33 Coordinate Transformations and Motor Planning in Posterior Parietal Cortex

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ABSTRACT The posterior parietal cortex is neither a strictly visual nor a strictly motor structure; rather it performs visuomotor integration functions including coordinate transformations for the determination of spatial locations and the formation of plans for movement. Coordinate transformations are an essential aspect of visually guided behavior and are required because sensory information is derived in the coordinates of the retina and must be transformed to the coordinates of muscles for movement. These transformations produce in the posterior parietal cortex a representation of space that uses a population code and is formed by a specific operation that systematically combines visual and eye position signals to form *planar gain fields*. Activity related to the planning of eye movements has been found in the lateral intraparietal area, a recently discovered cortical area that appears to be specialized for saccades. This planning-related activity appears to encode the movements that the animal intends to make.

Recent neurophysiological experiments suggest there exist intermediate and abstract representations of space interposed between sensory input and motor output. These intermediate representations are formed by combining information from various modalities. A *head-centered* representation refers to a coordinate system framed with respect to the head and is formed by combining information about eye position and the location of a visual stimulus imaged on the retinas (figure 33.1) A *body-centered* coordinate representation likewise is achieved by combining head, eye, and retinal position information (see figure 33.1). An even more complicated representation is one in *world-centered* coordinates (see figure 33.1), which can be achieved by combining vestibular signals with eye position and

retinal position signals. There is reason to believe that the brain contains and uses all these representations. This chapter focuses on head-centered representations of space formed by the combining of eye and head position signals in the posterior parietal cortex. The studies outlined here provide a glimpse into the internal operations of the brain that are the basis of our spatial perceptions and actions.

A second major aspect of sensorimotor integration is the planning of movements. At some point in this integration process, sensory signals give way to signals related to what the animal intends to do. In the second part of this chapter, I will discuss evidence that this step from sensory representation to decisions to make movements utilizes the neural circuitry within the posterior parietal cortex. Such studies have been aided by the recent discovery of a small area within the posterior parietal cortex, the lateral intraparietal area (LIP), which appears to be specialized in the processing of saccadic eye movements. This area carries not only sensory information related to the targets for eye movements but also signals related to the planning of eye movements.

Representation of space in area 7a of posterior parietal cortex

Lesions to the posterior parietal cortex produce profound spatial deficits in both humans and nonhuman primates. My colleagues and I thus chose to examine how space is represented in the posterior parietal cortex by examining the spatial receptive field properties of neurons in behaving monkeys. One might have imagined that locations in head-centered coordinates are encoded using receptive fields similar to retinal receptive fields but anchored in head-centered, rather than

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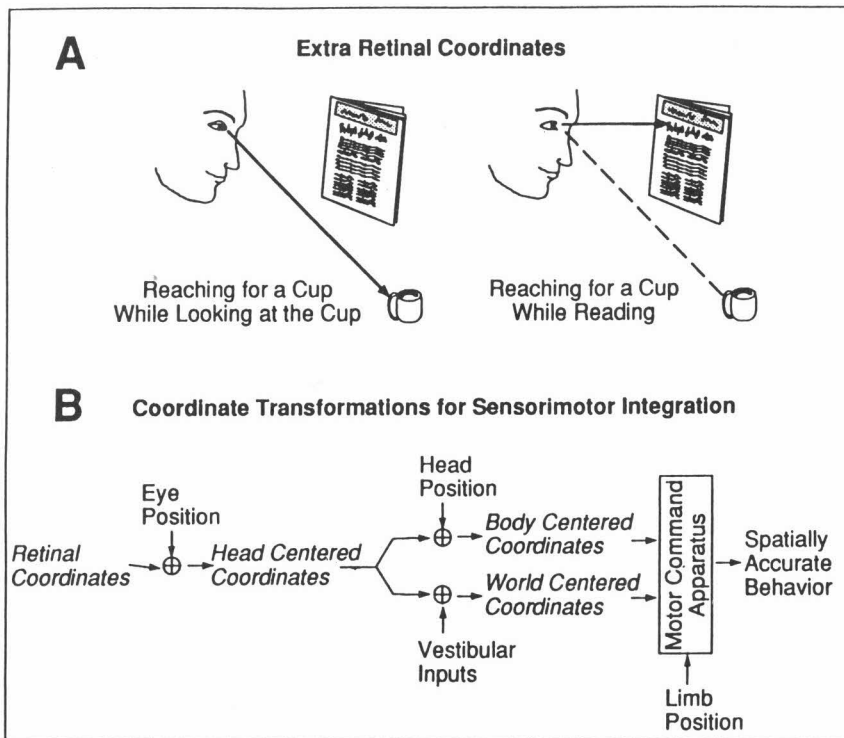
FIGURE 33.1 (A) Demonstration of why representations of space in extraretinal coordinates are required for accurate motor behaviors. The term *extraretinal* refers to the encoding of visual stimuli in higher-level coordinate frames than simple retinal coordinates. In the sketch on the left, a person is fixating the cup and it is imaged on the foveas, whereas on the right the subject is fixating the newspaper and the cup is imaged on a peripheral part of the retinas. In both cases, the individual is able to localize the cup with a reaching movement. Because different parts of the retinas are stimulated in the two conditions, information about eye position must also be available to determine accurately that the cup was at the same location in space. (B) Schematic showing how extraretinal coordinate frames can be computed from retinal coordinates. Visual stimuli are imaged on the retinas and are

input to the brain in retinal coordinates. Eye position signals can be added to form representations in head-centered coordinates, and body-centered coordinates can be formed by adding head position information. One way of forming world coordinates is to add vestibular signals, which code the location of the head in the world, to a head-centered coordinate frame. For illustrative purposes, the figure shows these signals being added sequentially. It is not known yet whether there is a hierarchical organization of extraretinal coordinate frames in the brain or whether several of these signals come together at once to form body- and world-coordinate frames, combined with information about limb position derived from proprioceptive inputs, to encode accurate reaching movements. (From Andersen et al., in press, with permission)

retinal, coordinates. If this were the case, each time the eyes would move the receptive field would change the location on the retina from which it derives its input, in order to code the same location in space.

PLANAR GAIN FIELDS Early investigations of area 7a of the posterior parietal cortex showed, however, that locations in head-centered coordinates could be coded in an entirely different format (Andersen and Mountcastle, 1983; Andersen, Essick, and Siegel, 1985). The receptive fields of the neurons did not change their retinal locations when eye position changed. Rather

the visual and eye position signals interacted to form *planar gain fields*, in which the amplitude of the visual response was modulated by eye position (Andersen, Essick, and Siegel, 1985) (figure 33.2). The gain fields were said to be planar because the amplitude of the response to stimulation of the same patch of retina varied linearly with horizontal and vertical eye position (Andersen, Essick, and Siegel, 1985).

These results indicated that spatial locations are not represented explicitly at a single-cell level using receptive fields in space. However, the location of a target in head-centered coordinates could still be easily deter-
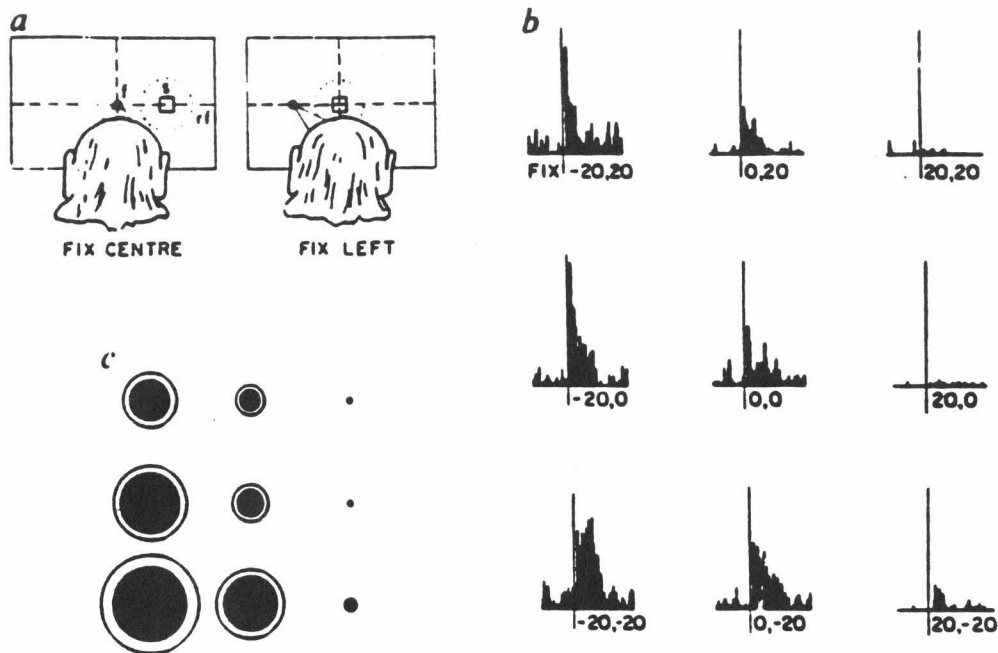
FIGURE 33.2 (a) Experimental protocol for determining spatial gain fields, with the projection screen viewed from behind the monkey's head. To determine the effect of eye position, the monkey, whose head is fixed, fixates on a point (f) at one of nine symmetrically placed locations on the projection screen. The stimulus (S) is always presented at the same retinal location, chosen as the maximum response zone of the retinal receptive field. The stimulus consists of 1°- or 6°-diameter spots flashed for 500 ms. Each measurement is repeated eight times. (b) Peristimulus histograms of a typical gain field determination. The nine histograms are located in the same relative positions as the fixations that produced them. The vertical line indicates the time of visual stimulus onset. (c) A graphical method for illustrating these data, in which the diameter of the darkened inner circle, representing the visually evoked gain fields, is calculated by subtracting the background activity recorded 500 ms before the stimulus onset from the total activity during the stimulus. The annulus diameter corresponds to the background activity that is due to an eye position signal alone, recorded during the 500 ms before the stimulus presentation. (Reprinted with permission from *Nature* 331:679–684. Copyright 1988 Macmillan Magazines Ltd.)

mined if the activity of several area 7a neurons were examined together; in other words, the representation of space is *distributed* in this area. Figure 33.3 demonstrates why this representation is distributed. The contour plot of activity is made for the variables of location in head-centered space and eye position. When examined in this fashion, it can be seen that area 7a neurons are tuned to a particular location in head-centered space but only for a limited range of eye positions. The location of maximum response in head-centered coordinates is a conjunction of the preferred eye position of the cell and the most responsive part of its retinal receptive field. To derive a signal for location in head-centered space independent of eye position requires the activity of a subset of parietal neurons, and thus the code is a distributed one. A distributed code of this sort is, of course, not unique to the posterior parietal cortex. Middle temporal (MT) neurons, for instance, are tuned to a limited range of temporal and spatial frequencies. For stimuli of different shapes to be perceived as moving at the same speed would require a population of cells tuned to different temporal and spatial frequencies. Thus, the perception of speed, independent of the exact texture or shape of a moving stimulus, appears to use a distributed code not unlike the one for spatial location.

Looking at the behavior of single cells as merely components of a much larger, distributed network has been critical in advancing our understanding of how the brain computes locations in space. Neural networks trained to convert inputs of eye position and retinal position into an output of locations in head coordinates develop a distributed representation in the hidden layer interposed between the input and output layers (Zipser and Andersen, 1988). This distributed representation appears to be the same as that found in area
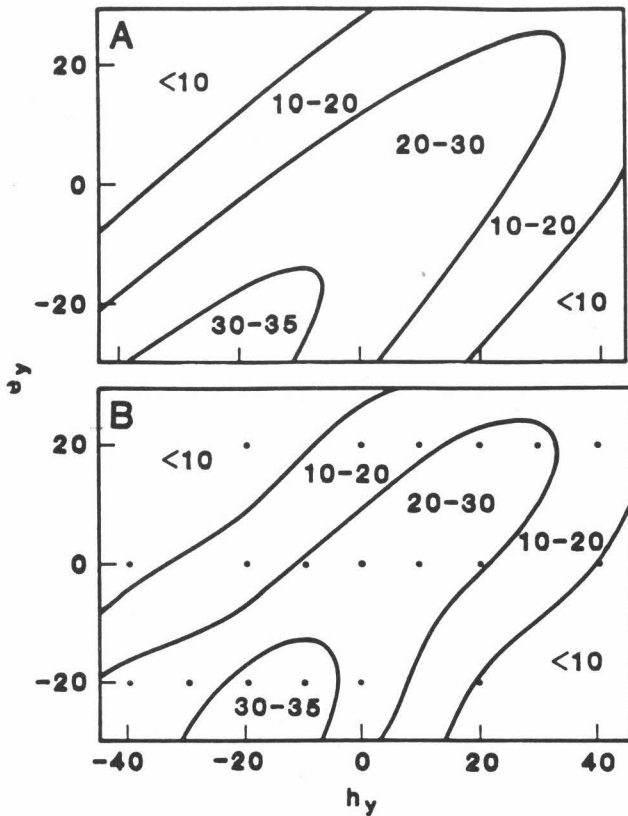
FIGURE 33.3 (A) Computer simulation of the response (in spikes per second) of an area 7a neuron predicted by multiplying the vertical axis of a planar gain field by the vertical axis of a gaussian receptive field. The results are represented on the contour plot with the stimulus head-centered coordinates (h_y) plotted along the abscissa and eye position (e_y) along the ordinate. (B) Contour plot of actual recording data for a cell with the same gain field and receptive field characteristics as the model neuron plotted in (A). Each data point represents the mean evoked response to eight repetitions of the stimulus. The average standard error for these data points was two spikes per second. (Reprinted with permission from Andersen et al., 1985. Copyright 1985 by the AAAS)

7a, with the hidden units exhibiting planar gain fields. A mathematical analysis of this network indicates that the planar gain fields are the basis of an algorithm for adding eye and retinal position vectors in a distributed network (Goodman and Andersen, 1990; Brotchie, Andersen, and Goodman, 1993). Thus, the method of integrating these two signals is not random but is systematic and requires that the gain fields be planar.

One of our neural network models for area 7a was trained to produce output units with receptive fields in head-centered coordinates (Zipser and Andersen, 1988). The middle layer of this model produced gain fields similar to those found in area 7a, suggesting that gain fields are an intermediate stage between retinal and spatial receptive fields. A possible objection to this model is that cells resembling its output (receptive fields in space) are not routinely found. However, we also trained a second network with an output representation similar to the activity found in oculomotor structures and motor centers in general. In this format, activity varies monotonically as a function of location with respect to the head. We have shown that such a network can be trained to make eye movements and have argued that receptive fields in space are an unnecessary encoding of spatial location (Goodman and Andersen, 1989; Andersen et al., 1990). Instead, we believe that cells with planar gain fields are an intermediate step in the transformation from visual to motor coordinates.

OTHER AREAS WITH GAIN FIELDS Recently, gain fields have been found in several areas besides 7a. In monkeys, these areas include cortical area LIP (Andersen et al., 1990), cortical area V3a (Galletti and Battaglini, 1989), the inferior and lateral pulvinar (Robinson, McClurkin, and Kertzmann, 1990) and premotor and prefrontal cortex (Boussaoud, Barth, and Wise, 1993), and in cats in the superior colliculus (Peck et al., 1992). In the cases where data were collected for a sufficient number of eye positions, the gain fields usually were linear for horizontal and vertical eye positions. These results suggest that gain fields are a typical format for representing spatial information in many areas of the brain.

It is interesting that the newer data just cited show that planar gain fields appear to be the predominant method of representing space and performing coordinate transformations. A clue to the predominance of this form of representation comes from Mazzoni, Andersen, and Jordan (1991a). We found that networks with multiple hidden layers trained to make coordinate transformations have gain fields in all the hidden layers. The planar gain field is an economical method for compressing spatial information (Goodman and Andersen, 1990).

It has been suggested that receptive fields in space also may exist in some cortical areas (Battaglini et al., 1990; Fogassi et al., 1992; MacKay and Riehle, 1992). These reports are preliminary, and further work is needed to substantiate such claims.

Distance, body-centered coordinates, and world-centered coordinates

The data in the preceding section indicate that there are representations with respect to the head in the two dimensions of elevation and azimuth. Recent recording experiments suggest that the third dimension of distance from the head is also contained within these representations, and the method of encoding distance is in the form of gain fields. Gnadt and Mays (1991; Gnadt, 1992) found LIP neurons in which the vergence angle modulated the magnitude of the visually evoked responses but not the disparity tuning of the cells. These types of gain fields are also predicted by neural network models similar to the Zipser-Andersen model but are trained to localize in depth (Lehky, Pouget, and Sejnowski, 1990).

Our earlier experiments tested the interaction of eye position and retinal position signals for animals with their heads mechanically immobilized. As a result, head-centered representations could not be distinguished from body-centered representations. With this in mind, Brotchie, Andersen, and Goodman (1993) have examined the effect of head position on the visual response of cells in the posterior parietal cortex. Neural network simulations performed prior to the experiments suggested that posterior parietal neurons should have gain fields for head position as well as eye position if they are representing space in body-centered coordinates. Furthermore, the eye and head gain fields of individual parietal neurons should have the same gradients (two-dimensional slopes), even though the gradients of different cells may vary considerably. The recording experiments from areas 7a and LIP bore out these predictions. Approximately half the cells with eye position gain fields were found to have similar head position gain fields. These results suggest that there may be two representations of space in the posterior parietal cortex, one in head-centered coordinates (units with gain fields for eye position) and the other in body-centered coordinates (units with gain fields for eye and head position).

Finally, recent recordings from our laboratory have shown that vestibular signals are integrated with the various other signals (Snyder, Brotchie, and Andersen, in press). When monkeys are rotated in the chair in the dark, many cells that show tonic activity related to eye position exhibit similar changes in activity for movement of the head relative to the room. Presumably, these cells are receiving an integrated vestibular signal. Because these cells code both location of the eye in the head and location of the head in the world, they are coding the direction of gaze in the world. Another subset of cells has retinal receptive fields with gain fields for eye position and chair rotation. The modulation of the visual response by a vestibular signal suggests that this population of cells may code locations of visual stimuli in world coordinates.

Biologically plausible learning rule

One criticism of neural network models has been that the learning rule used for training the networks is unlikely to be used by the nervous system. Mazzoni, Andersen, and Jordan, (1991a, b) trained a neural network to perform the transformation from retinal to head-centered coordinates using a reinforcement learning rule developed by Barto and Jordan (1987) that is more biologically plausible than backpropagation (figure 33.4). They found the reinforcement-trained networks produced the same gain fields that are produced by the backpropagation-trained networks and are found in the brain, which suggests that the algorithm discovered for computing the coordinate transformation is largely independent of the exact learning rule used to generate it. Likewise, it suggests that posterior parietal neurons could learn or adjust spatial representations using a learning paradigm that is more reasonable in terms of what is currently known about learning mechanisms in the central nervous system.

Microstimulation experiments

Goodman and Andersen (1989) examined the effects of microstimulating the Zipser-Andersen model for eye movements. Their model was connected to a simplified set of oculomotor muscles (four instead of six), and individual hidden units were maximally activated to simulate microstimulation. The most typical result of stimulating individual hidden units was the change in amplitude pattern seen with stimulation of area LIP (figure 33.5b). This model suggests that the change in amplitude pattern is indicative of a distributed representation of space in LIP. Because the representation of head-centered space is distributed, a single cell does not drive the eyes to a goal in space; rather, such behavior requires the activity of many LIP neurons. To demonstrate directly how these changes in amplitude patterns could code single locations among a group of
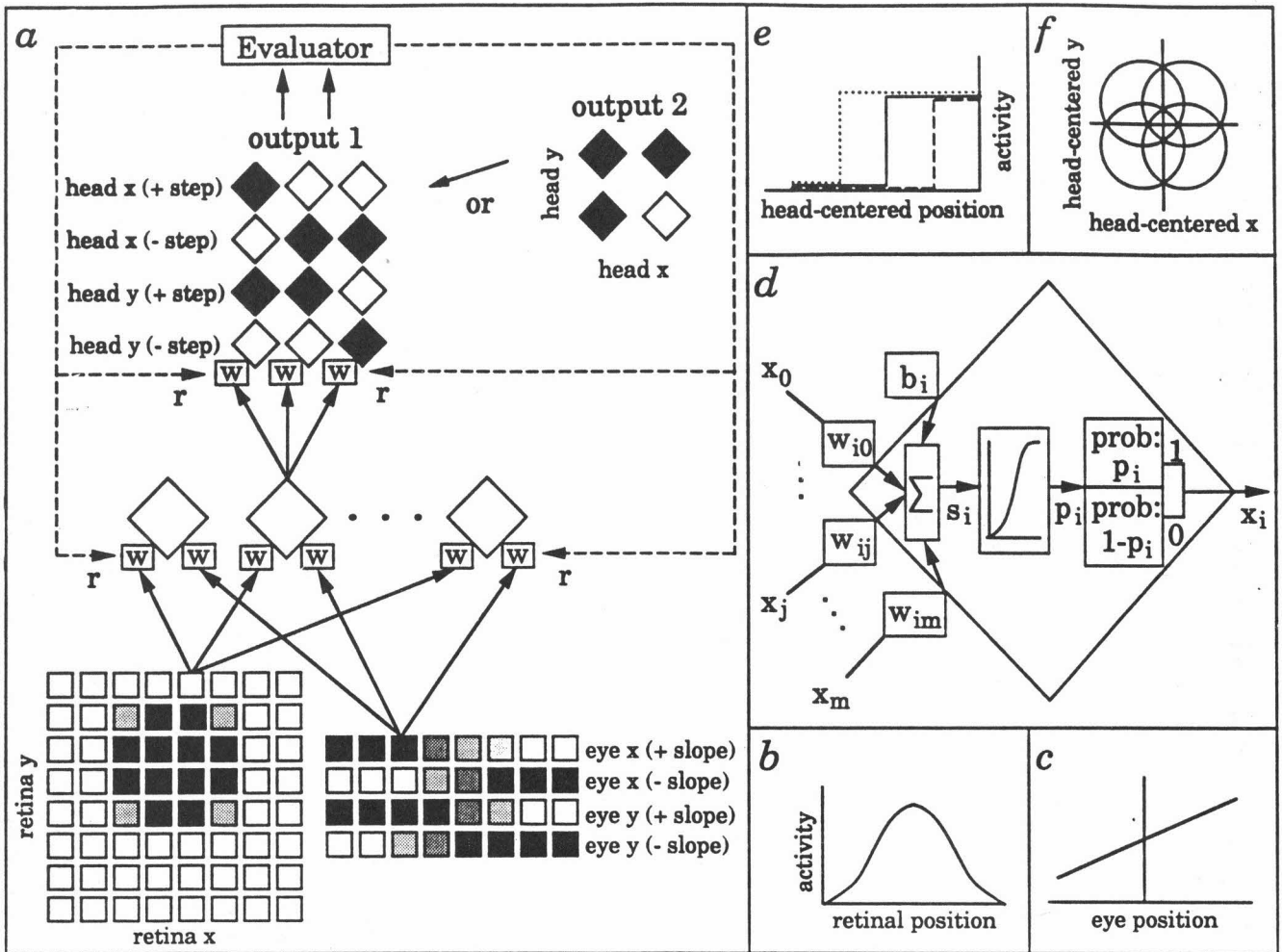
FIGURE 33.4 (a) Network structure. (b) Retinal input is encoded by 64 units with gaussian receptive fields, whereas eye position (c) is represented by 32 units with linear activation functions. In the retinal input, each unit has an output between 0 and 1, a $1/e$ width of $15°$, and a receptive field peak $10°$ apart from that of its horizontal and vertical neighbors. In the eye position input, the output of each unit (between 0 and 1) is a linear function of horizontal or vertical orbital angle, with random slope and intercept. These input formats reproduce properties of certain area 7a neurons that respond only to visual stimuli or to changes in eye position. The shading of each unit is proportional to its activity, with black representing maximum activity. The hidden and output layers are composed of binary stochastic elements (d), which produce an output of 1 with probability (prob) p equal to the logistical function of the sum of the weighted inputs $(s_i = \sum_{j=0}^{m} w_{ij}x_j)$, and 0 with probability $1 - p$. The jth unit in the network provides input x_j to ith unit via the connection w_{ij}; m is the number of inputs to the units, and b is a bias. The network used from two to eight hidden units. The output units encode head-centered locations according to one of two output formats. (e) In the binary-monotonic format, each unit produces an output of 1 or 0, depending on whether the encoded locations are to the right or to the left (or, for some units, above or below) a certain reference point. For example, a typical output layer consisted of four sets of three units, giving an output of 1 when the x (or y) craniotopic coordinate is greater than (or less than) -40, 0, or $+40$ degrees. This format is analogous to the eye position input format, in that four groups of units encode an increase in horizontal or vertical position angle by increasing or decreasing their activation monotonically. (f) Another format used is the binary-gaussian one, in which four units give an output of 1 when the spatial position is within $100°$ of their receptive field centers, which are located at $(\pm 60°, \pm 60°)$. This format is analogous to that of the retinal input, in that a position angle is encoded topographically by units with overlapping receptive fields.
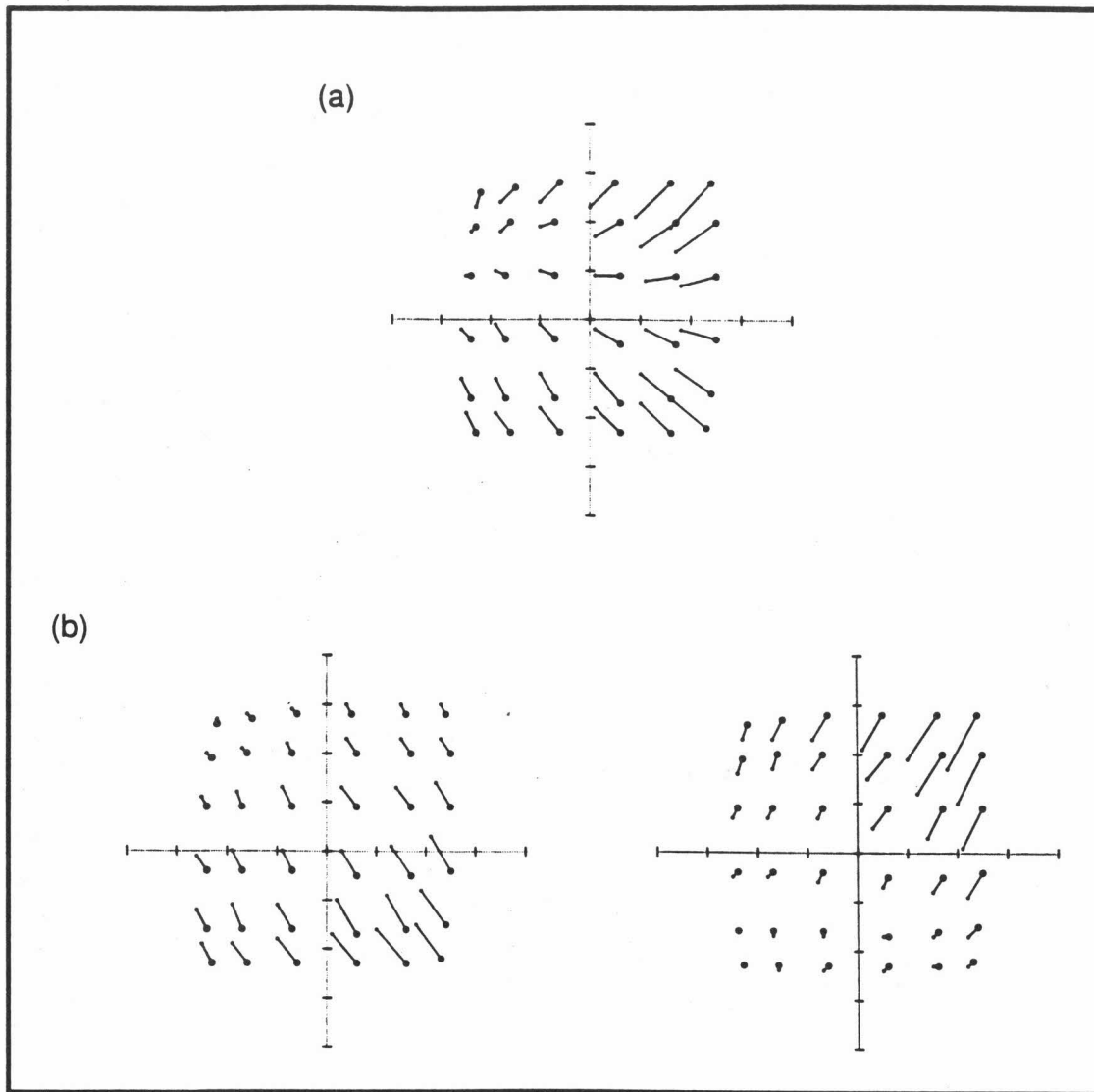
FIGURE 33.5   (a) Eye movements recorded when two hidden units of a monotonic output network are stimulated simultaneously. (b) Eye movements recorded when each of the two hidden units is stimulated alone. Note that the result of simultaneous stimulation, illustrated in (A), is more or less the vector addition of the two saccade fields that results from stimulation of the individual units. (Reprinted with permission from *J. Cogn. Neurosci.* 1:317–326. Copyright MIT Press 1989)

neurons, Goodman and Andersen (1989) showed that stimulation of two or more hidden units produced a pattern of eye movements that converge toward a single goal in head-centered space (figure 33.5a).

Area LIP

It has been appreciated for some time that the posterior parietal cortex is involved in the processing of eye movements. Balint (1909) described bilateral lesions to the posterior parietal cortex in human patients that resulted in the inability to will saccades, although spontaneous saccades were unaffected. In monkeys, electrical stimulation of the posterior parietal area produces saccadic eye movements (Fleming and Crosby, 1955; Wagman, 1964), and lesions to the parietal cortex also produce deficits in saccades (Keating and Gooley, 1988; Lynch and McLaren, 1989).

In the mid-1970s, Mountcastle and his colleagues embarked on cell-recording experiments within the

inferior parietal lobule (which encompasses approximately the posterior half of the posterior parietal cortex) and reported cells selective for saccades as well as neurons selective for smooth pursuit, reach, and fixation. Mountcastle's group (1975) reported that in electrode penetrations perpendicular to the cortex, all cells

tended to have the same functional properties, an observation consistent with a columnar organization. Lynch and coworkers (1977) later reported that these columns were not segregated by functional types into particular parts of the posterior parietal cortex, suggesting that repeating columns of each functional class
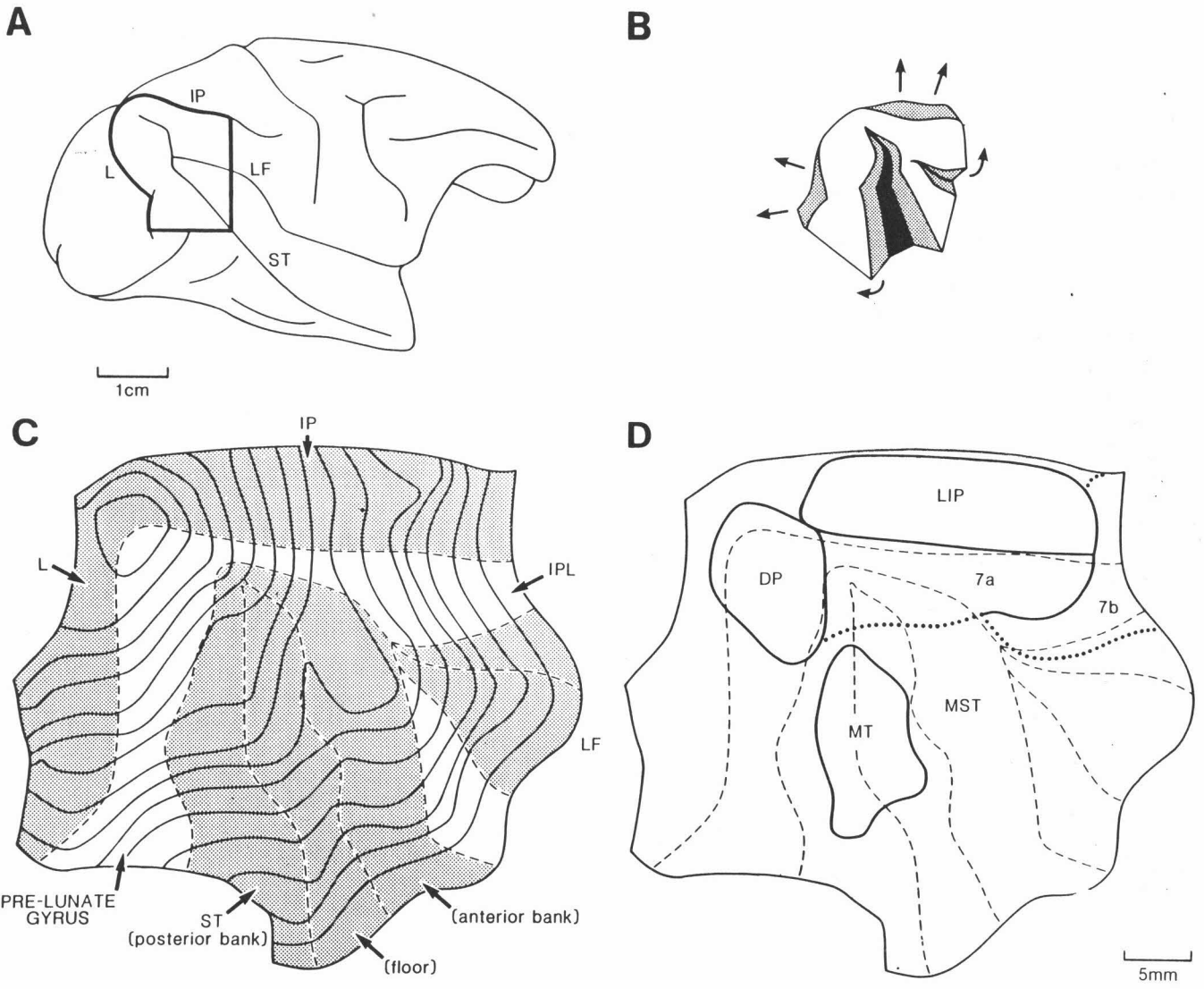

FIGURE 33.6 Parcellation of inferior parietal lobule and adjoining dorsal aspect of the prelunate gyrus used in this study. The cortical areas are represented on flattened reconstructions of the cortex. (A) Lateral view of monkey cortical hemisphere. The darker line indicates the area to be flattened. Cortical areas: L, lateral; IP, intraparietal; LF, lateral fissure; ST, superior temporal. (B) The same cortex isolated from the rest of the brain. Stippled areas are cortex buried in sulci, and the blackened area is the floor of the superior temporal sulcus. The arrows indicate movement of local cortical regions resulting from the mechanical flattening. (C)

The completely flattened representation of the same area. The stippled areas represent cortical regions buried in sulci, and the contourlike lines are tracings of layer IV taken from frontal sections through this area. Cortical areas as in (A); IPL, inferior parietal lobule. (D) Locations of several of the cortical areas. The dotted lines indicate borders of cortical fields that are not precisely determinable. Cortical areas: LIP, lateral intraparietal; DP, dorsoparietal; MT, middle temporal; MST, medical superior temporal. (Reprinted with permission from *J. Comp. Neurol.* 296:65–113. Copyright 1990 Wiley-Liss)

are rather evenly distributed across the inferior parietal lobule. These results had to be interpreted with some caution, however, as results were pooled from several different brains and referenced to sulcal patterns that vary considerably from animal to animal. Following up on these observations, Andersen, Asanuma, and Cowan (1985) reasoned that these different types of columns could be selectively labeled with anatomical tracers by assuming that they had connections with different brain structures. Thus, for instance, columns of cells with saccade-related activity would likely project to the frontal lobe in the region of the frontal eye fields . However, when retrograde tracers were injected into the frontal eye fields and adjoining dorsolateral prefrontal cortex, label was found · predominantly within the lateral bank of the intraparietal cortex. Andersen, Asanuma, and Cowan (1985) named this · area the *lateral intraparietal area* because it was located on the lateral bank of the intraparietal sulcus, lateral to the ventral intraparietal area (VIP) described earlier by Maunsell and Van Essen (1983) (figure 33.6). Subsequent recording experiments showed that most LIP cells had activity related to eye movements, and a majority of these responded prior to saccades (Gnadt and Andersen, 1988; Andersen et al., 1990; Barash et al., 1991a, b). Other studies showed that reach activity was confined largely to area 7b (Hyvärinen and Shelepin, 1979; Robinson and Burton, 1980a, b; Hyvärinen, 1981) and smooth-pursuit activity to the medial superior temporal area (MST) (Newsome, Wurtz, and Komatsu, 1988) (see figure 33.6). Fixation activity typically varies with direction of gaze (Lynch et al., 1977; Sakata, Shibutani, and Kawano, 1980; Andersen, Essick, and Siegel, 1987) and appears primarily to convey information about eye position (Andersen, Essick, Siegel, 1987; Andersen, 1989). These eye position–related activities are typically found in areas LIP and 7a (see figure 33.6). Thus, many of the functional types discovered by Mountcastle and colleagues (1975) are actually segregated into small cortical fields, of which area LIP is one, and not into interdigitated cortical columns.
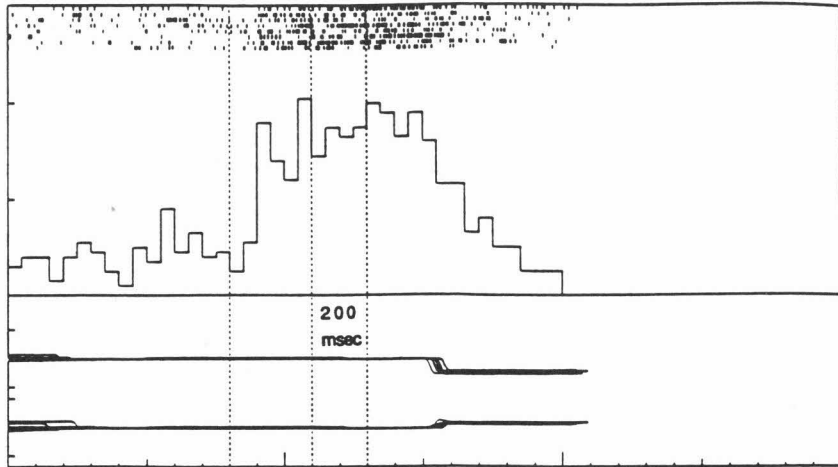
Physiology

VISUAL AND SACCADE-RELATED RESPONSES There was, briefly, some controversy about whether parietal neurons had saccade-related activity. When Mountcastle and colleagues (1975) first observed saccade re-

sponses, they proposed that the area issued general commands to make saccadic eye movements. Soon thereafter, Robinson, Goldberg, and Stanton (1978) observed visual responses from parietal neurons and they challenged Mountcastle's command hypothesis, arguing that the cells were responding in a sensory fashion to the saccade targets as visual stimuli rather than in a motor fashion related to the eye movement. Using a memory saccade task that separated sensory from motor responses, Andersen, Essick, and Siegel (1987) showed that posterior parietal neurons had both visual and saccade-related activity. These results suggested that it was more appropriate to consider posterior parietal cortex as being involved in sensorimotor integration rather than as strictly a sensory or a motor structure (Andersen, 1987).
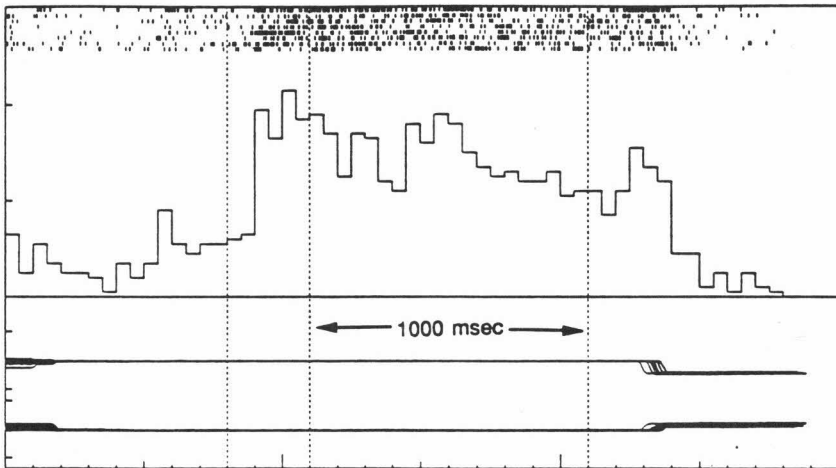
The visual and saccade activity in LIP has recently been studied in great detail by our laboratory (Barash et al., 1991a, b) and compared to visual and saccade activity in area 7a. Saccade-related responses in LIP generally begin prior to eye movements, whereas most area 7a saccade responses are postsaccadic, beginning after initiation of eye movements. This observation, and the reduced activity related to planning eye movements in 7a compared to LIP (see later), led these investigators to propose that LIP participates in the planning of eye movements, whereas area 7a appears to subserve other functions. These studies also showed that visual responses to saccade targets are generally weaker in 7a and have a longer latency and that the spontaneous activity in LIP is greater than in 7a. The visual receptive fields and motor fields of LIP neurons generally were found to overlay one another.

MEMORY ACTIVITY Andersen and colleagues (Gnadt and Andersen, 1988; Andersen et al., 1990; Barash et al., 1991a, b) described memory-related activity in LIP using a task that required monkeys to make saccades to remembered locations in the dark. The cells remained active during the period in which the animal withheld its response while remembering the location of an extinguished saccade target (figure 33.7). Using a double-saccade task similar to the one developed by Mays and Sparks (1980), Gnadt and Andersen were able to distinguish between whether the cells were coding the location of the sensory stimulus or whether they were coding the intention to make a saccade of a particular amplitude and direction. These investigators found that the activity could be evoked

A) 200 msec Delay

200
msec

B) 1000 msec Delay

← 1000 msec →

C) 1300 msec Delay

50 spikes/sec/div

25°/div

H   Saccade   Delay   Fixation Light
           Target   Off

V   ← 1300 msec →

100 msecs/div
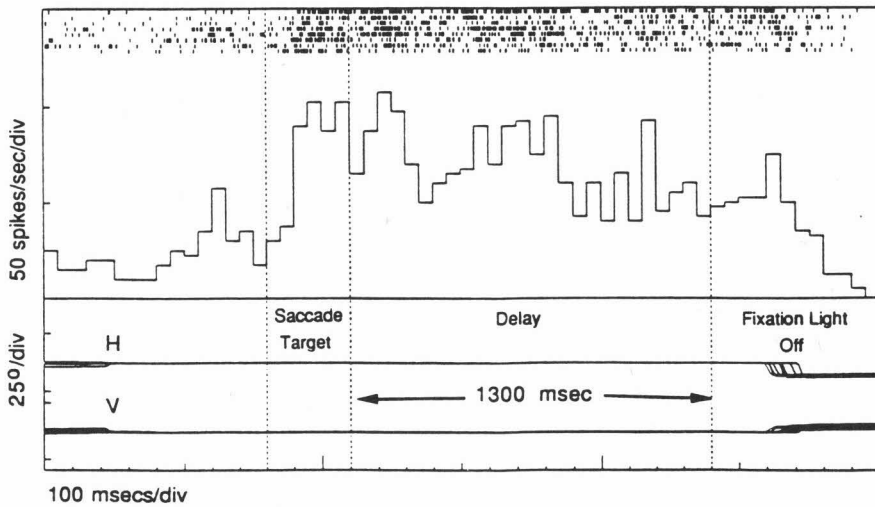
even when the sensory s nulus did not fall in the receptive field but the eye movement was made into the cell's motor field, arguing for the latter alternative (figure 33.8). They interpreted these activities as being part of a motor plan that has been triggered and remains active during the waiting period. Goldberg, Colby, and Duhamel (1990) and Barash and associates (1991a, b) confirmed these double-saccade results. We (Barash et al., 1991a, b) showed that the memory activity of LIP cells is directionally tuned, and these memory fields coincide with the visual and saccade fields. These results suggested the hypothesis that the memory activity reflects the intention of the monkey to make the next saccade.

To test the idea that this activity is related to intention, we (Bracewell et al., 1991) trained monkeys in a change-in-plan task, for which an animal was required to make an eye movement to a remembered target after a delay. However, during the delay period of some trials, the target would flash on at a new location, requiring a change in the direction of the planned saccade. It was found that the activity of the cells would turn on and off in a manner consistent with the motor plan that the animal had to formulate, as required by the task. The remarkable aspect of this result was that the plan to make an eye movement in a particular direction could be determined by examining the activity of the LIP cells without the animal emitting any behavior. To test this intention idea further, we (Bracewell et al., 1991) trained monkeys to make saccades to the remembered location of auditory targets. We found that many of the cells exhibited intended movement activity for both visual and auditory stimuli, consistent with the idea that the activity was more related to the plan to make an eye movement than to the modality of the sensory stimulus. Finally, in a memory double-saccade task, we (Bracewell et al., 1991; Mazzoni et al., 1992) showed that the memory activity was present only for the next intended movement. In this task, two targets were flashed briefly, and the animal had to remember the location of both targets. If the second target fell in the visual receptive field of a cell but both saccades were of a different amplitude and direction from the motor field of the cell, then the cells usually showed no response. Even when the task was configured so that the second saccade target fell in the visual receptive fields and the second saccade was made into the motor fields, the cells did not become active until after the first saccade.

In general, it is difficult to determine whether neural activity is related to attention or intention; for instance, Goldberg, Colby, and Duhamel (1990) have argued that the memory activity is related to the animal's *visual attention*, and not intention, to make movements. A visual attention interpretation would be consistent with the change-in-plan results but not with the auditory memory results, and so the interpretation must be broadened to posit that the attentional activity in this area is multimodal. Moreover, the memory double-saccade results do not appear to be consistent with any simple attention hypothesis, because the animal must attend and memorize both visual targets but most cells will have little or no memory activity for the visual targets in their receptive fields if the task does not require eye movements into their motor fields. A correlation of the memory activity with intention seems the most straightforward interpretation for these data.

Conclusions

Recent experiments, reviewed in this chapter, are shedding light on the nature of abstract representations of space. Spatial representations are derived by integrating visual signals with information about eye position, vergence angle, and head position. These signals are brought together in the posterior parietal cortex to form a specific, distributed representation of space that is typified by linear gain fields.

One issue for further research is whether the different representations of space, outlined previously, share

FIGURE 33.7 Memory saccade task with different delays demonstrating the memory character of the activity during the delay. Delays are (A) 200 ms, (B) 1000 ms, and (C) 1300 ms. The rasters show the actual neural activity used to make the histograms. The period between the first two dotted vertical lines represents the time the saccade target is present, and the period between the second and third lines is the delay period. The fixation light goes off coincident with the third dotted vertical line. Both horizontal (*H*) and vertical (*V*) eye position traces are shown. In this experiment, the saccade target appeared 15° to the left. There is a vertical component in the leftward eye movement; this upward component for horizontal eye movements is common for saccades to remembered locations made in the dark. (Reprinted with permission from Andersen et al., 1990. Copyright 1990 Society for Neuroscience)
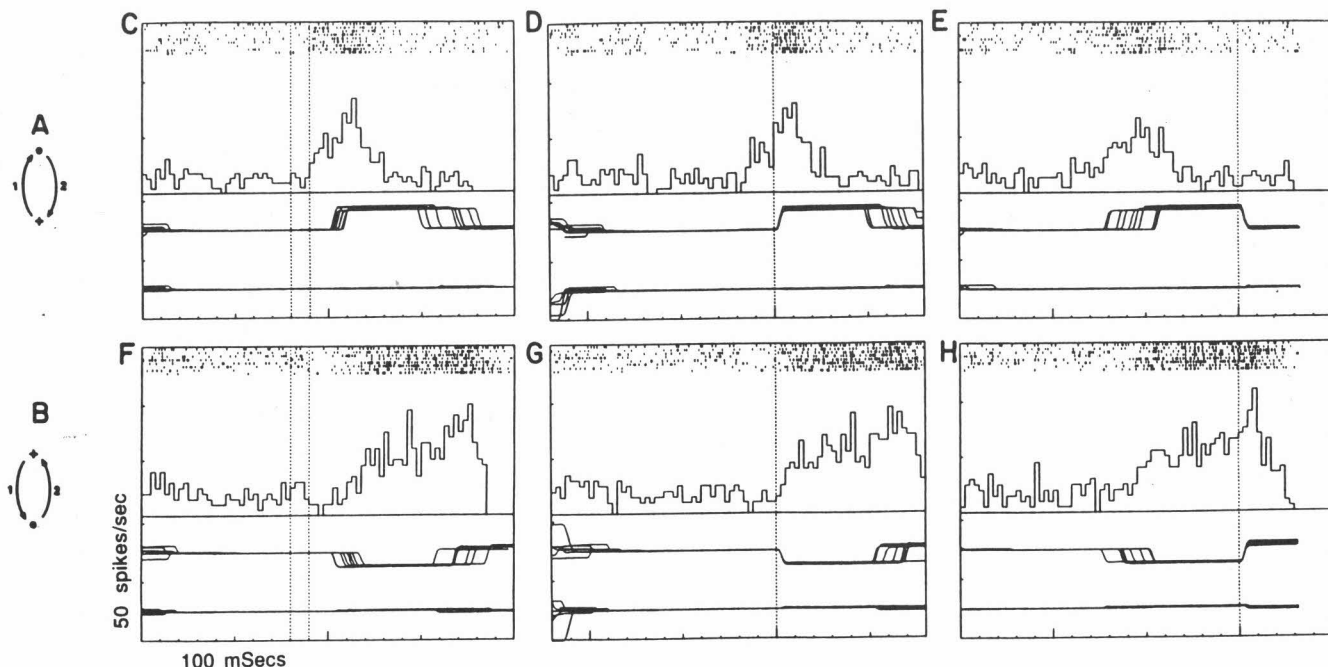
FIGURE 33.8 Back-saccade paradigm. (A, B) Scheme of the two saccades in the task. The first saccade is to the (single) target, whereas the second saccade is made in the dark back to the location of the original fixation point. (C–H) Activity in the back-saccade task of an LIP neuron. The preferred direction of this neuron, for the light-sensitive (LS), memory (M), and saccade (S) phases, is upward. Hence, in the top row, the visual stimulation and the first movement are in the preferred direction, and the second movement is in the opposite, nonpreferred direction. In the bottom row, the visual stimulation and the first saccade are in the nonpreferred direction, but the second saccade is in the preferred direction. (C) and (F) are aligned on the sensory stimuli. The first dotted vertical line denotes the offset of the fixation spot and the simultaneous onset of the target. The second dotted line represents the target offset. (D) and (G) are aligned on the beginning of the first saccade, and the dotted line denotes the time the first saccade begins. (E) and (H) are aligned on the beginning of the second saccade, and the dotted line denotes the time the second saccade begins. Shown in each panel, from the top, are the spike rasters, where each horizontal trace represents a trial and each tick within a line marks the time of occurrence of a spike; the resulting histogram; and the horizontal and vertical eye position traces of the various trials, superimposed. (Reprinted with permission from Barash et al., 1991a)

the same neural circuits. LIP is fascinating in that it appears to be an example of such an area. Cells in LIP integrate eye and head position with retinal signals to code space in head and body coordinates. Many cells here also carry vergence and disparity signals, enabling the representation of distance with respect to the body.

A related issue is whether the coordinate transformations proceed in a hierarchical fashion. For instance, are the body-centered cells of the posterior parietal cortex constructed by adding head position signals to the head-centered representation? Alternatively, the entire representation could be body-centered, with some cells exhibiting only retinal and eye position signals within this highly distributed representation (training networks to code in body-centered coordinates often generate some hidden units that carry only

eye and retinal signals). Is information about shoulder position added to the body-centered representation of space in areas 7a and LIP to generate arm-referenced representations? Are there additional representations of visual targets that code with respect to the hand? These and many other questions make this a rich area for future research.

In the past few years, substantial progress has been made in researching the role of LIP in processing saccades. This area appears to make interesting, high-level contributions to the processing of eye movements. Cells in this area integrate information on eye position, head position, and vergence angle as well as the usual retinal location information and appear to represent targets in head- and body-centered spatial coordinates. Recent studies also reveal memory-related activities in

LIP that may function in the formation of motor plans. These results point to a central role for LIP in directing gaze.

REFERENCES

ANDERSEN, R. A., 1987. The role of the inferior parietal lobule in spatial perception and visual-motor integration. In *Handbook of Physiology: Sec. 1. The Nervous System:* Vol. 5. *Higher Functions of the Brain* (part 2), F. Plum, V. B. Mountcastle, and S. R. Geiger, eds. Bethesda, Md.: American Physiological Society, pp. 483–518.

ANDERSEN, R. A., 1989. Visual and eye-movement functions of the posterior parietal cortex. *Annu. Rev. Neurosci.* 12: 377–403.

ANDERSEN, R. A., C. ASANUMA, and W. M. COWAN, 1985. Callosal and prefrontal associational projecting cell populations in area 7a of the macaque monkey: A study using retrogradely transported fluorescent dyes. *J. Comp. Neurol.* 232:443–455.

ANDERSEN, R. A., R. M. BRACEWELL, S. BARASH, J. W. GNADT, and L. FOGASSI, 1990. Eye position effects on visual, memory and saccade-related activity in areas LIP and 7A of macaque. *J. Neurosci.* 10:1176–1196.

ANDERSEN, R. A., G. K. ESSICK, and R. M. SIEGEL, 1985. Encoding of spatial location by posterior parietal neurons. *Science* 230:456–458.

ANDERSEN, R. A., G. K. ESSICK, and R. M. SIEGEL, 1987. Neurons of area 7 activated by both visual stimuli and oculomotor behavior. *Exp. Brain Res.* 67:316–322.

ANDERSEN, R. A., and V. B. MOUNTCASTLE, 1983. The influence of the angle of gaze upon the excitability of the light sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 3:532–548.

ANDERSEN, R. A., L. SNYDER, C.-S. LI, and B. STRICANNE, in press. Coordinate transformations is the representation of spatial information. *Curr. Opinion Neurobiol.*

BALINT, R., 1909. Seelenlähmung des "Schauens," Optische Ataxie, Räumliche Störung der Aufmerksamkeit. *Psychiatr. Neurol.* 25:51–81.

BARASH, S., R. M. BRACEWELL, L. FOGASSI, J. W. GNADT, and R. A. ANDERSEN, 1991a. Saccade-related activity in the lateral intraparietal area I. Temporal properties. *J. Neurophysiol.* 66:1095–1108.

BARASH, S., R. M. BRACEWELL, L. FOGASSI, J. W. GNADT, and R. A. ANDERSEN, 1991b. Saccade-related activity in the lateral intraparietal area II. Spatial properties. *J. Neurophysiol.* 66:1109–1124.

BARTO, A. G., and M. I. JORDAN, 1987. Gradient following without backpropagation in layered networks. In *Proceedings of the IEEE International Conference on Neural Networks* 2:629–636.

BATTAGLINI, P. P., P. FATTORI, C. GALLETTI, and S. ZEKI, 1990. The physiology of area V6 in the awake, behaving monkey. *J. Physiol.* 423:100P.

BOUSSAOUD, D., T. M. BARTH, and S. P. WISE, (in press).

Effects of gaze on apparent visual responses of frontal cortex neurons. *Exp. Brain Res.*

BRACEWELL, R. M., S. BARASH, P. MAZZONI, and R. A. ANDERSEN, 1991. Neurons in the macaque lateral intraparietal cortex (LIP) appear to encode the next intended saccade. *Soc. Neurosci. Abstr.* 17:1282.

BROTCHIE, P. R., R. A. ANDERSEN, and S. GOODMAN, 1993. The influence of head position on the representation of space in the posterior parietal cortex. Manuscript submitted for publication.

FLEMING, J. F. R., and E. C. CROSBY, 1955. The parietal lobe as an additional motor area: The motor effects of electrical stimulation and ablation of cortical areas 5 and 7 in monkeys. *J. Comp. Neurol.* 103:485–512.

FOGASSI, L., V. GALLESE, G. DI PELLEGRINO, L. FADIGA, M. GENTILUCCI, G. LUPPINO, M. MATELLI, A. PEDOTTI, and G. RIZZOLATTE, 1992. Space coding by premotor cortex. *Exp. Brain Res.* 89:686–690.

GALLETTI, C., and P. P. BATTAGLINI, 1989. Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *J. Neurosci.* 9:1112–1125.

GNADT, J. W., 1992. Area LIP: Three-dimensional space and visual to oculomotor transformation. *Behav. Brain Sci.* 15:745–746.

GNADT, J. W., and R. A. ANDERSEN, 1988. Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* 70:216–220.

GNADT, J. W., and L. E. MAYS, 1991. Depth-tuning in area LIP by disparity and accommodative cues. *Soc. Neurosci. Abstr.* 17:1113.

GOLDBERG, M. E., C. L. COLBY, and J.-R. DUHAMEL, 1990. The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harb. Symp. Quant. Biol.* 55:729–739.

GOODMAN, S., and R. A. ANDERSEN, 1989. Microstimulation of a neural-network model for visually guided saccades. *J. Cogn. Neurosci.* 1:317–326.

GOODMAN, S. J., and R. A. ANDERSEN, 1990. Algorithm programmed by a neural network model for coordinate transformation. In *Proceedings of the International Joint Conference on Neural Networks, San Diego,* Vol. 2. Ann Arbor, Mich.: IEEE Neural Networks Council, pp. 381–386.

HYVÄRINEN, J., 1981. Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res.* 206: 287–303.

HYVÄRINEN, J., and Y. SHELEPIN, 1979. Distribution of visual and somatic functions in the parietal associative area 7 of the monkey. *Brain Res.* 169:561–564.

KEATING, E. G., and S. G. GOOLEY, 1988. Disconnection of parietal and occipital access to the saccadic oculomotor system. *Exp. Brain Res.* 70:385–398.

LEHKY, S. R., A. POUGET, and T. J. SEJNOWSKI, 1990. Neural models of binocular depth perception. *Cold Spring Harb. Symp. Quant. Biol.* 55:765–777.

LYNCH, J. C., and J. W. MCLAREN, 1989. Deficits of visual attention and saccadic eye movements after lesions of parieto-occipital cortex in monkeys. *J. Neurophysiol.* 61: 74–90.

LYNCH, J. C., V. B. MOUNTCASTLE, W. H. TALBOT, and T. C. T. YIN, 1977. Parietal lobe mechanisms for directed visual attention. *J. Neurophysiol.* 40:362–389.

MACKAY, W. A., and A. RIEHLE, 1992. Planning a reach: Spatial analysis by area 7a neurons. In *Tutorials in Motor Behavior 2*, G. Stelmach and J. Requin, eds. New York: Elsevier.

MAUNSELL, J. H. R., and D. C. VAN ESSEN, 1983. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J. Neurosci.* 3:2563–2586.

MAYS, L. E., and D. L. SPARKS, 1980. Dissociation of visual and saccade-related responses in superior colliculus neurons. *Science* 43:207–232.

MAZZONI, P., R. A. ANDERSEN, and M. I. JORDAN, 1991a. A more biologically plausible learning rule for neural networks. *Proc. Natl. Acad. Sci.* 88:4433–4437.

MAZZONI, P., R. A. ANDERSEN, and M. I. JORDAN, 1991b. A more biologically plausible learning rule than backpropagation applied to a network model of cortical area 7a. *Cerebral Cortex* 1:293–307.

MAZZONI, P., R. M. BRACEWELL, S. BARASH, and R. ANDERSEN, 1992. *Soc. Neurosci. Abstr.* 18:148.

MOUNTCASTLE, V. B., J. C. LYNCH, A. GEORGOPOULOS, H. SAKATA, and C. ACUNA, 1975. Posterior parietal association cortex of the monkey: Command function for operations within extrapersonal space. *J. Neurophysiol.* 38:871–908.

NEWSOME, W. T., R. H. WURTZ, and H. KOMATSU, 1988. Relation of cortical areas MT and MST to pursuit eye movements: I. Differentiation of retinal from extraretinal inputs. *J. Neurophysiol.* 60:604–620.

PECK, C. K., J. A. BARO, and S. M. WARDER, 1992. Eye position effects on visual responses in the superior colliculus. *Invest. Ophthalmol. Vis. Sci. (Suppl.)* 33:1357.

ROBINSON, C. J., and H. BURTON, 1980a. Organization of somatosensory receptive fields in cortical areas 7b, retroinsular postauditory and granular insula of *M. fascicularis*. *J. Comp. Neurol.* 192:69–92.

ROBINSON, C. J., and H. BURTON, 1980b. Somatic submodality distribution within the second somatosensory (SII), 7b, retroinsular, postauditory and granular insular cortical areas of *M. fascicularis*. *J. Comp. Neurol.* 192:93–108.

ROBINSON, D. L., M. E. GOLDBERG, and G. B. STANTON, 1978. Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. *J. Neurophysiol.* 41:910–932.

ROBINSON, D. L., J. W. McCLURKIN, and C. KERTZMANN, 1990. Orbital position and eye movement influences on visual responses in the pulvinar nuclei of the behaving macaque. *Exp. Brain Res.* 82:235–246.

SAKATA, H., H. SHIBUTANI, and K. KAWANO, 1980. Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. *J. Neurophysiol.* 43:1654–1672.

SNYDER, L. H., P. R. BROTCHIE, and R. A. ANDERSEN, in press. World-centered encoding of location in posterior parietal cortex of monkey. In *Proceedings of Neural Control of Movement Third Annual Meeting*.

WAGMAN, I. H., 1964. Eye movements induced by electric stimulation of cerebrum in monkeys and their relationship to bodily movements. In *The Oculomotor System*, M. B. Bender, ed. New York: Harper & Rows, pp. 18–39.

ZIPSER, D., and R. A. ANDERSEN, 1988. A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* 331:679–684.