metric (amplitude and direction), the so-called movement or motor field of the neuron. These fields coincide with the visual receptive fields of other, purely visual, neurons in the superficial layers of the superior colliculus, which, in the primate, form a topographic map of the contralateral half of the visual field. The neurons in the deeper layers project to brainstem regions important for the initiation and control of saccadic eye movements. Several models of the generation of the saccade signals by these superior colliculus neurons have been proposed and David Sparks takes a critical look at the plausibility of three classes of model. Both Hoffmann and Sparks conclude that the output of the superior colliculus should be considered to be a request, rather than the command it is more commonly termed.

The representation of intention and spatial location in monkey posterior parietal cortex

Richard A. Andersen

The primate posterior parietal cortex (PPC), located between primary sensory and motor cortical areas, is known to be important for the processing of spatial information. Early studies established that it contributes to visuospatial behaviour, although the exact nature of this involvement was not clear (Mountcastle *et al.*, 1975; Robinson et al, 1978). Both human patients and non-human primates with unilateral or bilateral lesions in the PPC show deficits related to sensorimotor integration, one of the most prominent being optic ataxia. As well as a general impairment of visually guided motor control (Balint, 1909; see Jeannerod, 1994), oculomotor functions, such as smooth-pursuit eye movements and saccades, are also impaired.

A specific region of PPC in monkeys, the lateral bank of the intraparietal sulcus or lateral intraparietal area (LIP) has been found to participate in the control of voluntary saccades. Many neurons in LIP exhibit activity during a delay in a saccade task. I argue here that a large component of this activity represents the intention of the monkey to make a saccade rather than attention to the sensory information (see Goldberg, this volume, for another view).

Background

Recent studies of parietal lesions in both humans and non-human primates (in humans, only with lesions in the right hemisphere) revealed that impairments in saccades were restricted to voluntary movements; spontaneous saccades were unaffected. In monkeys, electrical stimulation of specific regions of the PPC elicited saccadic eye movements and retrograde tracers injected into the FEF, an area in frontal cortex known to be involved in the control of saccades, predominantly labelled LIP, now considered as the posterior eye field (Andersen *et al.*, 1990a; Barash *et al.*, 1991a, b).

The involvement of LIP in the generation of saccades was confirmed by single-unit recordings in the behaving monkey. Neurons in LIP produce a burst of activity during regular visually guided saccades. Using a memory-guided single saccade task demonstrated that this activity can be separated temporally into sensory and motor phases (Andersen, 1989). In this task, a visual stimulus is flashed briefly in a neuron's visual receptive field while the monkey fixates a central target; the saccade can be made only once the fixation light is switched off. Many LIP neurons revealed a tonic discharge during the delay period in addition to a visual response and a burst of activity tightly related to the onset of the saccade.

Nature of the delay-period activity

Does the activity in the delay period represent holding the sensory information in memory, i.e., the location of the target with respect
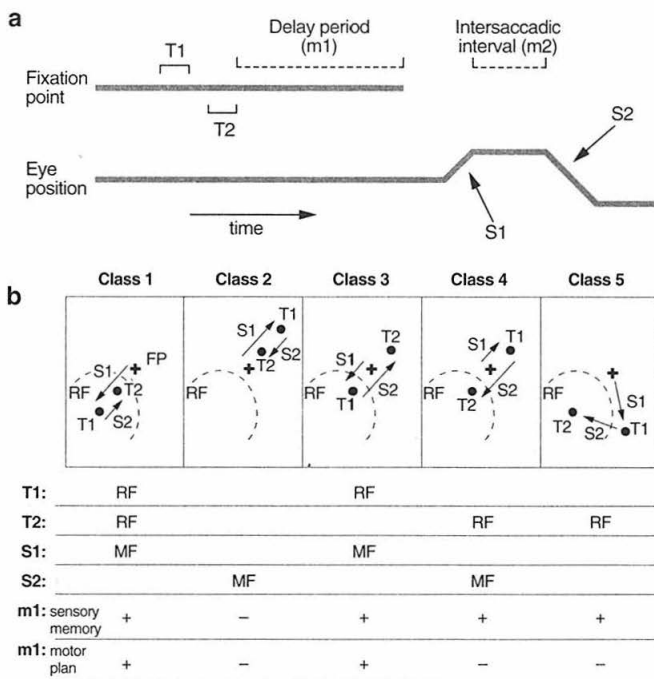
Figure 30. Delayed double saccade task designed to determine whether activity in LIP neurons is related to sensory memories or plans to make movements. *a*, timing of stimuli and eye movements in the task. The monkey fixates a point (continuous bar) while the first (T1) and second (T2) visual targets are flashed. Following T2, the fixation point remains illuminated for a delay period (m1), after which the monkey makes saccades (S1, S2) to the two targets (lower trace). The intersaccadic interval is the second memory period, m2. *b*, spatial arrangement of stimuli in the five classes of the delayed double saccade task and predictions of the responses during m1 that should be made if the neuronal activity represents either sensory memory or motor plan. Each panel shows the location of the fixation point (FP = cross), a neuron's receptive field (RF = dashed semicircle), the locations of the two visual targets (T1, T2 = spots). The size and direction of the arrows indicate the amplitude and direction of the saccades (S1, S2). The table below the diagram summarizes the target positions with respect to the RF and whether saccades are in the neuron's preferred direction, i.e., into its motor field (MF). Modified from Mazzoni et al., 1996.

to the receptive field, or does it reflect the plan to make a saccade towards the target? A delayed double saccade task, modified from the original double saccade task devised by Mays and Sparks (1980), was used to dissociate these possibilities. In the original task two saccade targets T1 and T2 are briefly flashed in sequential order at different spatial locations. The second target disappears within the shortest saccade reaction time. The movement required for the first saccade corresponds to the site of retinal stimulation but to make the second saccade the system has to take into account both the retinal position of the second target and the previous eye movement. Thus spatially tuned activity occurring after the first saccade but preceding the second should represent preparation for the impending saccade.

We have extended this task by introducing a delay period, m1, before the execution of the first saccade; the interval between the performance of the two saccades is here termed m2 (*Fig. 30a*). Five classes of delayed double saccade tasks using similar spatial locations but different temporal sequences (*Fig. 30b*) were employed to test activity in the delay period more systematically. The logic of this experiment is that the sensory-memory and motor-plan hypotheses should give the same activity in classes 1, 2 and 3 during the m1 period, because the movement the animal plans to make and the stimulation of the receptive field are spatially congruent. In contrast, in classes 4 and 5 the second stimulus appears in the receptive field but the first movement is planned outside the receptive field. The motor-plan hypothesis predicts no activity during m1, whereas the sensory-memory hypothesis predicts activity.

A neuron tested with class 1-4 tasks (*Fig. 31a*) revealed a response to a visual stimulus flashed in its receptive field and a build-up of activity during m1 in classes 1 and 3. In contrast, when tested with tasks of classes 2 and 4, where the first saccade is directed away from its receptive field, the neuron showed no visual response and no activity during m1; however it discharged during
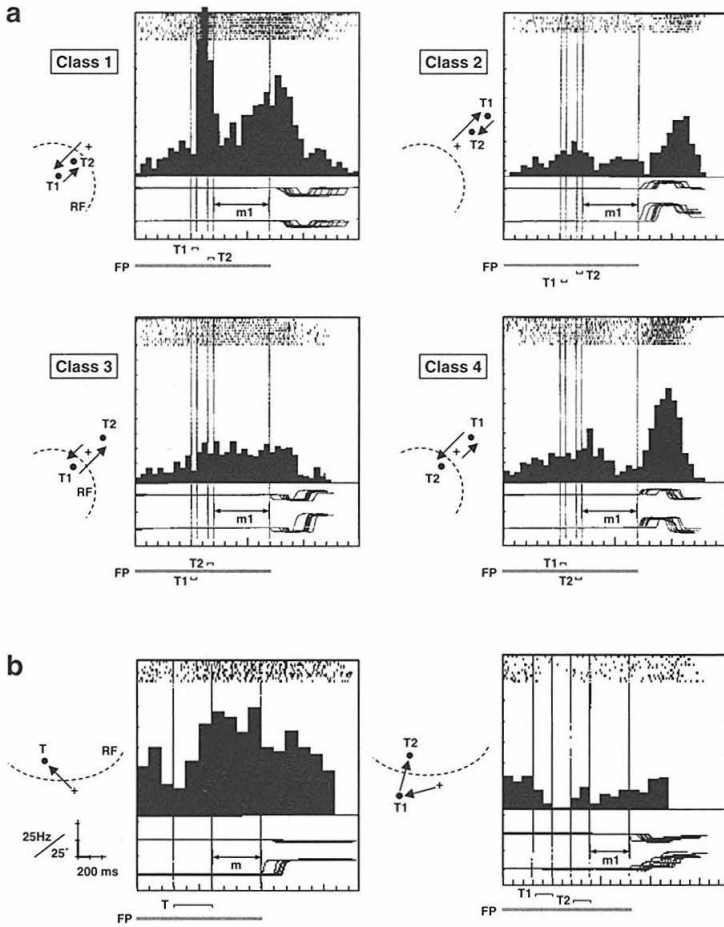
Figure 31. Examples of two LIP neurons showing that activity during delay periods in the task are more related to the planned movement than to the memory of the target location. *a*, activity of a neuron while the monkey performed classes 1- 4 of the delayed double saccade task. *b*, comparison of single (left) and double (right) saccade tasks shows that the second neuron was tuned to movement into its motor field (see text for details). Each panel includes: discharge rasters for each trial (top); time histogram of the firing rate (middle) and a trace of the horizontal and vertical eye positions (bottom). The vertical dotted lines and the thick lines below each panel show the presentation of the visual stimuli. On the left of each panel, the spatial arrangement of the task is shown (see Fig. 30). Modified from Mazzoni et al., 1996.

m2, when the saccade was towards the receptive field, even in class 2 where no stimulus ever appeared there. The lack of response in m1 in class 4 is consistent with the motor-plan hypothesis and not the sensory-memory hypothesis; the activity in m2 for classes 2 and 4 is also consistent with the motor-plan hypothesis. That is, the memory-delay activity was stronger before saccades whose amplitudes were more appropriate to the motor field of this neuron (m1 in the class 1 task and m2 in the class 4 task).

Tuning of the activity in the memory period to the direction of the saccade is also shown by comparing the discharges observed in a single memory-guided saccade task with those in a delayed double saccade task in class 5 (compare left and right panels in *Fig. 31b*). In the single memory-guided task, the saccade is made into the receptive field, whereas in the delayed double saccade task, the second stimulus falls in the same location as the stimulus in the single saccade task but the first eye movement is planned out of the receptive field. Activity was suppressed during the m1 period (as it was in this neuron in the single memory-guided saccade task for saccades away from the receptive field). This result is again consistent with the planning of a movement and not the coding of a sensory memory.

Out of 46 neurons recorded in two monkeys, in 38 (82%) the activity during the memory period fitted statistically with the motor plan hypothesis (*Fig. 32a*, motor plan group). The activity of the remaining 18% is compatible with the sensory-memory hypothesis (*Fig. 32a*, sensory memory group). The neuronal discharge during the first memory period, m1, was quantified using an activity index:

I_a = (m1 activity - background activity)/background activity

When I_a is zero, m1 activity is similar to background, whereas when it is close to 1.0, m1 activity is about twice the background level. When the mean values of I_a for the five classes of delayed double saccade task are plotted for the motor-plan group (*Fig. 32a*), I_a values are above 1.0 in the tasks where the first

saccade was made into the motor field of the neurons (class 1 and 3), whereas tasks requiring a first saccade in the opposite direction resulted in I_a values around zero (class 2, 4, 5). In contrast, for the sensory memory neurons I_a was between 0.5 and 1.0 for all tasks (*Fig. 32a*). The dependence on direction of movement is obvious, even when the values for both groups are combined (*Fig. 32b*).
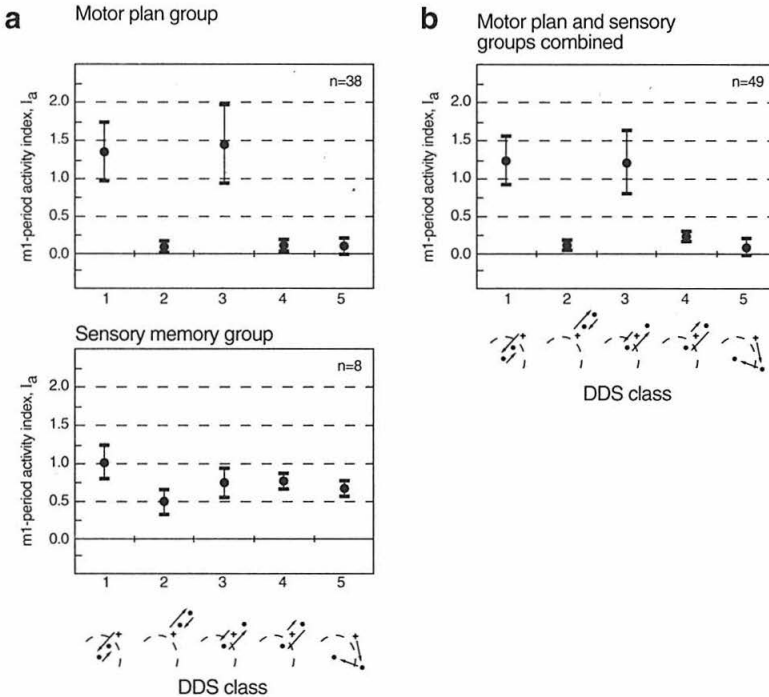

Figure 32. *Summary of data from 49 LIP neurons demonstrates that activity during the delay period in most of them reflected what the animal intended to do. In a few neurons activity related to the memorized location of the target.* ***a,*** *upper panel: the 38 neurons with m1 responses that fitted statistically with the motor-plan hypothesis. Lower panel: the eight neurons whose m1 response fitted the sensory-memory hypothesis.* ***b,*** *all neurons in this study. Mean values plus standard error of the m1 period activity index, Ia (see text), are given for the five delayed double saccade (DDS) classes. Modified from Mazzoni et al., 1996.*

Change in plan

Because most LIP neurons seem to code for the intended eye movement, their activity may represent the plan for making an eye movement independent of whether the movement is made. We therefore designed a task in which the animal's plan for making a specific eye movement was altered without any overt change in performance. This change-in-plan experiment comprised eight classes of saccade tasks presented in random order. In all of them, the monkey was required to perform a saccade to the most recent target.

Classes 1 and 2 are single memory-guided saccade tasks with the target either in the motor field of the neuron (*Fig. 33a*) or outside it (*Fig. 33b*). Classes 3 and 4 are single change-in-plan tasks with the first target in the motor field and the second target away from it (*Fig. 33c*) and vice versa (*Fig. 33d*). Here there was less activity after m1 in the class 3 task and an increase in m2 in the class 4 task. This outcome was even more obvious in the double change-in-plan tasks (class 7 and 8), where the first and third targets are in the motor field and the second away from it (*Fig. 33g*) and vice versa (*Fig. 33h*). Here the animal had to change the plan for the intended movement twice within one trial; the activity pattern of the neuron changed according to the direction of the intended movement.

The observation that LIP neurons are active for plans for movements which do not have an obligatory link to their execution may provide a unifying thread for a recent observation. When two lights are flashed and the animal makes a saccade to only one of them, activity appears after the first eye movement for the location that codes the oculomotor coordinates of the second stimulus, even if the stimulus is no longer present (Duhamel *et al.*, 1992). This result is similar to the memory double saccade experiment above (class 2) and earlier double saccade experiments (Gnadt and Andersen 1988), except that the second saccade is not made. Based on these results, Duhamel *et al.* (1992) proposed that LIP codes sensory signals in retinal coordinates
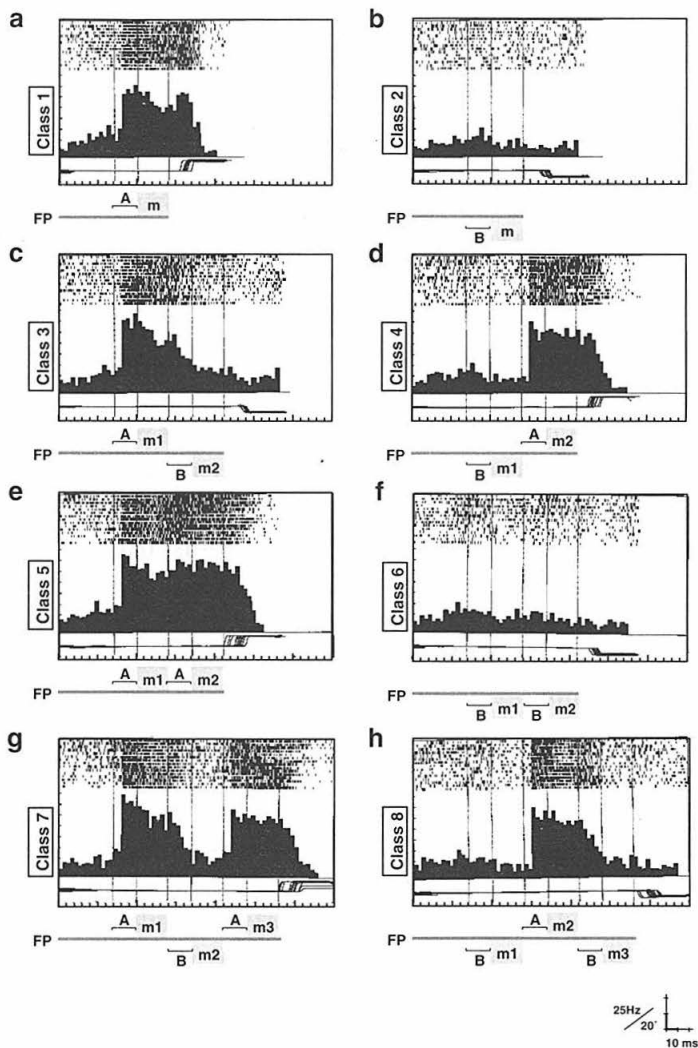
Figure 33. Activity of an excitatory LIP neuron coding the movement plan in the change-in-plan task. Changes in a planned movement resulted in changes in the neuron's activity, which also related to the intention to make movements even when they were not performed. **a - h**, for description of the eight classes of trial, see text. Conventions as in Figures 30, 31. A, target in the receptive field; B, target outside receptive field; m3, third memory (delay) period. Reproduced with permission from Bracewell et al., 1996.

and that the retinal location of the remembered sensory signal is remapped in retinal coordinates to anticipate reafference of retinal signals coding the second target after the eye movement. Our results provide an alternative explanation: that the animal does consider making an eye movement to the second target but this plan is not executed. In other words a majority of the neurons active in the memory period are coding intended movements in motor coordinates, rather than sensory signals in retinal coordinates.

Parietal cells code the type of movement being planned

A definitive test of intention is to show that the delay-period activity is contingent on the type of movement the animal plans to make. Bushnell *et al.* (1981) claimed that the activity of PPC neurons did not differentiate between the animal programming an eye movement or a reaching movement to a stimulus that was retinotopically identical. Moreover, if neurons showed a larger response when a stimulus was a target for a movement compared to when it was not, the enhancement was the same for both reaching and eye movements. This result was interpreted as proof that PPC is concerned with sensory location and attention and not with planning movements (Bushnell *et al.* 1981; Colby *et al.* 1995).

We have recently repeated these experiments, with different results (Snyder *et al.*, 1996). The monkey fixated a light in a button and pressed the button with its hand. Next a light appeared briefly in the visual field; depending on the colour, the animal had to plan either an arm or an eye movement to the remembered location. After a delay, it made the eye movement without moving the limb or vice versa. During the memory period, two-thirds of the neurons sampled (n = 276) in PPC were selective for the requirement to make an arm or an eye movement. Interestingly, nearly half of the sensory responses to the flashed targets also distinguished between the type of movement called for. Much of the activity in PPC is thus concerned with what the animal plans to do, that is with intentions.

These data lead us to conclude that a large component of delay activity in LIP neurons encodes the next movement rather than the memory of the spatial location of the target for a saccade. Some neurons do code the sensory memory but there are fewer of them. The tuning of the neurons implies that the coding is in motor coordinates. Their activity is not linked in an obligatory manner to overt behaviour but rather reflects the animal's intention or plan to make the next movement. Lastly, the activity of most neurons in PPC during the delay period is specific for the type of movement (reach or saccade) that the animal plans to make.

Attentional and spatial mechanisms in the parietal cortex

Michael E. Goldberg

Studies on patients with lesions in parietal cortex have also emphasized the role of the PPC in attentional processes dedicated to a specific region in space. These patients show several impairments in attention, such as a neglect contralateral to the lesion side or a shift of attention into one visual hemifield (for review, see Ungerleider and Mishkin, 1982). We have investigated the neural basis of these attentional processes in more detail using single-neuron recordings in awake behaving monkeys. Neurons in LIP discharge in response to behaviourally relevant stimuli, regardless of whether these are targets for an eye movement or not (see also Andersen, this volume). They differ in this from neurons in the FEF, a subset of which discharge only before purposive saccadic eye movements and do not respond to visual targets even if these are the target for a delayed saccade (Bruce and Goldberg 1985). Using several behavioural tasks, we have examined the activity of LIP neurons to characterize better their role in the processes underlying visuospatial attention.