12

Posterior Cingulate Cortex and Visuospatial Cognition: Properties of Single Neurons in the Behaving Monkey

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Monkeys are a natural subject for single-neuron recording studies of the cingulate gyrus because they are able to learn and tirelessly perform numerous cognitively demanding tasks. This is an invaluable asset in studies of a region of cortex to which a bewildering array of cognitive functions has been speculatively ascribed, including spatial memory (Goldberg, 1984; Mishkin and Bachevalier, 1986; Pandya and Yeterian, 1984; Sutherland et al., 1988), attention (Mesulam, 1981; Pandya and Yeterian, 1984), and emotion (Papez, 1937; MacLean, 1990).

The approach of monitoring single-neuron activity in primate cingulate cortex, however, has been employed in only a few studies to date. Paul MacLean and colleagues carried out the first and only broad survey of single neurons in primate cingulate cortex (Cuénod et al., 1965; Bachman and MacLean, 1971). They recorded from single units in the posterior cingulate cortex of anesthetized squirrel monkeys and in the anterior cingulate cortex of alert, but passively restrained, squirrel monkeys, while presenting stroboscopic flashes and comparably coarse stimuli in other sensory modalities. They found that only a minute fraction of cingulate neurons could be driven with their sensory stimuli.

Subsequent single-neuron studies in primates have focused exclusively on a narrow dorsal strip of anterior cingulate cortex, including area 24c, immediately adjacent to the supplementary motor area. This strip differs from the remainder of cingulate cortex in possessing strong and direct links to primary motor cortex and to the spinal cord (Muakassa and Strick, 1979; Chapter 14 of this volume). Niki and Watanabe (1976, 1979) monitored the activity of neurons in this region in Old World monkeys trained to perform delayed-response tasks. They observed modulation of neuronal activity during all three task epochs: the cue period (32% of task-related neurons), the delay period (59%), and the response period (76%). Shima et al. (1991) recorded from neurons in the same locale in macaque monkeys performing self-paced and stimulus-triggered arm movements. They found that neurons carry signals related to the preparation and execution of both types of arm movement. Finally, Brooks and colleagues recorded surface potentials around this region in monkeys learning to make wrist movements in response to visual stimuli (Brooks, 1986; Gemba et al., 1986). They describe "error potentials" that occur in conjunction with movements erroneously self-initiated in the absence of a triggering stimulus. Thus, previous studies have demonstrated that a thin strip of anterior cingulate cortex adjacent to the supplementary motor area contains neurons active during the planning and execution of arm movements, but the remainder of cingulate

Neurobiology of Cingulate Cortex and
Limbic Thalamus: A Comprehensive Handbook
Brent A. Vogt and Michael Gabriel, Editors

cortex, comprising more than 90% of its volume, is a virtual *terra incognita* as far as primate single-neuron recording studies are concerned.

The experiments described in this chapter involve monitoring the activity of single neurons in the posterior cingulate cortex of alert macaque monkeys trained to perform tasks requiring visually guided eye movements and the detection of visual events. Tasks of this type were employed because it appeared probable on connectional grounds that posterior cingulate neurons would carry visual and oculomotor signals. Posterior cingulate cortex in the macaque monkey is connected reciprocally to numerous cortical areas in which neuronal activity is correlated with vision and eye movements. These include, in descending order by pathway strength, periprincipalis prefrontal cortex (Barbas and Mesulam, 1985), posterior parietal association cortex (Cavada and Goldman-Rakic, 1989; Andersen et al., 1990a; Tian et al., 1991), supplementary eye field (Huerta and Kaas, 1990), and arcuate eye field (Barbas and Mesulam, 1981; Leichnetz and Goldberg, 1988).

The initial supposition has been confirmed in that many posterior cingulate neurons were found to undergo changes of activity in conjunction with eye movements and in response to visual stimulation. In particular, they fire tonically during periods of steady gaze, at a rate determined by the size and direction of the preceding eye movement and by the current angle of the eye in the orbit. We suggest that this pattern of sensitivity reflects the participation of cingulate circuitry in visuospatial cognition.

Oculomotor and Visual Correlates of Neuronal Activity

Experimental Approach

The methods employed in these experiments permit precise control of visual stimuli and accurate monitoring of eye movements. Under general anesthesia and with sterile surgical procedures, the monkey is fitted with scleral search coils for monitoring eye position (Robinson, 1963), a head holder, and a recording cylinder through which microelectrodes can subsequently be lowered into the brain. The monkey is trained to sit with head fixed in a chair facing a screen and to make eye movements to visible targets projected onto the screen under computer control. Variations in the task permit studying covert shifts of visual attention in the absence of overt eye movements and studying eye movements to remembered rather than to physically present visual targets. During task performance, the electrical activity of single neurons is recorded through a microelectrode lowered vertically by a transdural approach into the brain. A grid held in a chamber affixed to the skull permits placing electrode tracks in a precisely defined square array with 1 mm intertrack spacing and thus allows systematic sampling of neurons throughout a large volume of the posterior cingulate gyrus underlying the chamber (Crist et al., 1988).

On vertical approach to the cingulate gyrus, the electrode first traversed area 5 or area 4. Neurons in these areas are easily identified by the fact that they fire bursts of action potentials during voluntary movements of the contralateral body or in response to somatosensory stimulation, but not during eye movements. Exit from these areas was generally marked by a period of electrical silence as the electrode entered the cingulate sulcus. On further advance, when the tip of the electrode was brought into the cingulate gyrus, neurons no longer showed obvious somatic sensitivity and instead exhibited activity dependent on the monkey's oculomotor behavior. In the single monkey so far brought to histology, microlesions placed at selected recording sites before perfusion were demonstrated, as expected, to be in posterior cingulate cortex.

Quantitative data collection has been carried out on 374 neurons from four cerebral hemispheres in two monkeys. Neurons with task-related activity, as demonstrated by quantitative testing, have been encountered throughout the region of posterior cingulate cortex explored to date. The black dots in Figure 12.1*A* represent recording sites, reconstructed by histological analysis, at which task-related cells were present.

Prolonged Postsaccadic Activity

Each neuron was initially characterized by monitoring its activity, while the monkey performed a standard set of visually guided eye movements to small spots projected on a dimly illuminated screen. The monkey initiated each trial by fixating a small central spot as shown in Figure 12.1*B*. After 1.2 sec, this spot vanished and another identical spot appeared 16° away from it in one of four directions, whereupon the monkey was required to make a rapid eye movement bringing its gaze to bear on the new target. On interleaved trials, the target was presented at different locations, until at least 16 trials of each type had been completed. Out of 374 neurons tested by this method, 199 (53%) exhibited obvious task-related modulation.

Task-related activity consistently took the form of a prolonged shift in firing frequency following saccadic eye movements. An example is shown in Figure 12.1*C*. The histograms juxtaposed to the four arrows in this figure represent mean firing frequency as a function of time during trials in which the monkey made saccadic eye movements in the four corresponding directions. Each histogram is paired with a raster display representing action potentials (dots) as a function of time on a trial-by-trial (row-by-row) basis. The raster and histogram displays are aligned so that the time of onset of the saccade is at a standard position in each display, as indicated by a vertical line. The horizontal extent of each display is 2 sec. For the neuron shown in Figure 12.1*C*, the rate of firing increased after saccadic eye movements, with the most dramatic shift occurring after saccades with a rightward component. The broad tuning for direction evidenced by this neuron was characteristic of a large majority of neurons in the sample. Eye movements eliciting the strongest firing tended to be those directed away from the recording hemisphere, as indicated by the preponderance of rightward-directed rays in Figure 12.1*D*. In this figure each ray points in the corresponding neuron's direction of optimal discharge and the length of the ray is greater for a neuron with more pronounced direction selectivity.

The shift of firing occurred at a time that varied across neurons from close to the onset of the saccade to more than 200 msec following its completion. This pattern of timing indicates that the signal carried by these neurons is neither a motor command that would precede the eye movement nor a sensory response to the visual target that would take the form of a burst of action potentials time-locked to target onset rather than to the saccadic eye movement.

Influence of Orbital Position vs. Saccade Direction and Amplitude

Direction-selective firing as illustrated in Figure 12.1*C* could reflect either sensitivity to the direction of the saccade or sensitivity to the angle of the eye in the orbit at the conclusion of the saccade. To distinguish between these possibilities, further tests were carried out on neurons exhibiting task-related activity. Sensitivity to the angle of the eye in the orbit was examined by having the monkey execute saccades of constant size and direction from different starting points. Data gathered from a neuron with obvious orbital-position sensitivity are shown in Figure 12.2*A*. While the monkey executed 16° rightward saccades from four starting points, the level of tonic activity became higher or lower as a function of the angle of gaze, increasing as orbital position shifted farther to the right. This is evident both before and after the saccadic eye movement. Of 47 neurons tested using this task, 27 (57%) exhibited some degree of sensitivity to orbital position. Data gathered from a neuron with obvious sensitivity to saccade

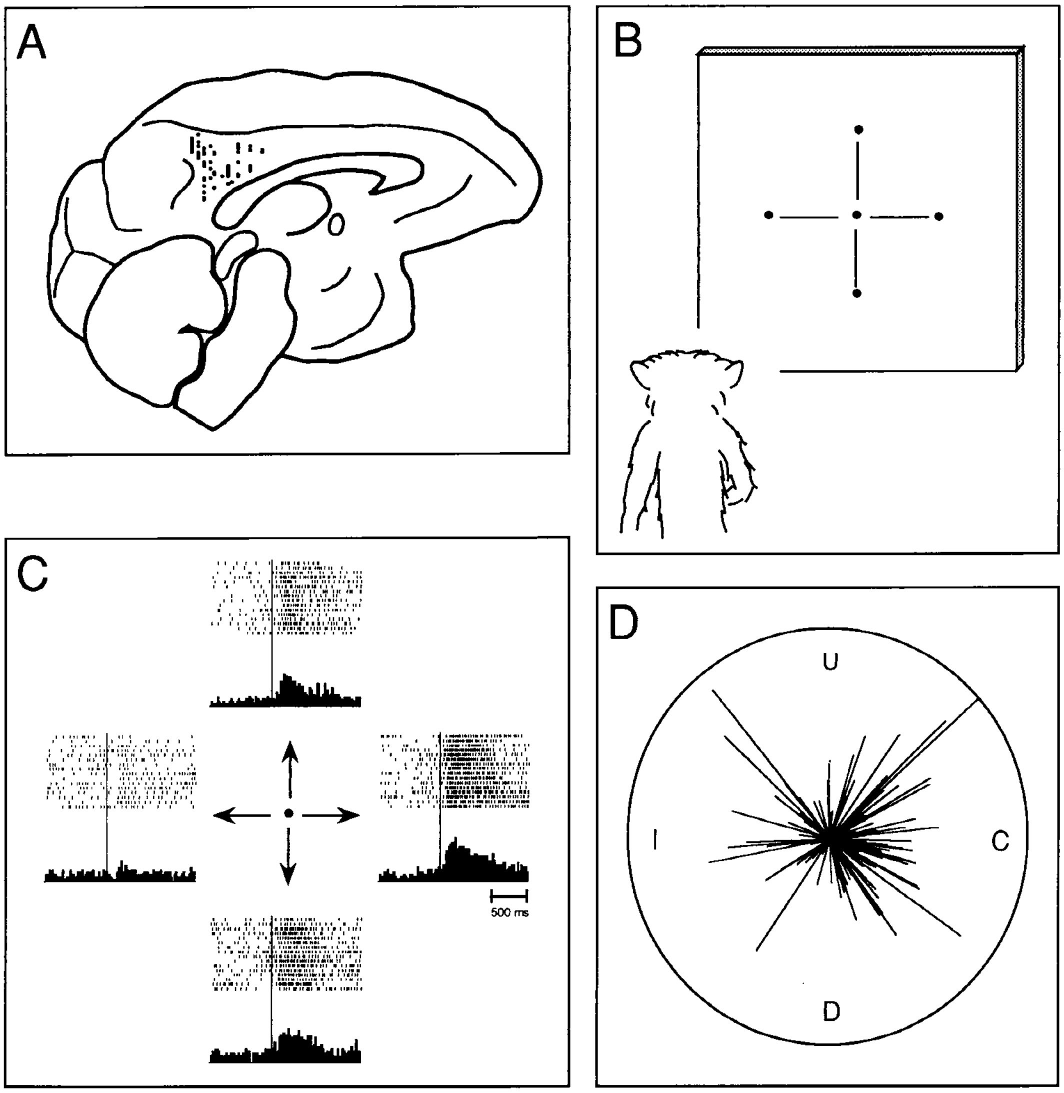

FIGURE 12.1. *A*. Each dot indicates the location of a neuron with task-related activity. Neurons from both hemispheres of a single brain in which histological reconstruction was carried out are projected onto a medial view of the left hemisphere.

B. The standard task employed for initial characterization of all neurons. The monkey maintained fixation of a central spot which was then extinguished, and a second spot was presented 16° from the center in one of four cardinal directions. The monkey was required to attain fixation of the second spot by means of a saccadic eye movement and to maintain fixation for 1 sec for a water reward.

C. Activity of a representative posterior cingulate neuron during performance of the standard task. Activity is represented as a function of time during the trial. Time was measured relative to the moment of onset of the saccadic eye movement (vertical line). In the raster displays, each row represents a trial and each dot represents an action potential. In the histograms, the height of each bar indicates mean level of activity across all trials. The activity of this neuron increased after saccadic eye movements, and firing frequency was especially high following rightward eye movements.

D. Summary of direction selectivity in the standard saccade task. Each ray represents a neuron, the angle of the ray indicates its calculated preferred direction and its length indicates the strength of direction selectivity (a ray touching the perimeter corresponds to a neuron giving no response when motion is orthogonal to the best direction). There is clear bias toward contraversive (C) direction selectivity (i.e., toward stronger firing when the eye is moved into the gaze field opposite the neuron's hemisphere). Downward, D; ipsiversive, I; upward, U.

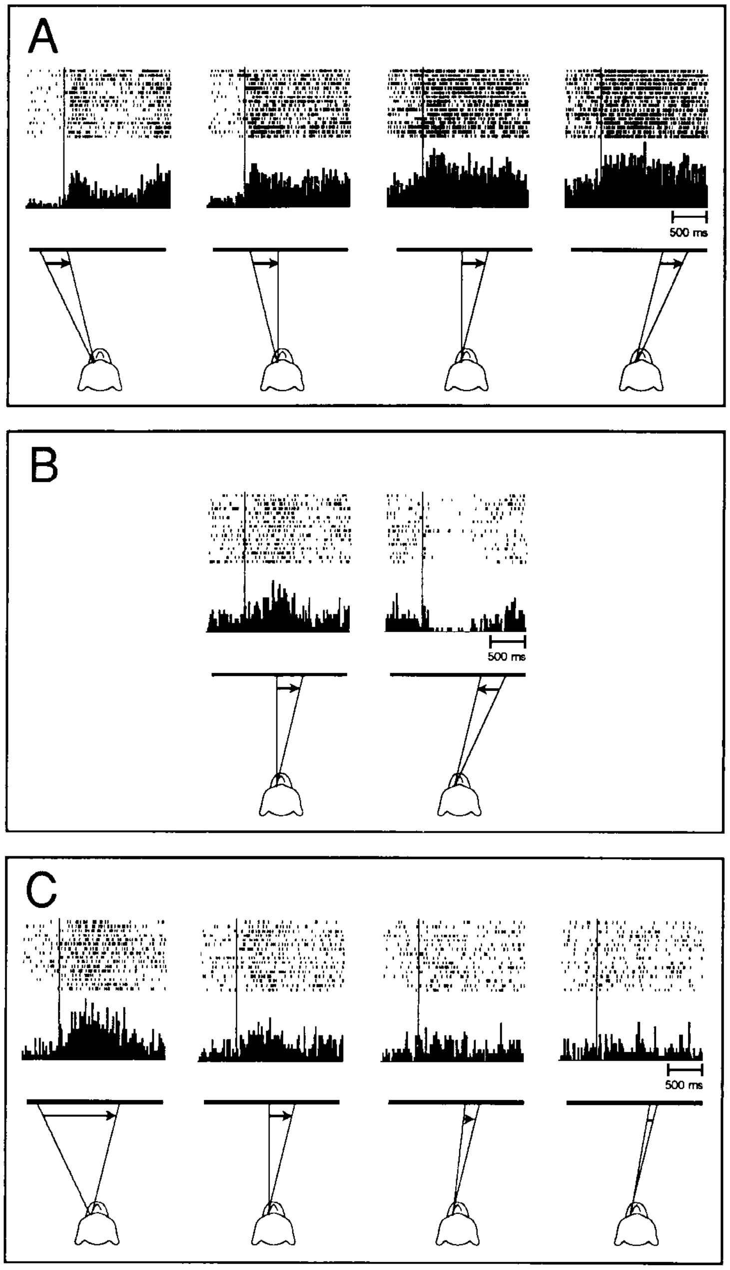

Figure 12.2. *A*. Activity of a neuron exhibiting sensitivity to orbital position. In each raster display and histogram, activity is represented as a function of time relative to the onset of the eye movement (vertical line). In four trial conditions, saccades of identical amplitude (16°) and direction (rightward) were initiated from different starting points. The conditions were imposed in interleaved sequence. Activity became greater as the eye was deviated farther to the right.

B. Activity of a neuron exhibiting sensitivity to saccade direction. In each raster display and histogram, activity is represented as a function of time relative to the onset of the eye movement (vertical line). In two trial conditions, saccades of 16° amplitude were directed to the same endpoint from diametrically opposed starting points. The conditions were imposed in interleaved sequence. Activity was greater following rightward saccades.

C. Activity of the same neuron as in *B* demonstrating sensitivity to saccade amplitude. On interleaved trials, saccades of different amplitude (4°, 8°, 16°, and 32°) were executed in the same direction to an identical endpoint. Postsaccadic activity was maximal after the largest eye movements.

direction are shown in Figure 12.2*B*. When the monkey executed 16° saccades to the same target from different starting points, firing was markedly higher after rightward saccades than it was after leftward saccades. This difference cannot be explained in terms of orbital position, since the position of the eye in the orbit was identical after eye movements in the two directions. Of 30 neurons tested using this task, 17 (57%) were sensitive to the direction of the eye movement. Neurons sensitive to saccade direction commonly were amplitude sensitive as well, firing more strongly after larger movements. Data gathered from a neuron with sensitivity to saccade amplitude are shown in Figure 12.2*C* (same neuron as in Fig. 12.2*B*). Following execution of 4°, 8°, 16°, and 32° rightward saccades ending at the same orbital position, firing attained progressively higher levels.

Although a few neurons were sensitive only to saccade direction or to orbital position, the activity of most neurons was influenced by both factors. For example, in a representative neuron exhibiting combined sensitivity, the rate of firing increased after any large rightward eye movement but the magnitude of the increase became greater as the starting point and endpoint of the movement shifted farther to the right. In a few neurons, the excitatory directions for saccades and orbital deviations were opposed, so that firing was maximal, e.g., after leftward eye movements executed with the eye deviated into the right-gaze field. For the majority of neurons, however, the excitatory directions for postsaccadic activity and orbital position were identical. We conclude that the signals of individual posterior cingulate neurons are complex, reflecting both saccade direction and orbital position.

Influence of Visual Reafference

What causes posterior cingulate neurons to fire during eye movements in certain directions or when the eye has assumed orbital angles in a particular range? One possibility is that these neurons monitor phasic and tonic efference-copy signals arising from the oculomotor system. Another possibility is that they are sensitive to the visual consequences of eye movements. Although visual responses to the small spots of light employed in the tasks described so far were not observed, these tests were carried out in a dimly lighted room. Consequently, every time the eyes moved, images—both of objects in the room and of the target itself—were swept across the retina. Every time the eyes arrived at a new position, images of objects in the room were projected onto a new set of retinal points. In this situation, a purely visual neuron might appear sensitive to saccade direction and gaze angle simply because images are swept across the retina in its preferred direction during certain eye movements and are brought into its receptive field only with the gaze maintained in a certain direction.

To determine whether the task-related firing of posterior cingulate neurons was dependent on visual reafferent stimulation, visual cues were eliminated in two steps. First, the standard visually guided saccade task, as summarized in Figure 12.1*B*, was repeated after placing the room in total darkness. This eliminated any possibility of visual stimulation from the background. Second, the monkey was required to execute saccades not only with ambient illumination eliminated but with the target of the eye movement itself not visible. To achieve the second condition, a memory-guided saccade paradigm was employed (Hikosaka and Wurtz, 1983). While the monkey fixated a continuously visible central spot, a target light was flashed on briefly and extinguished. Several hundred milliseconds later, the central fixation light was extinguished, whereupon the monkey was required to execute an eye movement to the point where the target had formerly appeared. This eye movement was executed in absolute darkness. The saccade target reappeared 400 msec after the monkey initiated the saccadic eye movement.

Both tests were carried out on 11 neurons that had exhibited clear task-related firing in the light. Out of this sample, 2 neurons continued to fire following saccadic eye movements even when the saccades were made in total darkness and without a visible saccade target. Data from one of these neurons are shown in Figure 12.3*A* where the three histograms represent activity as a function of time during identical eye movements executed under three conditions: in a dimly lighted room with the target visible at the time of the movement (left); in a dark room with the target visible at the time of the eye movement (middle); and in a dark room with the target extinguished at the time of the eye movement (right). The tendency for the rate of firing to increase after the eye movement survived the progressive elimination of reafferent visual stimuli. In contrast, the presence of visual background was found to be important for the majority of posterior cingulate neurons tested in this way. In 6 of 11 neurons tested, activity still increased postsaccadically when saccades were made to a visible target in total darkness but not when saccades were made in the absence of the visual target. In the remaining three neurons, task-related activity depended on the presence of a visible background. We conclude from these results that visual reafference exerts a marked influence on the firing of most posterior cingulate neurons.

To test the dependence of orbital-position sensitivity on visual feedback, an additional task was employed. In this task, visual stimulation was not eliminated but rather was held constant, while the angle of the eye in the orbit was varied. The monkey was required to execute saccadic eye movements between an identical pair of targets on successive blocks of trials. Between blocks of trials, the orientation of the head relative to the screen was adjusted by rotating the monkey's chair about a vertical axis. Thus the targets and visual background were identical from block to block of trials, but the angle of the eyes in the orbits varied across blocks as a function of the orientation of the head relative to the screen. In some but not all neurons, the level of activity exhibited an obvious dependence on orbital position even with visual stimulation held constant. Data from such a neuron are shown in Figure 12.3*B*. The firing frequency of this neuron was higher when the monkey looked straight ahead at targets 1 and 2 (top row) than when the monkey looked at the same targets by counterrotating the eyes leftward to compensate for a rightward rotation of the head (bottom row).

Influence of Overt Eye Movements vs. Covert Shifts of Attention

Every eye movement involves both a motoric component (the rotation of the eye itself) and an attentional component (the redirection of visual attention to a new location in the environment). It is conceivable that the postsaccadic activity of posterior cingulate neurons is a function not of the eye movement itself but rather of the accompanying shift in the spatial locus of attention. To permit assessment of this possibility, the monkey was trained to attend to peripheral stimuli while maintaining central fixation (Wurtz and Mohler, 1976; Robinson et al., 1981). The monkey initiated each trial by pressing a bar, triggering the illumination of a central spot on which he was then required to maintain fixation. After a variable time, a small spot appeared 16° away from the central target in one of four directions. While maintaining fixation of the central target, the monkey was required to shift attention to the peripheral spot and to report its faint dimming at a variable time 500 to 1500 msec after its appearance by releasing the bar. Thus, the monkey's attention shifted while his eyes remained stationary. To date, seven neurons exhibiting clear postsaccadic activity in the standard saccade task have been tested in this condition. No neuron in this population was activated at the time when attention shifted to the peripheral site, even on trials when the direction and amplitude of the attentional shift were identical to

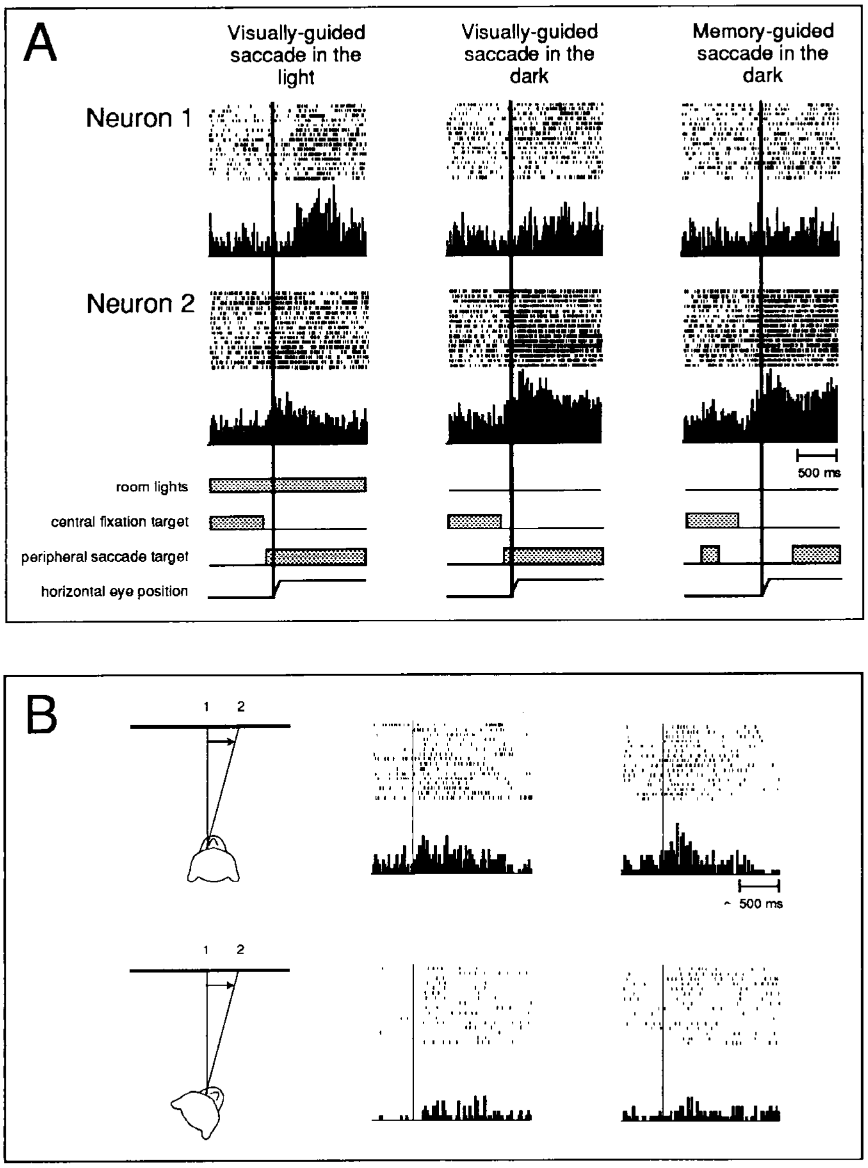

FIGURE 12.3. *A*. Activity of two posterior cingulate neurons following visually guided 16° rightward saccades made under three conditions in separate blocks of trials. Left column: The target and the environment were visible at the time of the eye movement. Middle column: The target alone was visible at the time of the eye movement. Right column: The eye movement was executed in total darkness. The postsaccadic activity of neuron 1 (top row) depended on visual feedback. The postsaccadic activity of neuron 2 did not. The apparent enhancement of responsiveness in the dark (neuron 2) may be the result of spontaneous drift in the level of responsiveness between blocks of trials.

B. The top panel shows activity obtained from an orbital position neuron during two separate blocks of trials in which the monkey made 16° rightward saccades with its head and body oriented toward the center of the screen. The bottom panel shows activity collected during two separate blocks of trials in which the monkey made a saccade between the same two targets with its head and body rotated 16° to the right with respect to the screen. The activity of this neuron is clearly related to the angle of the eye in the orbit.

the direction and amplitude of the eye movement eliciting maximal postsaccadic activation. Data from a representative neuron are illustrated in Figure 12.4*A*. We conclude that eye movements, as opposed to shifts of attention, are the necessary condition for activation of posterior cingulate neurons.

Phasic Responses to Visual Stimuli

Posterior cingulate neurons must be sensitive to visual stimulation, as indicated by the fact that postsaccadic firing is strongest in the presence of a visible target and in an illuminated room. Nevertheless, the onset of the saccade target, a small dim spot, does not elicit phasic visual responses in these neurons (see, e.g., Figs. 12.3*A* and 12.4*A*). We have carried out experiments to assess the possibility that other forms of visual stimulation might be more effective. In these experiments, visual stimuli were flashed at peripheral locations on the screen while the monkey maintained fixation of a central target. The results indicate that large textured patterns, in contrast to small spots, are an effective stimulus for many posterior cingulate neurons. For example, out of 25 neurons tested with a 16° diameter checkerboard, 18 (72%) gave obvious phasic visual responses. The receptive fields of these neurons were large and perhaps unlimited. In 11 neurons, including the one illustrated in Figure 12.4*B*, responses of equal strength were elicited regardless of the quadrant in which the stimulus was presented. It is noteworthy that a large textured stimulus lacking any behavioral relevance should drive neuronal activity effectively, whereas a small spot to which the monkey is actively attending should elicit no response (Fig. 12.4*A*–*B*).

Comparison to Other Areas in Macaque Cerebral Cortex

The posterior cingulate cortex of the macaque monkey is strongly linked by reciprocal pathways to a variety of high-order (as opposed to primary sensory and motor) cortical areas. These include anterior cingulate, prefrontal and premotor, inferior parietal, superior temporal, ventromedial temporal, and parahippocampal cortices (Vogt et al., 1979; Baleydier and Mauguiére, 1980; Vogt and Pandya, 1987; Chapter 8 of this volume). In several of these areas, neurons can be driven by visual stimuli and are active during eye movements. Cortical areas exhibiting oculomotor activity and possessing direct links to posterior cingulate cortex include: prefrontal cortex in and around the principal sulcus (Barbas and Mesulam, 1985), the prearcuate frontal eye fields (Barbas and Mesulam, 1981; Leichnetz and Goldberg, 1988), the supplementary eye field on the dorsomedial shoulder of the frontal lobe (Huerta and Kaas, 1990), area 7a on the convexity of the inferior parietal lobule (Cavada and Goldman-Rakic, 1989; Andersen et al., 1990a,b), and area LIP in the lateral bank of the intraparietal sulcus (Cavada and Goldman-Rakic, 1989; Andersen et al., 1990a,b). Posterior cingulate cortex is markedly different from most of these areas in terms of the functional properties of neurons.

Visual Signal

Many posterior cingulate neurons give phasic responses to visual stimulation arising from large textured patterns. Further evidence of visual sensitivity arises from the dependence of oculomotor firing on visual background in some neurons. Nevertheless, it is a striking and consistent finding that posterior cingulate neurons do not respond to the small dim spots employed as targets for eye movements in our experiments. Their failure to do so sets them apart from neurons in virtually every other known cortical oculomotor area. In the frontal eye fields, around one-half of neurons give excitatory responses to small spots employed as oculomotor targets (Mohler et al., 1973; Bruce and Goldberg, 1985). In the supplementary eye field, many visually responsive neurons are encountered (Schlag and Schlag-Rey,

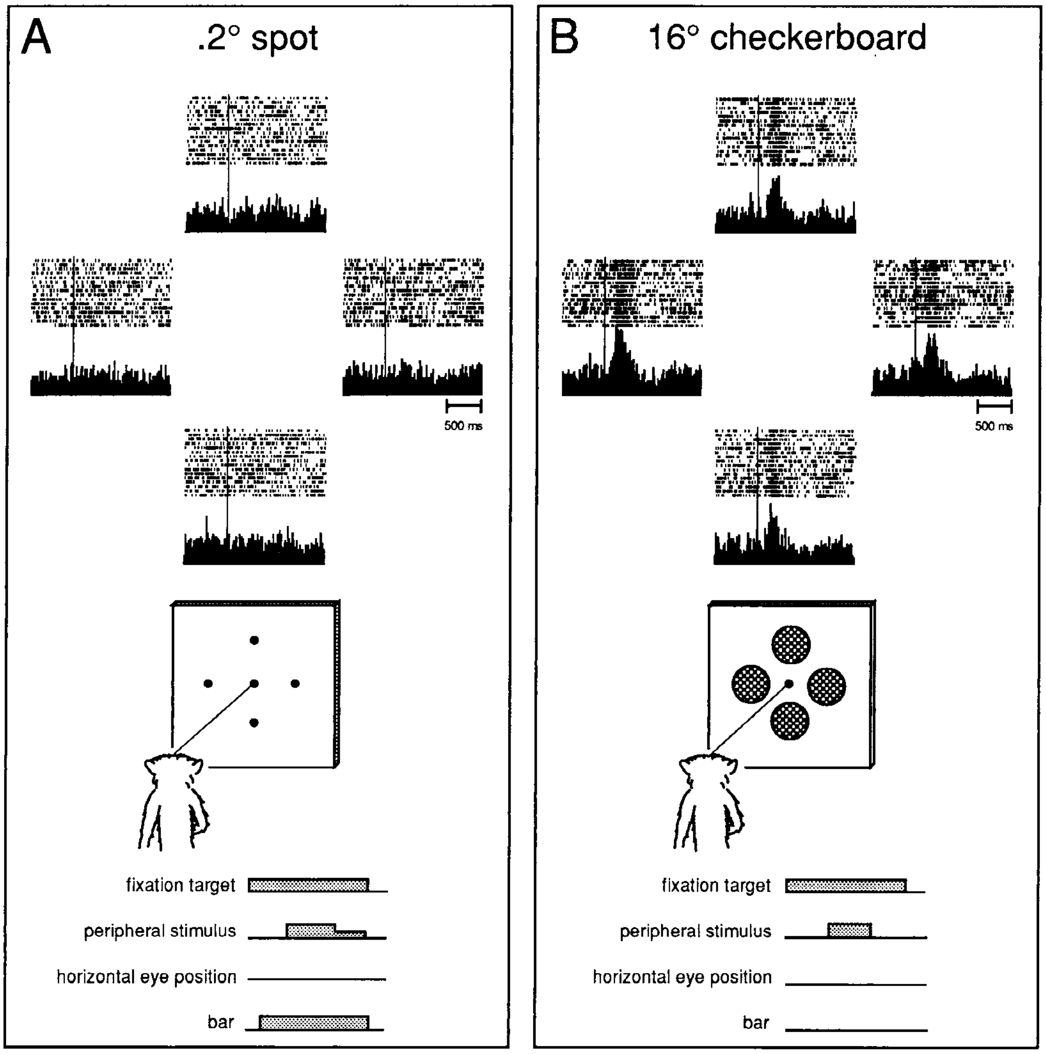

FIGURE 12.4. *A*. Activity in the peripheral attention task of a posterior cingulate neuron previously demonstrated, in the standard saccade task, to fire postsaccadically. In the peripheral attention task, the monkey maintained fixation of a central spot while awaiting onset of a peripheral spot at a variable location (the peripheral spot appeared 16° from the center in one of four cardinal directions). The monkey then attended to the peripheral spot so as to detect its dimming. Reward was contingent on the monkey's releasing a bar within a narrow time window following the dimming. Raster and histogram displays are aligned with respect to the time of onset (vertical line) of the peripheral spot. The small spot, in itself, elicited no visual response, and the covert shift of attention to the locus of the spot was not accompanied by neuronal firing.

B. Activity of the same neuron in response to a large textured stimulus without behavioral relevance. The monkey was rewarded for maintaining fixation of the central spot. During central fixation, the 16° checkered disk was presented with its center at 16° eccentricity in one of four cardinal directions (time of onset indicated by vertical line in each histogram and raster display). Despite the absence of any requirement for the monkey to attend to the disk, it elicited a vigorous neuronal response.

1987). In periprincipalis prefrontal cortex, most task-related neurons give sensory responses to eye-movement targets (Boch and Goldberg, 1989). The same is true in the posterior parietal region encompassing areas 7a and LIP (Robinson et al., 1978; Bushnell et al., 1981).

Orbital-Position Signal

The presence in posterior cingulate cortex of numerous neurons carrying an orbital-position signal is of interest because it seems to indicate that there is an affinity between the posterior cingulate and posterior parietal areas, as expected from their strong interconnection (Vogt et al., 1979; Baleydier and Mauguière, 1980; Pandya et al., 1981; Vogt and Pandya, 1987; Cavada and Goldman-Rakic, 1989). More than half of the neurons in the parietal region encompassing areas 7a and LIP carry a tonic signal related to the angle of the eye in the orbit (Sakata et al., 1980; Andersen and Mountcastle, 1983; Andersen et al., 1987, 1990b). In contrast, neurons carrying an orbital-position signal are extremely rare in the frontal eye fields (Bruce and Goldberg, 1985), in the supplementary eye field (Schlag and Schlag-Rey, 1987), and in periprincipalis prefrontal cortex (Suzuki and Azuma, 1983). The almost total confinement to posterior areas of neurons carrying orbital-position signals suggests that this information is of greater use in processing sensory input than in the execution of eye movements.

Postsaccadic Signal

In many posterior cingulate neurons, a reduction or increase of activity occurs in conjunction with each saccadic eye movement, beginning simultaneously with or shortly after the onset of the movement. Firing may return to baseline after a few hundred milliseconds or remain at the new level throughout the ensuing period of fixation. Presaccadic signals, bursts of activity that begin before eye movements and so conceivably could contribute to generating the movements, are rare or absent in posterior cingulate cortex. This feature distinguishes posterior cingulate cortex from all other cortical oculomotor areas. Neurons firing presaccadic bursts are far more common than neurons firing postsaccadically in the frontal eye fields (Bruce and Goldberg, 1985), the supplementary eye field (Schlag and Schlag-Rey, 1987), periprincipalis prefrontal cortex (Boch and Goldberg, 1989), and parietal area LIP (Andersen et al., 1990b). Only in parietal area 7a do most neurons firing saccade bursts exhibit a postsaccadic pattern, but even in that area firing begins before the saccade in approximately one-fifth of neurons (Andersen et al., 1990b). The preponderance of postsaccadic neurons in both posterior cingulate cortex and area 7a may reflect their especially close connectivity. The posterior cingulate cortex is linked far more strongly to area 7a on the convexity of the inferior parietal lobule, than it is to area LIP in the adjacent lateral bank of the intraparietal sulcus (Pandya et al., 1981; Vogt and Pandya, 1987; Cavada and Goldman-Rakic, 1989).

In frontal oculomotor areas, although most neurons begin firing before the onset of the saccade, a few neurons begin to fire only after saccade onset. In these postsaccadic neurons, selectivity for saccadic direction and amplitude is especially coarse (Schlag and Schlag-Rey, 1987; Boch and Goldberg, 1989; Goldberg and Bruce, 1990). Furthermore, in postsaccadic neurons of area LIP, the postsaccadic signal is unusual in that the direction and amplitude of the saccadic movement yielding the best postsaccadic signal are not matched to the location of the visual receptive field (Barash et al., 1991b). It is possible that neural connections between these areas and the posterior cingulate area involve subpopulations of neurons that carry postsaccadic signals. If so, then the relative nonselectivity of these neurons for the metrics of saccades may be related to the low degree of selectivity in posterior cingulate cortex.

Absence of Delay-Period Firing

On recording from posterior cingulate neurons while monkeys executed memory-guided saccades, we found that modulation of neuronal activity did not occur in the period between brief presentation of the visual target and subsequent execution of the delayed saccade. In contrast, in most other oculomotor areas, delay-period firing, reflecting the memory of the visual cue or the intention to execute an oculomotor response, does occur. Delay-period modulation related to the direction of the impending saccade occurs in one-fifth of frontal eye field neurons that carry motor signals (Bruce and Goldberg, 1985), in roughly one-half of task-related prefrontal neurons (Funahashi et al., 1989), and in around one-fifth of neurons in area LIP (Gnadt and Andersen, 1988). Neurons in the supplementary eye field have not been studied systematically in monkeys executing memory-guided saccades. Neurons exhibiting modulation during the delay period appear to be less frequent in area 7a than in area LIP (Barash et al., 1991a), although the exact percentage is unknown. The complete absence of delay-period firing in posterior cingulate neurons adds weight to the general conclusion that posterior cingulate cortex is involved in monitoring rather than in controlling eye movements.

Visuospatial Processing in Posterior Cingulate Cortex

Neurons in posterior cingulate cortex of the macaque encode the angle of the eye in the orbit and the size and direction of the saccadic eye movement by which the current epoch of fixation was initiated. The neurons respond to large textured visual stimuli and are influenced by background illumination but do not respond to small nonsalient visual stimuli even when these are detected by the monkey and are objects of attention, memory, and targeting eye movements. The basic observation that neurons in posterior cingulate cortex of the monkey carry oculomotor signals and respond to some visual stimuli agrees with reports on the rabbit (Sikes et al., 1988) and cat (Olson and Musil, 1992; Chapter 11 of this volume). Extensive behavioral tests possible only in the monkey have greatly extended this basic finding by permitting assessment of how firing is influenced by attention and memory and by allowing analysis of the parametric dependence of neuronal activity on orbital position and on the direction and amplitude of saccadic eye movements.

On the basis of the observed neuronal properties, posterior cingulate cortex stands apart from all other previously identified oculomotor areas of macaque cerebral cortex. In the other areas that have been characterized to date, neurons fire before eye movements, carrying signals related to onset of the visual target, attention to the visual target, the intention to move the eye, and the command to move. In contrast, in posterior cingulate cortex, changes of activity occur only at the time of or following the eye movement. Area 7a on the convexity of the inferior parietal lobule is most similar to posterior cingulate cortex in that it contains a substantial subpopulation of neurons in which the change of activity follows the eye movement. The functional similarity between the two areas reinforces the view, based on the existence of strong interconnections between them, that they subserve closely related functions.

The most plausible interpretation of oculomotor signals carried by posterior cingulate neurons is that they contribute to visuospatial cognition. It has been demonstrated that rats with posterior cingulate lesions are impaired on memory-guided navigation in a water maze (Sutherland et al., 1988; Chapter 16 of this volume) and that rats (Markowska et al., 1989) and monkeys (Murray et al., 1989) with extensive cingulate lesions perform poorly on a spatial delayed nonmatch-to-sample task. Monitoring eye movements and registering the current angle of gaze are necessary for the spatial interpretation of visual images because every movement of the eyes produces a shift of imagery on the retina. Parietal neurons reinterpret retinal images on the basis of signals from the oculomotor system (Duhamel et al., 1992). It is reasonable to speculate that posterior cingulate neurons also utilize oculomotor signals in the service of visual information processing.

Acknowledgments

This work was supported in part by grants to C.R.O. from National Institutes of Health (RO1 NS27287) and from the McDonnell-Pew Program in Cognitive Neuroscience. S.Y.M. was supported by a National Research Service Award (EY06202). We are grateful for the superb technical help from the staff of the Laboratory for Sensorimotor Research of the National Eye Institute: M. Smith for histology; T. Ruffner and C. Crist for mechanical construction; L. Jensen for electronic support; K. Powell, H. Magruder, and R. Bell for animal care; J. Steinberg for secretarial assistance; and J. Raber for invaluable veterinary care.

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