This is not the case. A second experiment uses a similar array, except there is no stimulus at the location to which the saccade had brought the receptive field in the stable array experiment. The monkey fixates so that no member of the array is in the receptive field, and then the task-irrelevant stimulus suddenly appears at the post-saccade location of the receptive field. Now the monkey makes a saccade to the center of the array, bringing the recently appeared stimulus into the receptive field, and the cell fires intensely (Figure 25–11C). When the monkey makes the saccade, the two arrays are identical. However, the stable stimulus is presumably unattended,

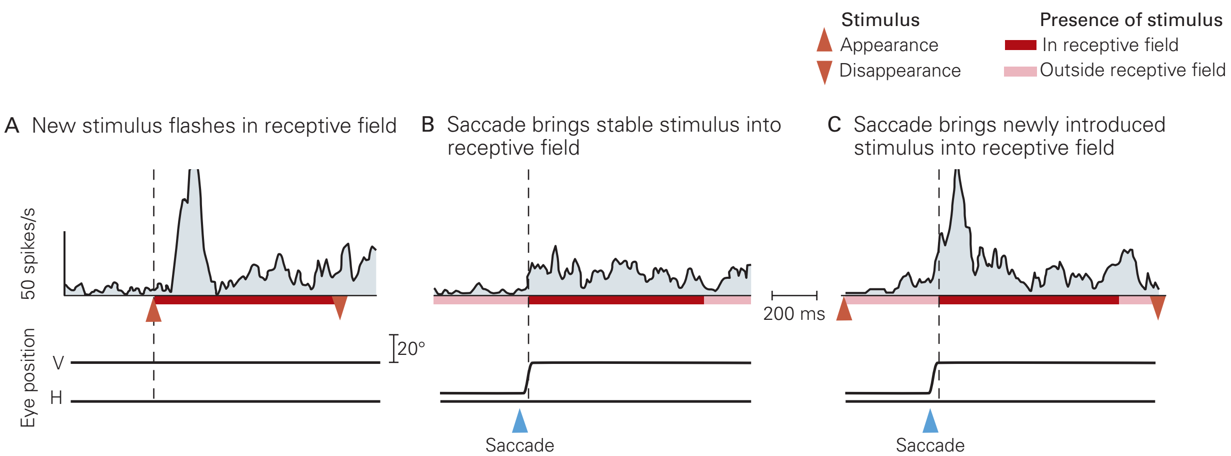

Figure 25–11 A neuron in the lateral intraparietal area fires only in response to salient stimuli. In each panel, neuronal activity and eye positions are plotted across time.

A. A stimulus flashes in the receptive field while the monkey fixates.

B. The monkey makes a saccade that brings a stable, task-irrelevant stimulus into the receptive field.

C. The monkey makes a saccade that brings the location of the recent light flash into the receptive field.

The neural operations behind visually guided movements involve identifying targets, specifying their qualities, and ultimately generating a motor program to accomplish the movement. Neurons in the parietal cortex provide the visual information necessary for independent movement of the fingers.

The representation of space in the parietal cortex is not organized into a single map like the retinotopic map in primary visual cortex. Instead, it is divided into at least four areas (LIP, MIP, VIP, AIP) that analyze the visual world in ways appropriate for individual motor systems. These four areas project visual information to the areas of premotor and frontal cortex that control individual voluntary movements (Figure 25–13).

Neurons in the medial intraparietal area describe the targets for reaching movements and project to the premotor area that controls reaching movements. The anterior intraparietal cortex has neurons that signal the size, depth, and orientation of objects that can be grasped. Neurons in this area respond to stimuli that could be the targets for a grasping movement, and these neurons are also active when the animal makes the movement (Figure 25–14). Neurons in the lateral

whereas the recently flashed stimulus evokes attention and a much larger response. Stable objects can evoke enhanced responses when they become relevant to the animal's current behavior.

A stable object can also be made behaviorally important. In that case, the neurons increase their firing rate when the monkey has to attend to the stable object brought into the receptive field by the saccade (Figure 25–12).

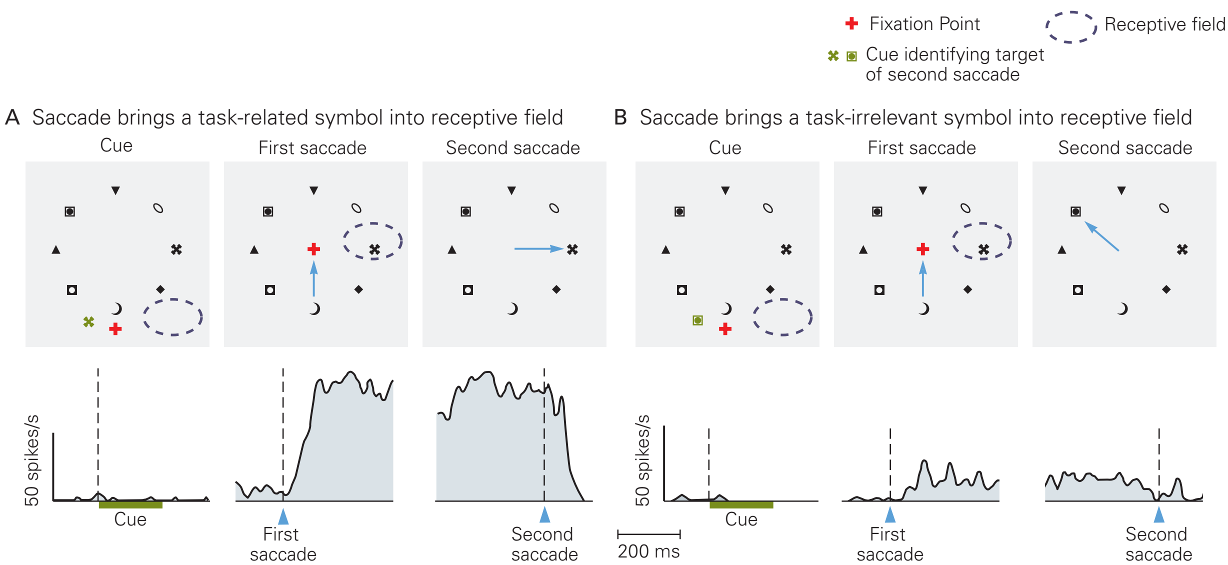

Figure 25–12 A neuron in the lateral intraparietal area fires before a saccade to a significant stable object. On each trial, one object in a stable array becomes significant to the monkey because the monkey must make a saccade to it. The monkey fixates a point outside the array, and a cue that matches an object in the array appears outside the neuron's receptive field. The monkey must then make a saccade to the center of the array and a second saccade to the object that matches the cue. Two experiments are shown (in parts A and B). The *left* panel shows the neuron's response to the appearance of the cue outside the receptive field, the *center* panel shows the response after the first saccade brings the cued object into the receptive field, and the *right* panel shows the response just before the second saccade to the cued object. The cues are shown here in **green** for clarity but were black in the experiment. The visual scene at the time of the saccade is identical in both experiments.

A. The monkey is trained to make the second saccade to the cued object; the cell fires intensely when the first saccade brings the object into the receptive field.

B. The monkey is trained to make the second saccade to an object outside the receptive field; the cell fires much less when the saccade brings the task-irrelevant stimulus into the receptive field.

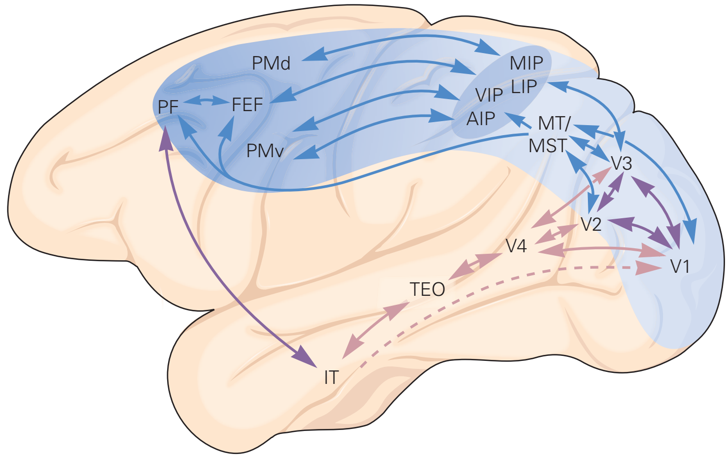

Figure 25–13 Pathways involved in visual processing for action. The dorsal visual pathway (**blue**) extends to the posterior parietal cortex and then to the frontal cortex. The ventral visual pathway (**pink**) is considered in Chapter 24. There are bidirectional projections from the inferior temporal cortex to the prefrontal cortex. (Abbreviations: **AIP**, anterior intraparietal cortex; **FEF**, frontal eye field; **IT**, inferior temporal cortex; **LIP**, lateral intraparietal cortex; **MIP**, medial intraparietal cortex; **MST**, medial superior temporal cortex; **MT**, middle temporal cortex; **PF**, prefrontal cortex; **PMd**, **PMv**, dorsal and ventral premotor cortices; **TEO**, occipitotemporal cortex; **VIP**, ventral intraparietal cortex; **V1–V4**, areas of visual cortex.)

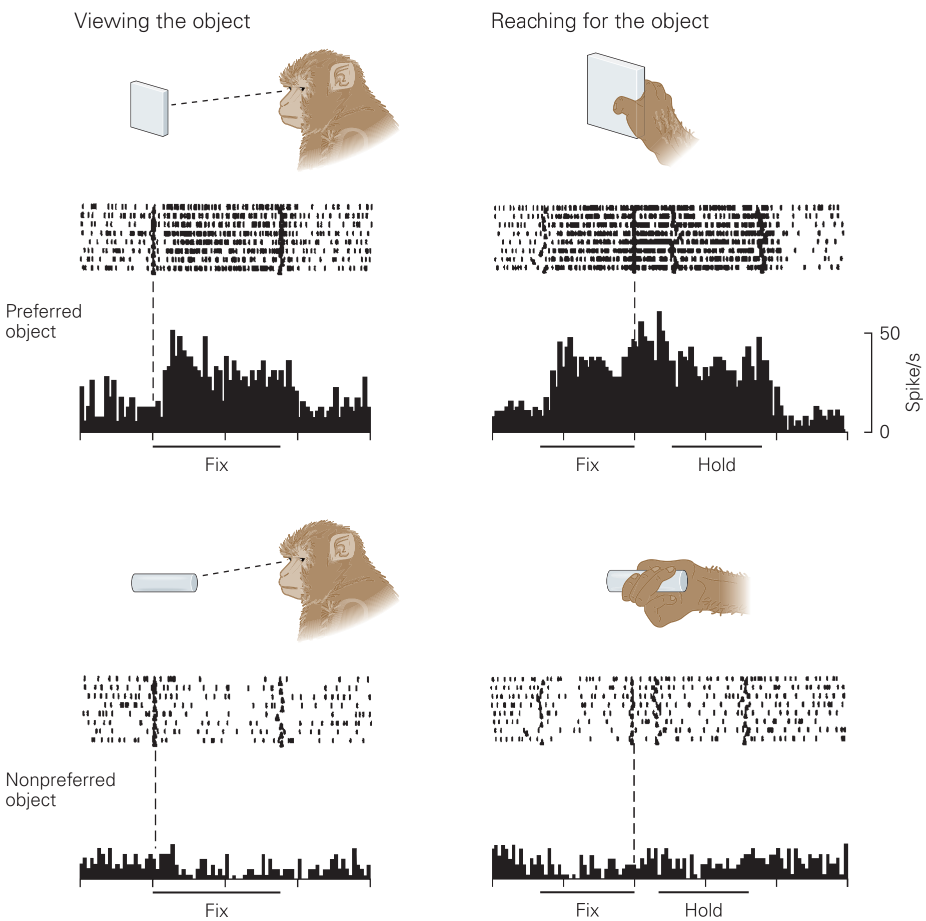

Figure 25–14 Neurons in the anterior intraparietal cortex respond selectively to specific shapes. The neuron shown here is selective for a rectangle, whether viewing the object or reaching for it. The neuron is not responsive to the cylinder in either case. (Reproduced, with permission, from Murata et al. 2000.)

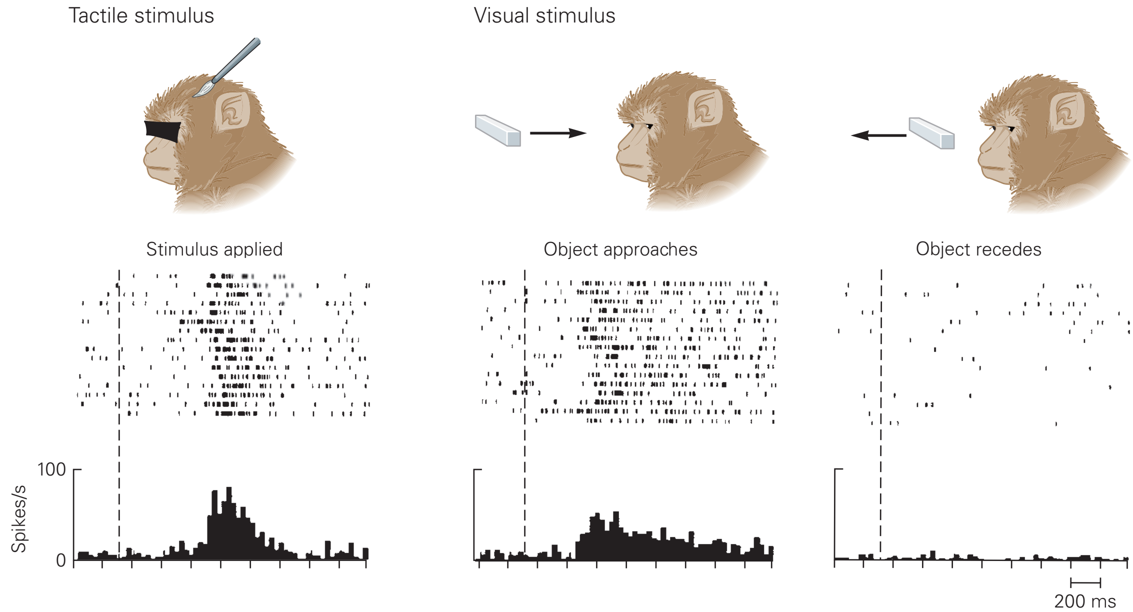

Figure 25–15 Bimodal neurons in the ventral intraparietal cortex of a monkey respond to both visual and tactile stimuli. The neuron shown here responds to tactile stimulation of the monkey's head or to a visual stimulus coming toward the head, but not to the same stimulus moving away from the head. (Reproduced, with permission, from Duhamel, Colby, and Goldberg 1998.)

intraparietal area specify the targets for saccades, and project to the frontal eye field.

Because a monkey cannot see its mouth, the ventral intraparietal area has bimodal neurons that respond to tactile stimuli on the face (Figure 25–15) and to objects in the visual world that are approaching the tactile receptive field, allowing the brain to estimate that an object is near the mouth. The ventral intraparietal area projects to the face area of premotor cortex.

Highlights

1. The image of the world enters the brain via the eye, which is constantly moving in the head. The visual system must compensate for changes in eye position to calculate spatial locations from retinal locations. Helmholtz postulated that the brain solves this problem by feeding back the motor signal that drives the eye to the visual system, to compensate for the effect of the eye movement. This motor feedback to the visual system is called corollary discharge.
2. Neurons in the lateral intraparietal area, which provides visual information to the oculomotor system, show evidence of this corollary discharge. Neurons that ordinarily do not respond to a particular stimulus in space will respond to it if an impending saccade will bring that stimulus into its receptive field.
3. This receptive field remapping depends on a pathway that goes from the intermediate layers of the superior colliculus to the medial dorsal nucleus of the thalamus to the frontal eye field. Medial dorsal nucleus inactivation impairs monkeys' ability to identify where their eyes land after a saccade, suggesting the corollary discharge has a perceptual as well as a motor role.
4. Sherrington postulated that the brain uses eye position to calculate the spatial location of objects from the position of their images on the retina. There is a representation of eye position in somatosensory cortex. Eye position modulates the visual responses of parietal neurons, and target position in space is simple to calculate from this modulation.
5. An unanswered question is how the brain chooses between the eye position and corollary discharge mechanisms to determine spatial position. Because corollary discharge precedes the change in eye position and proprioception follows it, could the brain use both positions at different times?
6. Attention is the ability of the brain to select objects in the world for further analysis. Without attention, spatial perception is severely limited. For

example, humans have great difficulty noticing a change in the visual world unless their attention is drawn to the spatial location of a change.

7. The activity of neurons in the parietal cortex predicts a monkey's locus of spatial attention as measured by their perceptual thresholds. The parietal cortex sums a number of different signals—motor, visual, cognitive—to create a priority map of the visual field. The motor system uses this map to choose targets for movement. The visual system uses the same map to find the locus of visual attention.
8. Lesions in the parietal cortex cause a neglect of the contralateral visual world.
9. Visual information provided by the parietal cortex enables the motor system to adjust hand grip to match the size of the object to which it reaches before the hand actually lands on the target. By contrast, patients with perceptual deficits caused by lesions in inferior temporal cortex adjust their grip perfectly well even though they cannot describe the nature or size of the object to which they reach perfectly.
10. There are at least four different visual maps in the intraparietal sulcus, each of which corresponds to a particular motor workspace.
11. Neurons in the anterior intraparietal area respond to targets for grasping, respond even when monkeys make grasping movements in total darkness, and project to the grasp region of premotor cortex.
12. Neurons in the ventral intraparietal area respond to objects coming toward the mouth, have tactile receptive fields on the face, and project to the mouth area of premotor cortex.
13. Neurons in the medial intraparietal area have a representation of arm position and respond to targets for reaching.
14. Neurons in the lateral intraparietal area respond to targets for eye movements and objects of visual attention, discharge before eye movements, and have a representation of eye position. Activity of these neurons is modulated by the position of the eyes in the orbit.
15. Neurons in the face region of area 3a in the somatosensory cortex have a representation of the position of the eye in the orbit that arises from the contralateral eye.

Michael E. Goldberg
Robert H. Wurtz

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