

7.6 Sensory-Motor Integration and the Posterior Parietal Cortex

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Experiments outlined here suggest that the posterior parietal cortex performs visuomotor integration functions including motor planning and coordinate transformations. Neural activity related to planning saccades is found in the lateral intraparietal area (LIP), a recently discovered cortical area specialized for saccadic eye movements. The planning related activity encodes the movements that the animal intends to make. Coordinate transformations are performed in area LIP and 7a of the posterior parietal cortex and produce a representation of space in both these areas. These representations are not explicit at a single cell level but rather utilize a population code. The coordinate transformations are achieved by a specific operation which systematically combines visual and eye position signals to form "planar gain fields".

7.6.1 Introduction

A major aspect of sensory-motor integration is the planning of movements. At some point in the sensory-motor integration process, sensory signals give way to signals related to what the subject intends to do. This chapter will discuss evidence that this step from sensory representation to decisions to make movements utilizes the neural circuitry within the posterior parietal cortex. We will focus on a recently discovered small area within the posterior parietal cortex, the lateral intraparietal area (LIP), which appears to be specialized for saccadic eye movements. This area carries sensory information related to the targets for eye movements and signals related to the planning of eye movements.

Coordinate transformations are a second major aspect of sensory-motor integration and are required because sensory information is derived in the coordinates of the retina and must be transformed to the coordinates of muscles for movements. The experiments discussed here suggest there exist, within the posterior parietal cortex, intermediate and abstract representations of space interposed between the sensory input and the motor output. These intermediate representations are formed by combining visual information with body position information to form representations of space in head-, body-, and perhaps even world-centered coordinates.

7.6.2 Area LIP

The posterior parietal cortex plays an important role in the processing of eye movements. Bilateral lesions to the posterior parietal cortex in human patients result in the inability to will saccades, although spontaneous saccades are unaffected (Balint 1909). Electrical stimulation of the monkey posterior parietal cortex produces saccadic eye movements (Wagman 1964; Fleming and Crosby 1955), and lesions to this region in monkeys produce deficits in saccades (Lynch and McLaren 1989; Keating and Gooley 1988).

Mountcastle and his colleagues (1975) reported cells in the inferior parietal lobule (which encompasses approximately the posterior half of the posterior parietal cortex) which were selective for saccades, as well as neurons selective for smooth pursuit eye movements, reaching movements of the limbs, and fixation. They reported that there appeared to be a columnar organization for these functional properties. Lynch et al. (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 are rather evenly distributed across the inferior parietal lobule. These results must be interpreted with some caution, however, since the data were pooled from several different brains and referenced to sulcal patterns which vary considerably from animal to animal. We reasoned that these different types of columns could be selectively labeled with anatomical tracers by assuming that they had connections with different brain structures (Andersen et al. 1985a). 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 we injected retrograde tracers into the frontal eye fields and adjoining dorsolateral prefrontal cortex, label was found predominantly in the lateral bank of the intraparietal cortex. We named this area the lateral intraparietal area (LIP) 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). Subsequent recording experiments showed that most area LIP cells had activity related to eye movements, and a majority of these cells responded prior to the 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 1981; Hyvärinen and Shelepin 1979; Robinson and Burton 1980a,b) and smooth pursuit activity to the medial superior temporal area MST (Newsome et al. 1988). Fixation activity typically varies with direction of gaze (Lynch et al. 1977; Andersen et al. 1987; Sakata et al. 1980), and conveys information about eye position (Andersen et al. 1987; Andersen 1989). These eye position-related activities are typically found in areas LIP and 7a. Thus, many of the functional types discovered by Mountcastle and colleagues (1975) are actually segregated

into small cortical fields rather than interdigitated cortical columns. Area LIP is the cortical field where saccade related activity is found.

7.6.3 Visual and Saccade Related Activities in Area LIP

There was a brief period of controversy regarding whether parietal neurons had saccade related activity. When Mountcastle and colleagues (1975) first observed saccade responses, they proposed that the area issued general commands to make 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 which separated sensory from motor responses, we showed that posterior parietal neurons had both visual and saccade related activity (Andersen et al. 1987). These results suggested that it was more appropriate to consider posterior parietal cortex as being involved in sensorimotor integration, rather than as a strictly sensory or motor structure (Andersen 1987).

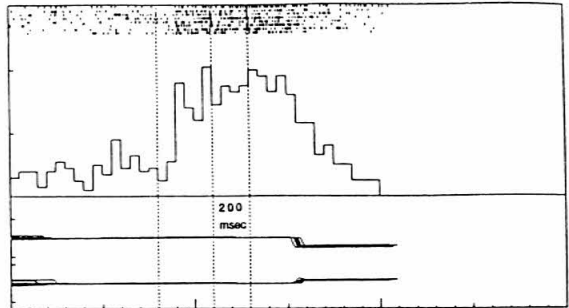
The visual and saccade activity in LIP has recently been studied in great detail by our laboratory and compared to visual and saccade activity in area 7a (Barash et al. 1991a,b). Saccade related responses in area LIP generally begin prior to eye movements, whereas most area 7a saccade responses are postsaccadic, beginning after initiation of eye movements. This observation, and the reduced activity related to planning eye movements in 7a compared to LIP (see below), led us to propose that area LIP participates in the planning of eye movements, whereas area 7a appears to subservise other functions. These studies also showed that the visual receptive fields and motor fields of LIP neurons generally were found to overlay one another.

7.6.4 "Memory" Related Activity in LIP

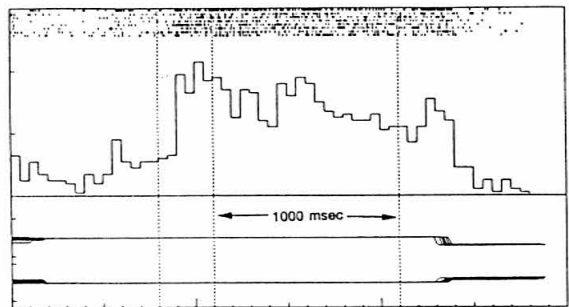
Recently, we found a memory related activity in area LIP using a task which required monkeys to make saccades to remembered locations in the dark (Gnadt and Andersen 1988; Andersen et al. 1990; Barash et al. 1991a,b). The cells remained active during the period in which the animal withheld its response while remembering the location of an extinguished saccade target (Fig. 1).

Using a double saccade task similar to the one developed by Mays and Sparks (1980), we were able to distinguish between whether the cells were coding the location of the sensory stimulus or whether the cells were coding the intention to make a saccade of a particular amplitude and direction. The

A) 200 msec Delay



B) 1000 msec Delay



C) 1300 msec Delay

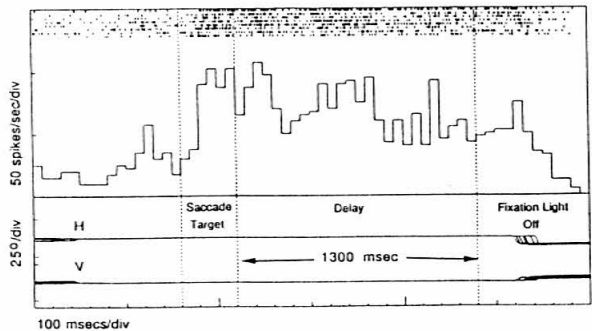


Fig. 7.6-1. A-C Memory saccade task with different delays demonstrating the memory character of the activity during the delay. Delays are 200 ms (A), 1000 ms (B), and 1300 ms (C). The rasters show the actual neural activity that is used to make the histograms. The period between the first two dotted 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)

activity could be evoked even when the sensory stimulus did not fall in the receptive field but the eye movement was made into the cell's motor field, arguing for the latter alternative (Fig. 2). We interpreted these activities as being part of a motor plan which has been latched in and remained active during the waiting period. The memory activity of LIP cells is directionally tuned, and these memory fields coincide with the visual and saccade fields. These results suggest that the memory activity reflects the intention of the monkey to make the next saccade.

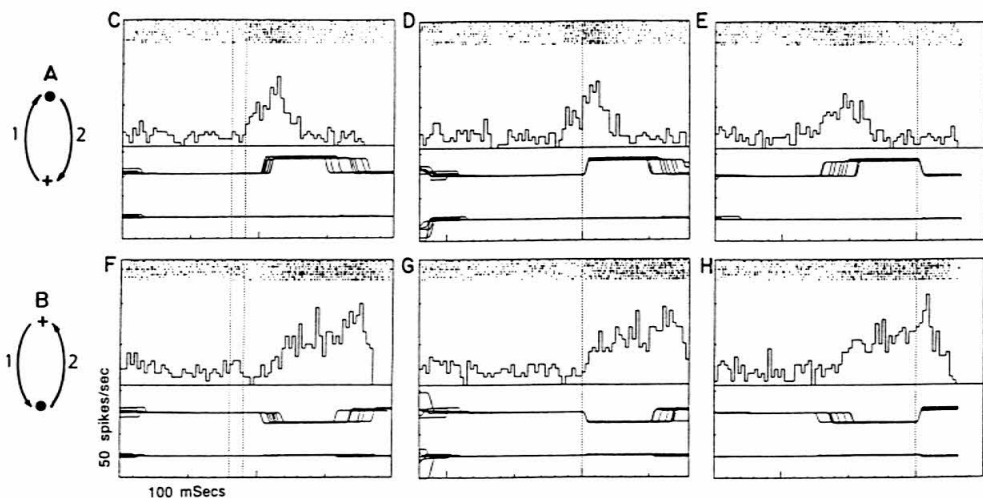


Fig. 7.6-2. Back-saccade paradigm. **A,B** Scheme of the two saccades in the task. The first saccade is to the (single) target, and the second saccade is made in the dark back to the location of the original fixation point. **C-H** Activity in the back-saccade task of an lateral intraparietal (LIP) neuron. The preferred direction of this neuron, for the LS (light-sensitive), M (memory), and S (saccade) 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. 1991b)

To test the hypothesis that this activity is related to intention, we have trained monkeys in a change-in-plan task. In this task, an animal was required to make an eye movement to a remembered target after a delay (Bracewell et al. 1991). 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. The activity of the cells would turn on and off consistently with the motor plan that the animal had to formulate, as required by the task. Remarkably, 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 further test this intention hypothesis we trained monkeys to make saccades to the remembered locations of auditory targets (Bracewell et al. 1991). We found many of the cells to exhibit intended movement activity for both visual and auditory stimuli, consistent with the idea that the activity is related more to the motor plan than to the modality of the sensory stimulus. Lastly, in a memory double saccade task, we showed that the memory activity was only present for the next intended movement (Bracewell et al. 1991; Mazzoni et al. 1992). 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 than 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 still did not become active until after the first saccade.

An important question is whether neural activity is related to attention or intention; for instance, Goldberg and colleagues (1990) have argued that the memory activity in area LIP is related to the animal's visual attention and not intention to make movements. A visual attention interpretation is consistent with the change in plan results, but is not consistent with the auditory memory results and requires that the interpretation be broadened to posit that the attentional activity in this area is multimodal. The memory double saccade results do not appear to be consistent with any simple attention hypothesis, since 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 is the most straightforward interpretation for these data.

7.6.5 Representations of Visual Space in Extraretinal Coordinates

Combining eye and body position information can form several frames of reference, depending on the type of body position information that is used. A head-centered representation is 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 (Fig. 3). A body-

centered coordinate representation is achieved by combining head, as well as eye and retinal, position information.

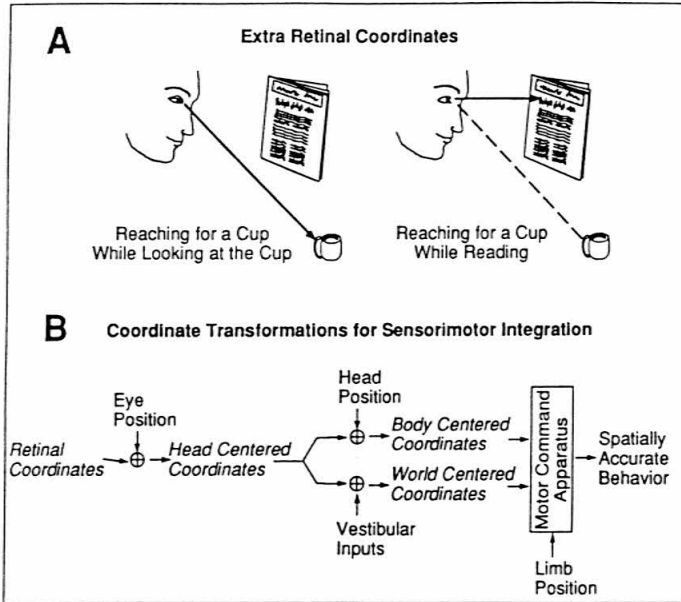


Fig. 7.6-3. A Demonstration of why representations of space in extraretinal coordinates are required for accurate motor behaviors. The term “extraretinal” refers to the encoding of visual stimuli in higher level coordinate frames than simple retinal coordinates. In the sketch on the *left* of the figure, a person is fixating the cup and it is imaged on the foveas, whereas on the *right* he or she is fixating the newspaper and the cup is imaged on a peripheral part of the retinas. In both cases, the subject is able to localize the cup with a reaching movement. Since different parts of the retinas are stimulated in the two conditions, information about eye position must also be available to accurately determine that the cup was at the same location in space. **B** How extraretinal coordinate frames can be computed from retinal coordinates. Visual stimuli are imaged on the retinas and are inputted 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 also 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. The figure shows these signals being added sequentially for illustrative purposes. It is presently not known whether there is a hierarchical organization of extraretinal coordinate frames in the brain or whether several of these signals come together at once to immediately form body and world coordinate frames. These signals, when combined with information about limb position derived from proprioceptive inputs, can encode accurate reaching movements. (Reprinted, with permission, from Andersen et al. 1993)

A world-centered coordinate frame (Fig. 3) can be achieved by combining vestibular signals with eye position and retinal position signals. The reason that it is world-centered is that the eye position information provides information about the location of the stimulus with respect to the head, and the vestibular information provides information about the location of

the head in the world. Below we will provide data consistent with all three of these representations being present in areas 7a and LIP of the posterior parietal cortex. The studies outlined here provide a glimpse into the internal operations of the brain which form the basis of our spatial perceptions and actions.

7.6.6 Representation of Space in Head-Centered Coordinates

We examined how space is represented in the posterior parietal cortex by exploring 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 retinal, coordinates. If this were the case, each time the eyes moved, 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.

Our 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 et al. 1985b). 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 et al. 1985b; see Fig. 4). The gain fields are 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 et al. 1985b). We later found similar gain fields for eye position in area LIP (Andersen et al. 1990).

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 can still be easily determined if the activity of several neurons is examined together; in other words, the representation of space is *distributed* in this area. Figure 5 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 neurons are tuned to a particular location in head-centered space, but only for a limited range of eye positions. To derive a signal for location in head-centered space independent of eye position it is necessary to examine the activity of a subset of parietal neurons and thus the code is a distributed one.

Looking at the behavior of single cells as only components of a much larger, distributed network has been crucial in advancing our understanding

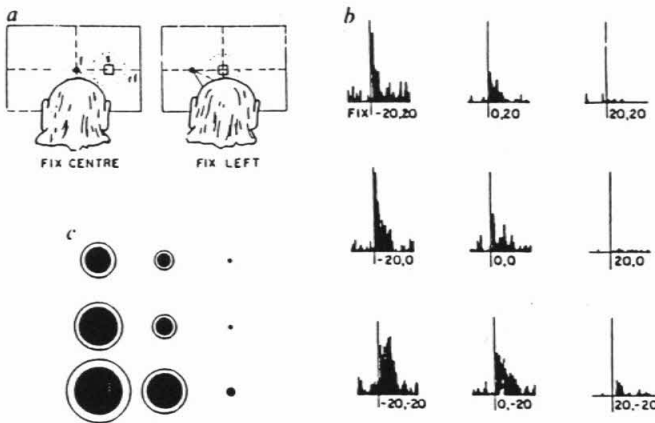
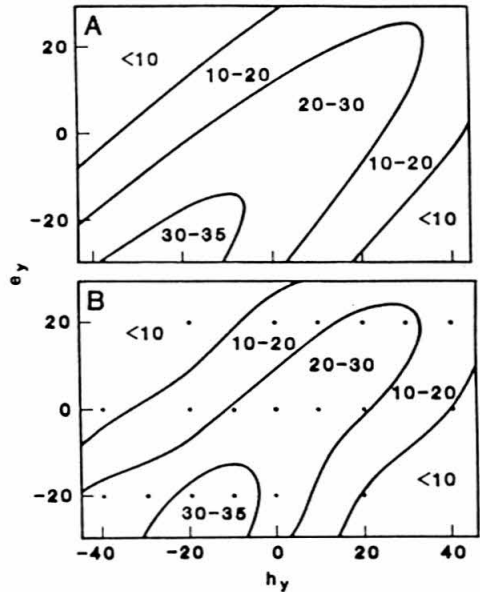


Fig. 7.6-4. **a** Experimental protocol for determining spatial gain fields, with the projection screen viewed from behind the monkey's head. To determine the effect of eye position, the monkey with head fixed, fixates on a point, *f*, at one of nine symmetrically placed locations on the projection screen. 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. Some cells were tested with 6° -diameter stimuli and others with 1° -diameter stimuli; however, stimulus size was not a relevant factor for this effect. 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 graphic 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* (Zipser and Andersen 1988); copyright 1988 Macmillan Magazines)

of how the brain computes locations in space. Neural networks trained to convert inputs of eye position and retinal position into locations in head coordinates at the output 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 areas 7a and LIP, 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). Thus the method of integrating these two signals is not random, but is systematic and requires the gain fields to be planar.

One of our neural network models for areas 7a and LIP 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

Fig. 7.6-5. **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 2 spikes/s. (Reprinted, with permission, from *Science* (Andersen et al. 1985); copyright American Association for the Advancement of Science)



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 (Andersen et al. 1990; Goodman and Andersen 1989). Instead, cells with planar gain fields appear to be an intermediate step in the transformation from visual to motor coordinates.

7.6.7 Body-Centered Coordinates and World-Centered Coordinates

The above 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 or world-centered representations. With this in mind, we have recently examined the effect of head position on the visual response of cells in the posterior parietal cortex (Brotchie et al. 1991). 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. About half of the cells with eye position gain fields were also found to have head position gain fields. When both these gain fields were present in individual cells their slopes were the same, consistent with the models prediction. 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). Recent recordings from our laboratory have shown that vestibular signals are also integrated with the various other signals (Snyder et al. 1993). When monkeys are rotated in the chair in the dark, many cells which show tonic activity related to eye position also have similar changes in activity for movement of the head relative to the room. Presumably these cells are receiving an integrated vestibular signal. Since 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 visual (retinal) receptive fields which have 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.

7.6.8 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. In response to this criticism we have trained neural networks to perform the transformation from retinal- to head-centered coordinates using a reinforcement learning rule developed by Barto and Jordan (1987), which is more biologically plausible than backpropagation (Mazzoni et al. 1991a,b). We found the reinforcement-trained networks produced the same gain fields which are produced by the backpropagation-trained networks and which are found in the brain. This result suggests the algorithm discovered for computing the coordinate transformation is largely independent of the exact learning rule used to generate it. It also 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.

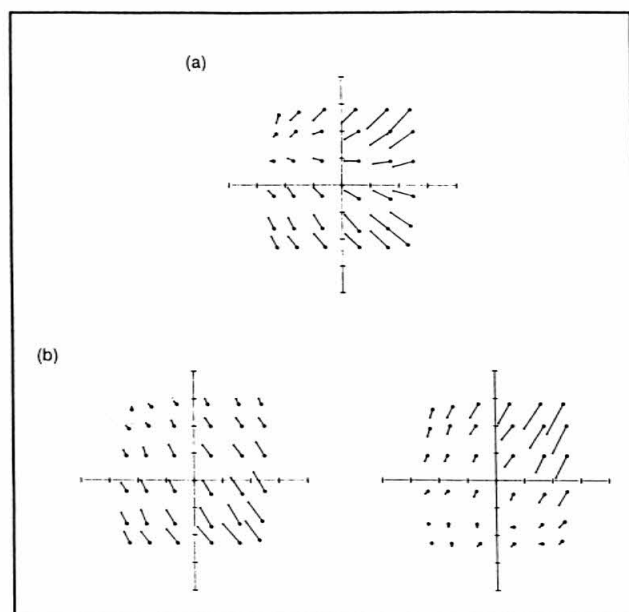


Fig. 7.6-6. a Eye movements recorded when two hidden units of a monotonic output network are stimulated simultaneously. b Eye movements recorded when each of the two hidden units is stimulated alone. Note that the result of simultaneous stimulation (a) is more or less the vector addition of the two saccade fields that result from stimulation of the individual units. (Reprinted, with permission, from *Journal of Cognitive Neuroscience* (Goodman and Andersen 1989); copyright MIT Press)

7.6.9 Microstimulation Experiments

We have also examined the effects of “microstimulating” the Zipser–Andersen model on eye movements (Goodman and Andersen 1989). Our 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 (Fig. 6b). 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 change in amplitude patterns could code single locations among a group of neurons, we showed that stimulation of two or more hidden units produced a pattern of eye movements which converge toward a single goal in head-centered space (Fig. 6a).

7.6.10 Conclusions

There has been substantial progress in research on the role of area LIP in the processing of saccades. This area appears to play an interesting, high-level role in the processing of eye movements. For instance, the memory activity in this area appears to be directly related to intention and motor planning.

The data reviewed here also shed light on the nature of abstract representations of space. Spatial representations are derived by integrating visual signals with information about eye position and head position. These signals are brought together in the posterior parietal cortex to form a specific, distributed representation of space which is typified by planar gain fields.

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References

- Andersen RA (1987) The role of the inferior parietal lobule in spatial perception and visual-motor integration. In: Plum F, Mountcastle VB, Geiger SR (eds) *The handbook of physiology*, Sect 1. The nervous system, vol 5. Higher functions of the brain part 2. American Physiological Society, Bethesda, pp 483-518
- Andersen RA (1989) Visual and eye-movement functions of the posterior parietal cortex. *Ann Rev Neurosci* 12: 377-403
- Andersen RA, Mountcastle VB (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 RA, Asanuma C, Cowan WM (1985a) 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 RA, Essick GK, Siegel RM (1985b) Encoding of spatial location by posterior parietal neurons. *Science* 230: 456-458
- Andersen RA, Essick GK, Siegel RM (1987) Neurons of area 7 activated by both visual stimuli and oculomotor behavior. *Exp Brain Res* 67: 316-322
- Andersen RA, Bracewell RM, Barash S, Gnadt JW, Fogassi L (1990) Eye position effects on visual, memory and saccade-related activity in areas LIP and 7A of macaque. *J Neurosci* 10: 1176-1196
- Andersen RA, Snyder L, Li C-S, Stricanne B (1993) Coordinate transformations in the representations of spatial information. *Current Opinion in Neurobiology* 3: 171-176
- Balint R (1909) Seelenlähmung des "Schauens", Optische Ataxie, Räumliche Störung der Aufmerksamkeit. *Psychiatr Neurol* 25: 51-81
- Barash S, Bracewell RM, Fogassi L, Gnadt JW, Andersen RA (1991a) Saccade-related activity in the lateral intraparietal area. I. Temporal properties. *J Neurophysiol* 66: 1095-1108
- Barash S, Bracewell RM, Fogassi L, Gnadt JW, Andersen RA (1991b) Saccade-related activity in the lateral intraparietal area. II. Spatial properties. *J Neurophysiol* 66: 1109-1124
- Barto AG, Jordan MI (1987) Gradient following without backpropagation in layered networks. *Proc IEEE Int Conf on Neural Networks* 2: 629-636
- Bracewell RM, Barash S, Mazzone P, Andersen RA (1991) Neurons in the macaque lateral intraparietal cortex appear to encode the next intended saccade. *Soc Neurosci Abstr* 17: 1282
- Brotchie PR, Andersen RA (1991) A body-centered coordinate system in posterior parietal cortex. *Soc Neurosci Abstr* 17: 1282
- Fleming JFR, Crosby EC (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

- Gnadt JW, Andersen RA (1988) Memory related motor planning activity in posterior parietal cortex of macaque. *Exp Brain Res* 70: 216-220
- Goodman S, Andersen RA (1989) Microstimulation of a neural-network model for visually guided saccades. *J Cognitive Neurosci* 1: 317-326
- Goodman SJ, Andersen RA (1990) Algorithm programmed by a neural network model for coordinate transformation. *Proc Int Joint Conf Neural Networks San Diego II*: 381-386
- Goldberg ME, Colby CL, Duhamel J-R (1990) The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbor Symp Quant Biol* 55: 729-739
- Hyvärinen J (1981) Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res* 206: 287-303
- Hyvärinen J, Shelepin Y (1979) Distribution of visual and somatic functions in the parietal associative area 7 of the monkey. *Brain Res* 169: 561-564
- Keating EG, Gooley SG (1988) Disconnection of parietal and occipital access to the saccadic oculomotor system. *Exp Brain Res* 70: 385-398
- Lynch JC, McLaren JW (1989) Deficits of visual attention and saccadic eye movements after lesions of parieto-occipital cortex in monkeys. *J Neurophysiol* 61: 74-90
- Lynch JC, Mountcastle VB, Talbot WH, Yin TCT (1977) Parietal lobe mechanisms for directed visual attention. *J Neurophysiol* 40: 362-389
- Maunsell JHR, Van Essen DC (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
- Mazzoni P, Andersen RA, Jordan MI (1991a) A more biologically plausible learning rule for neural networks. *Proc Nat Acad Sci USA* 88: 4433-4437
- Mazzoni P, Andersen RA, Jordan MI (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, Bracewell RM, Barash S, Andersen R (1992) Intended movement activity of area LIP neurons in delayed double saccade tasks. *Soc Neurosci Abstr* 18: 148
- Mays LE, Sparks DL (1980) Dissociation of visual and saccade-related responses in superior colliculus neurons. *Science* 43: 207-232
- Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command function for operations within extrapersonal space. *J Neurophysiol* 38: 871-908
- Newsome WT, Wurtz RH, Komatsu H (1988) Relation of cortical areas MT and MST to pursuit eye movements. I. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60: 604-620
- Robinson CJ, Burton H (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 CJ, Burton H (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 DL, Goldberg ME, Stanton GB (1978) Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J Neurophysiol* 41: 910-932
- Sakata H, Shibutani H, Kawano K (1980) Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. *J Neurophysiol* 43: 1654-1672
- Snyder LH, Brotchie PR, Andersen RA (1993) World-centered encoding of location in posterior parietal cortex of monkey. *Soc Neurosci Abstr* 19: 770
- Wagman, IH (1964) Eye movements induced by electric stimulation of cerebrum in monkeys and their relationship to bodily movements. In: Bender MB (ed) *The oculomotor system*. Harper and Row, New York, pp 18-39
- Zipser D, Andersen RA (1988) A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* 331: 679-684