

5. Individual cells in inferior temporal cortex can be highly shape-selective and respond selectively, eg, to a hand or a face. They can maintain selectivity across position, size, and even rotation—properties that might explain perceptual constancy.
6. Inferotemporal cortex comprises a yet-unknown number of areas with very different functional specializations. While the functional logic of the overall organization remains unknown, we do know that cells with similar selectivity group into cortical columns and that face cells are organized into larger units called face areas.
7. Face recognition is supported by multiple face areas, each with a unique functional specialization. Face areas are selectively coupled to form a face-processing network, which has emerged as a model system for high-level vision.
8. Inferotemporal cortex is interconnected with perirhinal and parahippocampal cortices for memory formation, with the amygdala for the assignment of emotional valence to objects, and with prefrontal cortex for object categorization and visual working memory. If associative memories are stored as patterns of connections between neurons, what then are the specific contributions of hippocampus and neocortical structures of the medial temporal lobe, and by what cellular mechanisms do they exert their influences? The confluence of molecular-genetic, cellular, neurophysiological, and behavioral approaches promises to solve these and other problems.
9. Objects are perceived as members of a category. This simplifies the selection of appropriate behaviors, which often do not depend on stimulus details. Neurons with categorical selectivity are found in dorsolateral prefrontal cortex, a main projection site of inferior temporal cortex.
10. Object recognition relies on past experience. Perceptual learning can improve the ability to discriminate between complex objects and refine neural selectivity in inferior temporal cortex.
11. Visual information can be held in short-term working memory to be available beyond the duration of a sensory stimulus. Neurons in temporal and prefrontal cortex can exhibit delay-period activity after the disappearance of a stimulus. How these networks establish the ability to keep information online is an open question.
12. High-level visual information processing changes with top-down modulation. The sensory experience of an image in view and the recall of the same stimulus from memory are subjectively

similar. Neurons in inferior temporal cortex exhibit similar activity during bottom-up activation and cued recall.

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## Visual Processing for Attention and Action

### The Brain Compensates for Eye Movements to Create a Stable Representation of the Visual World

Motor Commands for Saccades Are Copied to the Visual System

Oculomotor Proprioception Can Contribute to Spatially Accurate Perception and Behavior

### Visual Scrutiny Is Driven by Attention and Arousal Circuits

### The Parietal Cortex Provides Visual Information to the Motor System

### Highlights

**T**HE HUMAN BRAIN HAS AN AMAZING ability to direct action to objects in the visual world—a baby reaching for an object, a tennis player hitting a ball, an artist looking at a model. This ability requires that the visual system solve three problems: making a spatially accurate analysis of the visual world, choosing the object of interest from the welter of stimuli in the visual world, and transferring information on the location and details of the object to the motor system.

### The Brain Compensates for Eye Movements to Create a Stable Representation of the Visual World

Although the visual system produces vivid representations of our visual world, as described in preceding chapters, a visual image is not like an instantaneous photographic record but is dynamically constructed

from information conveyed in several discrete neural pathways from the eyes. When we look at a painting, for example, we explore it with a series of quick eye movements (saccades) that redirect the fovea to different objects of interest in the visual field. The brain must take into account these eye movements in the course of producing an interpretable visual image from the light stimuli in the retina.

As each saccade brings a new object onto the fovea, the image of the entire visual world shifts on the fovea. These shifts occur several times per second, such that after several minutes the record of movement is a jumble (Figure 25–1). With such constant movement, visual images should resemble an amateur video in which the image jerks around because the camera operator is not skilled at holding the camera steady. In fact, however, our vision is so stable that we are ordinarily unaware of the visual effects of saccades. This is so because the brain makes continual adjustments to the images falling on the retina after each saccade.

A simple laboratory experiment, shown in Figure 25–2, illustrates the biological challenge to the brain.

### Motor Commands for Saccades Are Copied to the Visual System

The first insight into the brain mechanisms underlying visual stability came from an observation by Hermann von Helmholtz in the 19th century. He saw a patient who could not move his eye horizontally toward his ear because of a paralysis of the lateral rectus muscle. Whenever the patient attempted to look toward his ear, the entire visual world jumped in the opposite direction and then returned to the center of gaze.



**Figure 25-1** Eye movements during vision. A subject viewed this painting (*An Unexpected Visitor* by Ilya Repin) for several minutes, making saccades to selected fixation

points, primarily to faces. Lines indicate saccades, and spots indicate points of fixation. (Reproduced, with permission, from Yarbus 1967).

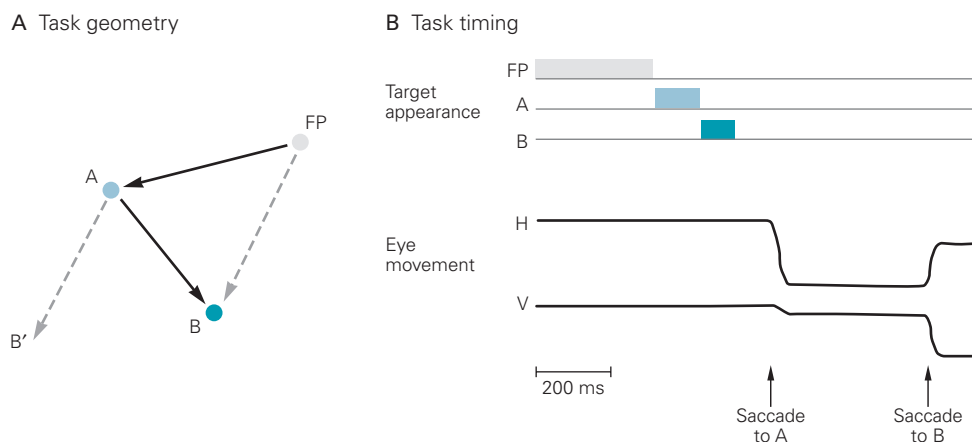
Helmholtz postulated that a copy of the motor command for each saccade was fed to the visual system so that the representation of the visual world could be adjusted to compensate for eye movement. This adjustment would lead to a stable image of the visual world. In the 19th century, Helmholtz called such a copy a “sense of effort,” and in the 20th century, it was named an efference copy or corollary discharge.

The corollary discharge solves the problem of the double-step saccade. In order for a corollary discharge to affect visual perception across eye movements, motor information has to affect the activity of visual neurons.

This is precisely what happens to neurons in the parietal cortex, frontal eye field, prestriate visual cortex, and superior colliculus when a monkey makes a saccade. Each saccade can be considered a vector with two dimensions—direction and amplitude. Although the retinal image is different after each saccade, the brain can use the vector of each saccade to reconstruct the whole visual scene from the sequence of retinal images.

The corollary discharge can be seen at the level of a single cell. Physiological studies in the Rhesus monkey, an animal whose oculomotor and visual systems resemble those of humans, have illuminated the





**Figure 25–2** The double-step task illustrates how the brain stabilizes images during saccades.

**A.** A subject starts by looking at a fixation point (FP) that disappears, after which two saccade targets **A** and **B** appear and disappear sequentially before the subject can make the saccade. The first saccade (to target **A**) is simple. The retinal vector (FP→**A**) and

the saccade vectors are the same. After the first saccade, the subject is looking at **A**. The retinal vector is **A**→**B'**, but the monkey must make a saccade whose vector is **A**→**B**. The brain must adjust the retinal vector to compensate for the first saccade.

**B.** Timing. The upper records show when the targets appear (colored bars). (Abbreviations: **H**, horizontal; **V**, vertical.)

problem. Every time a monkey makes a saccade, a stimulus currently not in the receptive field of a neuron in the lateral intraparietal area, and therefore incapable of exciting the neuron, will excite the neuron if the impending saccade will bring the stimulus into the receptive field, even before the saccade occurs (Figure 25–3). Thus, a corollary discharge of the impending saccade affects the visual responsiveness of the parietal neuron.

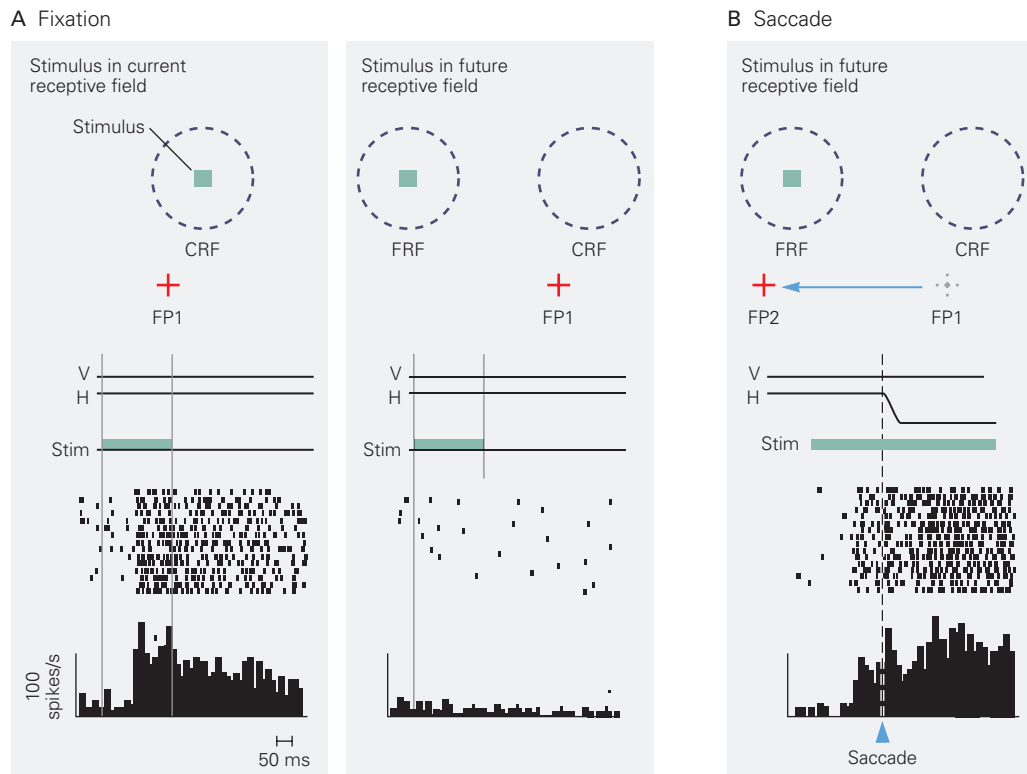
This transient remapping of the receptive field explains how subjects can perform the double-step task. Consider the diagram in Figure 25–2A. The task begins with the monkey directing gaze to the fixation point (FP). After the monkey makes the first saccade, the retinal vector **A**→**B'** is no longer useful for making the **A**→**B** saccade. However, the FP→**A** saccade remaps the activity of the cell describing the vector **A**→**B**, so it responds to the target at the retinal location of **B**, which was not in its receptive field when the monkey was looking at FP. Remapping is found in a number of cortical and subcortical areas, including lateral intraparietal area, frontal eye field, medial intraparietal area, intermediate layers of the superior colliculus, and prestriate areas V4, V3a, and V2. As we shall see, remapping facilitates both visual perception around the time of a saccade and the accuracy of visually guided movement.

The first question this raises is: How does the brain obtain the vector of the saccade that it feeds back to the visual system? We know from decades of research that the motor command for the vector is represented in the superior colliculus on the roof of the midbrain (Chapter 35). Each neuron in the superior colliculus

is tuned to saccades of a given vector, such that the neurons collectively provide a map of the vectors of all possible saccades. Inactivation of the superior colliculus affects the monkey's ability to make saccades. Electrical stimulation of the superior colliculus evokes saccades of the vector described by the neurons at the stimulation site. But this provides the vectors that actually drive the eye, not the vectors that inform perception about the vector of the saccade. How does the vector information used to move the eye become available to brain processes that do not move the eye but do require information about how it moved?

Since the vectors for moving the eye have been identified in the superior colliculus, it is reasonable to expect that this also might be the source of a corollary discharge. Indeed, it is. The superior colliculus has both descending pathways for generating the saccades and ascending pathways to the cerebral cortex that could carry the corollary discharge of the impending movement (Figure 25–4). The pathways to the cortex pass through the thalamus, as does all internal and almost all external information reaching the cerebral cortex.

The motor signal in the thalamus is not necessarily a corollary discharge; it could also be a movement command that simply passes through the cerebral cortex. That is not the case, however, because inactivation of this pathway in the thalamus does not alter the amplitude and direction of saccades. It is not driving saccades. It is more likely to be a corollary discharge. After inactivation of the thalamic pathway, monkeys cannot accurately perform the second saccade of the double-step task. In addition, inactivation disrupts the



**Figure 25-3** Remapping of the receptive field of a visual neuron in the parietal cortex of a monkey in conjunction with saccadic eye movements. (A [left] and B adapted, with permission, from Duhamel, Colby, and Goldberg 1992. A [right] reproduced with permission, from M.E. Goldberg.)

**A. Left:** The monkey looks at fixation point 1 (FP1), and the cell responds to the abrupt onset of a task-irrelevant stimulus in the current receptive field (CRF). Successive trials are synchronized on the appearance of the stimulus. (Abbreviations: H, horizontal

eye position; V, vertical eye position.) **Right:** The monkey looks at FP1, and the cell does not respond to a stimulus flashed in the future receptive field (FRF).

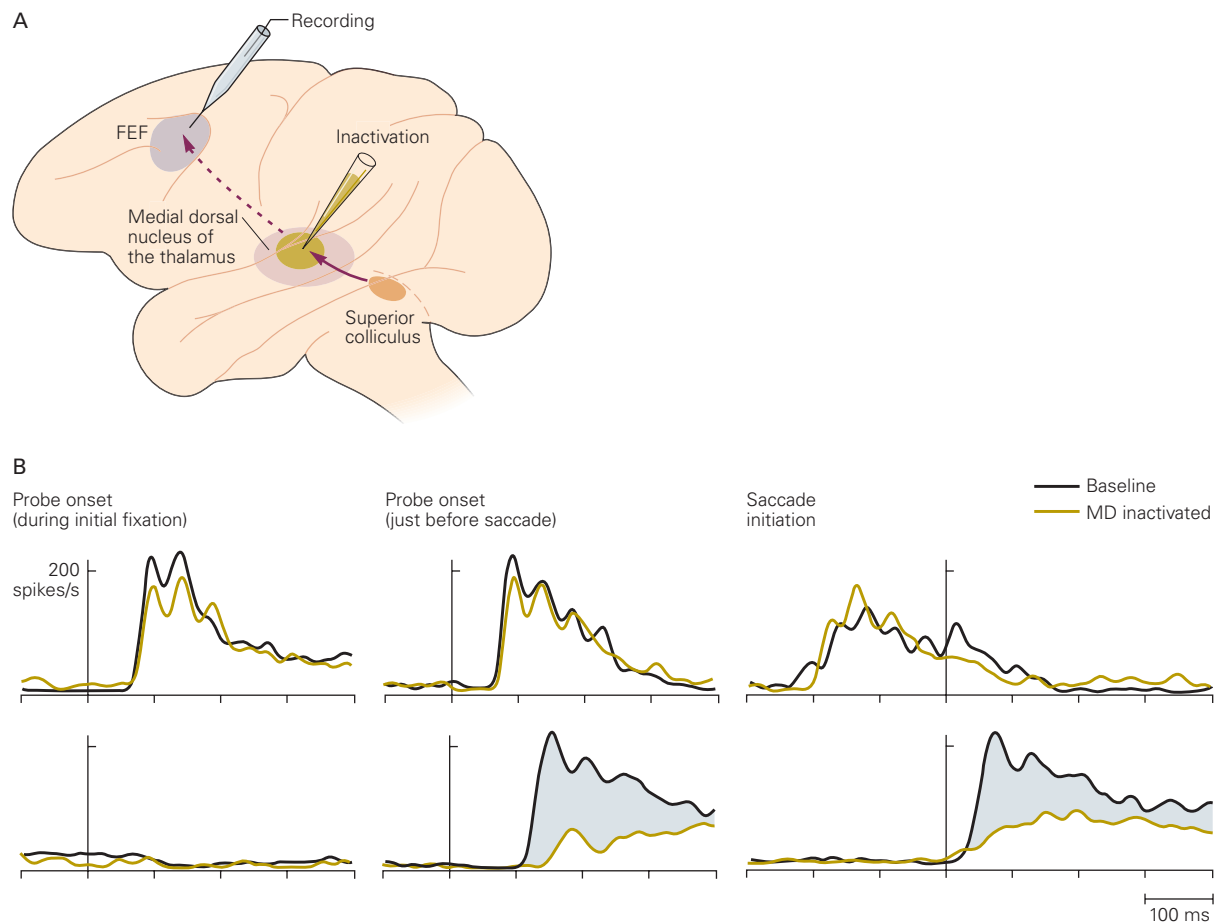
**B.** The monkey makes a saccade from FP1 to FP2, which will bring the cell's receptive field onto the stimulus in the FRF. Now the cell fires even before the saccade begins, which means that a corollary discharge of the saccade plan remapped the area of the retina to which the cell responds.

receptive field remapping described earlier (Figure 25-3B). Because disrupting the corollary discharge disrupts both receptive field remapping and the behavioral compensation for eye movements, it is likely that the corollary discharge is essential for solving the problem of spatial accuracy for action.

To determine whether the corollary discharge also provides the information that allows the visual system to perceive the location of objects that appeared before a saccade, the monkey is trained to indicate where it thinks its eyes are directed at the end of the saccade. We can measure where the motor system moved the eye, but what we want to know is the monkey's perception of the change in its eye direction with each saccade. This can be determined using a task developed for humans by Heiner Deubel and his colleagues and adapted for monkeys. In this task, the monkey looks at a fixation point and then makes a saccade to a target (Figure 25-5A). During the saccade, the target

temporarily disappears; when it reappears, it has been displaced to a location left or right of the original target. After the trial, the monkey moves a bar to the right or left to indicate the direction of the displacement (Figure 25-5A).

Over a series of trials, the monkey's responses are plotted to generate a psychometric curve (Figure 25-5B). This curve shows the actual intrasaccadic target displacement (horizontal axis) in the same (forward) or opposite (backward) direction as the initial saccade, and how frequently the monkey reports that it was moved forward (vertical axis). The monkey responded that the target had moved forward 100% of the time when the target was 3° to the right. When the target moved 3° to the left, the monkey responded that it had never moved forward. The point on the psychometric curve where the monkey reported forward and backward displacements with equal frequency (the 50% horizontal line) was taken as the perceptual null point.

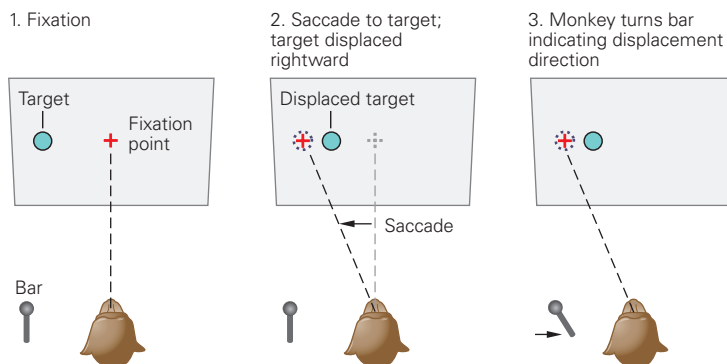


**Figure 25-4** A corollary discharge from the motor program for saccades directs a shift in location of the receptive field of frontal eye field neurons prior to the saccade. (Adapted, with permission, from Sommer and Wurtz 2008. Copyright © 2008 by Annual Reviews.)

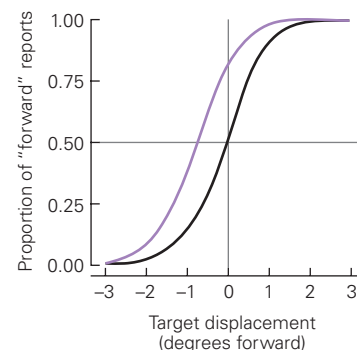
**A.** One possible pathway for the corollary discharge originates in saccade-generating neurons in the superior colliculus, passes through the medial dorsal nucleus of the thalamus, and terminates in the frontal eye field (FEF) in the frontal cortex.

**B.** When the medial dorsal nucleus (MD) is inactivated, the response of a frontal eye field neuron to a stimulus probe in the cell's current receptive field is unaffected (**upper records**), whereas the response to a stimulus in a future (post-saccade) receptive field is severely impaired (**lower records**). This result demonstrates that a corollary discharge from the saccade motor program directs the shift in the neuron's receptive field properties.

#### A Task for perceived eye direction



#### B Change in perceptual location



**Figure 25-5** Perceived saccade direction changes with disruption of corollary discharge.

**A.** At the start of each trial, the monkey fixates a target on a screen (1). When the fixation point is turned off, the monkey makes a saccade to the target; during the saccade, the target is displaced randomly (up to 3°) either to the left or to the right (2). After the saccade to the original target, the monkey receives a reward for manually moving a bar in the direction of the target displacement (3).

**B.** Psychometric curves before (black) and after (purple) inactivation of the medial dorsal nucleus of the thalamus, which contains the relay neurons for the corollary discharge in its pathway between the superior colliculus and the frontal cortex. The curve shows the proportion of forward (in the direction of the saccade) judgments (y-axis) for each target displacement (x-axis). The post-saccadic target location at which the monkey perceived no displacement is defined as the perceptual null location. (Adapted, with permission, from Cavanaugh et al. 2016.)

We take this point to be the monkey's perception of the original target location. If the target were not perceived to move, it must be in the same location as before the saccade; in a normal monkey, that point is close to zero (Figure 25–5B).

We now have a corollary discharge that can provide the vector for each saccade and a task for a monkey that allows us to determine where it perceives the target to be at the end of the saccade. If the corollary discharge contributes to the monkey's perception, then inactivating the corollary discharge should change the animal's perception of target location. It does. The purple curve in Figure 25–5B represents the perceived location after corollary discharge inactivation; the curve shifts to the left after inactivation of the medial dorsal nucleus of the thalamus. The conclusion is that the corollary discharge does provide the vector of the saccade, which is necessary for the monkey to perceive that the target had moved. With each saccade, corollary discharge information provides perceptual information for determining the amplitude and direction of the current saccade, and it does so with machine-like precision several times per second.

The corollary discharge provides the vector information available before the saccade is made, but it is not the only source of information. Two other types of information must be evaluated after the saccade has taken place: visual cues and eye muscle proprioception. Visual cues are unlikely to be a factor in the perceptual experiment described (Figure 25–5) because the experiment was done in total darkness except for light scattered from the very dim fixation point and saccade target. In the light, however, could visual cues be a factor? In fact, repeating the experiment in the light did not improve the monkey's judgment and frequently made it worse.

Oculomotor proprioception is unlikely to provide the vector information at the end of the saccade because, on average, the metrics of the saccades before and during inactivation do not change, so there is little reason to expect that the muscle proprioception will have changed. In addition, while the corollary discharge begins at least 100 ms before the saccade, neuronal activity from oculomotor proprioception reaches the lateral intraparietal area about 150 ms after the saccade. As we will see in the next section, the role of proprioception in perception might be to provide information long after the saccade ends.

Finally, there is a second potential disruption of vision produced by saccades: a blur as the saccade sweeps the visual scene across the retina. The blur is not seen, however, because neuronal activity in a number of visual areas is suppressed around the time of

every saccade. This so-called saccadic suppression was first seen in the superior colliculus and has subsequently been seen in the thalamus and areas of visual cortex beyond primary visual cortex.

A corollary discharge contributes to this neuronal activity suppression because the suppression occurs even in total darkness (no vision) and even if eye movement is blocked (no proprioception). Suppression can also be produced by visual masking, which occurs when one stimulus reduces the perception of a following or preceding stimulus. If a saccade starts in total darkness, and an object is then flashed and extinguished before the saccade ends, a blur can be seen during the saccade. If a mask is flashed after the saccade, the blur is suppressed. A correlate of such a masking effect is clearly seen in neurons in primary visual cortex. The suppression resulting from a corollary discharge is relatively weak but is present with all saccades; that from visual masking is much stronger but is present only in the light.

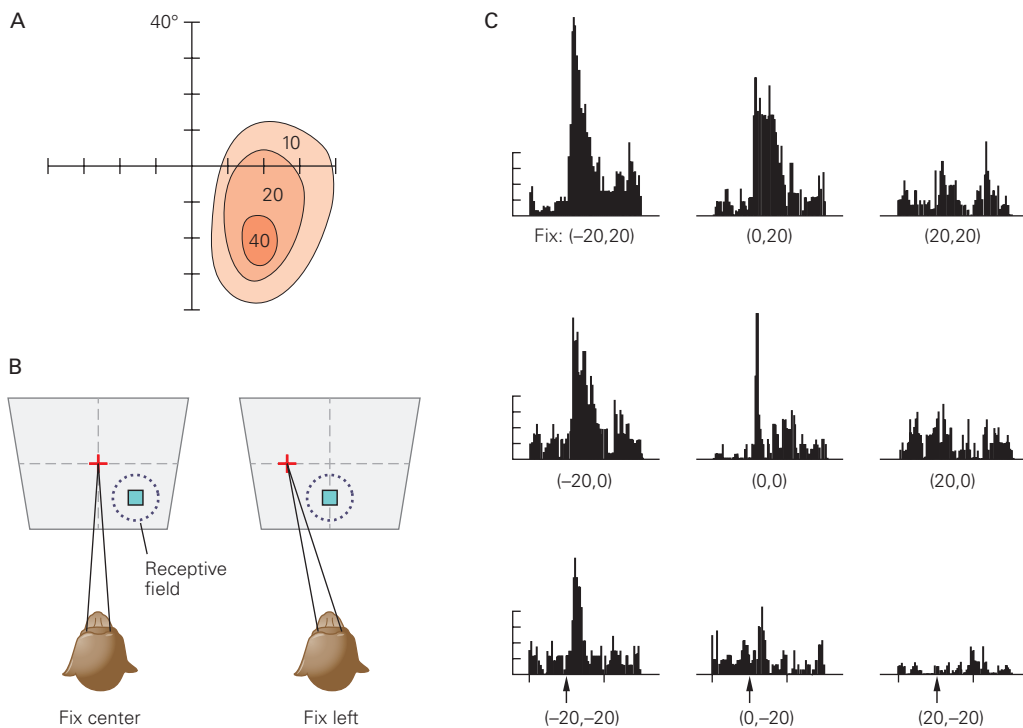
### **Oculomotor Proprioception Can Contribute to Spatially Accurate Perception and Behavior**

Charles Sherrington suggested that the way the brain compensates for a moving eye is to measure directly where the eyes are in the orbit and adjust the visual signal for changes in position. Richard Andersen and Vernon Mountcastle discovered that the responses of parietal visual neurons with retinotopic receptive fields are modulated by the position of the eye in the orbit in a linear fashion called the *gain field* (Figure 25–6). From this relationship, the position of an object in head-centered (craniotopic) coordinates can easily be calculated.

Where does the eye position signal that creates the gain fields come from? It could come from a corollary discharge of eye position, or it could come from a proprioceptive mechanism. Human eye muscles have two structures that could contribute to oculomotor proprioception: muscle spindles and myotendinous cylinders, or palisade endings, an eye-specific structure. Area 3a, the region of somatosensory cortex to which skeletal muscle spindles project, has a representation of the position of the eye, which arises from proprioceptors in the contralateral orbit (Figure 25–7).

However, the proprioceptive measurement of eye position lags changes in eye position by 60 ms, and for 150 ms after a saccade, the gain fields modulate the visual response as if the monkey were still looking at the presaccadic target, long after the corollary discharge has remapped the visual response. Therefore, the eye position signal creating the gain fields probably arises from a proprioceptive mechanism. The possibility





**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  $-20^\circ, 20^\circ$  to a minimum when the monkey fixates a point at  $20^\circ, -20^\circ$ . **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