

# Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) using a common coordinate frame

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*Abstract.* The posterior parietal cortex (PPC) has long been considered a sensory area specialized for spatial awareness and the directing of attention. However, a new, far reaching concept is now emerging that this area is involved in integrating sensory information for the purpose of planning action. Moreover, experiments by our group and others over the last two decades indicate that PPC is in fact anatomically organized with respect to action. PPC also is an 'association' cortex which must combine different sensory modalities which are coded in different coordinate frames. We have found, at least for two different cortical areas within PPC, that different sensory signals are brought into a common coordinate frame. This coordinate frame codes locations with respect to the eye, but also gain modulates the activity by eye and body position signals. An interesting feature of this coordinate representation at the population level is that it codes concurrently target locations in multiple coordinate frames (eye, head, body and world). Depending on how this population of neurons is sampled, different coordinate transformations can be accomplished by the same population of neurons.

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Historically, the posterior parietal cortex (PPC) has been considered a high-order sensory area important for the perception of space. The syndrome of neglect, in which patients with parietal lobe lesions have difficulty attending to stimuli or shifting their attention, first suggested that this area also plays an important role in attention (Critchley 1953, Andersen 1987 for review). Numerous physiological experiments in non-human primates demonstrated attention-related enhancements of activity in the PPC (see Colby et al 1995 for review). More recently, however, there have been a number of studies in humans and monkeys which suggest that the PPC is important in action and, more specifically, in transforming sensory signals

into plans for action (Mountcastle et al 1975, Gnadt & Andersen 1988, Goodale & Milner 1992, Andersen 1995, Mazzoni et al 1996b, Snyder et al 1997).

In fact, over the last few years there has been an emerging view that parts of the PPC contain an anatomical specialization — or map — of intentions. As will be covered in this review, the lateral intraparietal area (LIP) appears to be specialized for making saccades. A medial and posterior area, which may include the medial intraparietal area (MIP) and the occipital parietal area (PO) appears to be specialized for reaching movements. We have referred to this area as the parietal reach region (PRR). A third area anterior to LIP, the anterior intraparietal area (AIP), appears to be specialized for grasping. We will also review studies of the reference frame in which space is represented in LIP and PRR. How are different modalities, that are originally represented in different coordinate frames, integrated in PPC? Also, how is communication achieved between these different areas, which are highly interconnected anatomically (Andersen et al 1990, Blatt et al 1990), and whose outputs are presumably closely orchestrated for coordinated movements? As we will see, there appears to be a common coordinate frame used by these two areas for several modalities. This coordinate frame has an extremely interesting feature of being distributed, and can be read out by other areas in several different coordinate frames, e.g. eye, head, body or even world-centred. Finally, we will see that the representations of space in both LIP and PRR are updated across eye movements for the remembered locations of targets for movement.

### **Coding of intention to saccade and reach**

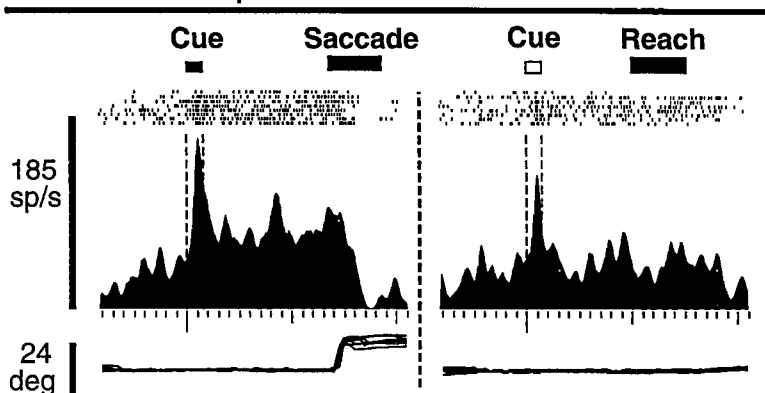
Although there has been considerable suggestion in the literature that the PPC may play a role in intention, it has been very difficult to approach this problem experimentally. This is because it is quite difficult to differentiate activities related to attention and intention. This difficulty is due to the obvious fact that animals attend to locations to which they plan movements. Recently we designed a task specifically to isolate activities related to these two cognitive functions. We reasoned that if PPC activity was simply related to attention, this activity should be indifferent to the type of movement an animal planned to make to a particular stimulus. On the other hand, if activity varied according to the animals' plans, given the same location and stimulus, then it is likely this activity reflects what the animal plans (intends) to do.

We trained monkeys to memorize the location of peripherally flashed lights and plan either an eye or an arm movement to that location (Snyder et al 1997). As demonstrated in Fig. 1, we found many cells that were active in the memory period only when an animal planned an eye movement and others that were only active when the animal planned an arm movement. In fact, about two-thirds of PPC neurons showed a significant response in the memory period for only one of

## SACCADE TRIALS

## REACH TRIALS

### A. Saccade-specific cell



### B. Reach-specific cell

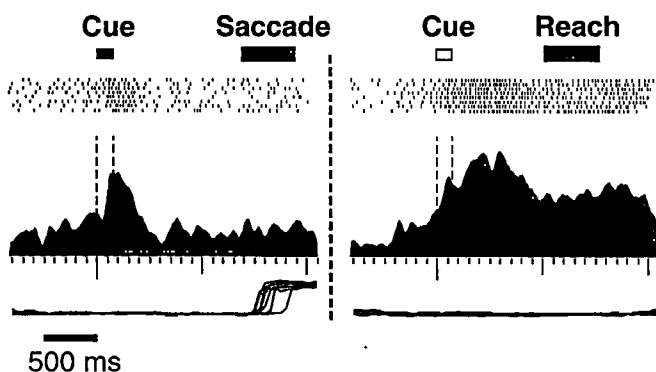


FIG. 1. Responses of two intention-specific neurons in the delayed-saccade (*left*) and delayed-reach (*right*) tasks. Each panel shows timing of peripheral flash ('Cue': red flashes indicated by filled bars, green flashes by open bars) and response ('Saccade' or 'Reach'); eight rows of rasters corresponding 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 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 non-specific. 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).

the two plans. The remaining one-third of the cells responded to both plans. This activity in many cases is not merely attention/sensory memory activity, as the control experiment in Fig. 2 shows. This cell had activity for flashes in its receptive field regardless of whether the animal planned a reach or a saccade there. However, we also had the animal perform a two movement task in which he planned and made eye and reach movements simultaneously in opposite directions. As can be seen in the bottom panels of Fig. 2, when the animal planned an arm movement into the receptive field of this same cell, but an eye movement outside the receptive field, the cell was still active; however, when the eye movement was to be into the receptive field and the arm movement outside, the cell was not active. We interpret this result as the animal making a 'default' plan to make a reaching movement that was not executed. Half of the remaining 'sensory' cells demonstrated a covert preference for either saccades or reaches indicating that over 80% of the PPC cells tested had activity during the memory period that specified the intent of the animal.

An important feature of this intended movement activity is that it is anatomically localized. The eye movement planning activities were found predominantly for cells in LIP. This observation is consistent with previous research in LIP which has shown presaccadic bursts of activity (Barash et al 1991), saccade deficits after lesioning (Lynch & McLaren 1989, Li et al 1998), strong axonal projections to other saccade centres (Lynch et al 1985, Asanuma et al 1985, Blatt et al 1990, Andersen et al 1990) and evoked saccades due to electrical stimulation (Thier & Andersen 1996). The reach-selective responses were also found to be anatomically segregated within a continuous swath of cortex which appears to include areas MIP to PO. We referred to this region as the parietal reach region (PRR).

It could be argued that the selectivity in LIP is due to the fact that the animals attend to where they plan to saccade but not to where they plan to reach, and the differential activity reflects this difference in attention. If this were the case, however, then PRR neurons also should only be active when eye movements are planned in their receptive fields; instead we see the reverse phenomenon, with activity being present only when reaches are planned into the receptive fields. Moreover, in the experiments reviewed next, attention is maintained at the same location and the animal is asked to change movement plans. In this case, where attention is identical across trials, the activity of PPC neurons changes dramatically depending on the animals' plans.

### **Activity related to changing movement plans**

A prediction of the above results is that activity should shift between areas LIP and PRR when monkeys change their movement plans. We decided to test this prediction directly with the paradigm shown in Fig. 3A (Snyder et al 1998). The experiment was similar to the one mentioned above, but once a target instructing a

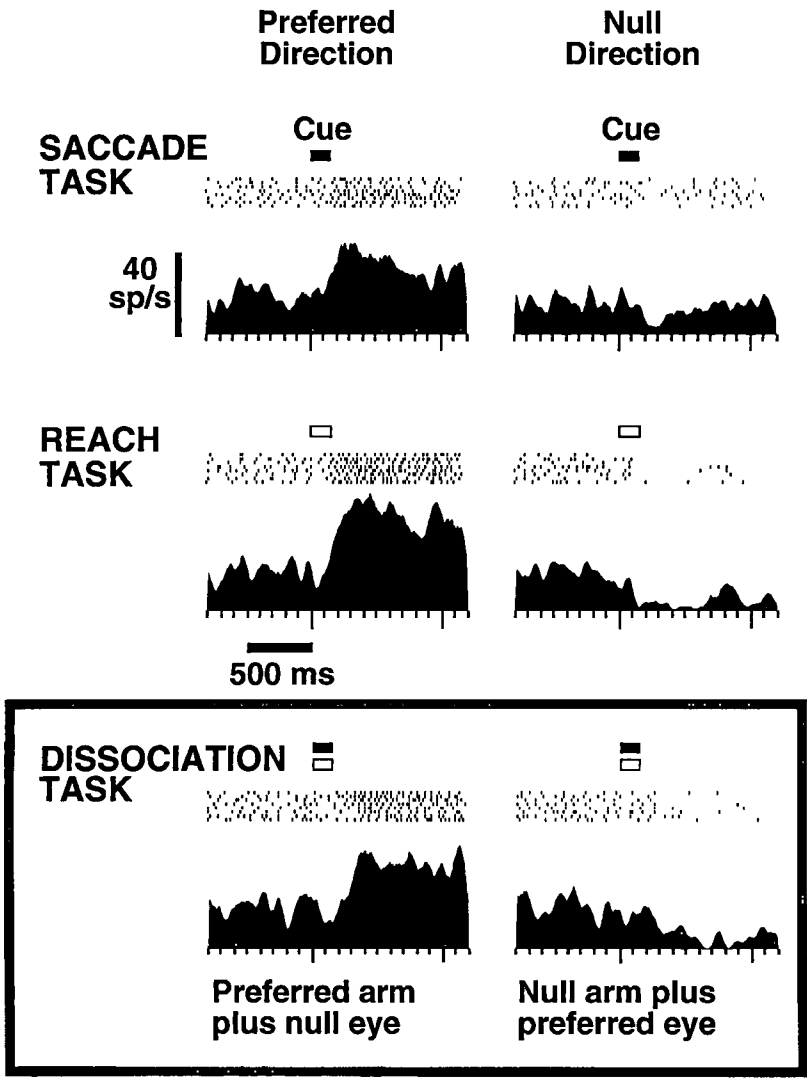
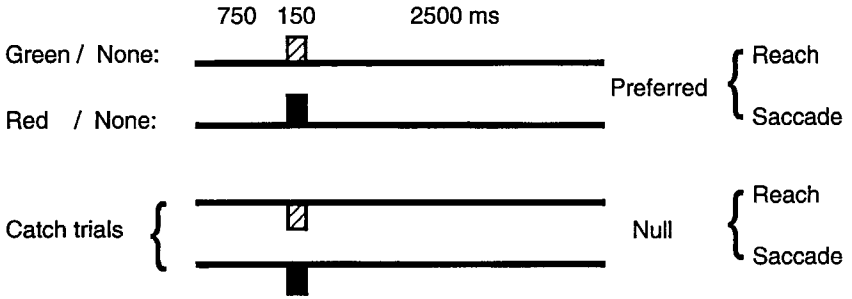


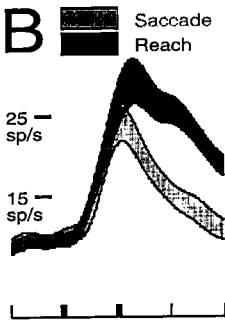
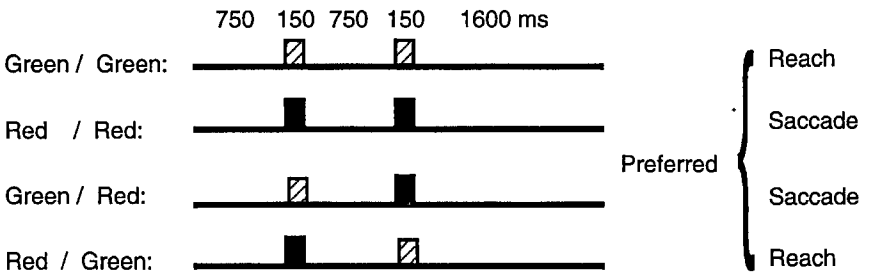
FIG. 2. An intention-specific neuron whose motor specificity was revealed by the dissociation task. Delay activity was greater before movements towards the receptive field ('Preferred direction', left column) compared to away ('Null direction', right column) in both delayed saccade (top row) and reach (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. 1. Every other action potential is indicated by one raster mark. Reprinted from Snyder et al (1997).

# A

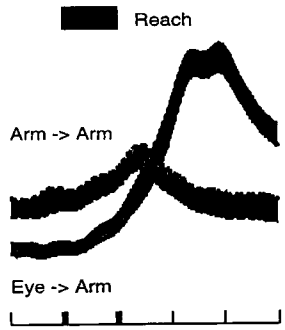
## Single flash trials:



## Double flash trials:

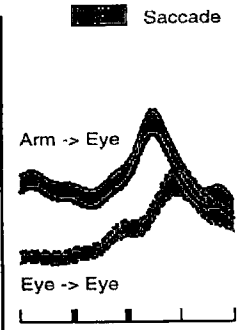


Response to first instruction



Response to second instruction that:

— Countermands first instruction  
 - - - Affirms first instruction



particular movement had been flashed in the receptive field of a cell, on some trials this plan would be changed by a second flash of a different colour, or reaffirmed by a flash of the same colour. Since the animal did not know what the subsequent flash would instruct, and since these flashes always appeared at the same location as the preceding flash, the monkeys' spatial attention was the same in these two conditions. However, the response to the flashes, and the subsequent activity in the memory period after the flash was strongly related to the animals' plans. An example of this plan dependency can be seen in Fig. 3B for the population response of reach neurons from PRR. The response to the first flash is always larger when it is green and thereby instructing a reach. This activity remains high during the first memory period when the monkey is still planning a reach. The middle part of the figure shows the responses to a second, green flash instructing a reach, segregated into two plots depending on whether this flash reaffirmed or changed the plan. It can be seen that the response to the identical flash, under identical attentional conditions, was much stronger if the animal changed his plan. This result indicates that a large component of activity to the flash reflects a shift in plans, suggesting that PPC may play a role in shifting plans. That this change-in-plan specific activity is not a result of the novelty of the stimulus is demonstrated in the plots on the right, which show the responses to the second flash when it is red and instructing an eye movement. The responses were small for the non-preferred plan, regardless of whether it was a change or reaffirmation of the previous plan. Thus the enhanced response to the flashes was only present when there was a change of plan to the preferred plan of the area. Essentially the same result was found for LIP neurons, but with saccades being the preferred plan.

### Coding the next planned movement in LIP and PRR

Using a memory double-saccade paradigm we recently found that a majority of LIP neurons code the next planned eye movement (Mazzoni et al 1996b). For instance,

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FIG. 3. (A) Time course of eight single and double flash trials. The experiment was designed to force the animal to attend to the spatial location and colour of both flashes. Second flashes never required a shift in spatial attention. See text for details. (B) Population data from PRR (average of 17 cells). Responses to initial flashes instructing a saccade (light) or reach (dark) are shown on the left. Centre and right panels, respectively, show responses when a second flash, at the same location as the first, instructed either the preferred or non-preferred movement. Preferred responses were larger than non-preferred responses. Responses to the second flash were further subdivided by whether they countermanded (solid lines) or affirmed (dashed lines) the instruction of the first flash. Countermanding flashes elicited a greater response when a preferred movement was instructed. When non-preferred movement was instructed, responses were much more similar. Standard error was calculated across cells and mean  $\pm$  1 SEM is shown. From Snyder et al (1998).

if the second target in a double eye movement task fell within the receptive field of an LIP cell, but the animal was planning the first eye movement outside of the receptive field, then this cell would not be 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. This result is consistent with a majority of the LIP neurons coding movement intention. There was also a minority of cells with activity for the second target during the memory phase, and we interpreted these cells as holding the memory of the location of the second target.

We have recently performed a similar experiment in PRR (Batista et al 1998). In this case we cue the monkey to a location for a reach. However, during the delay period we flash a second target which the animal uses to change his limb position. At the end of the delay the animal must make a second arm movement to the location of the first target. We find that, similar to LIP, the PRR cells typically will cease firing to the remembered location of the first reach target when the monkey is planning an arm movement to a location outside the receptive field of the cell. Thus PRR shares another similarity with LIP, i.e. PRR neurons code the next planned movement in double movement tasks. This result is consistent with the accumulating data that a large component of both PRR and LIP activity reflects the animals' plans or intentions for movement.

### Coordinates for representing space within area LIP

Cells in LIP have receptive fields much like cells in other visual areas. These receptive fields are in the coordinates of the retina or eye, and the location in space that will activate these cells will move with the eyes. However, we also found that the activity of these cells is modulated by eye position and head position. Neural network simulations show that these 'gain field' effects can lead to a distributed coding in other coordinates besides eye-centred. Thus, for instance, neurons in another part of the brain which receive projections from LIP could construct receptive fields in head-centred coordinates by exploiting the eye position gain fields. Likewise the combination of eye and head position gains can be used to construct body-centred coordinates (see Figs 4 and 5).

Area LIP is a classic extrastriate visual area. In the hierarchy of visual areas based on feedforward and feedback patterns of cortico-cortical connections (Maunsell & van Essen 1983), it is at approximately the same level as area V4 (Andersen et al 1990, Blatt et al 1990). In other words, it is an area deeply embedded in visual extrastriate cortex, and it occupies a processing position relatively early in the visual pathway (i.e. close to area V1). This fact is reflected in the response properties of LIP neurons, which have brisk responses to visual stimuli, even



The representation of space is a distributed code

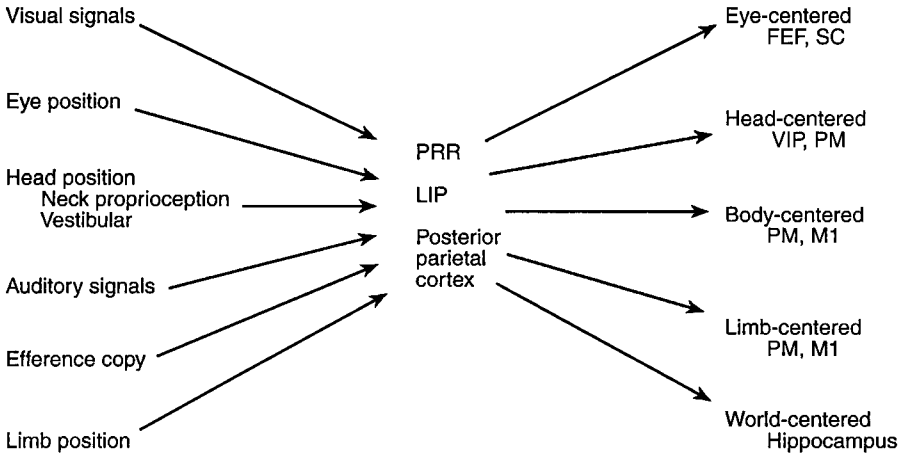


FIG. 4. Schematic of the inputs and outputs of areas PRR and LIP. These areas receive a variety of sensory signals and body position signals. These signals are integrated in a very specific fashion and the population code can be read out in a variety of coordinate frames by other areas of the brain. SC, superior colliculus; FEF, frontal eye field; VIP, ventral intraparietal area; PM, premotor cortex; M1, primary motor cortex.

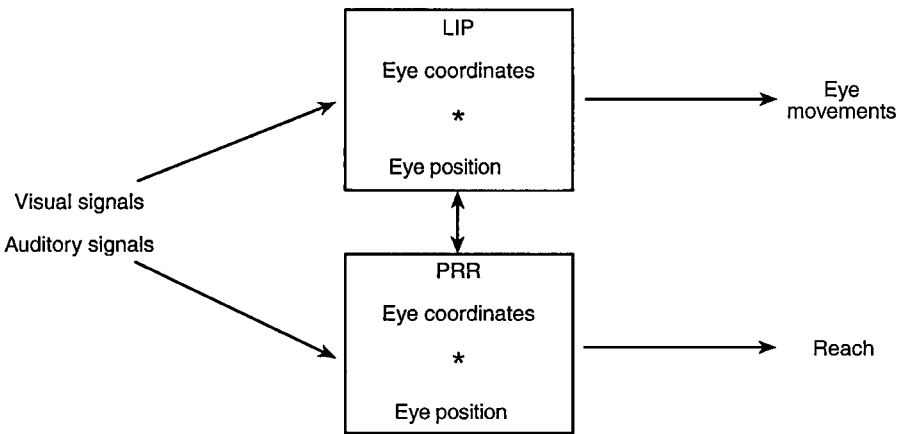


FIG. 5. Schematic of the common coordinate representation within LIP and PRR. Visual and auditory signals are both inputted to these areas. These signals are to a large degree represented in eye coordinates, but the receptive fields are gain modulated by eye position signals. As indicated in Fig. 4, these gain modulations enable LIP and PRR activity to be read out in multiple coordinate frames by other cortical areas and thus act as a mechanism for coordinate transformations. The outputs of LIP are primarily for the purpose of saccades, and those of PRR for limb movements.

when the animal is ignoring the stimulus (Linden et al 1997) or is anaesthetized (Blatt et al 1990).

LIP cells do not respond to auditory stimuli if they are not meaningful to the animal. However, since LIP plays an important role in saccades, and since monkeys can obviously make eye movements to auditory stimuli, we hypothesized that LIP cells would be active when the monkey used auditory stimuli for the purpose of making saccades. We found this to be true (Mazzoni et al 1996a, Grunewald et al 1997). Moreover, we determined the coordinate frames of these auditory-triggered responses in a memory guided eye movement task. In early parts of the auditory pathway the auditory receptive fields are in head-centred coordinates, constructed from interaural time, intensity and spectral cues. In LIP, however, only 33% of the cells were in head-centred coordinates while a surprising 44% were in eye-centred coordinates (Stricanne et al 1996). Another 23% were intermediate between these two coordinate frames. One possibility is that LIP is responsible for converting head-centred auditory signals into eye-centred coordinates. The neurons with auditory responses typically also have eye position gain fields. These gain effects could provide the mechanism for this coordinate transformation.

The finding that many LIP neurons code auditory signals in eye-centred coordinates when the animals are considering these auditory stimuli as possible saccade targets, has interesting implications. This result suggests that vision provides the basic map for spatial location in LIP. It also suggests that the mapping of auditory space onto visual space occurs only when these auditory stimuli are significant to the animal (Fig. 5). This is a very different view of multimodal integration from that which is commonly held. As we will see, these ideas can also be extended to PRR, and may be a fairly general way of representing space and integrating different modalities within a particular spatial representation. This concept may explain why visual stimuli tend to dictate the perceived spatial location of auditory stimuli. For instance, if we see someone's lips moving, but the sound is coming from a distant location in space, we none the less perceive the sound as coming from the speaker's lips.

### Coordinates for representing space in PRR

Recently we have examined the coordinates of the reach planning activity in PRR. One possibility is that the reach activity would be in the coordinates of the limb, as has been suggested for reach-related activity in the motor cortex. Alternatively, this activity could also be in the coordinates of the eye similar to LIP. We addressed this problem by having animals make the same reach, but with the eyes gazing in different directions, or alternatively to reach to the same location with respect to the eyes, but with the limbs starting from different initial positions. If the cells were coding in eye coordinates we would expect different activities for the

former condition, since identical reaches would be made to different retinal locations. On the other hand, if the cells were coding in limb coordinates we would expect the activity to vary in the latter condition, since limb movements in different directions are being made to the same location on the retina. We found that most PRR cells code reaches in eye coordinates, although some do code in limb coordinates or intermediate between the two frames (Batista et al 1998). The eye-centred responses also often showed gain modulation by eye position. Thus these cells represent space in a similar distributed manner as LIP neurons, with eye-centred receptive fields modulated by gain fields for eye position.

On the basis of the results of a common coordinate frame for both LIP and PRR, we were led to make a rather non-intuitive prediction. This prediction is that reaches to the remembered locations of sounds in the dark should be coded in eye-centred coordinates. Of course there is, in principle, no need for such a result. Head-centred auditory signals could be converted directly to limb coordinates for these reaches; there is no need to have an intermediate representation of these reach signals in eye coordinates. However, if there is a common distributed coordinate frame in PRR and LIP, then the reach activity should code the target location in eye-centred coordinates and be modulated by eye and limb position signals. Moreover, the results for auditory saccades in LIP, outlined above, would also predict that the auditory signals would be transformed into eye-centred receptive fields. This prediction was substantiated in recent experiments from our lab (Y. E. Cohen & R. A. Andersen, unpublished results 1998). We find that the reach activity is often in eye coordinates for auditory targets, and that these eye-centred receptive fields are strongly gain modulated by eye and limb position. Thus, auditory and visual signals are brought into the same distributed representation in both LIP and PRR, with eye-centred receptive fields modulated by eye and body position signals (see Fig. 5). The advantage of such a representation is the ease of coordinating activity between these two areas, and the ability to read out multiple coordinate frames from this common representation (Fig. 4).

### **Updating the spatial representations within LIP and PRR across saccades**

When a subject makes multiple saccades to different locations from memory, the remembered locations must be updated with each eye movement. This problem was first addressed in physiological experiments by Sparks & Mays (1980), who found that cells in the intermediate layers of the superior colliculus updated the location of the next planned eye movement in eye-centred coordinates across saccades. We later showed a similar phenomenon in area LIP (Gnadt & Andersen 1988). Duhamel et al (1992) extended these results to show that a second eye movement was not necessary for this updating to take place.

Although they interpreted this updated activity to be sensory, the results of Snyder et al (1997, 1998) and those outlined in a previous section ('Coding the next planned movement in LIP and PRR'), suggests that this activity may in fact represent default plans for eye movements to the flashed second targets.

Recently we asked if this same updating process might also occur in area PRR. To test this hypothesis we presented a visual target for a reach that the animal was required to remember. However, during the memory period we then had the animal make a saccade to fixate a new location in space. We found that the remembered location of the reach target was updated in eye coordinates to take into account the change in eye position (Batista et al 1998). For instance, if the monkey made a saccade that brought the remembered location of the target into the retinal receptive field of the PRR neuron, then the cell became active during the delay period prior to the reach. On the other hand, if the saccade brought the remembered location out of the receptive field of the PRR cell, then the cell fell silent. Again LIP and PRR were found to share an important similarity in updating remembered locations in eye coordinates across saccades (see Fig. 6).

This finding also has important implications for reading out the distributed representation of space accurately in non-retinal coordinates. For instance, if the eyes move, the eye position signals and gain modulations in LIP and PRR will change in accordance with the new eye position. If the remembered retinal location of a target remained the same after the eye movement it would be incorrectly coded in head or body centred coordinates. Thus the location in eye coordinates would by necessity need to be updated to read out the correct location with respect to the head or body.

## Conclusions

The results reviewed above indicate that the PPC is specialized for transforming sensory signals into action. Two prominent areas within the PPC, areas LIP and PRR, are specialized for saccades and reaches. For both areas, the visual system appears to serve as an anchor for representing space. Thus, both visual and auditory receptive fields are in the coordinates of the eye. However, these signals

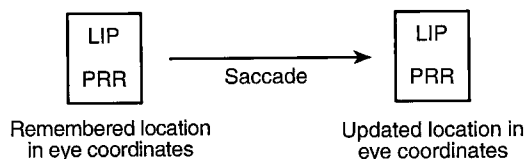


FIG. 6. Schematic showing that in both area LIP and PRR the remembered locations of targets are updated, in eye coordinates, across saccades.

are also gain modulated by eye and head position signals, and this gain modulation allows multiple reference frames to be coded simultaneously within these areas. Thus LIP and PRR contain a common, distributed representation of space. This representation is updated each time the eye moves. Not only are the eye position signals changing across eye movements, but also the retinal locations of remembered sensory targets. Thus this distributed representation of space can faithfully code the location of remembered targets across eye movements in eye, head or body-centred coordinates. This updating is obviously useful for making accurate movements in spite of intervening saccades. However, we also perceive space as stable in spite of eye movements. It is not clear whether the spatial constancy of perception is also supported by activity in PPC. Alternatively, PPC may only operate for action and not conscious awareness and activity in the ventral visual pathway may support visual awareness (Goodale & Milner 1992). If this is the case, then receptive fields in the ventral pathway may also update across eye movements, and this may be the basis for the spatial stability of perception. Likewise, there have been several reports of gain field effects in ventral extrastriate areas not unlike those found in PPC which may also contribute to perceiving space as constant across eye and head movements. Future experiments will need to be done to determine whether the updating mechanisms that are found in the motor and dorsal extrastriate areas are also found in the ventral extrastriate cortex. It is possible that updating of signals in eye coordinates, and the gain modulation of eye-centred receptive fields, are a very general phenomenon for large parts of the mammalian brain.

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## DISCUSSION

*Stein:* I didn't quite understand your reconciliation with Micky Goldberg. Micky says that there is an updating of the retinal meaning, as it were, of a receptive field before an eye movement. Many of your experiments suggest a

recalibration after the eye movement. I got the message from your paper that there is some reconciliation going on now, but I couldn't quite understand it.

*Andersen:* There is nothing much to reconcile, since we have both reported on updating of activity in LIP across saccades, that is in eye coordinates. Your question is about the timing of the update. When we look at memory responses, in that case the compensation usually occurs right at the time of the beginning of the eye movement or after, but not prior. Mickey looked at a different condition in which the stimulus was still visible and often saw the compensation occurring before the eye movement.

We have recently looked at the eye position signal itself. Interestingly, if a visual target is present, it begins to change prior to the eye movement. But if we look at a memory saccade, again it begins changing right about the time of the memory saccade. The idea is that the presence of the visual target somehow makes the compensation earlier in time.

*Stein:* But you never see it 100 ms before the eye movement?

*Andersen:* We haven't tried his experiment, but we do see the eye position signal updating sometimes even more than 100 ms prior to the eye movement. We think that the efference copy of the saccade command, possibly originating in the frontal lobe, is responsible, because the compensation is so early. This efference copy of eye displacement may be integrated by the parietal cortex to provide an eye position signal to then produce gain fields and maintain the spatial representation across eye movements.

*Thier:* You mentioned the early work by Mountcastle and co-workers on area 7a, in which they described the existence of saccade-related activity and reach-related activity in 7a (Mountcastle et al 1975). Now we have learnt, thanks to work from your lab and others, that there is a specific area involved in processing saccade-related information, area LIP, and another one, MST, processing pursuit-related information as well as signals related to optic flow. In addition, we now learn about another reach-related area in parts of the intraparietal sulcus, neighbouring area LIP. So what is left for area 7a to do?

*Andersen:* There are two answers. First, 7a does have reach activity. It also has eye movement activity but the responses are post-saccadic and not pre-saccadic; it's a very complicated area. As Dick Passingham was saying yesterday, it's all in the connections. If you look at 7a connections, it goes to the highest levels of the brain: the hippocampal gyrus, cingulate cortex and the anterior part of the superior temporal sulcus. It is not yet clear what area 7a does. Certainly, in the parietal reach region (PRR) the activity is incredibly robust; for saccades LIP is robust, and smooth pursuit seems to be found easily in area MST. No doubt in the early days when people were doing experiments in the posterior parietal region they were running electrode tracks deep through many of these regions. At that time 7a was defined as a much bigger area, which included areas LIP and

MST. Today, we define 7a as a much smaller area located on the surface of the inferior parietal lobule.

*Thier:* Does it also hold for the reach-related activity in 7a that it comes later than reach-related activity in the intraparietal sulcus?

*Andersen:* We haven't looked at that in detail. With this parietal reach area you can see in the rasters that the reach activity precedes the reach movement. In 7a their activity can also precede the reach, but we haven't analysed quantitatively whether 7a tends to have a higher proportion of post-reach responses.

*Miller:* I have trouble in understanding your interpretation of the last part of your extinction series of experiments. Wouldn't a fairly simple description be that as the eyes approach the edge of the oculomotor range, the monkey didn't care to look further in that direction and looked back?

*Andersen:* In the normal condition, when gaze is straight ahead the animal will choose with about equal frequency to look to the left and right targets. When the eyes are deviated to one side (say left), the monkey will generally choose to look in the direction that will centre the eye in the orbit (right). After LIP inactivation the monkey will generally not look into the unhealthy field even when the eye is deviated in the opposite direction. Thus the 'equilibrium' point for gaze direction at which the animal will choose the left and right targets equally shifts far into the ipsilesional field after inactivation. This result demonstrates an eye position (head-centred) deficit after LIP inactivation.

*Savaki:* Have you found any cells in area LIP which encode target position in head-centred coordinates?

*Andersen:* No it has always been in eye coordinates, but modulated by eye and head position.

*Savaki:* The discharge of cells which encode target position in head-centred coordinates (target *re* head position) should be completely unaffected by changes of eye position and affected only by changes of head position. As far as I know, you have not found any cells in area LIP coding target position in head-centred space. Moreover, a signal coding target *re* head position (even if it existed in area LIP) should be transformed back into a signal coding eye displacement *re* retina position to be used by the superior colliculi. Thus, cells in area LIP which send information out to the superior colliculi cannot be the LIP gain field neurons. Actually, the LIP output neurons have not been described yet. My impression is that the neurons which you have described to encode 'intention' or 'planning of movement' or 'memory of the intended eye-position' in area LIP have similar properties to the quasivisual (Qv) cells described in the deep layer of the superior colliculi by Mays & Sparks (1980). Moreover, it has been demonstrated by Moschovakis et al (1988) that these cells receive (a) visual retinotopic input from the superficial layer of SC (retinal error signal from L neurons) and (b) feedback input concerning the degree of eye displacement from RTLLB cells (cells which discharge in proportion to eye



displacement). Thus, retinal error minus eye displacement computation in Qv cells provides information about 'eye-position error' or 'memory of the desired eye displacement'. As far as I know, there is no anatomical support in any area of the brain, of eye position information subtracted from target *re* head position signal. Thus, LIP neurons may encode 'memory of the desired eye displacement' rather than 'memory of the intended eye-position'. The spatial hypothesis (which implies eye-position signal) is neither anatomically nor functionally substantiated, neither in area LIP nor in any other eye movement-related area. In contrast, the vector subtraction hypothesis (which implies eye displacement signal) has been substantiated in the superior colliculi both anatomically and functionally (Moschovakis et al 1996).

*Andersen:* That is the beauty of this distributed representation. I could think about looking to a remembered place in space, or a location with respect to some part of my body, through reading out that representation. In this distributed framework, the retinal location of a target is also retained, and a plan to move the eyes in eye-centred coordinates can also be read out from the population of LIP cells and used by the superior colliculus. Whenever you convert from a retinal receptive field to a receptive field in another coordinate frame, you lose information, whereas with this distributed representation you simultaneously have several coordinate frames that can be read out and you don't lose any information.

*Savaki:* But we haven't found the output cells of area LIP yet.

*Andersen:* I think cells that receive output from LIP that have other reference frames would be like VIP, which contains many cells which code the visual targets in head-centric coordinates. Dr Rizzolatti's experiments in F4 show coding with respect to body parts, and Graziano, Gross and colleagues have reproduced that result. Thus there are places in the brain which do combine information, and in a sense lose information when they make these conversions. An interesting question concerns why you would ever want to do that. In other words, the brain could stay within this distributed coordinate framework until motor cortex (M1) or the oculomotor nuclei.

*Ebner:* I'm interested in the general properties of the PRR cells. How is their amplitude tuning? Do these cells encode other parameters such as speed or velocity?

*Andersen:* That's a fascinating question, but we haven't looked at amplitude or speed tuning yet. We plan to look at this. My guess from what we know so far is that it will look like a receptive field, such as a retinal receptive field. Thus it would be amplitude tuned, but not velocity tuned.

*Ebner:* But your sense is that they're going to be spatially tuned; they're going to be tuned along an amplitude axis, as opposed to simply linear.

*Andersen:* Yes, but I'm guessing.

*Kalaska:* I want to follow up on the issue of directional tuning of these cells. When I looked at your results, I got the impression that the reach-related cells seemed to have more of a preferred spatial target location in retinal coordinates for reaching movements. They would discharge whenever the monkey moves into that target area but they're not actually tuned *per se* in terms of the metrics of the movement the monkey makes into that area — for instance, in which direction they must move the arm to get into the target location. Putting this another way, when you move into that field from many different directions, the cell seems to be active. It is non-directional in that sense. This clearly is quite different from motor cortical cells.

*Andersen:* That's the basis of my guess that it is going to be spatial because, as you say, the animal can move in two different directions but to the same location on the retina, and they're tuned with respect to the retina.

*Kalaska:* To continue along this line, you were recording a very medial location in the medial bank of the parietal sulcus. Donald Crammond and I recorded in an area that was slightly lateral to that, although still probably in MIP (Kalaska & Crammond 1995). The behaviour of the cells there didn't leave us with the impression or a suspicion that they had a retinotopic or eye-coordinate framework. I'm not upset about that: again, we're not in the same part of the brain, and also in our tasks we didn't fixate the eyes. The monkey is constantly saccading around and fixating at random throughout the performance of the task. When we turned on a target in a particular spatial location relative to where the hand was, in a delayed task, a cell would commonly emit a stable tonic discharge during the delay period before movement that was a function of the direction in which the monkey had to move to get to the target. In the meantime, during this delay period, the monkey is saccading all over. If the cells had retinotopic movement-target fields, the image of the spatial location of the movement-location signal we gave should fall on different locations on the retina relative to its movement-target field, and you should hear changes in the tonic discharge as the eye is saccading about during the delay period. However, we didn't see that property in those cells that we recorded in a part of area 5 only a few millimetres lateral to where you were recording. Instead, the tonic activity usually remained very stable. Thus there may be a very rapid shift in the nature of the coordinate frameworks, within a few millimetres along the bank of the intraparietal sulcus, from one that is retinotopic or at least strongly influenced by eye position, to one that appears to be more egocentric or even limb centred.

*Andersen:* Sure. This distinction of MIP from the convexity of area 5 is somewhat arbitrary. We have begun examining whether area 5 proper, up on the surface, was going to show a similar activity (C. A. Bueno, A. P. Batista & R. A. Andersen, unpublished observations). In this task the activity appears to be very different. We don't see the memory activity, by and large. Also, it appears to be

more limb related, but in some very complex way. Just as you discuss intrinsic coordinates, it is as if we're sampling a lot of the position signals from the limb from area 5; it is very different.

*Kalaska:* Donald Crammond and I saw exactly the same gradient: as we proceeded further laterally along the intraparietal sulcus and then onto the exposed surface of what most would still consider to be area 5, or the 2/5 transition area, the delay period discharge becomes much less prominent and cell activity becomes more coupled in time to the movements of the arm itself.

*Andersen:* We think this shared coordinate frame for PRR and LIP may help in hand-eye coordination, for instance. It would be nice and much simpler to plan arm movements under visual guidance in eye coordinates, and thus share a common coordinate frame with area LIP for that task.

*Goodale:* Would you like to comment on differences in the topology of what we know about the activation patterns that occur with reaching as opposed to those that occur with saccadic eye movements in neuroimaging studies of human brain? I'm thinking primarily of the recent work by Kawashima et al (1996), in which they showed that an area was activated in the intraparietal sulcus when subjects reached towards a visual target that was slightly more rostral and medial to the area that was activated when subjects made saccades towards the same targets. Is this a difference in the topological arrangement of the same areas that are seen in the monkey or are they different areas that have emerged in the human brain?

*Andersen:* I meant to mention at the end of the talk that Mel Goodale and his colleagues and I have been doing an fMRI experiment that shows the separation of saccade and reach in the parietal lobe of humans. The reach activation is located medial to the saccade area (similar to the monkey) but more anteriorly than we found in the monkey parietal lobe. There could be some difference in topography between the monkey and human.

Yesterday we touched briefly on some of the differences between monkeys and humans in terms of the superior and inferior parietal lobules. Also, in extrastriate cortex, the story is somewhat different between the two species: it is as if in human the monkey map has been dragged down and back. For instance, MT is located much more ventrally and posteriorly than we would have expected from monkeys. Although there are some small differences in topography between the species, it is important to emphasize that we can see the segregation for reach and saccade in the human and monkey parietal cortex.

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