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THE NEURAL ENCODING OF THE LOCATION OF TARGETS FOR SACCADIC EYE MOVEMENTS

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Summary

Current models of the saccadic system imply that there are at least three neural representations of a visual target to which a saccade is made: representations in retinal, spatial (head or body) and motor coordinates. This paper presents the evidence supporting these models and summarizes the available neurophysiological data concerning neural representations of target location. In the superior colliculus, neurones in the superficial layers encode target location in retinal coordinates. Neurones in the deeper layers responsive to auditory and visual stimuli carry motor error signals. Evidence is also accumulating that some neurones in the thalamus and the frontal and parietal cortex convey information about target position with respect to the head or body, but these studies are far from complete.

Introduction

Spatial perception and sensory-guided movements are thought to depend upon several different neural representations of the environment (see Jeannerod, 1982; Howard, 1982; Paillard, 1987, for references). These include representations of the positions of the various body components, representations of the spatial location of objects in the external environment, and representations of the location of objects with respect to the body. Information about the organization of these neural representations and where they might reside in the central nervous system (CNS) comes from a variety of sources. Sensory and cognitive psychologists have a long-standing interest in the question of how changing patterns of sensory stimulation produced by object movement or by movements of the observer are integrated into a coherent, stable perceptual representation (see, for example, Neisser, 1967; Treisman, 1977; Hochberg, 1978; Treisman & Gelade, 1980). Other researchers focusing on motor behaviour hypothesize that the neural control of limb movements is based upon an abstract code of the location of objects in space (see MacNeilage, 1970; Larish & Stelmach, 1982). Accumulating clinical data concerning disorders of spatial perception and spatially guided movements have led to refinements in the classification of neurological disturb-

Key words: superior colliculus, parietal cortex, frontal cortex, internal medullary lamina of the thalamus, receptive field, movement field, gaze field, saccades.

ances of spatial cognition (De Renzi, 1982). Recently, computational models of how the brain might represent spatial relationships have begun to appear (see, for example, Feldman, 1985; Grossberg & Kuperstein, 1986; Kuperstein, 1988).

Despite the increasing interest in spatially guided behaviour and the neural representation of the spatial location of objects, relatively few neurophysiological experiments have investigated these phenomena directly. Much of what is known about the neural mechanisms for encoding the location of an object in space comes from studies of the neural control of eye movements. In this paper, I describe models of the saccadic eye movement system making assumptions about the coordinate frames in which saccade targets are localized, present evidence that supports or fails to support these models, and summarize the available neurophysiological data concerning neural representations of target location.

Models of the saccadic system

Retinocentric models

Early models of the saccadic system (Young & Stark, 1963; Robinson, 1973) assumed that the visual system computed a signal of *retinal error* (RE, the distance and direction of the target image from the fovea) and that this signal was relayed directly to the oculomotor system which generated a command to correct for RE (see Fig. 1A). In these models, saccades were assumed to be preprogrammed or ballistic since the trajectory of the saccade was determined at saccade onset.

Early studies of the functional organization of the superior colliculus were interpreted as supporting retinocentric models. Schiller & Koerner (1971) hypothesized that the location of a visual target relative to the fovea was coded by the site of neural activity in the retinotopic map of the superficial layers of the superior colliculus. The discharge of visual neurones in the superficial layers was assumed to activate underlying regions of the superior colliculus containing neurones that discharge before saccades. Since the motor map of saccadic eye movements found in the deeper layers is aligned with the retinotopic map of the overlying superficial neurones, the ensuing saccade would direct the foveal projection towards the region of the visual field containing the target. However, subsequent experiments have revealed a number of problems with this hypothesis (Sparks & Mays, 1981; Sparks, 1986) and there is evidence that an alternative, spatial model of the saccadic system is correct.

Spatial models

More recent models of the saccadic system assume that visual targets for saccadic eye movements are localized with respect to the head or body and not with respect to the retina. A simplification of one such model (Zee *et al.* 1976) is shown in Fig. 1B. With the head stationary, the appearance of a visual target creates an RE signal that depends upon the position of the eye in the orbit (E/H). The RE signal and a copy of the command signal to move the eye are combined to form a representation of *target position with respect to the head* (T/H). After a

delay (D), a signal of the current position of the eye in the orbit is subtracted from T/H, resulting in a signal of *motor error* (ME). Motor error is the direction and amplitude of the saccade required to bring the image of the target onto the fovea. If eye position changes in the interval between the computation of RE and the command to move the eye, ME will be different from RE; otherwise, RE and ME are the same.

Spatial models differ from retinocentric models in three important ways (Sparks & Mays, 1983*a*). First, in spatial models, the direction and amplitude of a saccade are not determined by retinal information alone, but retinal signals are continuously combined with information about eye position to localize the target in a head or body frame of reference. Second, in spatial models, the motor command moves the eye to a certain position in the orbit; in retinocentric models, the command produces a movement of a certain distance and direction. Third, in some spatial models, the saccade is not preprogrammed or ballistic, but guided to its destination by a neural circuit that continuously compares actual and desired eye position.

Evidence for spatial models

The assertion that saccade targets are localized in spatial (head or body), rather than retinal, coordinates is supported by psychophysical and neurophysiological evidence. Saccades can be made on the basis of cues other than RE. Auditory cues that are localized in a head frame of reference (Zahn *et al.* 1978) and somatosensory cues can be used to initiate saccades. Hallet & Lightstone (1976) found that subjects could make a saccade to the location of a visual stimulus that was flashed, briefly, during a saccade. Since the position of the eye changed after the flash, RE

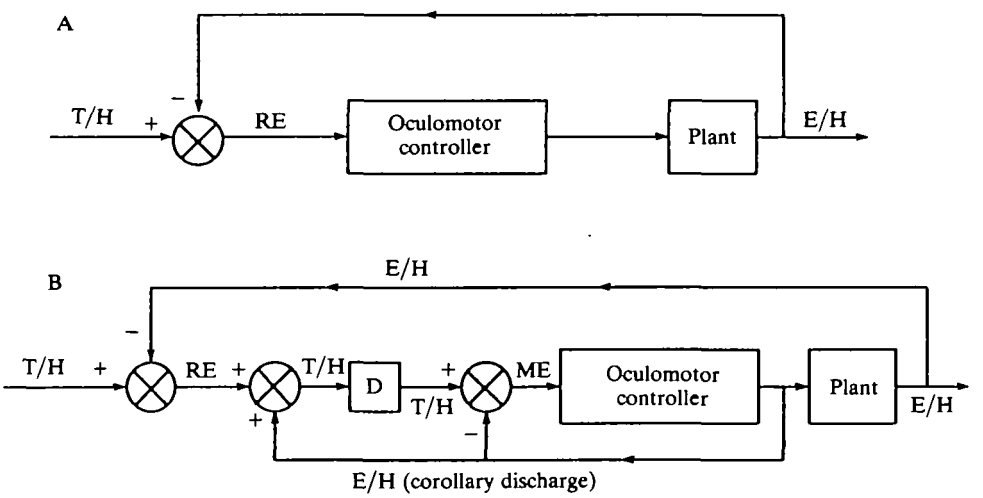

Fig. 1. Simplified versions of retinocentric (A) and spatial (B) models of the saccadic system. T/H, target position with respect to the head; E/H, position of the eye in the orbit; RE, retinal error; D, delay; ME, motor error. See text for further details. (Adapted from Sparks & Mays, 1983*a*.)

information alone could not be used to compute the direction and amplitude of the subsequent saccade to the position of the flashed target. The computation of the distance and direction of the second saccade must take into account information about the direction and amplitude of the first saccade.

Mays & Sparks (1980*a*, 1981; Sparks & Mays, 1983*b*) conducted experiments that also strongly support the view that saccade targets are localized in a nonretinocentric frame of reference. On a typical trial, the fixation target was extinguished and an eccentric target was illuminated for 50–100 ms. The monkey usually looked to the position of the target with a latency of 160–200 ms. Randomly, on 30 % of the trials, after the target was extinguished, but before the animal could begin a saccade, the eyes were driven to another position in the orbit by electrical stimulation of the superior colliculus. Under these circumstances, if the monkey attempts to look to the position where the target appeared, where will the animal look? Retinocentric models assume that the direction and amplitude of a saccade are based entirely upon an RE signal, and predict that the animal should produce a saccade with a predetermined distance and direction. Thus, the animal should produce a saccade that would direct gaze to a point in space that differs from the target location by an amount equal to the direction and amplitude of the stimulation-induced saccade. Spatial models assume that RE signals will be combined with information about the change in eye position produced by collicular stimulation and predict that the animal will look to the actual position of the target in space. Note that, except for the fixation target and the briefly flashed target, the task was performed in total darkness. Thus, the targets could not be localized using visual background cues as an external frame of reference. Also, the target was extinguished before the stimulation-induced saccade. If the animal made a saccade to the position of the target, it could not be based upon a visual update of target position.

Mays & Sparks (1980*a*, 1981) found that, regardless of the position of the target and regardless of the direction and amplitude of the saccade required to compensate for the stimulation-induced movement, the monkey made a saccade to the approximate position of the target in space. This finding supports spatial, rather than retinocentric, models since, on stimulation trials, saccades to the actual target locations could not be directed by RE alone. Furthermore, since the occurrence of the stimulation trials was completely unpredictable, compensation for the stimulation-induced perturbation could not have been predetermined; rather, the target must have been localized using both retinal information and information about the stimulation-induced change in eye position.

The original findings of Mays & Sparks using the stimulate/compensate paradigm have been extended in a number of ways. Sparks & Porter (1983) found that neurones in the superior colliculus discharging before saccades in response to visual targets also discharge before saccades compensating for stimulation-induced perturbations in eye position. This indicates that the computation of the trajectory of the compensatory saccade occurs at a relatively high level in the oculomotor circuitry. Schiller & Sandell (1983) found that animals compensate for displace-

ments of the eye produced by electrical stimulation of the frontal cortex (frontal eye fields) as well as stimulation of the superior colliculus and that neither the frontal eye fields nor the superior colliculus are necessary for compensation. Guthrie *et al.* (1983) found that animals compensate for stimulation-induced changes in eye position after extraocular muscle proprioceptive signals have been eliminated surgically. This result provides indirect support for the hypothesis that a central copy of the saccadic command provides precise information about the position of the eye in the orbit.

Neural representations of saccade targets

Identification of neurones encoding saccade targets in different coordinate systems

Spatial models of the saccadic system imply that there are at least three neural representations of a visual target to which a saccade is made (Fig. 2A); the first is a representation of the target as an RE signal; the second represents the target location in a head or body frame of reference and is based upon a combination of retinal and eye position information; and the third is a representation of ME, the difference between current and desired eye position. Sparks & Mays (1983*a*) described the response properties required of neurones encoding the position of a target in these three different ways, and the conditions necessary to identify these neurones.

Activation of neurones signalling RE is dependent upon excitation of receptors in a particular region of the retina. Accordingly, the receptive field moves with each change in gaze (Fig. 2B). Note, however, that neurones appearing to be responsive to activation of a particular region of the retina may actually be signalling ME. The distinction between neurones encoding RE and those encoding ME depends upon a critical test, described below.

Neurones representing a saccade target in a head or body frame of reference respond to targets in a specific region of the visual environment, regardless of the position of the eye in the orbit. Thus, as shown in Fig. 2C, the plot of the receptive field of such a neurone while the animal is fixating point 1 will be the same as the plot of the receptive field while the animal is fixating point 2. These neurones are responsive to stimuli occupying a particular region of visual space, regardless of the retinal locus of the target image and regardless of the position of the eye in the orbit. The spatial properties of these neurones would not be detected in an acute recording study or in a chronic recording experiment in which the receptive field was plotted with a single fixation point.

Neurones coding an ME signal alter their discharge rate when there is a certain difference between current and desired eye position. Motor error can be produced in two ways: by the appearance of a visual target located a certain distance and direction from the fixation point; or by a change in eye position after the appearance of a visual target. These situations are shown in Fig. 2D. On the left, the response field of a hypothetical ME neurone is represented as a circle (RF). With fixation straight ahead, the neurone discharges in response to a saccade

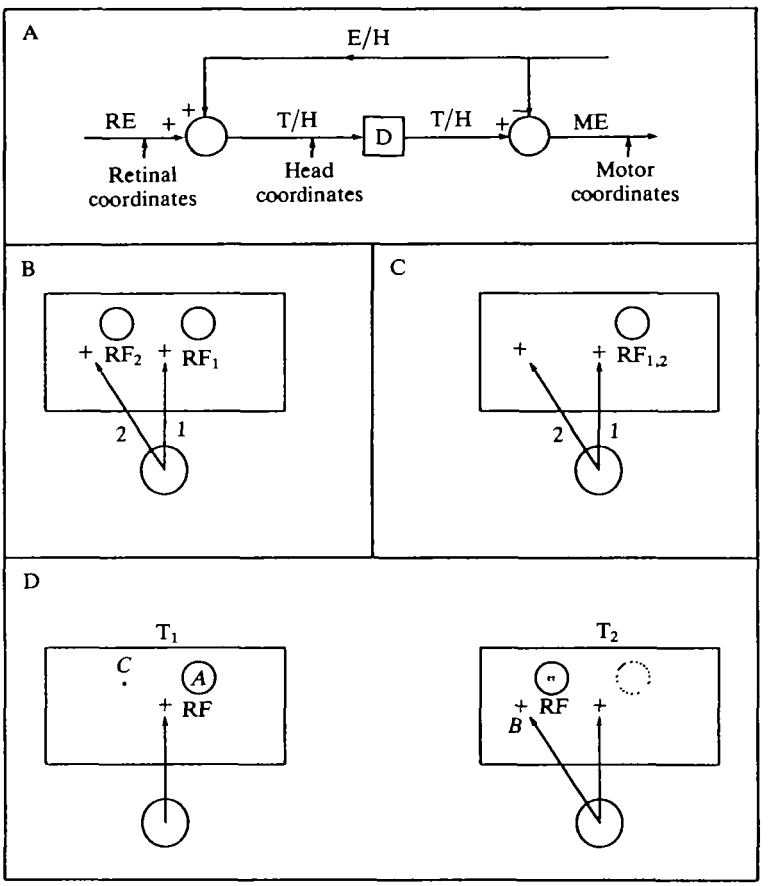

Fig. 2. Response properties of three types of hypothetical neurones. (A) Spatial models imply that there will be at least three neural representations of a saccade target: representations in retinal, head and motor coordinates. RE, retinal error; T/H, target position with respect to the head; E/H, position of the eye in the orbit; ME, motor error; D, delay. (B) Neurones signalling the position of the target in retinal coordinates have a retinal receptive field. With fixation of point 1, the neuronal discharge changes when stimuli activate a specific region of the retina (receptive field 1, RF_1). If the position of gaze changes (fixation of point 2), the receptive field moves (RF_2) since a specific region of the retina must still be activated to produce a neuronal response. (C) Neurones encoding the position of a target in head coordinates discharge whenever a stimulus appears in a specific region of the visual environment ($RF_{1,2}$), regardless of gaze direction (fixation 1 or fixation 2). The response of these neurones depends upon both retinal and eye-position information. (D) Response properties of neurones encoding motor error. Neurones conveying a motor error signal alter their discharge rate when there is a specific difference between current and desired eye position. This difference may occur because of the appearance of a visual target that produces a motor error (left) or because of a change in eye position after the brief appearance of a visual target (right). RF, response field of motor error neurone; *A*, *B*, *C*, target positions. T_1, Time period 1, central-fixation; T_2, Time period 2, after a leftward saccade. (Adapted from Sparks & Mays, 1983*a*.)

target (*A*) presented in the circular response field. The neurone discharges, not because a particular region of the retina was activated, but because, after the appearance of target *A*, the difference between current and desired eye position requires a saccade with a particular direction and amplitude. Note that if this is the only test applied, the discharge of the cell appears simply to reflect RE. A saccade target presented at position *C* outside the response field will not activate the neurone as long as fixation of the centre point is maintained. Suppose, however, after target *C* has disappeared, gaze is shifted to a new fixation point (*B*) but a saccade to the remembered location of target *C* is still required (Fig. 2D). After the first saccade, the difference between current and desired eye position is in the response field of the neurone and the neurone generates an increase in firing rate to signal this new ME. In this case, the ME signal is created not by the appearance of a new target, but by the change in eye position after the original target has disappeared.

Experimental data

Representations of retinal error and motor error

Mays & Sparks (1980*b*) reported that the superior colliculus contains an RE signal and a representation of ME. Monkeys were trained to perform a task like the one illustrated in Fig. 2D. After fixation of an initial centre target for a variable period, the offset of the centre fixation target was followed by successive presentations of two targets, *B* and *C*. Although the total duration of both targets *B* and *C* was less than the reaction time of the monkey, reward was contingent on the animal making a saccade to position B within 300 ms and a second saccade from *B* to *C* before an additional 500 ms elapsed. Thus, two saccades were made in succession; the first to *B* and the second from *B* to *C*.

Visually responsive neurones isolated in the superficial layers of the superior colliculus were activated by stimulation of a particular region of the retina. They responded only to the appearance of a visual stimulus in their receptive field, and the location of the receptive field shifted with each change in gaze. Thus, the site of neuronal activity in the retinotopic map of the superficial layers represents a map of RE.

One type of neurone that signals ME (the quasi-visual or QV cell) was identified in the intermediate layers of the superior colliculus. If these cells are tested while the animal maintains a single fixation position, they appear to be visually responsive, to have visual receptive fields and to respond to targets in their receptive field whether or not a saccade is made towards the target. But on trials requiring a change in fixation (Fig. 2D, right), QV cells begin to fire after the eye has reached position *B* and continue to fire until after the saccade from *B* to *C*. The cells firing in this case are not those whose receptive field contained the original target *C*, but cells whose receptive field would contain target *C* if the target were flashed again in the same spatial location after the eyes reached position *B*. In

other words, the activity of QV cells reflects motor error. Quasi-visual cells discharge whenever a saccade with a particular direction and amplitude is appropriate, regardless of whether the movement becomes appropriate because of the onset of a visual stimulus or because of an eye movement occurring after the disappearance of the target. Unlike neurones in the superficial layers that are activated if, and only if, a particular region of the retina is stimulated, QV cells can be activated by stimulation of any region of the retina if, after a subsequent movement of the eye, a saccade with a particular trajectory is required to look to the target. Since there are many combinations of sites of retinal stimulation and subsequent eye movements requiring a movement in the response field of a single QV cell, all regions of the retina must be mapped, at least indirectly, to each QV cell.

The hypothesis that the activity of QV cells encodes ME was tested in a separate experiment (Sparks & Porter, 1983) by recording their activity during trials in which the monkey compensated for stimulation-induced perturbations in eye position. Quasi-visual cells increased their discharge rate whenever there was a certain difference between current and desired eye position, regardless of whether this ME was produced by the sudden appearance of a visual target or by a stimulation-induced change in eye position after target offset. Based upon these and other findings, Sparks and colleagues conclude that the discharge of QV cells signals ME and holds this information in spatial register until a saccade occurs or is cancelled. Moreover, the mapping of target location in motor coordinates is a dynamic one: if the eyes move after a brief target disappears, the site of QV cell activity shifts to a location representing the new ME.

Recently, cells with properties almost identical to the QV cells of the superior colliculus have been discovered in the lateral bank of the intraparietal cortex (Gnadt & Andersen, 1988). Using the double saccade task of Mays & Sparks (1980*b*), Gnadt & Andersen found that the response of some cells in the parietal cortex is encoded in motor, rather than sensory, coordinates. Moreover, using a delayed saccade task, they discovered that these cells remain active throughout the memory interval, confirming the suggestion of Mays & Sparks (1980*b*) that cells of this type hold in spatial register the metrics of planned eye movements throughout the stimulus/response interval.

Experiments using auditory targets also support the view that the responses of sensory cells in the deeper layers of the superior colliculus are encoded in motor, rather than sensory, coordinates (Jay & Sparks, 1984, 1987). Monkeys trained to look to either visual or auditory targets in a completely darkened room were placed with their heads fixed in the centre of a semicircular track. Movement of a speaker (with a light-emitting diode attached) along the track and rotation of the track allowed targets to be presented at most locations on an imaginary sphere surrounding the animal. Three fixation lights separated by 24° were placed along the horizontal meridian. At the beginning of each trial, one of the three fixation lights was randomly activated. After a variable interval, an auditory (broad-band noise burst) or visual target was presented and the animal was required to look to

the target location in order to receive a liquid reward. A delayed saccade task was used to separate, temporally, sensory and motor activity.

The major objective of the experiment was to plot the receptive fields of sound-sensitive cells in the superior colliculus of alert monkeys while varying the direction of visual fixation. If the receptive fields of auditory neurones in the superior colliculus are based upon interaural cues and are organized in head-centred coordinates, the direction of fixation would have no effect. But, if the response of auditory neurones is organized in ME coordinates, then the response should depend upon both speaker position and fixation direction. Jay & Sparks (1984, 1987) found that the position of the eye in the orbit had a distinct effect upon the response of sound-sensitive cells in the superior colliculus. When the magnitude of the neural response was plotted as a function of the stimulus location in space, the receptive fields of the neurones shifted with the position of the eye in the orbit. But when the magnitude of the neural response was plotted as a function of the direction and amplitude of the movement required to look to the auditory target, the plots obtained with the different fixation positions were closely aligned. Thus, the discharge of sound-sensitive neurones in the superior colliculus is not determined solely by the position of the auditory stimulus in space, but depends upon ME, the trajectory of the saccade required to look to the target.

The mapping of the location of auditory targets in the superior colliculus is also dynamic. With each movement of the eye in the orbit, the population of neurones responsive to a stationary auditory stimulus in a particular location of the external environment changes to a new site within the superior colliculus, a site representing the new movement required for target acquisition.

Representations of target position in space

Neurones coding the position of a target in head or body coordinates were not found in the monkey superior colliculus. Nor have cells with properties identical to the hypothetical neurone illustrated in Fig. 2C been observed in other brain areas. This is not surprising, since few experiments have been conducted that would allow the detection of neurones encoding the location of a visual target in other than retinal coordinates. Nevertheless, spatial models of the saccadic system require a neural representation of the target in a head frame of reference and, presumably, the properties of QV cells in the superior colliculus and QV-like cells in the parietal cortex are based upon a subtraction of an eye-position signal from a stored representation of the position of the target in space. Neurones that could be used to construct a map of visual space in head or body coordinates have been observed in the internal medullary lamina (IML) of the thalamus and in the parietal cortex.

Schlag *et al.* (1980) and Schlag & Schlag-Rey (1983) found cells in the IML of the cat that responded only when the animal looked directly at a visual target or within a few degrees of it. These cells had central receptive fields but the visual response was more vigorous if the target appeared in a particular region of the visual field. These cells are described as discharging with a frequency related to eye position

when a target appears in the receptive field of the cell (Schlag & Schlag-Rey, 1983). Most of these cells display a discharge frequency related to eye position even in the dark, although the vigour of the response is reduced in the dark. A second type of cell in the IML with responses dependent upon gaze angle has large receptive fields that include the central retina. Consequently, gaze can be directed as much as 10° away from the target without a significant reduction in the visual response of the cell. Since visual responses are similar whether or not the animal fixates the target, firing rate is more related to the absolute position of the stimulus in space than to either eye position or retinal error.

The signals observed in the IML may be relayed to the parietal cortex, another brain region implicated in spatial perception and spatially guided behaviour. The discharge of many light-sensitive cells of the inferior parietal lobule is influenced by the direction of gaze (Hyvarinen & Poranen, 1974; Lynch *et al.* 1977; Andersen & Mountcastle, 1983). For many of these cells, visual stimuli delivered to the same region of the retina produce more or less vigorous responses, depending upon the location of the fixation target in the visual field. These neurones are said to have gaze fields, i.e. the increase in spike frequency during stimulus presentation is only observed if gaze is directed to a restricted region of the visual field. Control experiments by Andersen & Mountcastle (1983) indicate that these effects are not produced by changes in visual background associated with changes in the angle of gaze, by changes in fixation distance, or by variations in the intensity of stimuli viewed from different angles. It should be noted, however, that some of these cells show increased firing rates during particular directions of gaze, even in total darkness (Sakata *et al.* 1980).

Recently, Andersen and colleagues described the properties of cells in area 7a of the parietal cortex in more detail (Andersen *et al.* 1987; Andersen & Zipser, 1988). First, they mapped the receptive fields of light-sensitive neurones. Next, they presented a stimulus in the centre of the cell's retinotopic receptive field while the animal fixated targets at nine different locations in the visual field. Changes in the position of fixation produced systematic variations in the magnitude of the visual response. Moreover, the responses of the cell to stimuli presented at different points in the receptive field were all altered by an amount proportional to gaze angle, indicating a multiplicative interaction of the visual and eye-position signals. The receptive fields of these cells remain retinotopic since the peaks and symmetry of the receptive fields do not change; but the overall responsiveness of the cells is modulated by eye position.

These studies indicate that the visual response of many cells in the parietal cortex is jointly dependent on eye position and the location of the visual receptive field. But these cells do not encode absolutely the spatial location of visual stimuli; the spatial location of the visual stimulus cannot be determined from the cell's discharge unless the position of the eye in the orbit is known. Computer simulations developed by Zipser & Andersen (1988) show that a code of the position of a visual target in head coordinates can be achieved by considering the simultaneous activity of several neurones having the same retinotopic receptive

fields but different sensitivity to the angle of gaze. Thus, the convergence of the outputs of groups of cells in the parietal cortex onto cells in other regions of the parietal lobe or in still other brain structures could be used to generate a topographically coded representation of the location of a visual target in head or body coordinates. Zipser & Andersen (1988) suggest that this additional step of convergence is unnecessary for a signal of target position in head coordinates since this information can be extracted from the response of sub-populations of neurones in area 7a.

Some neurones in the frontal cortex display sensory activity seemingly related to the position of a stimulus with respect to a specific body region. Rizzolatti *et al.* (1981) isolated visually responsive neurones in the rostral part of area 6 just posterior to the arcuate sulcus. They described these neurones as 'peripersonal' cells since they were excited by visual stimuli within the animal's reach and also had tactile receptive fields on the hands or around the mouth and face. Visual receptive fields in front of or below the mouth were accompanied by tactile responsiveness to mouth and face or forearm stimulation. More recently, Gentilucci *et al.* (1983) described visually responsive neurones in the postarcuate region that are said to have visual receptive fields independent of eye position. The location of the visual receptive field appears to remain in register with the tactile receptive field even when the eyes move. This implies that the neurones are activated by visual stimuli in a particular region of 'egocentric' space, regardless of the site of retinal activation.

In summary, converging lines of clinical and experimental data implicate the posterior parietal cortex, the frontal and periarcuate cortex, the thalamic internal medullary lamina and the superior colliculus in the spatial localization of visual targets. The evidence that a topographically organized map of the visual environment organized in head or body coordinates resides in one or more of these brain regions is not yet compelling. Many of the early electrophysiological studies used informal and uncontrolled test procedures or failed to use methods capable of detecting neurones encoding the location of visual targets in other than retinal coordinates. Additional experiments continuing to explore, systematically, the implicated brain areas using electrophysiological methods capable of detecting neural representations of the visual environment organized in nonretinal coordinates are needed.

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