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Motor Intention Activity in the Macaque's Lateral Intraparietal Area I. Dissociation Of Motor Plan From Sensory Memory

PIETRO MAZZONI, R. MARTYN BRACEWELL, SHABTAI BARASH, AND RICHARD A. ANDERSEN
Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

SUMMARY AND CONCLUSIONS

1. The lateral intraparietal area (area LIP) of the monkey's posterior parietal cortex (PPC) contains neurons that are active during saccadic eye movements. These neurons' activity includes visual and saccade-related components. These responses are spatially tuned and the location of a neuron's visual receptive field (RF) relative to the fovea generally overlaps its preferred saccade amplitude and direction (i.e., its motor field, MF). When a delay is imposed between the presentation of a visual stimulus and a saccade made to its location (memory saccade task), many LIP neurons maintain elevated activity during the delay (memory activity, M), which appears to encode the metrics of the next intended saccadic eye movement. Recent studies have alternatively suggested that LIP neurons encode the locations of visual stimuli regardless of where the animal intends to look. We examined whether the M activity of LIP neurons specifically encodes movement intention or the locations of recent visual stimuli, or a combination of both. In the accompanying study, we investigated whether the intended-movement activity reflects changes in motor plan.

2. We trained monkeys (*Macaca mulatta*) to memorize the locations of two visual stimuli and plan a sequence of two saccades, one to each remembered target, as we recorded the activity of single LIP neurons. Two targets were flashed briefly while the monkey maintained fixation; after a delay the fixation point was extinguished, and the monkey made two saccades in sequence to each target's remembered location, in the order in which the targets were presented. This "delayed double saccade" (DDS) paradigm allowed us to dissociate the location of visual stimulation from the direction of the planned saccade and thus distinguish neuronal activity related to the target's location from activity related to the saccade plan. By imposing a delay, we eliminated the confounding effect of any phasic responses coincident with the appearance of the stimulus and with the saccade.

3. We arranged the two visual stimuli so that in one set of conditions at least the first one was in the neuron's visual RF, and thus the first saccade was in the neuron's motor field (MF). M activity should be high in these conditions according to both the sensory memory and motor plan hypotheses. In another set of conditions, the second stimulus appeared in the RF but the first one was presented outside the RF, instructing the monkey to plan the first saccade away from the neuron's MF. If the M activity encodes the motor plan, it should be low in these conditions, reflecting the plan for the first saccade (away from the MF). If it is a sensory trace of the stimulus' location, it should be high, reflecting stimulation of the RF by the second target.

4. We tested 49 LIP neurons (in 3 hemispheres of 2 monkeys) with M activity on the DDS task. Of these, 38 (77%) had M activity related to the next intended saccade. They were active in the delay period, as expected, if the first saccade was in their preferred direction. They were less active or silent if the next saccade was not in their preferred direction, even when the second stimulus appeared in their RF.

5. The M activity of 8 (16%) of the remaining neurons specifically encoded the location of the most recent visual stimulus. Their firing rate during the delay reflected stimulation of the RF independently of the saccade being planned. The remaining 3 neurons had M activity that did not consistently encode either the next saccade or the stimulus' location.

6. We also recorded the activity of a subset of neurons (n = 38) in a condition in which no stimulus appeared in a neuron's RF, but the second saccade was in the neuron's MF. In this case the majority of neurons tested (23/38, 60%) became active in the period between the first and second saccade, even if neither stimulus had appeared in their RF. Moreover, this activity appeared only after the first saccade had started in all but two of these neurons. In general, the neurons' responses thus did not anticipate the saccades in the DDS task.

7. The majority of LIP neurons have activity related to the next intended saccade. Cells in LIP also carry a signal coding the memory of the location of the sensory stimulus, although at the population level this signal is less prominent than the intended movement signal in the DDS task. The intended movement signal is not simply an attention signal for a spatial location because it was reduced or absent when a location required attention but not a saccade to it. The posterior parietal cortex is thus not only involved in sensory and attentional processing but also participates in the formulation of movement plans.

INTRODUCTION

The posterior parietal lobe of the primate brain has been implicated in a variety of functions subserving sensorimotor integration. Certain regions of the posterior parietal cortex (PPC) seem especially important for the production of saccadic eye movements. Lesions of these regions in humans and monkeys impair the perception of spatial relationships in the visual field and the ability to make voluntary saccades (e.g., Balint 1909; Hécaen and De Ajuriaguerra 1954; Holmes 1918; Lynch 1980; Lynch and McLaren 1989), and electrical stimulation of this region produces saccadic eye movements (Shibutani et al. 1984; Thier and Andersen 1991). Neurophysiological studies in awake behaving monkeys have revealed single-unit activity in the PPC related to saccadic eye movements (Hyvärinen and Poranen 1974; Lynch et al. 1977; Mountcastle et al. 1975).

Initially, there was a controversy as to whether the activity occurring around the time of a saccade was a motor command (Mountcastle et al. 1975) or rather an artifact of sensory stimulation (Robinson et al. 1978). Later studies (Andersen et al. 1987) addressed this issue by recording the activity of posterior parietal neurons in a "delayed" or "memory" saccade task (introduced by Hikosaka and Wurtz

1983, in studies of the basal ganglia). In this task a peripheral visual stimulus appears briefly while a monkey maintains fixation on a light spot; after a delay the fixation spot is turned off, which instructs the monkey to make a saccade, in the dark, to the location where the stimulus appeared. The memory saccade paradigm separates temporally the sensory and motor components of the saccade task. The initial studies showed that PPC neurons often carry both visual and saccade-related signals (Andersen et al. 1987). The exact role these signals played in the production of saccades, however, remained unclear.

The visual and saccade-related signals are especially prominent in the lateral intraparietal area (area LIP), a subdivision of the PPC characterized by strong projections to eye movement centers (especially the frontal eye fields, FEF, and the superior colliculus, SC) as well as multiple inputs from other extrastriate visual areas (Andersen et al. 1990a; Blatt et al. 1990; Lynch et al. 1985). The responses of neurons in this area have been characterized with the use of the memory saccade task (Andersen et al. 1990b; Barash et al. 1991a,b). These signals are spatially tuned. Visual responses vary across the visual field, being strongest for stimuli in a circumscribed sensory response field (receptive field, RF). Saccade-related responses are broadly tuned for amplitude and vary with saccade direction, reaching a maximum for saccades in the neuron's preferred direction (MF). The spatial tuning of the visual and saccade-related responses in LIP generally coincide, that is, the RF is in the same direction, relative to the fovea, as a saccade into the neuron's MF. Besides responding during the visual stimulus' presentation and during the saccade, many LIP neurons maintain sustained activity during the delay period of a memory saccade (Andersen et al. 1990b; Barash et al. 1991a; Gnadt and Andersen 1988). This "memory" (M) activity has similar spatial tuning to the visual and oculomotor responses (Barash et al. 1991b). It could reflect a memory of the stimulus' location, a covert shift of attention within the visual field, or the intention to execute the upcoming saccade.

The studies by Gnadt and Andersen (1988) and Barash et al. (1991b) showed that the responses of LIP neurons are coded in oculomotor coordinates. With the use of a double saccade paradigm, these experiments showed that LIP activity appears before a saccade made in the neuron's preferred direction even without RF stimulation. These authors thus proposed that the M activity is a memory trace of what the animal intends to do.

Other studies of area LIP have offered another interpretation of the role of this area in sensorimotor integration (Duhamel et al. 1992; Goldberg et al. 1990). According to these studies the major role of area LIP is to construct a perceptual map of visual space by encoding the locations of visual stimuli and maintaining this representation anchored to a retinally based reference frame across eye movements (Duhamel et al. 1992; Goldberg et al. 1990). Neural activity in this area would thus indicate that a stimulus is or has been at a particular location in the visual field, independently of whether the animal wants to foveate that location.

In this study we examined whether LIP neurons only encode the locations of visual stimuli (*sensory memory* hypothesis), or whether their memory activity also encodes movement intention (*motor plan* hypothesis). To answer this question we extended the double saccade task used by Gnadt and Andersen (1988) and Barash et al. (1991a,b). In a double saccade task (1st described by Hallett and Lightstone 1976, and applied to experiments in monkeys by Mays and Sparks 1980), two peripheral targets are presented in very fast sequence while the monkey fixates. The monkey must then make a sequence of two saccades to the locations of the two targets. By choosing appropriate locations of the targets relative to a neuron's RF, one can tease apart the relationships of the neural activity to the locations of sensory stimuli and to saccade metrics.

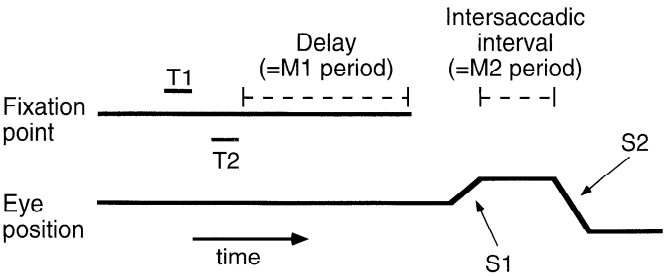

FIG. 1. Timing of stimuli and eye movements in the delayed double saccade (DDS) task. Horizontal bars indicate the appearance of the visual stimuli. Below these traces is a sketch of a typical eye position trace illustrating the monkey's behavior in the task. T1, 1st visual target; T2, 2nd visual target; M1, memory, or delay, period; S1, 1st saccade; S2, 2nd saccade.

Because in a simple double saccade task the monkey makes the eye movements as soon as possible, the visual and saccade-related responses cannot be separated (the reaction time before the 1st saccade being on the order of 150 ms). We thus added a delay requirement to this task. In the "delayed double saccade" (DDS) task, two visual stimuli appeared in sequence at different locations while the monkey maintained fixation and were followed by a delay (Fig. 1). After the delay the fixation point was extinguished, and the monkey had to make two saccades, in darkness, to the remembered location of each stimulus. During the delay period the monkey had to remember the locations of two visual stimuli and plan a saccade to the location of the first stimulus and then to that of the second one. Because in the delay period he was maintaining fixation, we could observe neural activity underlying sensorimotor integration uncontaminated by sensory or motor events.

By varying the locations of the stimuli relative to a neuron's RF, the location of sensory stimulation can be dissociated from the metrics of the saccade being planned. Gnadt and Andersen (1988) and Barash et al. (1991b) arranged the two stimuli so that they both fell outside the neuron's RF, but so that the second saccade was in the neuron's MF. Most LIP neurons became active between the first and second saccade, showing that sensory stimulation is not required to elicit LIP responses and that these responses predict the upcoming saccade vector.

For LIP activity to *specifically* encode the plan for the next saccade (as in the motor plan hypothesis), it should *1*) appear every time the monkey prepares to make a saccade in the neuron's MF, whether the stimuli were inside or outside the RF (as Gnadt and Andersen 1988 and Barash et al. 1991b showed); and *2*) be reduced or absent when the next saccade is away from the MF, even if the RF is stimulated.

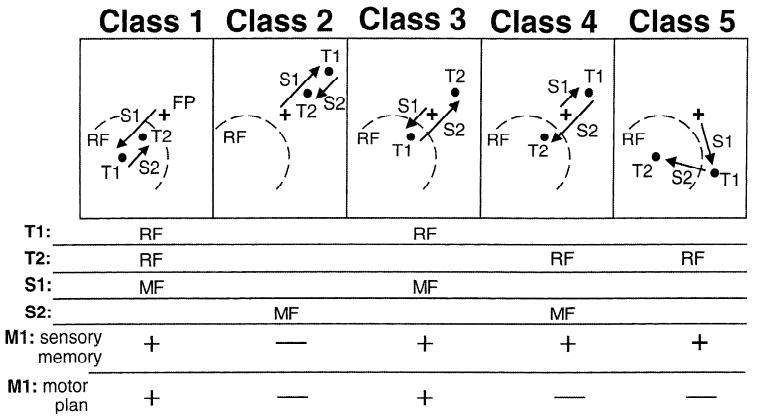

FIG. 2. Spatial arrangement of stimuli in the 5 classes of the DDS task and predictions of M1 period responses. Each panel in the top row shows the location of the fixation point (+), a sample neuron's receptive field (dashed semicircle), the locations where the 2 visual targets appear (●), and the amplitude and direction of the saccade the monkey must make (arrows). The table below the row of diagrams indicates which stimuli, in each class, fall in this neuron's receptive field and which saccades are in the neuron's preferred direction. The table's bottom 2 rows show whether or not M1-period activity is expected in each class according to the sensory memory hypothesis and according to the motor plan hypothesis. FP, fixation point; T1, T2, 1st and 2nd visual targets, respectively; RF, receptive field; MF, motor field.

Alternatively, LIP responses could encode the presence of a stimulus or the allocation of attention to a salient location in the visual field (sensory memory hypothesis), as Goldberg et al. (1990) and Duhamel et al. (1992) have suggested. In this case, these responses should appear every time a salient target (such as a saccade target) appears in the neuron's RF, regardless of whether the monkey plans the next saccade to that location or not.

We employed five different arrangements of stimulus locations (shown in Fig. 2, which will be described in more detail below). In two of these arrangements (classes 1 and 3) the first visual target fell in the RF, and the first saccade was in the MF. These stimulus classes established a neuron's M response when the saccade planned was toward the neuron's RF (*congruent conditions*).

In two other classes (classes 4 and 5) the first target was outside the RF, and the second one was inside the RF. The first saccade was thus away from the MF in spite of stimulation of the RF (*incongruent conditions*). The motor plan hypothesis predicts that M activity should be absent or reduced in the incongruent condition relative to the congruent condition. The sensory memory hypothesis, on the other hand, predicts that M activity should be similar in both conditions.

In the experiments described in this paper, the M activity of most LIP neurons carried information specific to the next planned saccade, although a number of cells also carried sensory information in the memory period. When the activity of the neuronal population as a whole is considered, the code for the next planned saccade predominates. In the companion paper (Bracewell et al. 1996), we show that this planned movement activity appears when the monkey plans to make a saccade in a certain direction independently of whether the saccade is actually made; that is, when the animal selects a different target for a movement, the movement vector encoded in area LIP shifts to reflect this change in plan. Area LIP activity includes a monkey's intention to make a specific saccade. These results suggest that the parietal lobe plays a role not only in the analysis of the sensory world but also in the preparation for movement.

METHODS

Animals, surgery, and animal care

We used two adult male rhesus monkeys (*Macaca mulatta*) in this study. We prepared each monkey for chronic recording of eye position and cortical neural activity through three surgical procedures. These were conducted with the monkey under general anesthesia [10 mg/kg im ketamine followed by pentobarbital sodium (Nembutal, 10 mg/kg iv) titrated as needed throughout the surgery] with the use of aseptic techniques. In the first procedure we implanted a scleral search coil in one eye (Judge et al. 1980; Robinson 1963) and mounted a metal head post in dental acrylic on the skull. In two separate procedures we implanted a recording chamber on each hemisphere over the posterior parietal cortex (Brodmann's areas 5 and 7). After each procedure the monkeys received analgesics and systemic antibiotics and rested for a week.

We trained the monkeys via operant-reinforcement techniques in several saccade tasks including the ones used in this study. During the training and recording periods, the monkeys' access to water was restricted to that obtained in the lab as reward for correct task execution, supplemented by additional water at the end of each session to reach the required daily ration. They had at least 2 days of rest per week with unrestricted access to water. The monkeys received routine veterinarian care, and their well-being was observed in accordance with National Institutes of Health guidelines.

Experimental setup and data collection

The monkeys sat in a completely dark room facing a large featureless tangent screen placed 57 cm away. Small light spots (~0.5° diam, ~45 cd/m^2) were back-projected onto the screen from two projectors through galvanometer-controlled mirrors. A laboratory computer (Digital Equipment, PDP 11/73) presented the stimuli and monitored the monkey's behavior. We sampled eye position at 500 Hz using the scleral search coil method, and we recorded extracellularly the action potentials of single cortical neurons with glass-coated Pt-Ir microelectrodes (Wolbarsht et al. 1960) mounted on a Chubbuck microdrive. The computer stored the eye position samples and the time of occurrence of action potentials for off-line analysis.

Behavioral tasks

Each monkey learned to perform several tasks involving saccades for the purposes of several studies. The ones used in this study are the memory saccade task and the delayed double saccade task.

A *memory saccade* (MS) trial started when a spot was turned on directly in front of the monkey, at eye level, and the monkey started fixating on it. After 800 ms of fixation, a peripheral stimulus was presented for 300 ms. The monkey was trained to continue to fixate for another 400 ms after stimulus offset (M period). At this

point the fixation spot was extinguished, and the monkey was rewarded for making a saccade, in the dark, to the remembered location where the stimulus had appeared. The stimulus was placed at an eccentricity of 5–25° along one of eight directions (the 4 cardinal and the 4 diagonal directions).

The responses of most LIP neurons during a MS trial consist of at least one of three components. These are a sensory response (LS, appearing during light stimulus presentation), a saccade-related response (SR, coincident with saccade execution), and sustained activity during the delay between stimulus presentation and fixation spot offset (memory activity, M) (Barash et al. 1991a,b; Gnadt and Andersen 1988). These signals are spatially tuned. LS responses vary across the visual field, being strongest for stimuli in a circumscribed sensory response field (receptive field, RF). SR responses vary with saccade direction (and to some extent with amplitude), reaching a maximum for saccades in the neuron's motor field (MF). The spatial tuning of the visual and saccade-related responses in LIP generally coincide, that is, the RF is in the same direction, relative to the fovea, as a saccade in the neuron's MF. The spatial tuning of the M activity generally matches that of the LS and SR responses (Barash et al. 1991b). LIP neurons thus have up to three spatially tuned fields, corresponding to the sensory, memory, and motor period of the MS task, and these fields are generally aligned in their spatial tuning. We used MS trials to identify each neuron's spatial tuning.

If a neuron had sustained M activity in MS trials with targets at 10 or 20° eccentricity, we then tested it in the DDS paradigm. This task was outlined in the INTRODUCTION. Here we give details of its parameters. A trial started when the monkey began fixating on the FP straight ahead. After a period of simple fixation (400 or 500 ms) the first visual stimulus (target 1, T1) appeared and was followed, after a brief interstimulus interval, by the second stimulus (T2). T2 was followed by a delay (the M1 period) during which the animal continued to maintain fixation. At the end of this delay, the FP was extinguished and the monkey was rewarded for making two saccades (S1 and S2) in darkness, first to the remembered location of T1 and then to the remembered location of T2. For most cells the targets were presented after 500 ms of fixation, for 50 ms each, separated by 50 ms, and followed by an M1 period of 500 ms. For a few cells the targets appeared after 400 ms of fixation, for 200 ms each, separated by 200 ms, and followed by an M1 period of 400 ms. The monkeys also made pauses of variable lengths between the first and second saccade. We refer to the period between the two saccades as M2. The timing of the stimuli was the same in all classes (Fig. 1).

We used five classes of DDS stimuli, each having a particular arrangement of the saccade targets relative to the neuron's RF (Fig. 2). In class 1 both targets (T1, T2) fall in the neuron's RF, and the first saccade (S1) is in the neuron's MF. In class 2 neither target falls in the RF, and the second saccade (S2) is in the MF. In class 3 only the first target falls in the RF and the first saccade is in the MF. In class 4 only the second target stimulates the RF, and the second saccade is in the MF. Note that in classes 3 and 4 the visual stimuli are at the same locations but are shown in opposite sequence. In class 5 the second target is in the RF but neither saccade is in the MF. The possible patterns of neuronal activity for each of these classes will be described below.

Histology

The neurons described in this study were isolated in area LIP of the right and left hemispheres of one monkey (*monkey 87-33*) and from the right hemisphere of a second monkey (*88-18*). Recordings were obtained from both hemispheres of both monkeys in the experiments described in this paper and the following one as well as in other unrelated experiments. In the last few weeks of experiments involving these monkeys, several marking lesions were made in both hemispheres by passing small DC currents through the recording electrode at different depths. Other markings were made by injecting various fluorescent and nonfluorescent dyes (Chicago sky blue, fast blue, nuclear yellow, hrp-gold, and rhodamine) at selected recording-chamber sites and depths. At the conclusion of the experiments, the monkeys were killed in separate sessions via an overdose of pentobarbital sodium and then perfused via a transcardiac route with heparinized saline, followed by buffered Formalin. Guide wires were lowered into the brain at selected recording-chamber coordinates immediately after the animals were killed. The wires were used as landmarks for blocking the posterior parietal cortex and for determining the locations of neurons that had been recorded at penetration sites not marked by a DC lesion or dye. Good agreement was found between the locations of the guide wires and the coordinates of the marking lesions and injections, indicating that the locations determined from the microdrive's coordinate system were reasonably accurate.

Forty-micrometer-thick sections were cut and were alternately stained with thionine for cytoarchitecture and by the Gallyas method for myeloarchitecture (Gallyas 1979). Areas within the PPC were identified on architectural and physiological criteria (Andersen et al. 1990a).

Figure 3 shows the estimated sites of recordings of neurons described in the present paper recorded from the right hemisphere of *monkey 88-18*. The sites are drawn on tracings of coronal sections, and the approximate anteroposterior location and angle from vertical for these sections are indicated on a tracing of a photograph of *monkey 88-18*'s brain.

Data analysis

We focused our analysis on neural activity during the M1 period of each task. For each neuron we computed the average firing rate during the delay period (except for the 1st 100 ms) and subtracted from it the average background firing rate (averaged over all classes, and computed from 300 to 800 ms from the start of each trial for cells tested with an 800-ms fixation period, and from 100 to 400 ms for cells tested with a 400-ms fixation period). We defined the resulting net firing rate as a neuron's M1 response for each behavioral class. We applied two-tailed t-tests (α level = 0.05) to each neuron's class 1 M1 response and determined whether it was positive (excitatory), negative (inhibitory), or absent. If this response was not absent, a one-tailed t-test (α level = 0.05) was used in classes 2–5 to determine whether an M1 response of the same sign as the class 1 response was present. If such a response was present in an incongruent class, it was then compared with the appropriate congruent class response (class 1 with class 5 and class 3 with class 4) to test for a significant difference. Thus, although t-tests were used extensively, they were mostly orthogonal tests because they were applied usually only once, and at most twice, on each cell's response in a given class, and thus a correction factor was not applied. A few neurons had M1 responses that were very large but clearly started after the 1st 100 ms of the delay period. For these neurons the beginning of the M1 period was adjusted manually to between 100 and 200 ms after the start of the delay period. For each neuron, however, a single definition of each period was applied to all classes of trials.

The responses and index values of a neuron in certain DDS classes were excluded from the analysis according to the following criteria. Because classes 1 and 2 tested the pattern of memory-period responses for stimuli located at 20° eccentricity, these classes were excluded from the analysis for neurons that showed no M1 responses for stimuli at 20° eccentricity (that is, no response in class 1). Classes 3 and 4, on the other hand, tested the pattern of memory-period responses for stimuli located at 10° eccentricity.

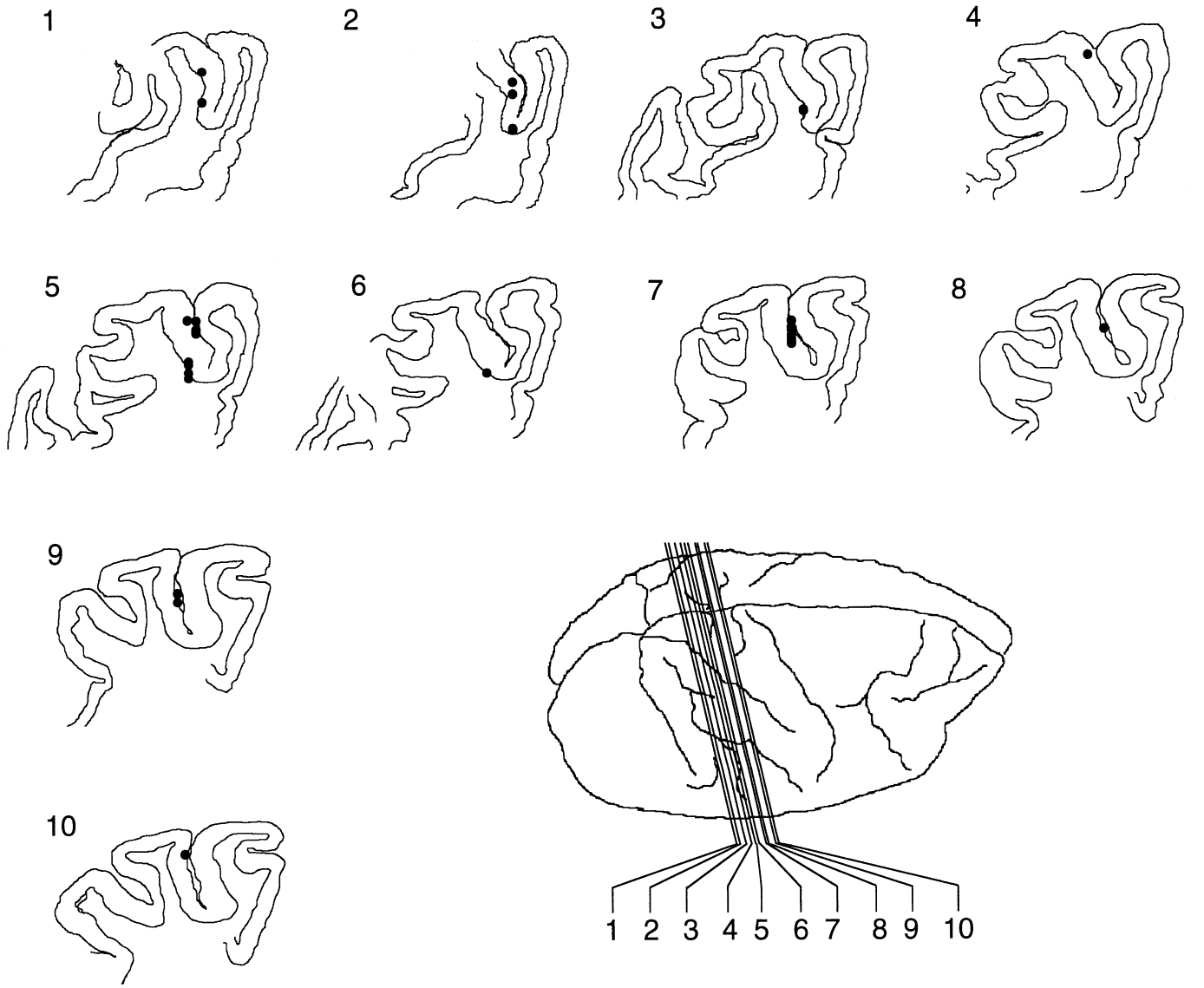

FIG. 3. Reconstructions of the locations of neurons recorded in the right hemisphere of the 1st monkey (*88-18*). *Panels 1–10* show the reconstructed locations of recording sites drawn onto representative coronal sections. The panel in the *bottom right* indicates the approximate locations of coronal sections 1–10 on a drawing of the monkey's brain viewed from a right, superior-oblique vantage point.

They were thus excluded from the analysis for neurons that had no M1 responses for stimuli at 10° eccentricity (that is, no response in class 3).

We also computed the net response of most neurons in the intersaccadic (M2) period of classes 2 and 4. We did this by aligning each trial on the beginning of the first saccade and then manually choosing a time segment that did not overlap with any part of the first or second saccade in any trial within that class. These time segments were between 100 and 200 ms. We took the difference between the average firing rate in this segment and the background firing rate as the M2 response. For several neurons the time between the two saccades was too short to compute an M2 response.

Calculation of activity indexes

As detailed further below (see *Predictions*), a difference in M-period responses between corresponding congruent and incongruent classes (i.e., between classes 1 and 5 or between classes 3 and 4) reflects a component of M activity that encodes the next planned saccade. This difference is thus an index of how much a neuron's M activity reflects a motor plan rather than a memory of the stimulus. We chose classes 3 and 4 to compute a quantitative index of motor plan encoding. We refer to this index as the *plan index,* I_p, and it is computed as

$$I_p = [(\text{class 3 M1 response} - \text{class 4 M1 response})/\text{abs}(\text{class 3 M1 response})] \times 100\%$$

where "response" refers to the difference between the M1 firing rate and the neuron's baseline, or background, firing rate, and "abs( )" refers to the absolute value function. This index expresses the component of a neuron's M1 response encoding the saccade plan as a percentage of the neuron's total response in the congruent condition. It is 100% when the entire response encodes the motor plan, and it is 0 when the entire response encodes the sensory memory.

To study the overall activity patterns of the population of neurons in the various trial classes, we first computed for each neuron an activity index, I_a, based on its M1 response. This index is the signal-to-noise ratio of the M1 response, defined as

$$I_a = (\text{average M1 FR} - \text{average background FR})/(\text{average background FR})$$

where "FR" stands for action-potential firing rate. For inhibitory cells we computed the absolute value of this index so that we could display index values of excitatory and inhibitory cells in the same plot. This index removes some of the bias in a neuron's activity that is due to the neuron's intrinsic baseline firing rate. The distribution of activity values measured by such an index is thus less skewed than the distribution of firing rates or firing rate differences, allowing for a more meaningful analysis of population-level patterns using simple measures of central tendency such as mean and standard error.

Note that the plan index, I_p, described above, can be expressed in terms of the activity index, I_a, as

$$I_p = [(\text{class 3 } I_a - \text{class 4 } I_a)/\text{abs}(\text{class 3 } I_a)] \times 100\%$$

Calculation of M2 response latency

The latency of onset of the M2 response in class 2 was obtained by first computing the time histogram of a neuron's class 2 activity with the use of 20-ms bins, aligning each trial with the beginning of the first saccade (saccades were defined as instances when the eye's tangential velocity became higher than 50°/s for at least 25 ms; the beginning of a saccade was defined as the time at which the velocity increased to >10°/s) (see Barash et al. 1991a). We then compared via a *t*-test the firing rate in each 20-ms bin to the firing rate during a baseline period within the M1 period. This baseline period was from 300 to 0 ms before the first saccade for most neurons. A few neurons had a steady decline of firing rate during the delay period of class 2; applying a strict definition of the baseline period to these neurons would give an artificially high baseline, leading possibly to an overestimation of their M2 response latency. Because we were most interested in estimating at least a lower bound of the M2 latency (to test for the possibility of predictive remapping; see DISCUSSION), we manually adjusted the baseline period of these neurons so as to exclude the period of changing activity. We were also careful to avoid averaging into the background any increase in activity before the beginning of the saccades. The latency was defined as the lower bound of the first of either *1*) two bins in which the activity was significantly different ($P < 0.05$) from the activity in the baseline period, or *2*), three consecutive bins in which the activity was different from background at a P value of 0.1. Of the latency values produced by criteria *1*) and *2*), we picked the one that produced the earlier latency value. We included criterion *2*) in order to avoid overestimating the latency of a few neurons whose M2 response developed gradually. It must be noted that it was not necessary to subtract a "visual reafference" period from the response latency because there was no stimulus present for at least 500 ms before the start of the saccade.

RESULTS

Memory-period activity in the memory saccade task

We have previously reported (Andersen et al. 1990b; Barash et al. 1991a,b; Gnadt and Andersen 1988) that the delayed saccade task allows us to distinguish three basic phases of activity in LIP cells: visual, delay period, and saccade-related. Figure 4*A* illustrates the activity of a typical LIP cell while the monkey makes a memory saccade. There is a visual response (LS) that begins after the onset of the stimulus in the RF, then prolonged, sustained activity (M) during the delay period (during which there is no stimulus in the RF, and the monkey is not making any eye move-

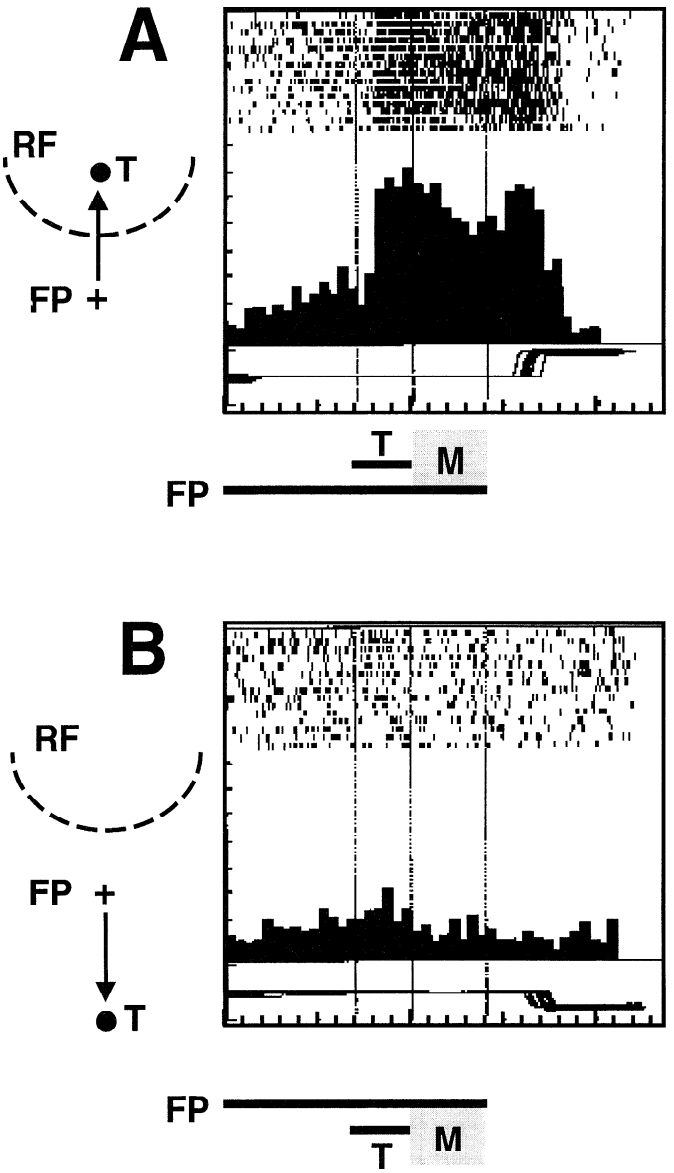

FIG. 4. Activity of a lateral intraparietal area (area LIP) neuron in 2 types of single memory saccade trials. The abscissa in each panel represents time (100 ms/division) during each trial of the task. Within each panel are plotted, from top to bottom, rasters of tick marks representing the occurrences of action potentials in each trial (1 trial/row); a time histogram (binwidth, 50 ms) of the neuron's average rate of action potential firing over all trials (20 Hz/division); and a trace of the monkey's vertical eye position (20°/division). Onset and offset times of stimuli during the trials are indicated both by the thin vertical lines within each panel and by the thick horizontal lines below each panel. To the left of each panel is a sketch of the arrangement of the visual target (dot) and the saccade made by the monkey (arrow) relative to the neuron's receptive field (dotted semicircle). FP, fixation point; RF, neuron's receptive field; T, visual target; M, memory, or delay, period. *A*: the visual target falls in the neuron's RF, and the saccade is in the neuron's MF. *B*: the visual target falls outside the RF, and the saccade is in the direction opposite the MF.

ments), and finally a second peak of activity (SR) occurring at the time of the saccade. Because the saccade is made in darkness to the remembered location of the target, the saccade-related response cannot be an artifact of visual stimulation. These findings have been described in detail by Barash et al. (1991a,b). Not all LIP neurons show all three phases of activity. In this study we further investigated the responses of units that exhibited clear M activity.

Figure 4 illustrates another key aspect of LIP neurons' responses: they are spatially tuned. In Fig. 4*A,* target is presented 15° above the fixation spot, and the neuron clearly shows LS, M, and SR activity. However, when the target is presented 15° below the fixation spot, the cell has negligible activity in all phases of the trial (Fig. 4*B*). The LS, M, and SR fields of any given neuron are typically broad (~90° width at half-maximal activity) but aligned with one another (Barash et al. 1991b). To be selected for further study in the present experiments, units had to show spatially selective M responses (the vast majority of LIP neurons were sufficiently narrowly tuned to meet this criterion).

Database

Our database consists of 49 neurons isolated in area LIP in 3 hemispheres of 2 monkeys while the animals were performing the DDS task. These neurons are a subset of a large number of PPC neurons that we isolated for this experiment and for others that we performed in parallel (Barash et al. 1991a,b; Bracewell 1991; Bracewell et al. 1991, 1996; Mazzoni 1994; Mazzoni et al. 1996). The neurons were selected according to the following criteria: first, assignation to area LIP (as described in METHODS); second, presence of clear, spatially tuned M1 period activity (significant in class 1 of the DDS task or in a simple memory saccade task by 2-tailed *t*-test at an α level of 0.05).

All 49 neurons had spatially selective M1 activity. Nineteen neurons were recorded from *monkey 87–33* and 30 from *monkey 88–18.* The M1 activity was excitatory in 34 neurons and inhibitory in 15. Most neurons were tested in DDS classes 1–4 (see *Quantitative analysis*). To test a neuron in class 5, we further required that its M1 field be narrow enough so that the first saccade would clearly be outside its RF. Our sample for this class consists of 19 neurons.

Predictions

We designed the DDS task to distinguish between two hypotheses. During the first memory period (M1) the monkey must remember and attend to the locations of two sensory stimuli. Some amount of attention must be assigned to these locations because they are goals of future saccades. By attention we mean an enhanced allocation of perceptual resources to a selected locus in the visual field. Neural activity during the delay could reflect such processing of the locations cued by the stimuli (sensory memory/attention hypothesis). The monkey, on the other hand, is also planning the next saccade during this period. Neural activity could reflect some aspect of the formulation of this motor plan (motor plan hypothesis).

Because in the DDS task the metrics of sensory stimulation and planned saccade do not always coincide, we expect different response patterns based on whether or not the neural activity reflects motor planning processes. The response patterns predicted for the five DDS classes by each hypothesis are summarized in Fig. 2. If a neuron's M activity reflects a memory of the stimulus' location or a shift of attention to that location, then this activity should appear every time a saccade target appears in the neuron's RF, regardless of whether the monkey plans the *next* saccade to that location. In every trial the monkey must attend to and memorize the location of the second stimulus as well as the first one's location. Therefore we should see activity in the delay period (M1) of classes 1, 3, 4, and 5. If the M activity encodes, on the other hand, planning for the upcoming saccade, it should appear whenever the monkey prepares to make a saccade in the neuron's MF, whether the stimulus was inside or outside the RF. Thus we should observe activity during the M1 period of classes 1 and 3, and between the first and second saccades (period M2) in classes 2 and 4. M1 activity should be significantly decreased compared with other classes, or possibly *not* appear at all, in classes 4 or 5, where the RF is stimulated but the first saccade (class 4) or both saccades (class 5) are not in the neuron's MF. It must be emphasized here that the motor plan hypothesis does not require that a neuron give no response at all in the M1 period of incongruent (class 4 or 5) trials. Because the only experimental variable between congruent and incongruent trials is the saccade plan under identical RF stimulation, any significant difference in M-period responses between these conditions must reflect a component of the M1-period activity that encodes the next intended saccade.

Activity in classes 1–4

The response pattern of an area LIP neuron in the first four classes of the DDS task is shown in Fig. 5. In class 1 both targets are in the neuron's RF, and the first saccade is in its MF. The neuron responds to T1 with a high-frequency burst of spikes and then maintains sustained M1 activity until the first saccade is made (Fig. 5*A*). This activity is predicted by both the sensory memory and motor plan hypotheses (Fig. 2) and simply confirms the neuron's preference for stimuli in and saccades toward the lower left quadrant.

In class 2 neither stimulus falls in the RF. The activity in the M1 period remains not significantly different from the background level, as predicted by both hypotheses. The neuron does become active, however, in the period between S1 and S2 (period M2; Fig. 5*B*) before a saccade in its MF, even in the absence of RF stimulation.

Classes 3 and 4 have identical spatial arrangements of stimuli. Because these appear in opposite order in the two classes, however, the saccade plans are different. In class 3 T1 is in the RF and S1 is in the MF. We see activity in M1 and not in M2, as predicted by both hypotheses (Fig. 5*C*). Note that the M1 response of class 3 is smaller than that of class 1. This is because the RF of LIP neurons are graded, giving maximal response near the RF center (Blatt et al. 1990), and T1 in class 3 is nearer the edge of the RF than in class 1. In class 4, T2 is in the RF and S2 is in the MF. Activity is absent in M1 but prominent in M2 (Fig. 5*D*). This response pattern supports

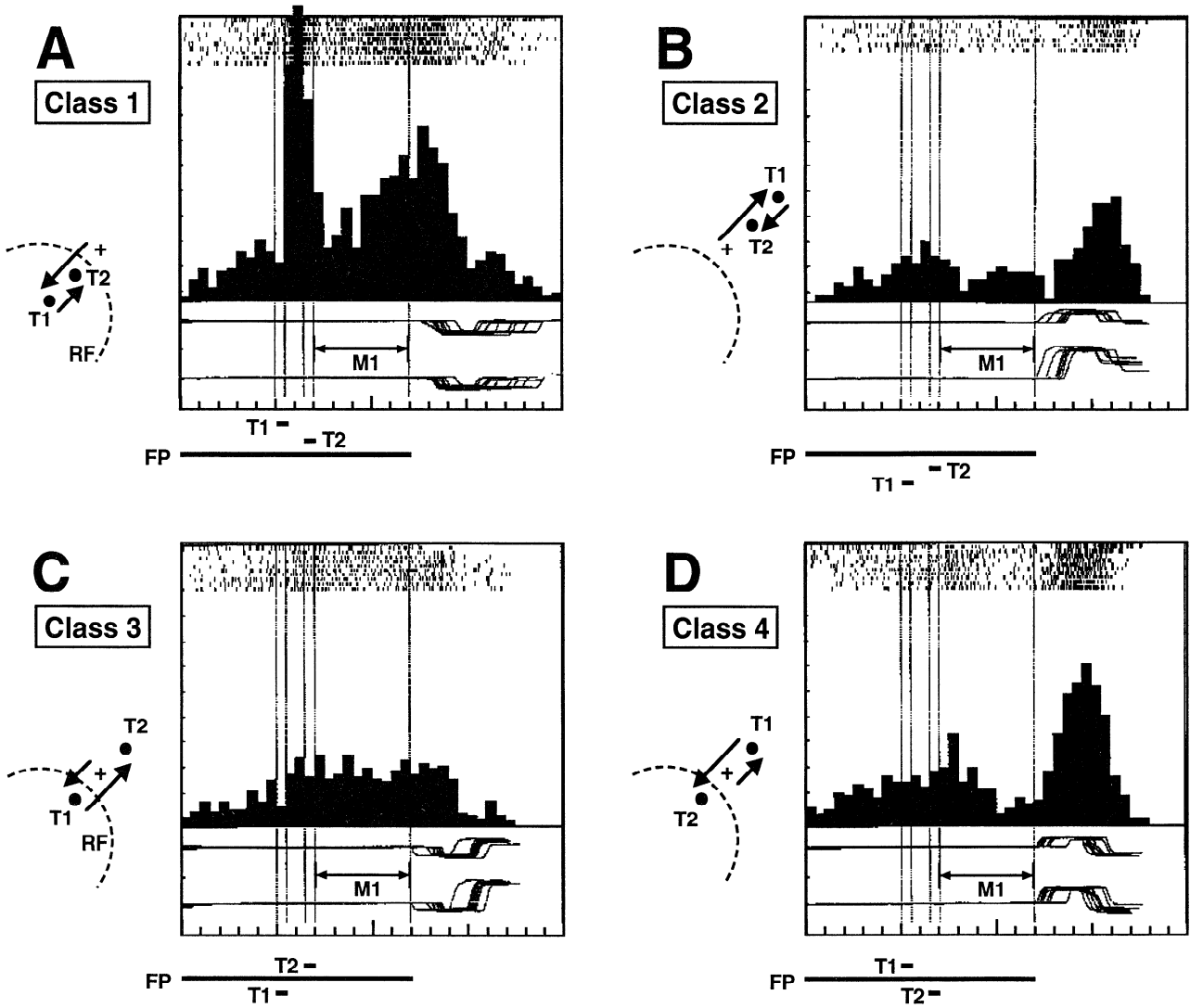

FIG. 5. Activity of an LIP neuron in classes 1–4 of the DDS task. As in Fig. 4 each panel has a plot that includes, from top to bottom, the spike rasters for each trial, the time histogram (binwidth, 50 ms) of the firing rate (20 Hz/division in *A–C*, 25 Hz/division in *D* and *E*), and the horizontal 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 1st and 2nd target (T1 and T2, respectively), the 1st and 2nd saccades (arrows), and the neuron's receptive field (RF). *A*: class 1. *B*: class 2. *C*: class 3. *D*: class 4.

the motor plan hypothesis because during M1 the planned saccade is opposite the MF, whereas S2 is in the MF. According to the sensory memory hypothesis the activity should have started in M1, immediately after stimulation of the RF by T2, and be maintained throughout M2, as the monkey had to remember the location of T2 throughout both M periods.

The M activity of the neuron of Fig. 5, when present, is of different magnitude in the various DDS classes. This can be explained by the fact that there are two sizes of retinal stimulation vectors and saccade vectors, one of 10° and one of 20°. LIP neurons are often tuned for the amplitude, as well as the direction, of the stimulation and saccade vectors (Barash et al. 1991b). When we tested this neuron on trials of single memory saccades of different sizes, it produced higher M activity in the 20° memory saccades than in the 10° memory saccades (not shown). This tuning is reflected in the different amplitudes of responses in the DDS trials (Fig. 5). High M activity always precedes 20° amplitude saccades (M1 in class 1, M2 in class 4), whereas lower (but still significant) M activity precedes 10° saccades (M2 in class 2, M1 in class 3).

Note that in Fig. 5 and in subsequent figures showing eye position traces, the eye positions after each saccade do not exactly match the target's positions, but rather tend to be shifted above the target. This "upshift" is an intrinsic feature of memory saccades made in darkness and has been described in macaque monkeys and humans (Gnadt et al. 1991). It does not affect our interpretation of M1 activity because this activity occurs while the animal is fixating straight ahead, before any saccade is made.

Activity in class 5

In class 5, as in class 3, the second target was in a neuron's RF. In contrast to class 3, however, T1 was positioned so

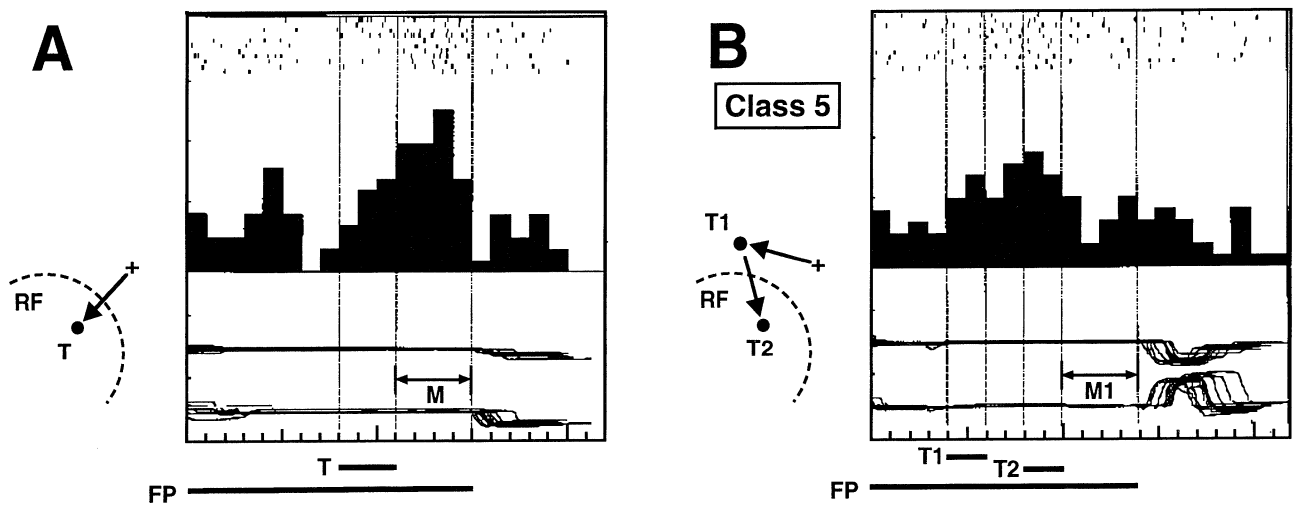

FIG. 6. Activity of an LIP neuron in a single memory saccade (*A*) and in class 5 of the DDS task (*B*). Panels are arranged as in Figs. 4 and 5, using the same abbreviations. The vertical scale for the histogram is 10 Hz/division. All other scales are as in Fig. 5.

that neither saccade would be in the MF. Class 5 thus complemented class 2 in contrasting the memory and plan hypotheses. In class 2 the RF was never stimulated, but a saccade in the MF (S2) was planned. In class 5, conversely, the RF was stimulated, but neither saccade was in the neuron's MF.

Figure 6 (see also Fig. 11) shows the activity of an LIP neuron in this class. In trials of single memory saccades directed into the lower left quadrant, the neurons showed clear M activity (Fig. 6*A*). In DDS class 5 trials (Fig. 6*B*), T2 elicits a response during its appearance. This response is suppressed, however, near the beginning of the delay period and remains suppressed throughout the execution of both saccades. There is no significant activity during the M1 period of class 5 (Fig. 6*B*), whereas it is clearly present in the memory period of the single memory saccade (Fig. 6*A*). Thus as the monkey formulates his plan, during the delay period of class 5, to make the first saccade, the neuron's activity expresses this plan and not the recent sensory stimulation.

Quantitative analysis

INDIVIDUAL NEURONS. After a neuron was selected for recording based on the criteria detailed above, its activity was recorded in various classes of trials. Most neurons were recorded on randomly interleaved trials of classes 1–4. It was not always possible, however, to test all classes of trials in all neurons. Moreover, a few neurons had memory response fields small enough to be activated by stimuli in class 1 but not in class 3, or vice versa. In these cases, only the activity from the relevant classes was included in the analysis. All trials in a class submitted to analysis, however, were always randomly interleaved with trials from the corresponding comparison classes involved in the analysis; specifically, class 3 trials were always randomly interleaved with class 4 trials. Of the 49 neurons in the data base, 33 were tested in class 1, 32 in class 2, 41 in classes 3 and 4, and 19 in class 5.

Most of the LIP neurons we studied showed the response pattern illustrated in Figs. 5 and 6. We compared the activity in the M1 period within the pairs of classes 1 and 5, and classes 3 and 4. Within each class pair the RF stimulus appeared at identical eccentricities (20° in classes 1 and 5; 10° in classes 3 and 4; see Fig. 2), but the first saccade was in the MF in only one class in each pair (classes 1 and 3). The motor plan hypothesis predicts that responses in class 4 should be absent or smaller than in class 3, and that responses in class 5 should be absent or smaller than in class 1. Smaller, but significant activity in the M1 response for classes 2 and 4 suggest that both motor planning and sensory memory contribute to the cell's M1 activity.

Of the 49 neurons in our sample, all of which had significant responses ($P < 0.05$, 2-tailed t-test) in at least one of the congruent conditions (classes 1 and 3), the majority ($n = 38$, or 77%) had no significant (or had significantly smaller) M1 responses in the corresponding incongruent conditions (classes 5 and 4, respectively; $P < 0.05$, 1-tailed t-test for lack of change or decrease in amplitude of response).

Figure 7*A* shows the average M1 response index values (that is, I_a, the signal-to-noise ratio of the M1 responses; see METHODS for details) in the five DDS classes for these neurons. The activity across this population is high in classes 1 and 3, with mean values of 1.35 and 1.44, respectively (i.e., M1 activity is 2.3 and 2.4 times greater than background), whereas it is lower or absent in classes 4 and 5 (mean 0.08 and 0.08, respectively). The activity of these neurons thus fits the quantitative predictions of the motor plan hypothesis. Because their M activity is significantly smaller after the appearance in their MF of a visual stimulus that is not the target of the next saccade, these neurons' M activity includes a component that encodes the next intended saccade. We refer to these neurons as the "motor plan" group. This term does not imply that these neurons encode only the motor plan, but rather that this is one of the signals they carry.

Of the remaining neurons, eight (16%) had activity consistent with the memory/attention hypothesis. Their M1 re-

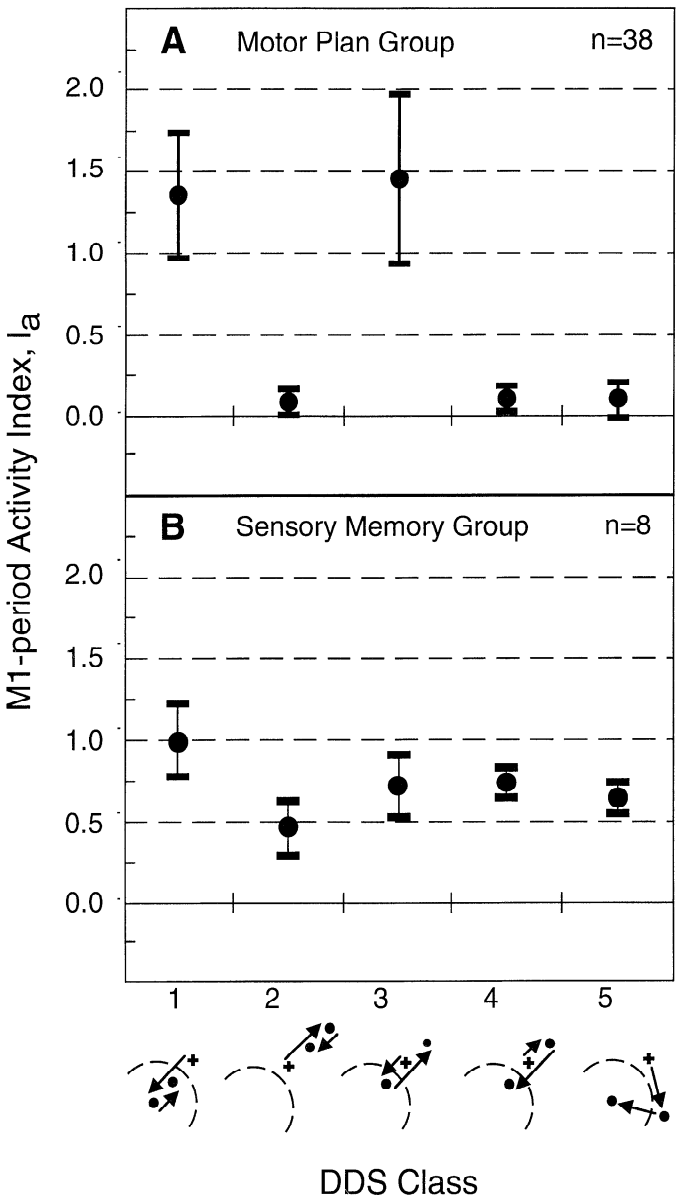

FIG. 7. *A*: mean values of the M1-period activity index, I_a, in the 5 DDS classes for the 38 LIP neurons whose M1 responses fit the motor plan hypothesis by statistical tests. Shown for each class are the class means ± SE. $n = 29$ neurons for class 1, 28 for class 2, 33 for classes 3 and 4, and 17 for class 5. *B*: mean values of the M1-period activity index, I_a, in the 5 DDS classes for the 8 LIP neurons whose M1 responses fit the hypothesis by statistical tests. Shown for each class are the class means ± SE. $n = 4$ neurons for classes 1 and 2, 8 for classes 3 and 4, and 2 for class 5.

sponses in classes 4 and 5 were not significantly lower than in classes 3 and 1, respectively ($P > 0.05$, 1-tailed t-test). Figure 7*B* shows the average I_a values in the five DDS classes for these neurons. The activity across this population is high in classes 1 (mean 0.99), 3 (mean 0.71), 4 (mean 0.72), and 5 (mean 0.629), whereas it is lower or absent only in class 2 (mean 0.45). Note that, although the mean index value for the class 2 response was 0.45, this response was not significantly different from 0 for any of the 8 neurons in this group. These neurons' responses thus always encoded the fact that a visual stimulus had appeared in their RF, regardless of the monkey's eye movement intention. We refer to these neurons as the "sensory memory" group. We use this term to emphasize that these neurons' activity does not encode a motor plan, but it does not imply that these are the only neurons encoding the stimulus' location.

The division of the neuronal data base into the motor plan and sensory memory groups just described emerged purely from differences in response patterns in the DDS task. The recording sites for cells in both groups appeared randomly interspersed, with no clear segregation of one group from the other.

The three remaining neurons had response patterns that could not be interpreted to fit either the motor planning or sensory memory hypothesis. They passed our criteria for inclusion in the data base because they had significant M1 responses in class 1 for at least one run of trials, but their response pattern varied from one run to the next. These neurons presumably encoded parameters that were not under experimental control. Alternatively, these neurons may have passed the inclusion criteria by chance, given that the α-level for inclusion was 0.05. Their activity was thus not further analyzed. We refer to these neurons as the "ambiguous response" group.

NEURONAL POPULATIONS. Because it is not known whether LIP activity is interpreted by other parts of the brain at the single neuron level or as a population activity pattern, we examined the patterns of responses for the combined populations of neurons sampled. Assuming a scenario in which a component of the nervous system receives input from all LIP neurons with clear M1-period responses, without any labeling information identifying these neurons as belonging to a sensory memory group, a motor plan group, or an ambiguous response group, what would be the net output of area LIP? Would its neurons encode primarily information about a stimulus' location, or is a code of the saccade plan available for transmission by the neuronal population as a whole?

Figure 8 shows, for each DDS class, the values of index I_a averaged over the entire population of neurons in our data base, i.e., neurons in the motor plan, sensory memory, and ambiguous groups ($n = 49$). The activity across this population is high in classes 1 and 3, with mean values of 1.24 and 1.23, respectively (i.e., the responses are on average 2.2 times greater than background), whereas it is lower or absent in classes 2, 4, and 5 (mean 0.12, 0.22, and 0.08, respectively). Analysis of variance (ANOVA) revealed a significant effect of DDS class on I_a [ANOVA with $F(4, 175) = 5.06$, $P < 0.001$]. Post hoc tests showed significantly smaller index values in classes 2 and 4 than in classes 1 and 3 (Tukey multiple comparison tests, $P < 0.05$). Moreover, there was no significant difference in the population's responses in classes 4 and 5 (in which the RF was stimulated) from its response in class 2 (in which the RF was not stimulated; Tukey multiple comparison tests, $P = 1.00$). These response patterns are the ones predicted by the motor plan hypothesis. Thus the LIP neurons we sampled express a signal specifying the next planned saccade not only at an individual neuron's level, but also at the level of the neuronal population. This signal is robust enough that it can be extracted from the average activity of a mixed population of LIP neurons, without the need to identify a priori a specific subset of neurons within area LIP.

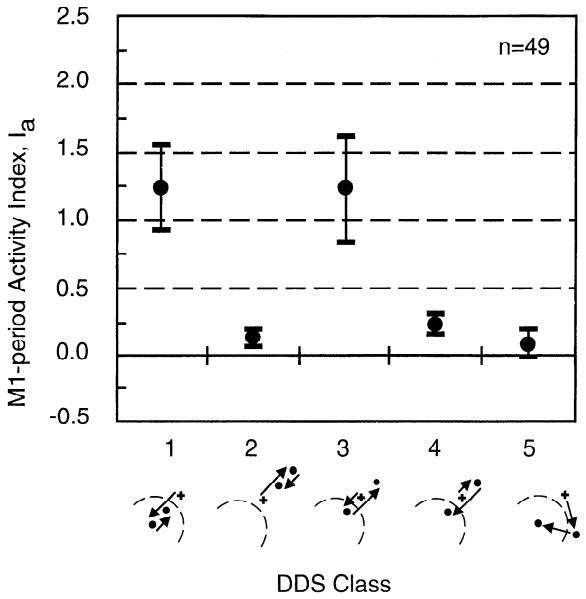

FIG. 8. Mean values of the M1-period activity index, I_a, in the 5 DDS classes for the entire population of LIP neurons in this study's data base. Shown for each class are the class means ± SE. n = 36 neurons for classes 1, 35 for class 2, 44 for classes 3 and 4, and 21 for class 5; total n = 49 neurons.

INDEX OF ACTIVITY ENCODING THE MOTOR PLAN. Figure 9 shows, for each neuron in our data base, the neuron's M1 response index (I_a) in class 4 versus its response index in class 3. Indexes for neurons encoding sensory memory alone should cluster around or above the line $y = x$ on this plot, indicating that the absence of a saccade plan in class 4 does little to reduce their responses to a visual stimulus. For seven of eight neurons in the sensory memory group, the response index values lie above a line through the origin with slope = 0.85, and five of these neurons have response indexes lying above the line with slope = 1. This indicates that changing the task conditions from motor intention in the preferred direction (class 3) to motor intention in the opposite direction (class 4) only reduces M1 activity by 15% or less for seven of eight neurons, and it *increases* the activity of five of eight neurons.

Values below the line $y = x$ indicate that sensory memory does not account for the entire class 3 response. This is the response pattern expected for neurons whose M1 activity includes a component reflecting the saccade plan, because their responses in class 4 are reduced compared with class 3. All neurons in the motor plan group but one have values below a line with slope 0.8. About one-half of these neurons have values clustering around or below the x-axis, indicating that the motor plan is not only a component of the neuron's response, but indeed the predominant signal they carry. The remaining neurons in this group have class 4 responses intermediate between 0 and their class 3 responses, indicating that their response is determined by the saccade plan as well as by the stimulus' location.

A more quantitative way to describe the data in Fig. 9 is to compute a measure of the component of a given neuron's M1 activity that encodes the next planned saccade. This is the "plan index," I_p, which measures the percentage of the M1 period response in class 3 (when a saccade in the preferred direction is being planned) that disappears in the corresponding period in class 4 (when the saccade being planned is in the opposite direction; see METHODS for de-

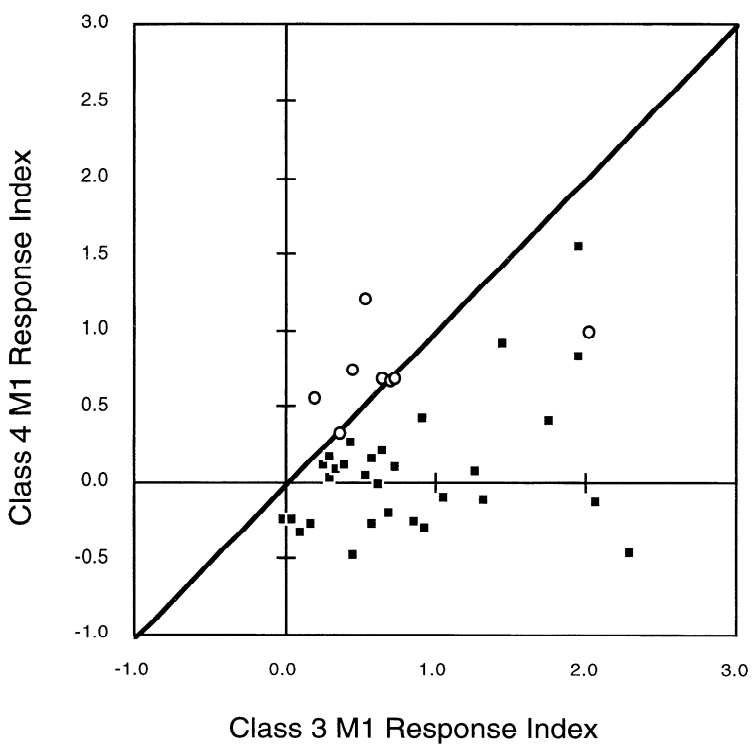

FIG. 9. Scatterplot of the M1 response index I_a in class 4 vs. the response index in class 3. Black squares indicate values for the neurons in the "motor plan group"; open circles indicate values for neurons in the "sensory memory" group. Not appearing on this plot are the 2 points (4.56, 0.32) and (17.50, 0.62).

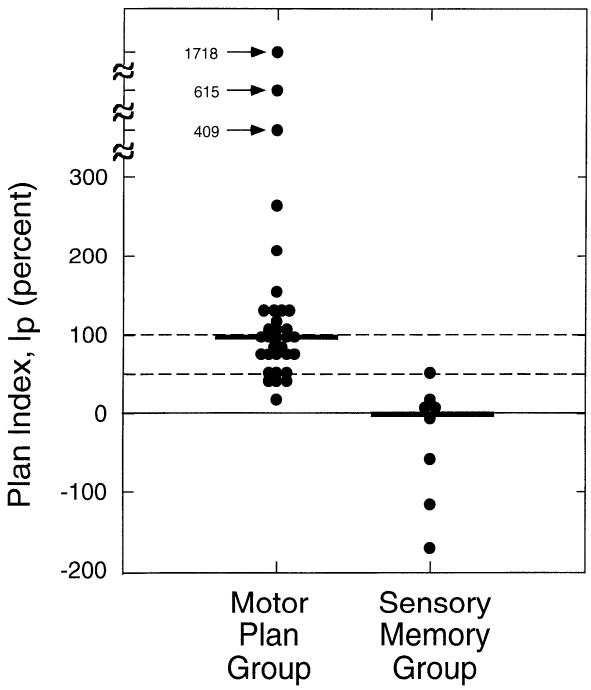

FIG. 10. Plan index, I_p, for neurons in the motor plan and sensory memory groups that were tested in classes 3 and 4. $n = 33$ neurons for the motor plan group and 8 neurons for the sensory memory group. The plan index is the percent change in a neuron's class 4 net response compared with its class 3 response (see METHODS for details). Thick horizontal bar marks the median value of each population of indexes.

tails). The values of I_p for neurons in the motor plan and sensory memory groups are shown in Fig. 10. I_p of 100% means that the entire response is accounted for by the motor plan, whereas 0 indicates that all activity is related to the sensory stimulus. Neurons in the motor plan group changed their response between 20 and 1,700% (median 94%; quartiles 72%, 130%) from class 3 to class 4. Index values >100% mean that the response changed sign (i.e., changed from excitatory to inhibitory or vice versa), indicating that the neuron's entire response during the M1 period encodes the saccade plan. Fifteen of 33 (45%) motor plan neurons had plan index values >100%, and all but 2 (94%) had values >40%. The motor plan component of these neurons' activity is thus a considerable—and in more than half the cases overwhelming—portion of their M1-period responses.

The responses of neurons in the sensory memory group, on the other hand, changed between −176 and 52% (median 2.5%; quartiles −77%, 10%; Fig. 10). An index of 0 or negative indicates that the entire response codes the sensory location. A negative plan index value indicates that the response was greater in class 4 than in class 3. Four of the cells (50%) had negative I_p values, and all but one cell (87%) had values <15%, indicating that most of these neurons strictly maintain their M1-period responses to visual stimuli regardless of what the eye movement plan is. The stronger response in class 4 than class 3 (for neurons with negative index values) may be partly due to an effect on these cells of stimulus recency, because the stimulus falling in the RF (T2 in class 4, T1 in class 3) appeared second in class 4.

Responses occurring between the first and second saccades

The two hypotheses of our study predict different response patterns in the M2 period (between the 1st and 2nd saccades; Fig. 1) of class 2. Most of the 38 neurons that fit the motor plan hypothesis had M2 responses in classes 2 and 4, as predicted by the same hypothesis. In class 2 these responses were present even though no stimulus had ever appeared in the neuron's RF. These responses reached significance in class 2 for 25 of the 38 (66%) neurons with motor planning activity that were tested in this class ($P < 0.05$). Of the eight cells whose M activity reflected the stimulus' location, six were tested in class 2. Of these, three had responses in the M2 period of class 2 ($P < 0.05$).

It should be noted that two variables may potentially affect M2 activity. Because the intersaccadic intervals were often short and of variable duration (between 100 and 200 ms), responses in this period could be contaminated by postsaccadic activity after S1 and presaccadic activity preceding S2. Additionally, any difference between the position of T1 and the eyes' actual position after the first saccade (including vertical drifts due to the upshift of memory saccades mentioned above) may introduce variation in the plan for the second saccade. Any such variations in metrics would be small relative to the size of LIP neurons' response fields, and would thus be unlikely to affect the responses significantly. However, for these reasons the M2 response is not as reliable an index of a neuron's sensory memory/motor planning activity as is the M1 response.

RFs versus tuning curves

The firing of LIP neurons for different stimulus locations and saccade vectors is usually better described by broad tuning curves than by sharply defined RFs (Barash et al. 1991b). These neurons are thus not simply either fully active or completely silent: their firing rate changes in a graded manner with changes in the location of a visual stimulus and in the amplitude and direction of the saccade required to foveate it. We would therefore expect that the firing rate during the memory period of the DDS task would reflect the direction and amplitude of the upcoming saccade according to a neuron's very broad tuning curve.

Neural activity in DDS class 5 confirmed this prediction for different saccade directions. The M activity before S1 and between S1 and S2 in class 5 generally matched the activity observed in single memory saccade trials for those directions. A clear example is offered by a cell that was excited before saccades into one quadrant and inhibited before saccades into the adjacent quadrant (Fig. 11). This cell produced clear excitatory M activity for single memory saccades directed up-left, up, and up-right (Fig. 11, *A* and *B*), and clear inhibitory M activity for down-left saccades (Fig. 11*C*). We tested this neuron in a version of class 5 with T2 falling in its excitatory RF and S1 in its inhibitory RF. The neuron showed *inhibitory* M1 activity (Fig. 11*D*), again reflecting the planned saccade and not the recent sensory stimulation. The motor planning activity of this LIP neuron contributes to the next saccade plan in a graded manner over the entire range (360°) of possible directions.

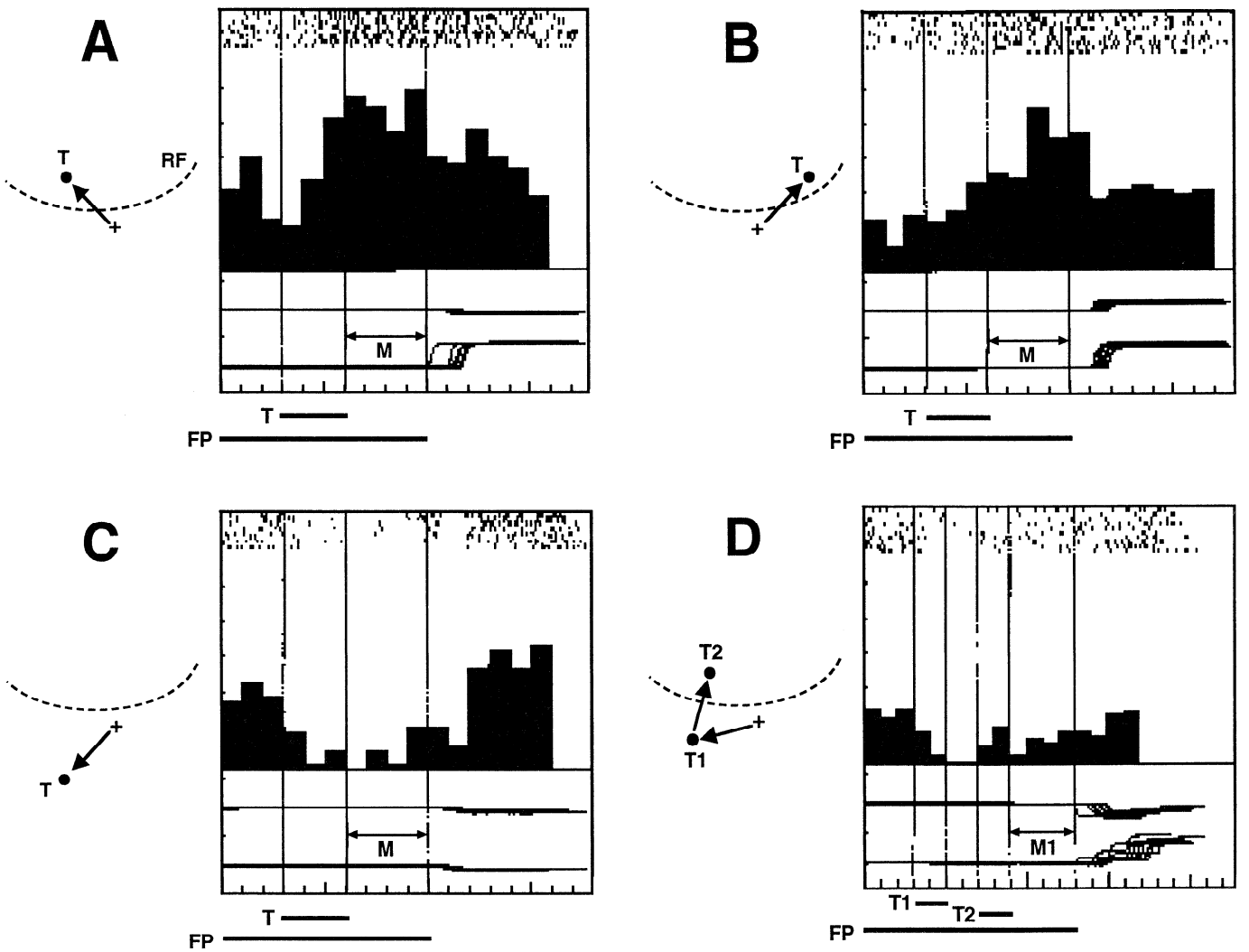

FIG. 11. Tuning of M activity for the direction of the next saccade. *A–C* show the activity of an LIP neuron in single memory saccade trials. *D*: activity of the same neuron in class 5 of the DDS task. Scales are as in Fig. 5.

Interaction of sensory response and motor plan

The neuron in Fig. 11 shows an interesting pattern of responses to sensory stimuli. A stimulus in the left upper quadrant, when presented alone (Fig. 11*A*), elicits a strong response during the stimulus-presentation period itself (LS response). When the same stimulus (T2, Fig. 11*D*), however, appears after an inhibitory stimulus in the lower left quadrant, the excitatory response is absent. We observed absent or attenuated LS responses, following a stimulus outside the excitatory RF, in 10 neurons. It is as if a neuron decided, based on the first stimulus, the direction of the saccade to be made, and from then on maintained the appropriate firing rate for that saccade plan, thus attenuating or abolishing any sensory responses to subsequent stimuli. Some neurons thus appear to express the saccade plan quite early, and to respond to sensory stimuli based on the context of the current saccade plan.

Timing of onset of M2 responses

During the delay period of classes 2 and 4, the monkey is planning a saccade away from a given neuron's RF, but also knows that immediately after the first saccade he will make the second one toward its RF. The second motor plan is reflected in the M2 activity of the neurons encoding the next saccade. The first saccade, therefore, brings the neuron's RF over the location of the next planned saccade. It has been reported that the RFs of some LIP neurons shift in advance of a saccade that will bring a visual stimulus into their RF, a process that has been termed "predictive remapping" of the RF (Duhamel et al. 1992). Therefore we asked at what time, relative to the intervening first saccade, the motor planning activity (in this case the M2 response) first appeared. To this end we measured the latency of onset of M2 responses relative to the beginning of the first saccade in class 2. In this class no stimulus ever appears in a neuron's RF, allowing us to measure the motor planning component of a neuron's activity without the contamination of stimulus-related activity.

Figure 12 shows the latency of class 2 M2 responses for 23 neurons with clear M2 responses. These responses started well after the beginning of the saccade in most neurons (141 ± 17 ms, mean ± SE). In only two neurons did the activity begin before saccade onset, and in all but four neu-

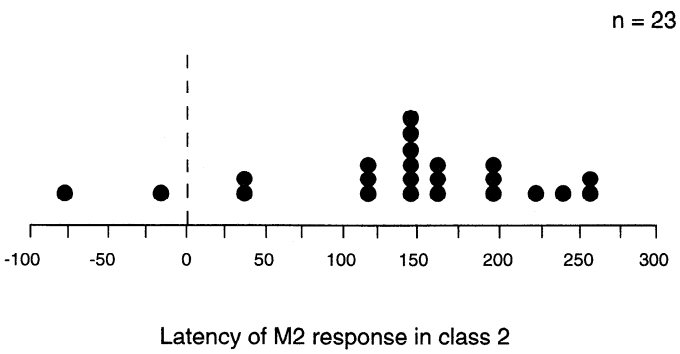

FIG. 12. Latencies of the M2 responses in class 2 of 23 LIP neurons with motor planning memory activity. The latency indicates the onset of these responses relative to the beginning of the 1st saccade. Each dot in this plot marks the latency of 1 neuron.

rons the activity started later than 100 ms after saccade onset. The activity of almost all LIP neurons in our sample thus did not begin in advance of the saccade, which is not consistent with a shift in the RF before an eye movement.

DISCUSSION

Motor intention

The most important finding of this study is that the activity of a majority of neurons in area LIP carries a signal encoding the next planned saccade. It had already been shown with the use of a double saccade task that LIP neurons become active before a saccade into their motor response field even in the absence of sensory stimulation (Barash et al. 1991b; Gnadt and Andersen 1988). In those experiments, however, the monkeys made the saccades immediately after the stimuli had appeared. The components of neural activity related to sensory memory and motor planning were thus potentially confounded with those related to sensory stimulation and saccade execution. In the present study we imposed a delay between presentation of the stimuli and saccade execution. During the delay the monkeys had to hold in memory two locations and plan the next saccade while maintaining fixation. The M activity we recorded could thus only be related to covert processes such as sensory memory, allocation of visual attention, and saccade planning.

We created a conflict, in our experiments, between the location of sensory stimulation and the planned saccade by presenting a stimulus (the 2nd target), in the neurons' sensory response field (the RF), that was not the goal of the next saccade. M activity in this condition was reduced or completely absent in most neurons compared with when the same stimulus was also the goal of the next saccade. Sensory stimulation alone is thus not sufficient to activate many LIP neurons during the delay period. We also replicated the finding of Gnadt and Andersen (1988) and Barash et al. (1991b) that LIP neurons do not require sensory stimulation to manifest motor planning activity. Most became active between two saccades if the second one will be into their motor response field, even when no stimulus had appeared in their sensory response field. Thus in the period between a visual stimulus and a saccade, many LIP neurons clearly encode, in motor coordinates, the next intended saccadic eye movement.

As mentioned above, if the M activity were a memory trace of a stimulus location or an attention shift to that location, it should have been triggered every time a stimulus appeared in a neuron's RF, independently of what saccade was being planned. Some neurons in our sample showed this pattern of responses. Their M activity may serve to allocate visual attention. This role is consistent with area LIP's extensive inputs from other visual areas (Blatt et al. 1990) and with the strong responses of this area's neurons to visual stimuli. Bushnell et al. (1981) have shown that parietal neurons produce enhanced responses to visual stimuli when a monkey actively attends to them. Alternatively, these neurons may hold a representation of a visual stimulus for later use by the visuomotor apparatus. In a double saccade task, for example, the location of the second target may need to be held in memory until the first saccade is completed, in order to program subsequent saccades. The neurons in the sensory memory group may participate in maintaining such a signal. Indeed, after being activated by the second target in class 4 of the DDS task, most neurons in this group tended to remain active throughout the first saccade, as would be expected for a neuron maintaining the target's location in memory.

The large majority of the neurons we studied, however, responded as predicted by the motor plan hypothesis. This prediction is that a component of a neuron's activity during the memory period of a delayed double saccade trial is contingent on whether the next saccade is to be made in the neuron's preferred direction. Thus even if the second target were flashed in the RF, it should evoke significantly less M activity than when the stimulus is also the goal of the next saccade. The cell should only express its full M activity *after* the first saccade, if the second saccade were in its preferred direction. About four-fifths of the cells we recorded showed this response pattern. Finally, a subset of cells had reduced activity during the M1 period in classes 4 and 5, but still had a significant response in this period. This result suggests that a group of LIP neurons have components of activity related to the sensory stimulus and the motor plan.

By observing neural activity during an imposed delay between a monkey's perception of a visual stimulus and an orienting eye movement to it, we have identified a neural correlate of the animal's oculomotor intention. The overall activity of area LIP during the M period reveals what saccade the animal intends to make next. The pattern of responses we observed cannot be explained as only reflecting shifts of attention in the visual field. Such covert attention shifts are reliably elicited by behaviorally relevant stimuli (Posner et al. 1984), such as saccade targets. In the DDS task the monkeys had to attend to two spatial locations, because both were targets of future saccades. The majority of M activity, however, was maintained only if the stimulus in the RF was also the target of the next saccade, and thus did not reflect the allocation of visual attention.

It may be argued that a saccadic eye movement is preceded by a special type of attention shift, characterized by the fact that it *always* precedes a saccade, and that the M activity of LIP neurons reflects only the allocation of atten-

tion to the subject's immediate target. An attention shift of this type, however, requires the concurrent intention to shift gaze to a given location and thus cannot be operationally distinguished from motor intention itself. We therefore regard such an attention shift—specific to the target of a saccade being planned—as part of motor intention.

Our results show that the M activity of most LIP neurons is not solely determined by sensory and perceptual processes but also carries information about the upcoming eye movement. A related question is whether the activity predicts the upcoming saccade in an obligatory fashion. LIP neurons often discharge just before, during, and after a saccade (Barash et al. 1991a). It is thus possible that the M activity is simply an early expression of the activity that will coincide with the saccade, that is, the motor command rather than the motor plan. If the M activity truly reflects the intention to make the saccade, on the other hand, it should be independent of the actual execution of the movement. We performed another set of experiments to address this question. These are described in the following paper (Bracewell et al. 1996). Briefly, we found that the M activity is indeed not contingent on actual saccade execution, and thus encodes the animal's intention rather than purely premotor processes.

Timing of onset of motor planning activity

Duhamel et al. (1992) have reported that, when a saccade is about to move a visual stimulus into the RF of an LIP neuron, the visual response of 44% of LIP neurons anticipates the saccade. The authors suggested that the response fields of these neurons temporarily shift, near the time of saccade execution, in the direction of the upcoming saccade; that is, they are predictively remapped. We found that anticipation occurs only rarely for the motor planning activity (2 out of 23 LIP neurons tested). As Fig. 12 shows, most LIP neurons remain silent as long as an intervening saccade outside their motor field is being executed. Generally, the motor planning response fields of these neurons are not remapped in advance of saccades and do not shift. One possible explanation for this apparent difference is that, although Duhamel et al. (1992) report that the RFs are remapped "in advance of the eye movement," they considered cells to be predictively remapped if the onset of activity relative to the beginning of the saccade was less than the latency of the cell's response to a visual stimulus. It is therefore likely that many of their cells began firing during or after the eye movement. A second possibility is that the memory reponse is not predictive, whereas the visual response is. Duhamel et al. (1992) do not report latency information for the remapping of memory activity. On the one hand, this possibility seems less likely because there is much more time to anticipate the consequences of the impending eye movement in the memory saccade task. On the other hand, visual responses are often more robust and perhaps it is easier to discern their onset given a limited number of trials.

Implications of motor plan encoding

Although most the results of the present study cannot be compared directly with those obtained by Duhamel et al. (1992) in support of their predictive remapping hypothesis, our findings do suggest alternative interpretations. By their view, LIP neurons have retinocentric RFs and carry predominantly visual and visual memory signals. This retinal map takes eye movements into account by remapping memory-related activity such that it always codes the retinal location of a remembered stimulus. They propose that some LIP neurons' visual RFs undergo a temporary shift in location just before a saccade, shifting back to their original locations at some point during or after the saccade is made.

Their model would yield predictions like those of the sensory memory hypothesis. It would predict that the cells code the remembered location of a stimulus and thus there should be strong activity during the M1 period in classes 4 and 5. Instead we found weak activity in these classes, indicating that most cells coded the direction of the planned movement, and not the remembered location of the stimulus during the M1 period.

The proposed remapping of remembered sensory signals is based on their finding responses when an eye movement brought the location of a recently flashed stimulus into a cell's retinal RF. An alternative possibility is that the eye movement also brought the location into the motor field of the neuron, and the animal was considering an eye movement to the flashed target location. In their experiments the animal did not make a second eye movement to the stimulus, but in the companion paper we show that the animal only needs to consider, and not execute, an eye movement in order to evoke planning-related activity. The presence of M2 activity in our experiment is consistent with both their retinal remapping hypothesis and our motor plan hypothesis. In class 4, however, the absence of activity in the M1 period argues against the M2 activity that follows being a memory of sensory stimulus location because the stimulus location was in the RF during both the M1 and M2 periods. This lack of activity in the M1 period cannot be due to a very early remapping of the RF because *1*) T2 would still be in the RF and *2*) such an early remapping would result in no activity in the M1 period in classes 1 and 3, a result that was not found.

The proposed temporary shift in RF locations was based on the finding that many responses seemed to anticipate eye movements (Duhamel et al. 1992). However, these authors first subtracted a visual latency from each of their latency measurements. These visual latencies are quite long (median 110 ms) (Barash et al. 1991a), and so it is likely that many "predictive" signals occurred during or even after the eye movements. The rationale for subtracting these long visual latencies was that, in the absense of prediction, the reafferent visual signal would require a full visual latency before appearing. On the other hand, if the activity in LIP codes the vector of a planned eye movement, then this signal can be updated by efference copies of movement commands without taking into account the reafference of sensory signals. From this point of view, it makes no sense to subtract visual latencies, and many fewer cells would be considered predictive.

Finally those cells that actually do begin responding before an eye movement do not necessarily require their RFs to temporarily jump to a new location and back if they are coding in motor rather than sensory coordinates. If a monkey

prepares a sequence of two eye movements, as in the DDS task, a majority of LIP neurons encode the plan for the first saccade, while a small number specifically encode the memorized locations of the two targets. As the execution of the first saccade approaches, the activity of the neurons carrying the motor plan changes so that the ones encoding the first saccade stop firing while those that will encode the second saccade become active. This shift in the activity between the two neuronal populations occurs around the time of the first saccade. It is possible that some of the cells that will carry the plan for the second saccade may begin firing just before the beginning of the first saccade, although most begin after the first saccade has begun. The anticipation suggests that whatever function the motor plan signal serves (being transmitted, for example, to a premotor area), this function is completed for some neurons before the first saccade starts. Thus the anticipatory component may occur in the shift in activity from one population of cells to another rather than the temporary jumping of the response fields of individual neurons. Further experiments will need to be done to distinguish between these two possibilities.

Context-dependent visual responses

Does a stimulus, if it falls in the RF of an LIP cell, always evoke a visual response? Although this appears to be true for the majority of LIP cells, in some the sensory response is attenuated or absent if the stimulus is the second in the sequence. We suggest that this is a result of the behavioral significance of the stimulus: when presented first it cues the next saccade, whereas when second it cues the second saccade. This suggests that the behavioral significance of the stimulus in part determines the "visual" response of some LIP neurons.

These findings are reminiscent of the observations of many workers in other higher order motor regions of the brain, where "sensory" responses to stimuli are typically only observed when the stimuli are cues to move. For instance, Godschalk et al. (1985) observed visual responses in the premotor cortex only if the stimuli cued an arm movement. Similarly, Seal and Commenges (1985) recorded responses to auditory stimuli in area 5 of the PPC only when these stimuli instructed the monkey to reach for a target.

Role of area LIP activity

It has been suggested (Duhamel et al. 1992; Goldberg and Colby 1992; Goldberg et al. 1989, 1990) that a major role of area LIP is the spatial analysis of the visual scene. The hypothesis is that one function of area LIP is to remap the visual scene before a saccade is made in order to predict what the reafferent visual input will be after the eye movement. Such a role would be consistent with the "where" function (i.e., the localization of visual stimuli) ascribed to the occipitoparietal pathway of cortical visual areas (Ungerleider and Mishkin 1982), which includes area LIP. By spatially dissociating sensory stimulation from the planned saccade, however, we have shown that a majority of LIP neurons encode (during an imposed delay) the monkey's intention to make the next saccade, independently of sensory stimulation. Thus, although the locations of sensory stimuli are clearly encoded in the responses of LIP neurons (in their stimulus-period responses, as well as in the memory-period activity of some LIP neurons), these neurons also carry an unambiguous code of the monkey's oculomotor intention. The role of area LIP thus cannot be limited to visual spatial analysis, but extends to a participation in movement planning.

The motor planning activity of LIP neurons demonstrated in this study is the first expression of motor intention identified in a visual cortical area. Activity encoding the upcoming movement is also common in cortical areas in the frontal lobe that are directly involved in movement preparation and execution, such as the motor (Georgopoulos et al. 1989), premotor (Bruce and Goldberg 1985; Weinrich and Wise 1982; Wise et al. 1992), and prefrontal cortex (Funahashi et al. 1990). The planning activity in the parietal cortex is quite abstract and is distinct from signals related to the execution of movements. The planning activity is not a trigger or command to make a movement, nor does it convey percise information about the dynamics of the movement.

The broad directional tuning of LIP neurons' response fields (Barash et al. 1991b) is consistent with a role of this area in encoding the next planned saccade. Such tuning allows an entire population of neurons to participate in the coding of one vector, creating a distributed representation of a single signal that is much less sensitive to the noise in the firing rate of individual neurons than a code expressed only at the single-cell level. This coding strategy seems commonly employed in nervous system structures encoding movements (Georgopoulos et al. 1986, 1988; Lee et al. 1988). The drawback of broad tuning curves is that only a few spatial signals can be encoded simultaneously. This feature of LIP neurons thus also makes it less likely that area LIP represents the visual scene, as has been suggested (Duhamel et al. 1992).

Our results, combined with the fact that area LIP is indeed located in the cortical visual pathway specialized for analyzing spatial relationships (Ungerleider and Mishkin 1982), support the revision of the role of the occipitoparietal pathway recently proposed by Goodale and Milner (1992). These authors described a patient with a posterior parietal lesion who could visually discriminate the sizes of various objects but could not adjust the size of her hand grip when grasping the objects (Goodale and Milner 1992). A similar deficit was obtained in monkeys following ablation of the cortex in the superior parietal lobule (Halsband and Passingham 1982). Goodale and Milner (1992) proposed that the role of the occipitoparietal cortical stream is to figure out not only "where" a sensory stimulus is, but also "how" to prepare an action based on the stimulus' spatial attributes. Our results would place the memory signals of LIP neurons near the final answer to such a question. Given the location of a sensory stimulus, LIP neurons "prepare" an intended saccade that will align the stimulus' location with the fovea.

By expressing only an intention to move the eyes, LIP neurons encode a pivotal point in the formulation of a motor plan, a point at which the action being prepared is unambiguously encoded but at which the plan can be freely altered as new behavioral contingencies are perceived. Area LIP

thus seems to establish a direct interface, along the extrastriate visual pathways, between the sensory and motor domains by encoding the transition from spatial perception to movement plan in the activity of its neurons.

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Address for reprint requests: R. A. Andersen, Division of Biology, 216-76, California Institute of Technology, Pasadena, CA 91125.

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