# Evidence for the lateral intraparietal area as the parietal eye field

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It has long been appreciated that the posterior parietal cortex plays a role in the processing of saccadic eye movements. Only recently has it been discovered that a small cortical area, the lateral intraparietal area, within this much larger area appears to be specialized for saccadic eye movements. Unlike other cortical areas in the posterior parietal cortex, the lateral intraparietal area has strong anatomical connections to other saccade centers, and its cells have saccade-related responses that begin before the saccades. The lateral intraparietal area appears to be neither a strictly visual nor strictly motor structure; rather it performs visuomotor integration functions including determining the spatial location of saccade targets and forming plans to make eye movements.

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## Introduction

When oculomotor physiologists discuss the cortical control of eye movements, they are typically referring to a small area in the frontal lobe called the frontal eye fields. More recently two other areas of cortex have become popular areas for eye movement research, the supplementary eye fields [1], also in the frontal lobe, and the lateral intraparietal area (LIP) in the posterior parietal cortex [2]. This review will discuss recent experiments that have examined aspects in the overall processing of saccadic eye movements that area LIP appears to perform. The activity of cells in this area has attributes of both the sensory stimulus and the motor response, suggesting that the area's primary function is in visual-motor integration. Among the visual-motor functions area LIP appears to subserve are the encoding of spatial locations of saccade targets and the planning of eye movements.

## Historical perspective

That the posterior parietal cortex is involved in the processing of eye movements has been appreciated for some time. Balint [3] described bilateral lesions to the posterior parietal cortex in human patients, which resulted in the inability to will saccades, although spontaneous saccades were unaffected. Electrical stimulation of monkey posterior parietal area produces saccadic eye movements [4,5], and lesions to monkey parietal cortex result in deficits in saccades [6,7].

In 1975, 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 *et al.* [8] 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. Later, Lynch *et al.* [9] 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 had to be interpreted with some caution, however, as they were pooled from several different brains and referenced to sulcal patterns that vary considerably from animal to animal. Following up on these observations, Andersen *et al.* [2] reasoned that the 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 probably project to the frontal lobe, in the region of the frontal eye fields. 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 *et al.* [2] 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 [10]. Subsequent recording experiments showed that most area LIP cells

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**Abbreviations**

**LIP**—lateral intraparietal area; **VIP**—ventral intraparietal area.

had activity related to eye movements, and a majority of these cells responded before saccades [11,12,13••,14••]. Other studies showed that reach activity was confined largely to area 7b [15–18], and smooth pursuit activity to area MST [19]. Fixation activity typically varies with direction of gaze [9,20,21], and appears primarily to convey information about eye position [20,22]. These eye position related activities are typically found in areas LIP and 7a. Thus, many of the functional types discovered by Mountcastle and colleagues [8] are actually segregated into small cortical fields, of which area LIP is one, rather than interdigitated cortical columns.

## Anatomical organization and topography

Besides strong connections to the frontal eye fields, area LIP provides a projection to the intermediate layers of the superior colliculus, whereas area 7a provides only a meager projection [23,24]. Area LIP also projects to different combinations of the pontine nuclei than are found for other areas within the posterior parietal cortex, and the LIP pattern is very similar to that reported for the frontal eye fields [25]. Thus, area LIP and the frontal eye fields appear to be part of a closely linked network that also includes the intermediate layers of the superior colliculus and the cerebellum (via the pontine nuclei). This network appears to be a major pathway for voluntary saccades.

Area LIP has a unique pattern of connections with the thalamus when compared with other areas in the posterior parietal cortex. The major thalamic projection to area LIP is from the pulvinar. Besides receiving inputs from the medial pulvinar [26•], as does area 7a [24,27–33], area LIP has strong connections to the lateral pulvinar [24]. Area 7b connects primarily to the oral pulvinar [24].

The connections of area LIP with other cortical areas are complex as it has reciprocal connections with at least 17 other cortical fields [34]. However, several important distinctions between LIP and the other areas of the parietal cortex are apparent from recent anatomical studies [33,34]. Area LIP receives inputs from extrastriate cortical areas that are rather low in the hierarchy of extrastriate areas. As mentioned above, it projects to saccadic eye movement centers, and also provides a weak projection to the dorsolateral prefrontal cortex, and a projection to areas in the rostral superior temporal sulcus. Area 7a is higher in the hierarchy of cortical areas, receiving 'feed-forward' projections from area LIP. Area 7a has connections with much higher level cortical areas than LIP including strong connections to the cingulate cortex, parahippocampal gyrus, presubiculum, and prefrontal cortex. Area 7b is unique in having connections with somatosensory areas, including area 5 and the insular cortex, although it also shares common cortical targets with area 7a [27,30,35–41].

There has recently been some discussion in the literature about the exact boundaries of area LIP. Seltzer and Pandya [42] originally described a densely myelinated zone on the lateral bank of the intraparietal sulcus, which was a part of their larger area POa. Area LIP encompasses approximately the posterior half of area POa [34,43]. The original description of LIP included this densely myelinated zone, but also cortex extending approximately 2 mm dorsal to this zone. Ungerleider and Desimone [44] reported a projection from MT to the densely myelinated zone, and not to the more dorsal aspect of LIP. They labeled the densely myelinated zone VIP*, as area VIP also receives input from MT. Blatt *et al.* [34] studied the anatomical connections of the dorsal and ventral aspects of LIP by injecting them separately with anatomical tracers. They confirmed the observation of Ungerleider and Desimone for the differential MT projection. Overall, however, they found that the two parts of area LIP had almost the same pattern of cortical connections, with only a few minor exceptions. Blatt *et al.* [34] named the dorsal cortex, LIPd, and the ventral cortex, LIPv. This approach recognizes differences between these two areas in terms of myelination and a few connections, but also emphasizes the similarity of the two regions, especially when compared with the physiological responses and anatomical connections found in area 7a.

Barash *et al.* [13••,14••] did not find any differences in the functional properties of the two subdivisions of LIP. Colby and Duhamel [45•] have found that the transition from visual activity found in area LIP to somatosensory receptive fields found in area VIP conforms to the ventral border of the densely myelinated region. These studies add further support to the idea that the ventral and dorsal aspects of area LIP are similar enough to consider them as a functional unit.

## Physiology

### Visual- and saccade-related responses

There was a brief period of controversy about whether parietal neurons had saccade-related activity. When Mountcastle and colleagues [8] first observed saccade responses they proposed that the area issued general commands to make saccadic eye movements. Soon thereafter Robinson, Goldberg and Stanton [46] observed visual responses from parietal neurons and 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 *et al.* [20] showed that posterior parietal neurons had both visual- and saccade-related activity. These results suggested that it is more appropriate to consider posterior parietal cortex as being involved in sensorimotor integration, rather than as a strictly sensory or motor structure [47], and that posterior parietal neurons carry a variety of signals that are integrated in very specific ways. Recent results outlined below indicate that the activity of area LIP neurons conveys eye position, head position, vergence, auditory, and memory signals, as well as visual and saccade signals.

The visual and saccade activity in area LIP has recently been studied in great detail by Barash *et al.* [13••,14••] and compared with visual and saccade activity in area 7a. Saccade-related responses in area LIP generally begin before 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 area 7a compared with area LIP (see below), led these investigators to propose that area LIP participates in the planning of eye movements, whereas area 7a appears to subserve other functions. This set of studies also shows that visual responses to saccade targets are generally weaker in area 7a and have a longer latency, and that the spontaneous activity in area LIP is greater than in 7a. The visual receptive fields and motor fields of LIP neurons were generally found to overlay one another.

### Memory activity

Gnadt and Andersen [11] described memory-related activity in area 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. Using a double saccade task similar to the one developed by Mays and Sparks [48], Gnadt and Andersen were able to distinguish 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. They found that the activity could be evoked even if the sensory stimulus did not fall in the receptive field, as long as the eye movement was made into the cell's motor field, arguing for the latter alternative. They interpreted these activities as being part of a motor plan which has been memorized, and remains active during the waiting period. Goldberg and colleagues [49] and Barash *et al.* [13••,14••] have confirmed these double saccade results. Barash *et al.* [13••,14••] have shown that the memory activity of area LIP cells is directionally tuned, and that these memory fields coincide with the visual and saccade fields. The results suggest 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, Bracewell *et al.* (RM Bracewell, S Barash, P Mazzoni and RA Andersen: *Soc Neurosci Abstr* 1991, 17:1282) trained monkeys in a change in plan task. An animal was required to make an eye movement to a remembered target after a delay. During the delay period of some trials, however, 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 further test the intention idea Bracewell *et al.* (RM Bracewell, S Barash, P Mazzoni and RA Andersen: *Soc Neurosci Abstr* 1991, 17:1282) trained monkeys to make saccades to the remembered location of auditory targets. They found that many of the cells exhibited intended movement activity for both visual and auditory stimuli, consistent with the idea that the activity was related more to the plan to make an eye movement than to the modality of the sensory stimulus. Finally, in a memory double saccade task, Bracewell *et al.* and Mazzoni *et al.* (RM Bracewell, S Barash, P Mazzoni and RA Andersen: *Soc Neurosci Abstr* 1991, 17:1282; P Mazzoni, RM Bracewell, S Barash and RA Andersen: *Soc Neurosci Abstr* 1992, 18:148) showed that the memory activity was only present 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 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 into the cells' visual receptive fields, and the second saccade was made into their motor fields, the cells still 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 and colleagues [49] 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 would not be consistent with the auditory memory results, and requires that the interpretation 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, as 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.

### Orbital position effects

The fact that we can make saccades to remembered locations in space, as well as to visual targets, suggests that the saccadic system has access to representations of space that are not strictly retinotopic. Gaze shifts often include head movements, and representation of targets in body coordinates has been proposed as a possible stage in the programming of these movements [50–52]. In earlier experiments in area 7a, a majority of the cells had been found to combine eye and retinal information in a manner consistent with adding these vectors to form a distributed representation of space in head-centered coordinates [53,54]. Recent experiments in area LIP now suggest that this area also combines eye position signals with retinal signals and can encode the location of targets with respect to the head [12]. Approximately 15% of cells recorded from area LIP had their response modulated primarily by eye position, with little or no activation by visual stimuli. Of the remaining cells that had visual, memory and/or saccade-related activity, approximately two thirds had their activities significantly modulated by eye position. The gain functions were labeled 'planar gain fields' as they are roughly linear for horizontal and vertical eye positions. Eye position also had a modulating effect on the memory- and saccade-related activities of LIP neurons. Individual LIP neurons, which often had visual-, memory- and saccade-related responses, all showed approximately similar gain functions for eye position. For instance, if the visual receptive field was most responsive when the animal was looking up and to the left, then the memory and saccade responses were also greatest for up, left eye positions.

As mentioned above, it would be convenient for gaze control to represent targets for saccades in body-centered coordinates. In a theoretical paper, Goodman and Andersen [55] trained a neural network to represent space in body-centered coordinates. Their network predicted that posterior parietal neurons should have planar gain fields for head as well as eye position, and that the head and eye gain fields should be the same for individual neurons. They further showed mathematically how the network could compute spatial positions by adding the retinal, eye and head position vectors using the gain fields. To test the prediction of this model, Brotchie and Andersen (P Brotchie and RA Andersen: *Soc Neurosci Abstr* 1991, 17:1281) trained monkeys with heads free in the horizontal dimension (most eye movement experiments are performed with the head fixed to better stabilize the recording conditions). The animals were trained to make saccades from different combinations of eye and head positions. They found that for both areas LIP and 7a, half the neurons with eye gain fields also had head gain fields, and the eye and head gain fields were similar for individual neurons. These data confirm the predictions of the model and provide additional support for the idea that these areas are representing the positions of targets in spatial coordinates.

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. Following the suggestion by Crick [56], Mazzoni *et al.* [57•,58] trained a neural network to perform the transformation from retinal- to head-centered coordinates using a reinforcement learning rule developed by Barto and Jordan [59], which is more biologically plausible than back-propagation. They found that the reinforcement-trained networks produced the same gain fields as those produced by the back-propagation-trained networks, and as those found in the brain. This result suggests that the algorithm discovered for computing the coordinate transformation is largely independent of the exact learning rule used to generate it. It also suggests that area LIP neurons can learn or adjust spatial representations using retinal, eye and head position signals.

Recently, Goldberg and colleagues [49,60••] argued that visual inputs to area LIP are mapped directly into oculomotor coordinates without an intermediate spatial representation. They suggest that information about saccades is used to update the entire oculomotor map by subtracting the change in eye position from the retinal input. This scheme is consistent with the shift in movement vectors that occurs in double saccade tasks. The computation would require that each cell have the same activities for the same retinal stimulus at different eye positions, otherwise the change in activity due to eye position would be incorrectly interpreted as a change in the retinal input vector. This is not the case for LIP cells because of their gain fields. A subtraction of vectors, but using population-encoded spatial vectors rather than retinal vectors, can account for both the eye position effects and the shifts in the movement vectors in double saccade tasks (P Brotchie and RA Andersen, unpublished data).

### Vergence activity

Modulation of activity of parietal neurons by eye position has been most extensively studied as a function of horizontal and vertical eye position. Under these circumstances, locations in space can be represented on a plane facing the animal, but distance from the animal cannot be varied. To encode distance of an object requires combining the vergence angle of the two eyes, which indicates the distance of the point of fixation, with the disparity, which determines the relative distance of an object from the fixation point. Sakata and colleagues [21] showed that eye position cells in the posterior parietal cortex are tuned to viewing distance as well as horizontal and vertical direction of gaze on a plane. Thus, these cells appear to carry the necessary information to encode the location of the fixation point relative to the animal's head in all three dimensions. Gnadt and Mays (JW Gnadt and LE Mays: *Soc Neurosci Abstr* 1991, 17:1113) have recently shown that many of the visually responsive neurons in area LIP are also disparity tuned, and that the gain of the response, but not the disparity tuning, is modulated as a function of vergence angle. These data indicate that gain fields exist for distance, and could be used to encode the distance of a visual stimulus from the head. Lehky *et al.* [61] have shown that a neural network similar to the Zipser-Andersen model, but trained to determine distance, develops gain fields for vergence and disparity that are similar to the results of Gnadt and Mays. Trotter *et al.* [62••] have recently shown that V1 disparity sensitive cells are also often affected by viewing distance, with the response magnitude but not the disparity tuning being affected. This result is rather surprising, as it indicates that the effects recorded for viewing distance in area LIP also appear to be present as early as area V1.

## Microstimulation

Electrical stimulation of the posterior parietal cortex evokes various types of eye movements. Shibutani *et al.* [63] obtained saccades when stimulating the lateral bank of the intraparietal sulcus. Thresholds were higher (on average 86 μA) than for stimulation of the frontal eye fields and superior colliculus. Kurylo and Skavenski [64••] have mapped area PG (which encompasses roughly the caudal half of the inferior parietal lobule) using microstimulation, and found three types of eye movements corresponding roughly to different cortical regions. Stimulation of caudal regions of area PG produces fixed vector saccades in which the same amplitude and direction movement is evoked independent of the initial eye position before stimulation. More rostral zones produce goal-directed saccades that can change direction depending on initial orbital position, such that they are always directed to a single final position in the orbit. A third type of eye movement pattern, intermediate between the other two types, is found scattered throughout the inferior parietal lobule.

Thier and Andersen (P Thier and RA Andersen: *Soc Neurosci Abstr* 1991, 17:1281) have found that microstimulation can be used to clearly demarcate areas 7a, LIP, and an area in the floor of the intraparietal sulcus. Stimulation at relatively low current levels (50 μA) generates eye movements reliably from LIP. The initial orbital position of the eye before the stimulation-evoked saccade generally did not affect the direction of the eye movement, but usually affected its amplitude. This change in amplitude usually resulted in smaller saccades when the initial position of the eye was more in the direction of the evoked saccade. For instance, if the stimulation-evoked saccades were up and to the right, fixations up and to the right would result in considerably smaller stimulation-evoked saccades than fixations down and to the left. Stimulation of the floor area also produces saccades at low thresholds, but these are goal-directed. They are usually accompanied by movements of the head, face muscles, pinnae, and shoulders, whereas LIP stimulation at low currents only produces eye movements. Stimulation of area 7a produces eye movements at very high currents (typically 200 μA) that are erratic in trajectory and often goal-directed. Blinking eye movements are also common with area 7a stimulation.

Goodman and Andersen [65] examined the effects of 'microstimulating' the Zipser–Andersen model on 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 stimulate microstimulation. The most typical result of stimulating individual hidden units was the change in amplitude pattern seen with stimulation of area LIP. This model suggests that the change in amplitude pattern is indicative of a distributed representation of space in area 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.

## Conclusions

The past year has seen substantial progress in research on the role of area LIP in the processing of saccades. It appears to play interesting, high-level roles in 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. These new studies also show memory-related activities in the area, which may play a role in the formation of motor plans. The results point to a central role for LIP in directing gaze.

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