



# Intention-related activity in the posterior parietal cortex: a review

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## Abstract

Over the last few years it is becoming increasingly apparent that an important role of the posterior parietal cortex is to process sensory information for the purpose of planning actions. We review studies showing that a large component of neural activity in area LIP is related to planning saccades and activity in a nearby parietal reach region (PRR) to reaches. This intention related activity dominates the delay period in delayed movement tasks, and also comprises a substantial component of the transient response. These findings, along with additional anatomical and physiological evidence, lends support to the idea that different cortical areas within the PPC represent plans for different actions. We also found strong modulation of activity when movement plans were changed without changes in the locus of attention. This result suggests that PPC, which has been postulated to play a role in shifting attention, may also play a role in changing movement intentions. Sensory related activity was also present in these tasks and may be related to the stimulus or to attention. These experiments show that there are intention and sensory related activities in the PPC consistent with its proposed role in sensory-motor transformations. These studies also show that care must be taken to measure intention-related signals and not assume that all task dependent modulation in the PPC reflects attention. © 2000 Elsevier Science Ltd. All rights reserved.

*Keywords:* Intention-related activity; Posterior parietal cortex; Process sensory information

## 1. Introduction

There has been considerable discussion over the last few years about the functions of the posterior parietal cortex. Early studies emphasized sensory-attentional (Robinson, Goldberg & Stanton, 1978) or motor-behavioral (Mountcastle, Lynch, Georgopoulos, Sakata & Acuna, 1975) roles for this region. Several years ago we proposed that PPC has components of both, being intermediate in a cortical pathway for sensory-motor transformation (Andersen, 1987). Lesion studies also support the idea that the PPC is part of a specialized pathway for programming actions (Goodale & Milner, 1992). As more became known about the organization of this area, it became clear that different cortical areas of the PPC are specialized for different behaviors (Asanuma, Andersen &

Cowan, 1985; Rizzolatti, Riggio & Sheliga, 1994; Sakata, Taira, Kusunoki, Marata & Tanaka, 1997). A number of studies have suggested that the PPC has activity related to sensory stimuli, attention, and more recently to intentions to move.

Here we review some recent experiments which examine activity related to the intentions to make saccades and reaches. Intention related activity for spatially guided movements has two components, target selection and movement selection. Thus, for example, a cup is selected for a reach, or a face is selected for a saccade. We do not at this point know how elaborate a plan is coded in PPC, but it is possibly nascent, and elaborated by frontal cortical areas to which PPC is connected.

In the experiments reviewed below we find that a large component of activity in the PPC is intention related. This activity is anatomically segregated into cortical areas suggesting an anatomical map for representing intended movements. We also find changes in activity in PPC when the animal changes movement plans without changing the locus of attention.

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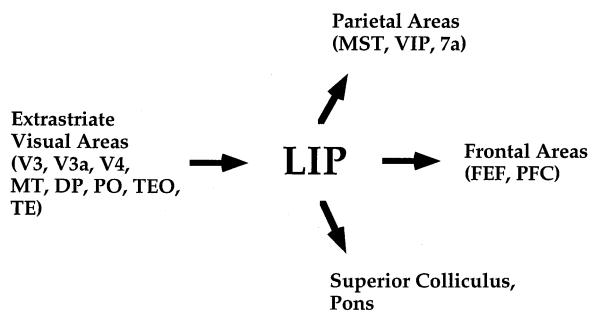


Fig. 1. Schematic of connections of LIP with other brain areas.

## 2. Evidence that LIP and PRR are nodes in saccade and reach networks

Area LIP receives inputs largely from extrastriate cortex including areas V2, V3, V4, MT, PO and IT as well as having connections with other visually related areas of the PPC (Asanuma et al., 1985; Blatt, Andersen & Stoner, 1990). Its outputs are directed toward saccade centers including the superior colliculus, frontal eye fields, and the cerebellum via the lateral pontine nuclei (see Fig. 1). A number of other lines of evidence

suggests that LIP is part of a saccade network. Microstimulation of LIP at low currents produce saccadic eye movements without other body movements (Thier & Andersen, 1996, 1998). Temporary inactivation of LIP with muscimol produces saccade deficits (Li, Mazzoni & Andersen, 1998). Many LIP neurons demonstrate bursts of activity before saccades (Barash, Andersen, Bracewell, Fogassi & Gnadt, 1991).

PRR includes area MIP and dorsal aspects of area PO (area MDP or V6a). These areas receive inputs from visual extrastriate areas and somatosensory areas and project to dorsal premotor cortex (Blatt et al., 1990; Caminiti, Ferraina & Johnson, 1996; see Fig. 2). Thus, like area LIP for saccades, area PRR appears to be a node in a reach network and provides a gateway between sensory and motor areas (Caminiti et al., 1996).

## 3. Intentions to saccade and reach

It has been very difficult to design experiments that dissociate intention related activity from activity related to attention because monkeys (and humans) attend to

# PRR is part of a cortical network for reach movements

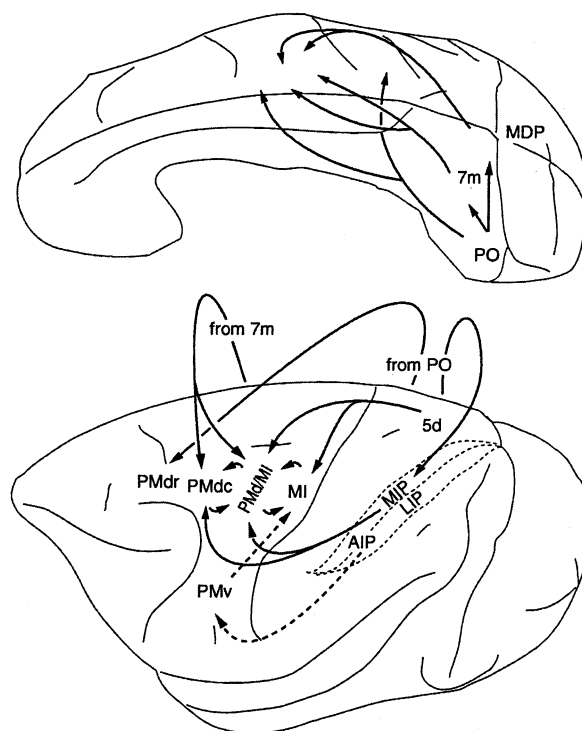


Fig. 2. Network of reach areas, which include areas MIP and MDP, which appear to be included in PRR. From Caminiti et al. (1996).

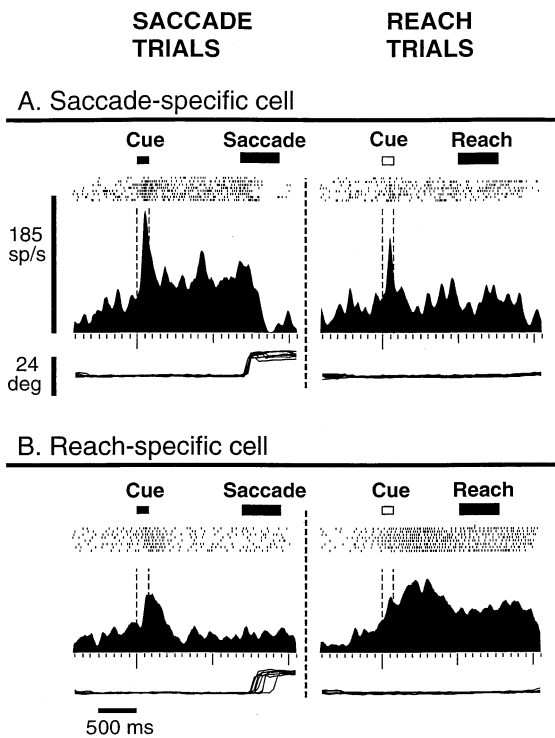


Fig. 3. Responses of two intention-specific neurons in the delayed-saccade (left) and delayed-reach (right) tasks. Each panel shows timing of peripheral flash ('cue': red flashes indicated by filled bars, green flashes by open bars) and response ('saccade' or 'reach'); eight rows of rasters corresponding to every third action potential recorded during each of eight trials; a spike density histogram of neuronal activity, generated by convolution with a triangular kernel<sup>27</sup> aligned on cue presentation, with cue onset and offset indicated by dashed lines; and eight overlaid traces showing vertical eye position. Neuronal responses in the cue interval (50 ms before to 150 ms after cue offset) were nonspecific. However, during the delay interval (150–600 ms), firing depended specifically on motor intent. (a) A cell showing elevated delay period firing before a saccade (left) but not before a reach (right). For illustration purposes, data for this cell were collected using a fixed delay interval. (b) A second cell showing reach rather than saccade specificity during the delay interval. Reprinted from Snyder et al. (1997).

locations where they plan to make movements. In a recent study we designed a task to specifically isolate intention related activity (Snyder, Batista & Andersen, 1997). We reasoned that activity in PPC should be indifferent to the type of movement planned by the animal if it is only related to attention. Thus if the monkey planned a reach or a saccade to the stimulus at the same location, there should be little or no difference in activity if it is primarily dependent on attention. However, if the activity does depend strongly on the movement the monkey plans, then this activity would be related to the animal's intention.

Monkeys were trained to memorize the location of briefly flashed visual stimuli in an otherwise dark room, and to plan either an eye or an arm movement to the cued location, the type of movement being instructed

by the color of the flashed stimulus. Fig. 3 demonstrates our typical result, that the activity in the delay period depended on the type of movement the animal planned. Approximately two thirds of PPC neurons showed a significant response in the memory period for only one of the two movement plans. The remaining one third of the cells responded to both plans. Even the transient response to the cue depended on the movement plan for nearly half the cells.

Fig. 4 shows the average activity for the population of 18 LIP neurons and 23 PRR neurons from one monkey for which a dual-movement task was also performed (described in Section 4). It is apparent that when a saccade is planned, LIP cells with response fields corresponding to the location of the target increase their activity compared to when a target appears at the same location and calls for a reach. The reverse behavior is seen in PRR, with increased activity when a reach is instructed and decreased activity when a saccade is instructed. It has been argued that the decrease we see in LIP when a reach is instructed is due to less attention being required for a reach compared to a saccade (Colby & Goldberg, 1999). However, this reasoning would also predict that the activity in PRR would be similarly lower for reaches than saccades, but the reverse is seen. Thus the 'double dissociation' we see between LIP and PRR argues against an attention explanation and in favor of the activity increasing and decreasing depending on the action the animal is planning.

Colby and Goldberg (1999) have also argued that LIP 'selects targets from the environment for possible but easily cancelable saccades.' We agree that LIP does not simply code attended locations in space. Instead, the fact that LIP activity is reduced when a reach is planned compared to when a saccade is planned (Fig. 4) demonstrates that LIP activity is specifically related

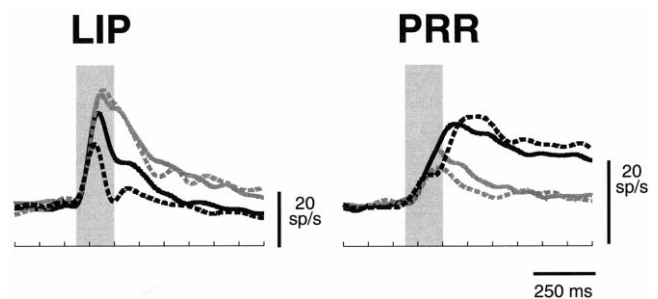


Fig. 4. Population response from one monkey for areas PRR and LIP. Cells had significant activity for either the reach or saccade condition during the memory period. Light traces are for saccades into the response field and dark traces for reaches. Dashed lines plot activity in the dual-movement task, again with light traces for saccades into the response field and dark for reaches into the response field. Histograms show the activity averaged over the population of cells and smoothed with a 181 point digital low pass filter with a  $-3$  dB point at 9 Hz.

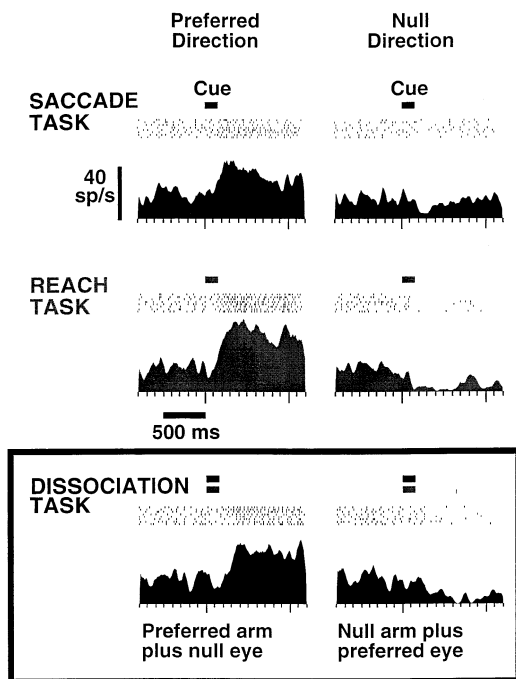


Fig. 5. An intention-specific neuron whose motor specificity was revealed by the dissociation task. Delay activity was greater before movements towards the receptive field ('preferred direction', left column) compared to away ('null direction', right column) in both delayed saccade (top row) and reach (middle row) tasks. Thus in single-movement tasks, the neuron appears to code remembered target location independent of motor intent. However, motor specificity was revealed in the dissociation task (bottom row). Firing was vigorous before a preferred reach combined with a null saccade (bottom left), but nearly absent before a preferred saccade plus null reach (bottom right). Thus when both a reach and a saccade were planned, delay activity reflected the intended reach and not the intended saccade. Panel formats are similar to Fig. 3. Every other action potential is indicated by one raster mark. Reprinted from Snyder et al. (1997).

to the intention to perform a particular type of movement (a saccade) to a particular spatial location.

#### 4. Covert plan related activity

About one half of the cells responding for both movements appeared to actually be selective for a particular type of movement, as shown in an additional control. We examined whether these cells might have activity coding 'covert' plans for movement. An example of this covert planning activity is shown in Fig. 5. This cell had activity during the memory period regardless of whether the animal planned a reach or a saccade into its receptive field. In the control experiment we had the animal perform a two movement task, in which he planned and made eye and reach movements simultaneously in opposite directions. The bottom panels of Fig. 5 illustrate that, when the animal planned an arm movement into the receptive field but an eye movement

outside the receptive field, the cell was active, but when he planned the eye movement into the receptive field and the arm movement outside of the receptive field the cell was not active. Thus it would appear that the cell's activity in the single movement task reflected a 'default' plan to reach that was not executed. Since half of the cells responding to both plans demonstrated a covert preference for either saccades or reaches, overall 84% of the PPC cells tested had activity during the memory period reflecting the intent of the animal.

Fig. 4 shows that, in the population response, when the preferred movement is being planned out of the response field of a cell, then there is no activity in the delay period to a flash in the response field instructing the non-preferred movement. Moreover, even the activity evoked by the cue shows a substantial additional reduction. However, there is also remaining activity which is sensory related and may be a visual sensory response or activity related to attention. These studies show that care must be taken to measure intention-related signals and not assume that all task dependent modulation in the PPC reflects attention. For instance, when recordings are made in LIP while monkeys perform saccade tasks it has been inferred that activity evoked by stimuli which are targets for saccades must be attention related. However, given the above results it is likely that a good deal of the increased activity seen in that study was related to the saccade the animals planned.

It has been proposed that the reduced activity in this two movement task when saccades are outside the response field of LIP neurons is due to divided attention (Colby & Goldberg, 1999). If this argument were to be tenable it would require that activity would be reduced in all two movement tasks in LIP and PRR, whereas inspection of Fig. 4 shows that activity is not reduced when the preferred movement is planned into the field. Moreover, the double dissociation in which activity goes up in one area and down the other depending on the plan argues against a simple reduction due to split attention which would lead to a simultaneous reduction in activity in both areas.

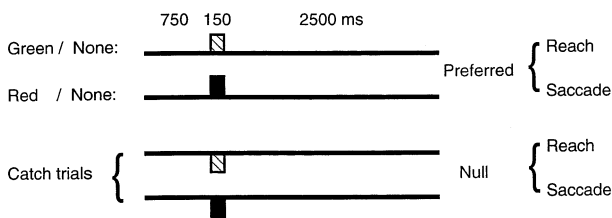
The intention related activity was anatomically segregated depending on whether it was specific for saccades or reach. Perhaps not surprisingly, eye movement related activity was found predominantly in LIP. This finding is very consistent with previous research which has indicated that LIP can be considered the 'posterior eye field' for the processing of saccadic eye movements, discussed above. The reach selective responses were found medial and posterior to LIP, in a band of cortex that likely includes areas MIP to dorsal PO. We referred to this functionally defined region of the PPC as the parietal reach area (PRR) since it appears to include more than one anatomical subdivision of PPC.

As mentioned above, the fact that activity goes up in one area and down in another depending on the plan argues against a generalized attentional effect and for activity related to movement selection. As we will see in the next section, there is activity in PPC linked to changes in plans independent of attention.

### 5. Changing movement plans without changing the locus of attention

Activity in area 7A of PPC is greater to a flashed stimulus when attention is shifted to the stimulus than if attention is already directed at the location of the flash. This result was interpreted as area 7a playing a role in shifting attention. We tested whether activity in LIP and PRR might similarly reflect changes in movement plans, tested with the paradigm shown in Fig. 6 (Snyder, Batista & Andersen, 1998). The experiment began in a similar manner to the one mentioned above with a flash of light instructing a particular type of movement to the location of the flash (red for saccade, green for reach). However, in the later period of some of the trials this plan was either changed by a second flash of a different color, or reaffirmed by a flash of the same color. The animals did not know what the subsequent flash would instruct, or whether it would appear at all, and these trials were all randomly interleaved.

#### Single flash trials:



#### Double flash trials:

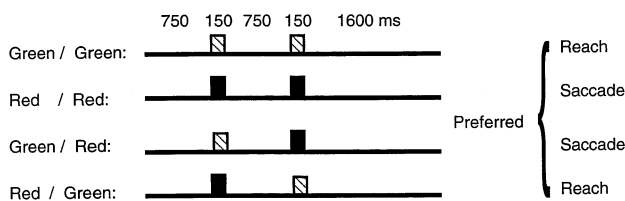


Fig. 6. Time course of eight single and double flash trials. The experiment was designed to force the animal to attend to the spatial location and color of both flashes. A 150 ms flash appeared 750 ms after fixation began. Red and green flashes instructed saccades and reaches, respectively. On half of the trials a second flash occurred 750 ms later at the same as the first, sometimes instructing a change in the motor plan but never shifting spatial attention. Fixation light offset, 2.5 s after the first flash, signaled the animal to perform the most recently instructed movement. For one animal, double flash trials also occurred for the null direction (not shown). Reprinted from Snyder et al. (1998).

Since these second flashes always appeared at the same location as the first flashes, a reasonable assumption would be that the monkeys focus their attention on the location of the impending second flash. However, if the animals are not attending to this location the attentional condition across the trials will be the same because the monkeys do not know what the second targets will instruct, or if they will appear at all.

The response to the flashes was strongly related to the animals intentions. The plan dependency across the population of PRR cells can be seen in Fig. 7A. The response to the first flash is always larger when it is green and is therefore instructing a reach. This reach-planning activity remains high during the first delay period. The middle panel shows the responses to a second, green flash instructing a reach, segregated into two plots depending on whether this second flash reaffirmed or changed the plan. In this instance, the response to the identical green flash, under identical attentional conditions, was much stronger if the animals were required to change their plans. Thus it can be concluded that a large component of the flash-triggered activity actually reflects a change in plans. The plots on the right in Fig. 7A show that this change-in-plan specific activity is not a result of stimulus novelty. These plots show the responses to the second flash in PRR when it is red and instructing an eye movement. These responses were small for the non-preferred plan, regardless of whether it was a change or reaffirmation of the previous plan. In other words, the enhanced response to the flashes was only present when there was a change of plan to the preferred plan. Fig. 7B shows that the same result was found for LIP neurons, but with saccades being the preferred plan.

### 6. Coding the next planned movement

Using a memory double saccade paradigm we found that a majority of LIP neurons code the next planned eye movement (Mazzoni, Bracewell, Barash & Andersen, 1996a,b). As shown in Fig. 8D for a representative neuron, when the second target of the planned sequence of movements fell within the receptive field of the LIP cell, but the animal was planning the first eye movement outside of the receptive field, then this cell showed only a brief response to the stimulus and was not active in the memory period. However, if the same target fell within the receptive field of the cell and it was the target for the first eye movement, then the cell was active during the memory period (Fig. 8C). This result is typical of a majority (77%) of the LIP neurons. There was also a minority of cells with activity for the second target during the memory phase, and these cells appear to hold the memory of the location of the second target. The remaining 7% could not be classified into one or the other.

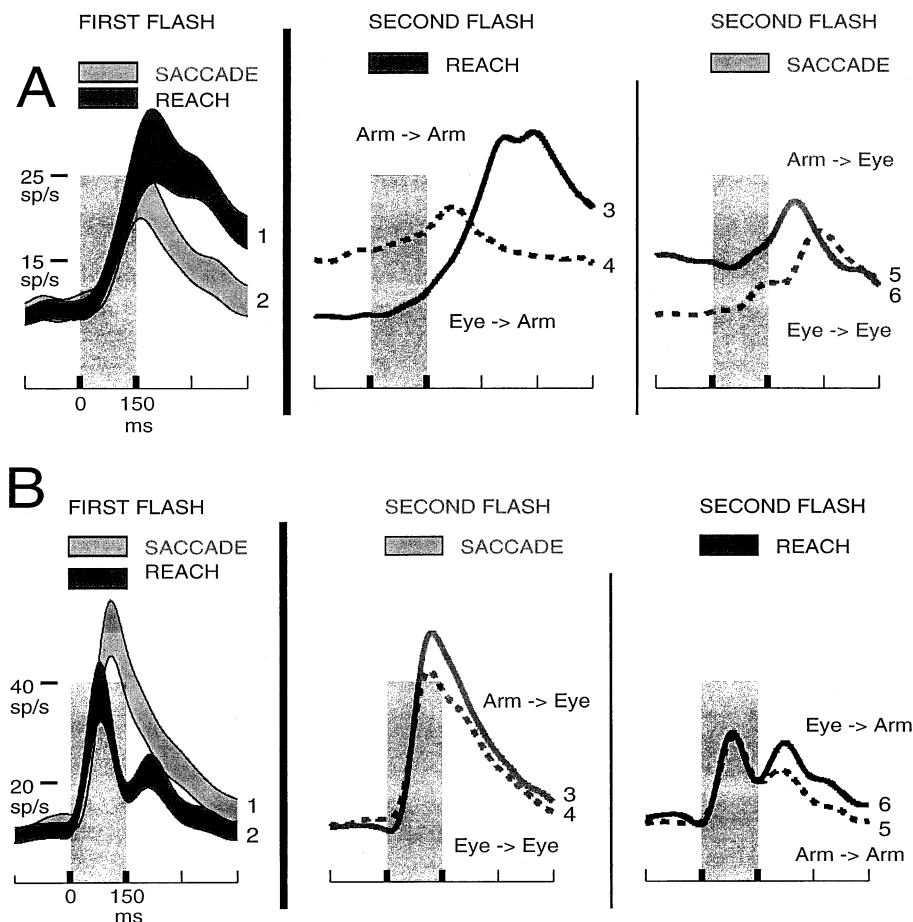


Fig. 7. Population data from PRR (A: average of 17 cells) and LIP (B: average of 20 cells). Responses to the first (left panel) and second (right and middle panels) flashes, instructing either a saccade (light) or a reach (dark) are shown. Second flashes could instruct a preferred (middle) or nonpreferred (right) movement, and this instruction could countermand (traces 3 and 5) or affirm (traces 4 and 6) the original instruction. Response to a preferred countermanding flash was larger than to a preferred affirming flash (three versus four) and comparable with the response to a preferred first flash (1). For nonpreferred movements, countermanding and affirming flashes elicited similar comparatively small responses (five versus six). Each ribbon is  $\pm$  SE was calculated across cells (left). Shading indicates the time of one 150 ms flash. Data were smoothed before plotting (121 point digital low-pass filter, transition band 20–32 Hz), but all reported values were obtained before smoothing. Reprinted from Snyder et al. (1998).

We have recently performed a similar double movement experiment in PRR, but requiring the monkey to plan two reaches instead of two saccades (Batista, Snyder, Buneo & Andersen, 1998). In this task we first cued the monkey to a location for a reach within the response field of the neuron. However, during the delay period, if we flashed a second target outside the response field of the cell, the animal was now required to make the reach first to that target. At the end of the delay the animal reached to this second target and another delay period began in which he now planned a movement to the first flashed target location. At the end of this second delay the animal made a second limb movement to the remembered location of the first target. We found that, similar to LIP, the PRR cells ceased firing in relation to the remembered location of the first reach target if the monkey was plan-

ning an arm movement to the location of the second target, outside the receptive field of the cell. Moreover, we found when we reversed the sequence of targets so the second target and first reach were in the response field, the activity was still always only present when the next planned movement was into the response field. Thus PRR shares another similarity with LIP; both areas code the next planned movement in double movement tasks. This result adds further support for the idea that a large component of both PRR and LIP activity reflects the target the monkey has selected for the next planned movement. Combined with the results above showing that large components of LIP and PRR activity reflect the movement the animal has selected, we can conclude that there is activity reflecting the intention of the animal in spatially guided movement tasks.

## 7. Discussion

It is clear from the evidence presented in this review that the posterior parietal cortex plays an important role in the planning of actions, with one area specialized for eye movements (LIP) and one for reach movements (PRR). The activity in these regions cannot be explained as simply a result of sensory memory or of non-specific, sensory attention, since which area is active depends the type of movement being planned, independent of the sensory stimulus.

However, an important question is what is the extent and nature of the intended movement activity in the PPC? It is clear that the endpoint of the movement is fully specified, and the type of movement is largely specified. However, it is currently not known what aspects, if any, of the dynamics of the movement are specified. Also it is not yet been determined if the path of the movement is encoded in PRR. It seems unlikely that fully formed movement plans are specified in PRR

or LIP given what we know about the physiology and anatomy of the sensory-motor pathway. Instead, the intended movement activity more likely represents early plans at the interface between sensory and movement systems. It will be an interesting area of future research to determine what additional components of the movement plans are and are not coded in PPC.

Two possible hypotheses for the architecture of sensory-motor processing are a hierarchical scheme and a distributed scheme. A hierarchical scheme would posit that the activity in the parietal cortex represents plans for movements that are an abstract and early stage in movement planning, and that the plans will be more fully elaborated and executed — or inhibited — at later stages in motor cortex. Consistent with this idea is the finding that PRR represents reach plans in eye coordinates, rather than the motor (limb) coordinates that would be expected at later stages in reach processing (Batista, Buneo, Snyder & Andersen, 1999). Inactivation to LIP produces deficits in eye movements that

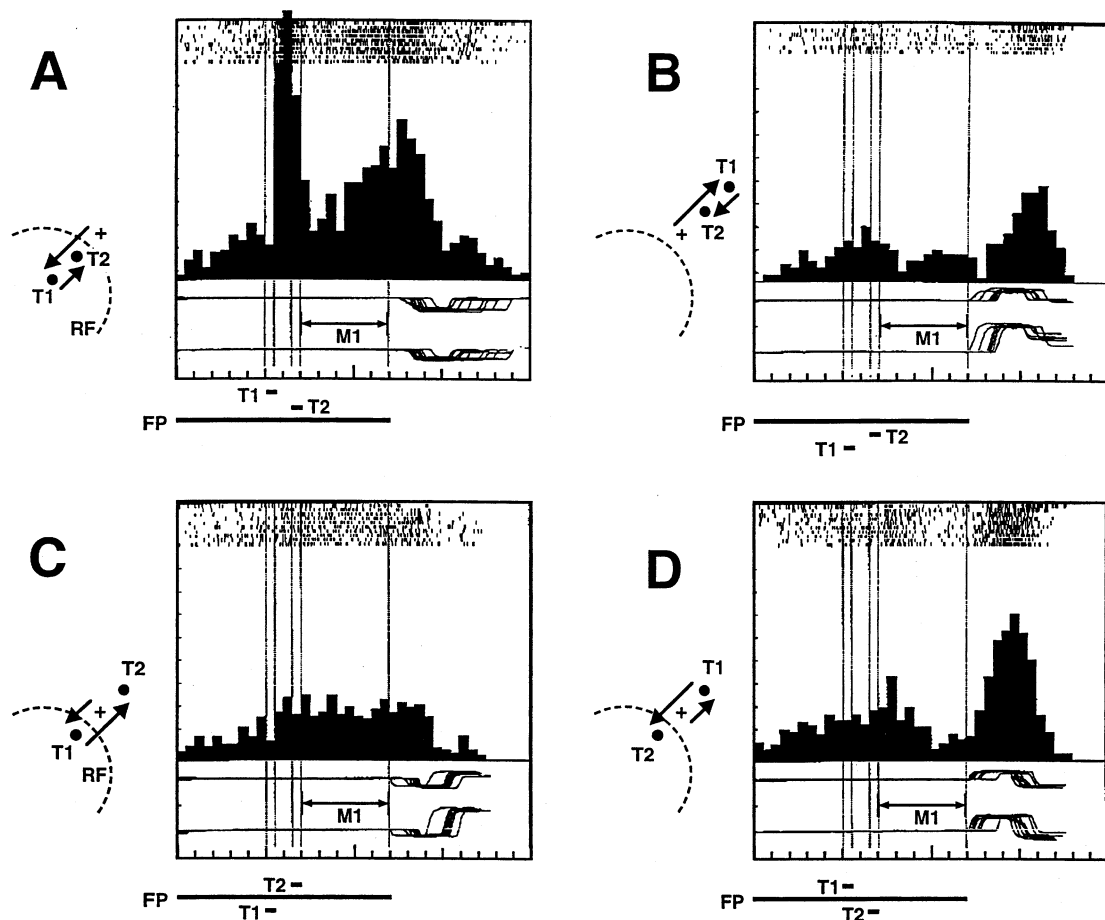


Fig. 8. Activity of an LIP neuron in four different sequences of a double saccade paradigm. Each panel has a plot that includes, from top to bottom, the spike rasters for each trial, the time histogram (binwidth, 50 ms) of the firing rate (20 Hz/division in A–C, 25 Hz/division in D), and the horizontal and vertical eye positions (25°/division; abscissa: 100 ms/division). Vertical dotted lines and the thick horizontal lines below each panel again show the onset and offset of the visual stimuli. Diagrams to the left of each panel show the spatial arrangement of the first and second target (T1 and T2, respectively), the first and second saccades (arrows), and the neuron's receptive field (RF). Reprinted from Mazzone et al. (1996).

are high level and cognitive, such as the ability to perform memory saccades or to decide between two targets for an eye movement (Li et al., 1998; Li, Grieve & Andersen, 2000). Inactivation to FEF produces these problems, as well as problems in executing eye movements (Schiller & Chou, 1998; Dias & Segraves, 1999). Kalaska and Crammond (1995) have shown in no-go tasks that many area 5 neurons continue to fire for the cancelled movement plan if no other plan has been put in place, whereas premotor neurons stop firing. Wurtz, Basso, Pare and Sommer (2000) have similarly shown that 1/3 of LIP neurons cancel their activity in the no-go condition, whereas 2/3 of superior colliculus neurons cancel their activity. On the other hand we know that if an alternative movement plan is put in place, then the activity specifying the old plan is cancelled and activity specifying the new plan appears (Mazzoni et al., 1996a,b; Snyder et al., 1997, 1998).

The alternative hypothesis is that the visual-motor pathway is distributed. By this proposal, neither parietal or frontal lobes are strictly sensory or motor, but rather work together in the sensory-motor transformation process. As a result, sensory as well as motor related activities will be present in both areas, which in fact has been shown in a number of studies (Bruce & Goldberg, 1985; Andersen, 1987; Goldman-Rakic, 1988; Carpenter, Georgopoulos & Pellizzer, 1999; Schall & Thompson, 1999). Additionally activity related to decision making for saccadic eye movements has been seen in both LIP and FEF (Shadlen & Newsome, 1997; Platt & Glimcher, 1999; Schall & Thompson 1999; Li et al., 2000). The anti-saccade, that requires the reflexive movement to a suddenly appearing target be cancelled and a new movement calculated and executed in an opposite direction, is thought to be the product of frontal lobe computations since frontal lesions release inhibition for reflexive movements and produce deficits in anti-saccade tasks (Schlag-Rey, Amador, Sanchez & Schlag, 1997). However, even in LIP, a small number of cells reflect the newly computed saccade and, in PRR, the majority of cells appear to reflect the new movement in an anti-hand tracking task. The greater number of cells showing this behavior in PRR may reflect the fact that saccades are the over-riding response to suddenly appearing targets, whereas hand movements tend to not be so tightly linked to such stimulus onsets.

To resolve between these two possibilities will require additional research. However the data presented above suggest that aspects of both proposals are true. One possible hybrid model is that both areas work together cooperatively, but also have specific functions that set them apart. One speculation along these lines is that the parietal cortex operates to produce on-line, rapid decisions and plans for movements. This area also is important for attention, target selection, coordinate

transformations, and other integrative functions that are closely linked to perceptual processes. The frontal lobes may also contribute to these same functions, and may elaborate them by inhibiting reflexive movements, storing locations of targets in a movement sequence beyond the most eminent movement (Shima & Tanji, 1998; Carpenter et al., 1999), and perhaps even emitting the final commands to make a movements. An efference copy of the movement commands may account for some of the most motor-like responses found in the parietal lobe. This signal may be used for, among other things, spatial constancy computations for both motor (Andersen, 1987; Gnadt & Andersen, 1988; Batista et al., 1999) and perceptual (Duhamel, Colby & Goldberg, 1992) purposes.

## 8. Conclusions

A large component of activity in the posterior parietal cortex reflects movement selection. LIP activity is greater when monkeys plan saccades and PRR activity is greater when monkeys plan reaches. This intention selectivity is strongest during the delay period in delayed movement tasks, but is also present in the transient response to flashed cues. There is a component of activity in LIP and PRR which is specific for changes in plans independent of the spatial locus of attention. This result is similar to recent findings that there is activity related to shifts in the spatial locus of attention in area 7a, but in this case the activity is related to changes in movement plans — that is, intention. Finally most activity in PRR and LIP is related to the next planned movement in sequential movement tasks, and not to the memory of spatial locations. These results suggest that activity in the PPC reflects both target and movement selection. These results are consistent with the PPC playing a role in visual motor transformations for spatially guided behaviors.

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