Visual and Visual-Motor Functions of the Posterior Parietal Cortex

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Abstract.   Recent research into the role of the posterior parietal cortex in motion perception, spatial perception, and visual-motor integration is reviewed in this paper. Lesion experiments have established that area MT, which feeds motion information to the posterior parietal cortex, is part of a motion processing pathway important for the perception of motion. Interestingly, deficits in motion perception recover quickly after these lesions, suggesting that either there is a compensatory reorganization of MT or parallel pathways are recruited or strengthened to subserve motion analysis. Cells in area 7a of the posterior parietal cortex integrate information about eye position and retinal position to produce an eye-position dependent tuning for the location of visual targets in head-centered coordinate space. A recently formulated network model indicates how the distributed representation of head-centered space in area 7a might be formed and read out. Area LIP in the posterior parietal cortex contains cells with response properties very similar to those found in the frontal eye fields and it is likely that this area plays a role in the processing of saccades. A newly discovered class of cells in area LIP has memory-linked activity coding, in motor coordinates, the intent to make eye movements.

INTRODUCTION

Lesions to the posterior aspect of the parietal lobe in humans produce a fascinating array of deficits in spatial perception and behavior. These deficits include the inability to localize visual targets, disturbances in the spatial distribution of attention, loss of spatial memories, and the inability to represent spatial relations in models or drawings. Over ten years ago Mountcastle and his colleagues began single cell recording experiments in behaving monkeys to examine the neural mechanisms that give rise to the

spatial abilities lost with parietal lesions. The work of Mountcastle, Lynch and colleagues; Hyvarinen and colleagues; Robinson, Goldberg and Stanton; and Sakata and colleagues during this period has provided a foundation for exploration into this intriguing corner of the brain. In this paper I will review three new research directions presently being explored from this foundation: (a) the role of the posterior parietal cortex and the pathways into this region in processing visual motion; in particular, visual areas within the posterior parietal cortex may play a role in extracting higher level motion information including the perception of structure-from-motion; (b) neural mechanisms for spatial constancy within the posterior parietal cortex; information about eye position is integrated with visual inputs to produce head-centered representations of visual space; and (c) the processing of eye movements made under visual guidance; a previously unexplored area within the intraparietal sulcus has been found whose cells hold in memory planned eye movements. Special experimental protocols have shown that these cells code the direction and amplitude of intended movements in motor coordinates and suggest that this area is important for motor planning.

Motion analysis. There is a substantial body of evidence to suggest that visual motion analysis is treated by specific brain regions. Brain lesions in humans can produce deficits in motion perception without deficits in other forms of vision. Recording experiments by a number of investigators have suggested that there are areas in the dorsal aspect of extrastriate cortex that may be specialized for motion analysis. These recording experiments have delineated a pathway which begins in primary visual cortex and ends in posterior parietal cortex. The anatomical determination of this presumed motion processing pathway is an important first step in understanding the neural mechanisms accounting for motion perception.

Direction selective cells in layers 4b and 6 of primary visual cortex project to the middle temporal area (MT) (V5 of Zeki). Recording experiments in MT indicate that nearly all cells in this area are direction selective, compared to only about 20% in area V1. There is a functional architecture for direction selectivity in MT similar to the functional architecture for orientation found in V1 (Albright et al. 1984). Area MT neurons also exhibit behaviors that may account for certain features of motion perception. Some cells are selective for the global direction of motion of patterns, rather than for the motion of those components of the pattern occuring orthogonally to the preferred orientation of the neurons (Movshon et al. 1985). Some cells are speed invariant over a wide range of spatiotemporal frequencies (Movshon 1985). MT cells also exhibit opponent center/surround organizations for direction selectivity with strong inhibition resulting when motion in the surround is in the same direction as motion in the center (Allman et al. 1985; Tanaka et al. 1985). These surround mechanisms are quite large and

often include the entire visual field. These cells may play a role in processing motion parallax (important for extracting depth from motion cues) or in distinguishing movement of objects in the world from motion generated by eye movements. These data have led to the suggestion that area MT is specialized for processing motion; however, until recently it had not been shown that damage restricted to area MT disrupted motion perception.

Area MT projects to the immediately adjacent medial superior temporal area located in the posterior parietal cortex within the anterior bank of the superior temporal sulcus. Recording experiments suggest that area MST contains cells selective for rotation and expansion of velocity fields (Saito et al. 1985; Sakata et al. 1985; Sakata et al. 1986). Area MST in turn projects to area 7a in the posterior parietal cortex. Cells in this region show an opponent direction organization with respect to the fixation point and it has been suggested that this property is important for the analysis of visual flow fields during locomotion (Motter and Mountcastle 1981).

Thus there may exist a hierarchy for visual motion analysis within the dorsal extrastriate cortex. Area MT processes more complex aspects of motion than the direction selective cells of V1 and, in turn, areas MST and 7a appear to analyze aspects of structure-from-motion.

Area MT is necessary for the perception of motion. The results of recent lesioning experiments have established that area MT is part of a motion processing system responsible for the perception of motion. Of equal interest is the observation that after at least small area MT lesions, the ability to perceive motion recovers in a matter of days.

Newsome, Wurtz, Dursteler, and Mikami (1985) were the first to test the effect of MT lesions on behavior requiring motion analysis. They found that small ibotenic acid lesions placed at retinotopically identified loci in area MT produced defects in smooth pursuit. During the early, open loop stage of tracking the animals underestimated the speed of the target. The deficit was specific to the retinal locus of the lesion, indicating that it was a deficit in estimating the speed of the target rather than a motor defect. Furthermore, the animals could make saccades accurately to the retinotopic locus of the lesion, indicating that the deficit was specific to motion and was not due to the animal not being able to see in the affected area.

These important experiments did not, however, establish that the monkeys could not see motion, only that they could not use this information to make smooth pursuit eye movements. In two ongoing studies it has been shown that the perception of motion is in fact disrupted with area MT lesions.

In the first of these experiments Siegel and Andersen trained animals to perform motion psychophysical tasks to determine prelesion thresholds for the detection of shear motion and structure-from-motion (Andersen and Siegel 1986; Siegel and Andersen 1986). Small ibotenic acid lesions to area

MT produced an eightfold increase in shear motion thresholds. This increase in thresholds was found only for those areas in the visual field that corresponded to the retinotopic locus of the lesion in area MT. The deficit was specific for motion since contrast sensitivity thresholds were not affected at the same locations in the visual field as the motion deficit. Since the animals were only required to determine whether or not they saw motion, and not any of the parameters of the motion such as direction, it was interpreted that the animals had a deficit in the *detection* of motion. Thus, restricted lesions to area MT produced motion scotomas in the visual field. Interestingly, the deficits were transient, the animals recovering in four to five days. This was a similar time course to the recovery of the tracking deficit recorded in the experiments of Newsome et al. (1985). In one hemisphere the effects of MT lesions on structure-from-motion thresholds were also tested. The monkey's task was to determine if it saw a revolving hollow cylinder in a moving dot pattern. The amount of structure of the stimulus was varied to generate psychometric functions. The animal could not do the structure-from-motion task after the area MT lesion even when there was no noise in the structure. Moreover, the structure from motion deficit remained for 23 days (at which time the animal was sacrificed), well after the motion detection thresholds had returned to normal.

In a second set of experiments, Newsome and Pare (1986) tested the ability of monkeys to determine the direction of correlated motion imbedded in noise. They found a transient deficit after MT lesions.

These experiments indicate that area MT is part of a motion processing system important for detecting motion. The thresholds for the shear detection tasks after MT lesions were so large that it is likely the animal could use positional cues to solve the task at very large amplitudes of shear. The transient nature of the deficit was common to all the experiments, being seen for pursuit, motion detection, and direction detection. The recovery could result from either a reorganization of area MT or from a parallel pathway which, being recruited or strengthened to serve in motion processing, normally does not function as a main line in the motion pathway. These two possibilities could be tested by completely destroying area MT. If the motion thresholds do not return, the recovery is due to reorganization of area MT; if they do recover, parallel pathways are involved in the recovery.

Another question regarding recovery is whether training is required for it to occur. The monkey performs thousands of trials on the motion detection task before the thresholds recover. If the animals were to be placed in the dark after an MT lesion and brought out a week later, would the thresholds recover spontaneously, or would they still be elevated indicating that the retraining had played a significant role?

Finally, the single observation of a more permanent deficit in structure-from-motion perception, if it is found in subsequent experiments, will

indicate that: (a) structure-from-motion computation is performed in area MT and no other pathway can assume this task; or (b) some other area such as area MST requires preprocessing for the structure-from-motion computation that only area MT can provide.

Spatial Constancy

There are two reasons to believe that the brain contains nonretinotopic representations of visual space. The first is the observation that when the eyes move the visual world remains stable. This result suggests that information about eye position changes are used to compensate for movements of the visual scene focused on the retinas. It could be argued that purely sensory signals are used to stabilize the visual world; i.e., that a complete translation of the retinal image indicates an eye movement and not movement of the world. However, this explanation is not tenable since moving the eyes passively, which generates the same retinal stimulus as a willed eye movement, produces the impression that the world has moved. The second line of evidence for spatial representations is the fact that we can make motor movements such as reaching accurately to visual targets without visual feedback during the movement. This observation indicates that the motor system uses representations of the visual stimulus mapped in body-centered rather than retinal coordinates.

The most likely brain region to find nonretinotopic representations of visual space is the posterior parietal cortex. Lesions to this area in humans produce *visual disorientation*, a syndrome in which patients cannot reach accurately to visual targets and have difficulty navigating around seen obstacles. These patients can see but appear to be unable to associate the locations of what they see with their body position.

Recent recording experiments have established the way in which visual space is represented in area 7a of the posterior parietal cortex (Andersen et al. 1985). In these experiments visual receptive fields are mapped with monkeys fixating at different eye positions. The heads of the experimental animals are fixed simplifying space to a head-centered coordinate frame. Under these conditions two possible results would be either that the retinal receptive fields move with the eyes so that visual space is mapped in retinal coordinates, or that the receptive fields do not move with the eyes but rather remain constant for a location in head-centered space. In fact neither representation was found. Instead, the receptive fields moved with the eyes (were retinotopic) but the responsiveness of these receptive fields to retinotopically identical stimuli varied as a function of the angle of gaze. The interaction of eye position and retinal position was found to be multiplicative, and the activity of area 7a neurons to visual stimuli could be described as a gain that was a function of eye position, multiplied by the

response profile of the retinal receptive field. This interaction produces a neuron tuned for locations of targets in head centered space but this tuning is eye position-dependent. To illustrate this fact in a simple example, consider a cell that has a receptive field 10 degrees to the right and is only responsive when the animal looks 10 degrees to the right from straight ahead. Such a cell will respond only for stimuli located 20 degrees to the right in head-centered space (spatial tuning), but only if the animal is looking 10 degrees to the right (eye position dependence). Cells have never been found that code the location of a target in space in an eye position-independent fashion; however, sufficient information for such a coding is present in the population response of area 7a neurons. A major question is how such a distributed code could be "read out" or interpreted by the brain. One possible solution would be the presence of some topographic organization for spatial tuning in the cortex; however, recording experiments so far have not found such a map and present data indicate that if such a map does exist it is likely to be very crude or highly fractured.

Zipser and Andersen (1987) have recently created a parallel network model that learns spatial location given eye position and retinal position inputs. The model uses a 3 layer network trained for spatial position using a back-propagation learning algorithm. Interestingly, this mathematical model generates receptive field properties similar to those found for actual posterior parietal neurons. The first input layer consists of 100 units in a 10 by 10 array that samples at equidistant points from a continuous two-dimensional retinal field, and 4 eye position inputs that code horizontal and vertical eye positions similar to the eye position cells found in area 7a. The intermediate layer has 9 units that receive inputs from all the input units, and in turn project to four units in the output layer that code horizontal and vertical positions in head-centered space for any pair of arbitrary retinal and eye position inputs. After training is complete the middle layer "hidden" units have receptive fields that remain retinotopic, but their activity becomes modulated by eye position in a manner similar to that seen in recording data from area 7a neurons. The retinal receptive fields of the model cells appear very similar to area 7a fields, being large and occasionally complex but smoothly varying in shape.

These intriguing results show that training a parallel network to do coordinate transformations creates the same sort of distributed code as that found in the posterior parietal cortex. This similarity could be a coincidence; however, it is more likely that, since both the cortex and the model share a layered parallel architecture, it represents a fundamental property of solving coordinate transformations in such a parallel architecture. It will be important to investigate other parallel networks that have more complicated structures analogous to those found in the brain to determine whether they also produce this form of distributed coding. These initial simulation results

suggest that the posterior parietal cortex may learn to associate visual inputs with eye position. Thus such neural coding may be an example of a distributed associative memory. The spatial code in the model is by definition nontopographic; yet, it can be read out or interpreted because it was learned and thus became an inherent property of the synaptic structure of the network. This learning mechanism suggests that area 7a need not require a topography for spatial tuning in order to read out eye position-independent spatial locations. Finally, the similarity of the retinal receptive fields of the network units and those of the cells suggests that parietal neurons may have access to the entire retina (as a result of the multistage divergence of the corticocortical projections from V1 to area 7a) and that the eventual receptive fields of area 7a neurons are a result of competition during the learning process.

Role of Parietal Lobe in Visual-Motor Integration

In the initial and pioneering neurophysiological studies of the posterior parietal cortex by Mountcastle and colleagues, cells were found with activity correlated to the motor and oculomotor behaviors of the animals (Mountcastle et al. 1975; Lynch et al. 1977). They proposed a command hypothesis for the function of the posterior parietal cortex: that this area synthesized sensory and motivational information from several cortical areas and issued commands of a general nature for motor behaviors. In a subsequent study by Robinson, Goldberg and Stanton (1978) it was found that many of these same neurons could be driven by sensory stimuli. They argued that the motor-related activity seen by Mountcastle and colleagues was in fact due to sensory stimulation, either from the targets for movement or as a result of sensory stimulation due to the movement. They further found that the response to a sensory stimulus was enhanced if that stimulus was behaviorally relevant to the animal, and proposed that the parietal lobe was important for attention rather than for generating motor commands.

Subsequent to this work a number of investigators have designed experiments to separate sensory- from motor-related responses, which had generally been linked in the earlier studies (Sakata et al. 1980; Sakata et al. 1983; Andersen et al. 1987; Wurtz and Newsome 1985; Bioulac and Lamarre 1979; Seal et al. 1982; Seal et al. 1985). It has been found that neurons generally have both sensory- and movement-related responses. For instance, cells responding to reaching behavior also have somatosensory inputs; and cells responding to smooth pursuit, saccades, or fixations also respond to visual stimuli. The idea emerging from these observations is that the parietal lobe should not be viewed primarily as a sensory or a motor structure (Andersen 1987). Rather, it appears to function somewhere in between these two points, integrating sensory information to be used for

the formulation of motor behaviors. Simply stated, the area is involved in sensorimotor integration.

Another recent finding is that there appears to be a functional segregation within the posterior parietal cortex (Hyvarinen 1981; Andersen et al. 1985b, 1985c). Area MST contains cells responding to smooth pursuit; area 7b contains the reach cells; area LIP appears to be involved in saccades; and area 7a contains many of the space tuned and fixation neurons.

Area LIP and its role in motor planning. An area has recently been found within the lateral bank of the intraparietal sulcus (the lateral intraparietal area—LIP) that appears to play a role in programming saccadic eye movements. This area is similar to the frontal eye fields in many respects.

Many of the LIP neurons have memory-linked activity (Gnadt and Andersen 1986, 1987). These memory-related responses are demonstrated in saccade tasks in which the animal must remember in total darkness the spatial location of a briefly flashed target for several seconds before making a saccade. The neurons become active 50 to 100 msec after the onset of the flash and remain active in the absence of any visual stimuli until the saccade is made. Thus these cells appear to act as latches, maintaining a steady rate of firing during the entire period that the saccade is withheld.

The memory-linked activity could represent three possibilities: (a) the memory of the retinotopic locus of the stimulus; (b) the memory of the spatial location of the stimulus; or (c) the memory of the movement that the animal intends to make. These three alternatives can be experimentally separated by asking in which coordinates the memory-linked response is mapped. By using special tasks that separate sensory from motor coordinates it was found that these cells were encoding the intended amplitude and direction of movements in motor coordinates (Gnadt and Andersen 1986, 1987). Thus these cells are holding in register the intent to make movements of a particular metric. This observation suggests that area LIP is involved in aspects of motor planning.

CONCLUSION

In this review, we have seen that the posterior parietal lobe functions in various aspects of visual-spatial perception and behavior including motion perception, maintenance of spatial constancy, and visual-motor integration. In the motion domain, the posterior parietal cortex is at the pinnacle of a presumed hierarchy in motion processing. The area that feeds parietal cortex, area MT, has been shown to be part of a motion processing pathway important for perceiving motion. The fast recovery of motion thresholds after MT lesions introduces several testable experiments into the mechanisms of cortical compensation and reorganization after cerebral lesions. The

motion psychophysics/MT lesion paradigm is well suited for asking these questions since the pathways involved are well understood and the experiments are rigorously controlled.

Recent experiments have indicated the distributed nature of the nonretinotopic representation of space in the parietal cortex. The network model has been valuable in suggesting that this spatial representation is learned. Learning the associations between visual space and body position is logical since this system would need constant recalibration during growth. Experiments to determine how plastic this representation is seem to be in order. For instance, distortions of space resulting from wearing prisms can be rapidly compensated for by learning (prismatic adaptation). Does this learning result in cells in area 7a changing their tuning characteristics? Would the network model make predictions about these changes that may turn up in the recording data?

Finally, area LIP contains neurons that reflect the intent of the animal to make motor movements. These cells may provide a useful handle in dissecting the formulation of motor plans for sequences of movements and the recomputation of spatial transformations following each movement of a sequence. These problems can be addressed by observing the dynamic changes in the representation of intended movements in area LIP as an animal performs a sequence of saccades programmed by memorizing a sequence of flashed sensory targets.

The results of single cell recording experiments in the posterior parietal cortex have been instrumental in establishing a framework of issues concerning its role in spatial functions. Future experiments using these same techniques will be able to address how the brain recovers visual-spatial functions after injury, how associations between visual space and body position are learned and stored, and how sequential motor activities are planned and executed.

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