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Saccade-Related Activity in the Lateral Intraparietal Area II. Spatial Properties

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SUMMARY AND CONCLUSIONS

1. Single-neuron activity was recorded from the inferior parietal lobule (IPL) of *Macaca mulatta* monkeys while they were performing delayed saccades and related tasks. Temporal characteristics of this activity were presented in the companion paper. Here we focus on the spatial characteristics of the activity. The analysis was based on recordings from 145 neurons. All these neurons were from the lateral intraparietal area (LIP), a recently defined subdivision of the IPL.

2. Delayed saccades were made in eight directions. Direction-tuning curves were calculated for each neuron, during each of the following activity phases that were described in the companion paper: light sensitive (LS), delay-period memory (M), and saccade related (S); the latter further partitioned into presaccadic (Pre-S), saccade coincident (S-Co), and postsaccadic (Post-S).

3. Width and preferred direction were calculated for each direction-tuning curve. We studied the distributions of widths and preferred directions in LIP's neuronal population. In each case we included only neurons that showed clear excitatory activity in the phases in question.

4. Width was defined as the angle over which the response was higher than 50% of its maximal net value. Width distributions were similar for all phases studied. Widths varied widely from neuron to neuron, from very narrow (<45°) to very wide (close to 360°). Median widths were ~90° in all phases.

5. Preferred-direction distributions were also similar for various phases. All directions were represented in each distribution, but contralateral directions were more frequent (e.g., 69% for S-Co).

6. For each neuron the alignment of the preferred directions of its various phases was determined. Distributions of alignments were calculated (again, phases that were not clearly excitatory were disregarded). On the level of the neuronal population LS, M, and Pre-S were well aligned with each other. S-Co was also aligned with these phases, but less precisely.

7. A set of "narrowly tuned" neurons was selected by imposing a constraint of narrow (width, <90°) LS and S-Co direction tuning. In this set of neurons, the LS and S-Co preferred directions were very well aligned (median, 12°). The fraction of narrowly tuned neurons in the population was 40% (25/63). Thus, in a large subpopulation of area LIP, a fairly precise alignment exists between sensory and motor fields.

8. An additional set of 82 area LIP neurons were recorded while the monkey performed delayed saccades to 32 targets located on small, medium, and large imaginary circles. Preferred directions were calculated for each activity phase of each neuron, separately for each of the three circles. Preferred directions of the same phase were well aligned on the different circles. This observation supports the existence of direction preference, not strictly dependent on eccentricity. We also calculated alignment between different phases, separately for each circle. The distributions of alignments were similar, indicating that our results are not a peculiarity of the eccentricities used.

9. The Post-S activity was not well aligned with the Pre-S phases. The distribution of alignments of the Post-S activity with the Pre-S phases was flat.

10. We recorded 33 neurons while the monkey was performing back- and double-saccade paradigms. Neurons in LIP become active in anticipation of a saccade made into their motor field even if no visual stimulation has occurred in their receptive field, that is, these neurons code in motor coordinates.

11. These characteristics of the activity in area LIP suggest that this cortical region is involved in the transformations of visual information for the planning of saccadic eye movements.

INTRODUCTION

The lateral intraparietal area (LIP) is a subdivision of the inferior parietal cortex (IPL) originally defined by its strong anatomic connections to established saccade centers, e.g., the superior colliculus and the frontal eye fields (Andersen et al. 1985; reviewed in Andersen 1987). These anatomic connections lead to the hypothesis that, within the IPL, area LIP is specialized for processing saccades. Here and in the companion paper (Barash et al. 1991), we investigate the saccade activity in area LIP, in the light of this hypothesis.

An important paradigm in investigating the IPL as well as other saccade-related structures has been the delayed-saccade task (Hikosaka and Wurtz 1983). With the use of this paradigm, Andersen and colleagues (Andersen et al. 1987) showed distinguishable light-sensitive (LS) and saccade-related (S) activities in IPL neurons. Further, Gnadt and Andersen (1988) described a third type of activity, specific to the delay period, called memory (M), because it was presumed to be related to the memory of the location of the target for the movement. However, these and other earlier studies did not explore the distribution of these types of activity within the subdivisions of the IPL. In the companion article (Barash et al. 1991) we showed, with the use of delayed saccades, that area LIP contains vigorous LS, M, and saccade-coincident (S-Co) activity. In contrast, in neighboring area 7a, another major part of the IPL, these types of activity are weaker in delayed saccades, with the exception of the postsaccadic (Post-S) activity. Moreover,

we showed that the majority of area LIP neurons that have S activity become active before the saccade, whereas in area 7a presaccadic (Pre-S) neurons are only a small minority. Thus the hypothesis that area LIP is involved in saccades is corroborated.

In the present article we study the spatial characteristics of LIP neurons' activity. We find that the LS, M, and S components of activity are all direction tuned. At the single-cell level, these three components are generally aligned with one another. In special double saccade tests we found that the M activity is coded in motor, not sensory, coordinates, indicating that this activity is related to the planning of saccadic eye movements.

Preliminary reports of parts of this work have been published elsewhere (Andersen and Gnadt 1989; Barash et al. 1988, 1989; Gnadt and Andersen 1988).

METHODS

The general framework of the experiment has been described in the METHODS section of the companion paper (Barash et al. 1991). Here we add information specific to the present paper.

Delayed saccades to eight locations

For the 145 neurons that are the primary data base of this study, the nine target stimuli were usually positioned 15° apart, on an imaginary grid centered on the fixation point. A grid was more suitable than a circle for other studies carried out in parallel on these neurons (Andersen et al. 1990). We directly compared the responses of 15 neurons in the standard task with the responses obtained when the targets were placed on a circle with 15 or 20° radius. In both conditions, responses were similar.

The end points of the saccades were usually not identical to the locations of the targets. This is typical of saccades to remembered locations. The performance of both monkeys and humans for M saccades was studied by Gnadt et al. (1991). Their main findings were as follows: *1*) for delay durations of hundreds of milliseconds, the longer the delay between target disappearance and fixation-point offset, the larger are the errors. *2*) Saccades directed down are usually hypometric, whereas saccades directed upward are normal or hypermetric. *3*) Horizontal saccades are often, but not always, hypometric. *4*) M saccades are often curved. *5*) The accuracy of M saccades depends critically on the visual background; the large errors seen in total darkness are often dramatically reduced by introducing a textured, random dot background. Our observations were consistent with the first four findings. (We did not investigate the effect of visual background in the present study.)

We wished to examine whether the results of the present analysis depend on the differences between the target locations and the actual end points of the saccades. Therefore, for 25 neurons, we carried out the analysis described in the rest of this paper in parallel for both the locations of the targets and the locations of the actual end points of the saccades and compared the two sets of data in detail. The results of the two sets were similar. In the rest of this paper, we define the direction of the saccade as the direction of the target.

Delayed saccades to 32 locations

An additional group of 82 neurons was recorded from the second hemisphere of the second monkey in a complementary study, examining the activity fields at a higher grain of 32 locations. The criteria for classifying the neurons to area LIP were those described in the METHODS section of the companion paper. The delayed-saccade paradigm was the same as described above, except for the location of the targets: in three distinct blocks of trials, targets were placed in directions $\theta_i = 45° \cdot i$ ($i = 1, \ldots, 8$), on circles of radii 7.5, 15, and 22.5°, respectively (sometimes the radii were, instead, 5, 15, and 25°). In the fourth block targets were placed on a 15° circle, in directions $45° \cdot i + 22.5°$. The order of the blocks was varied from one neuron to another.

Definition of the activity phases

For the convenience of the reader, we reiterate here the activity phases used in this paper, which were defined in the companion paper (Barash et al. 1991) (in a few neurons the times of the slices were slightly changed, to fit their pattern of activity): *1*) background, 300–700 ms from "fixation attained"; *2*) LS, 75–275 ms from target onset; *3*) M, 200–400 ms from target offset; *4*) Pre-S activity, 200–25 ms *before* the beginning of the saccade; *5*) S-Co, 25 ms before the saccade to 75 ms after the beginning of the saccade; *6*) Post-S, 200–500 ms after the beginning of the saccade. The last three phases are based on alignments of the trials on the beginning of the saccade, as previously described.

Double-saccade and back-saccade tasks

The double-saccade and back-saccade tasks (Mays and Sparks 1980) were designed along similar lines to the delayed-saccade task (for a description of the delayed-saccade task, see METHODS of the companion paper). The first part of a trial was identical in all tasks: a fixation spot was turned on, and the monkey had to foveate it within 1 s. Fixation attained was defined as the time point in which the eye entered a specified window around the fixation spot. If the monkey failed to fixate the spot within the given 1 s, the trial was aborted, declared a "miss," and an intertrial interval was begun.

In the double-saccade task, 1 s after fixation attained, the fixation spot was extinguished, and at the same time the first peripheral target spot was flashed for 60 ms; simultaneously with the offset of this first target spot, a second target spot appeared, also lasting 60 ms. The extinction of the fixation spot served as a "go" signal for the saccade. Because the latency of the first saccade was always >120 ms, both saccades were made in complete darkness. Within 500 ms of fixation-spot offset, the monkey had to make a first saccade to the location of the first target. Then, within 1,000 ms, but not before 100 ms, a second saccade had to be made to the location of the second target. After the second saccade the monkey had to keep his eye at the location of the second target for an additional 300 ms. If the monkey fulfilled all these conditions, the trial came to a successful end (a "hit"), and the animal received a reward, a drop of apple juice. If a trial had reached the fixation-attained stage but failed to satisfy any of the subsequent conditions, the trial was aborted and declared an "error." (In some cases these timings were slightly varied.)

In the most frequent arrangement of target positions, eight classes of trials were randomly interleaved. In the first class, an up stimulus, $(x,y) = (0,15)$, was followed by an up-and-right stimulus (15,15). In the second class, a right stimulus (15,0) was followed by up and right. The other classes consisted of the analogous paths in the other quadrants.

In the back-saccade task the fixation spot was extinguished 800 ms after fixation attained, and at the same time one peripheral target spot was flashed on the screen for 100 ms. Here, too, the offset of the fixation spot served as a go signal for the saccade. Because the saccadic latency was longer than the lifetime of the target spot, all movements were made in the dark. Within 500 ms of fixation-spot offset, the monkey had to make a first saccade to the location of the first target. Then, within 1,000 ms, but not before 100 ms, a second saccade had to be made back to the location of the initial fixation spot. After the second saccade, the mon-

key had to keep his eye inside the fixation-point window for an additional 300 ms (again, these are typical timings). Fulfillment of all these conditions led to declaring the trial a hit and to rewarding the monkey; otherwise (if the fixation-attained stage has already been reached) the trial was aborted and declared an error. A typical run consisted of two randomly interleaved classes of trials. The peripheral stimulus appeared in these classes in opposite positions, e.g., down (0,−15) in one class, up (0,15) in the other. (Sometimes these were mixed with 2 additional classes, in which the fixation spot would reappear, facilitating the animal's task.)

The spatial windows used in back saccades and double saccades were similar to those of the delayed saccades (Barash et al. 1991).

Direction tuning

A direction-tuning curve is defined as eight points in a polar plot, (r_i, θ_i), $i = 1, \ldots, 8$, characterized by the following two conditions. *1*) The directions of the points are 45° apart: $\theta_i = 45° \cdot i$, where 0° is horizontal contralateral, and 90° is upward. *2*) The distance of the point from the origin, r_i, is proportional to the

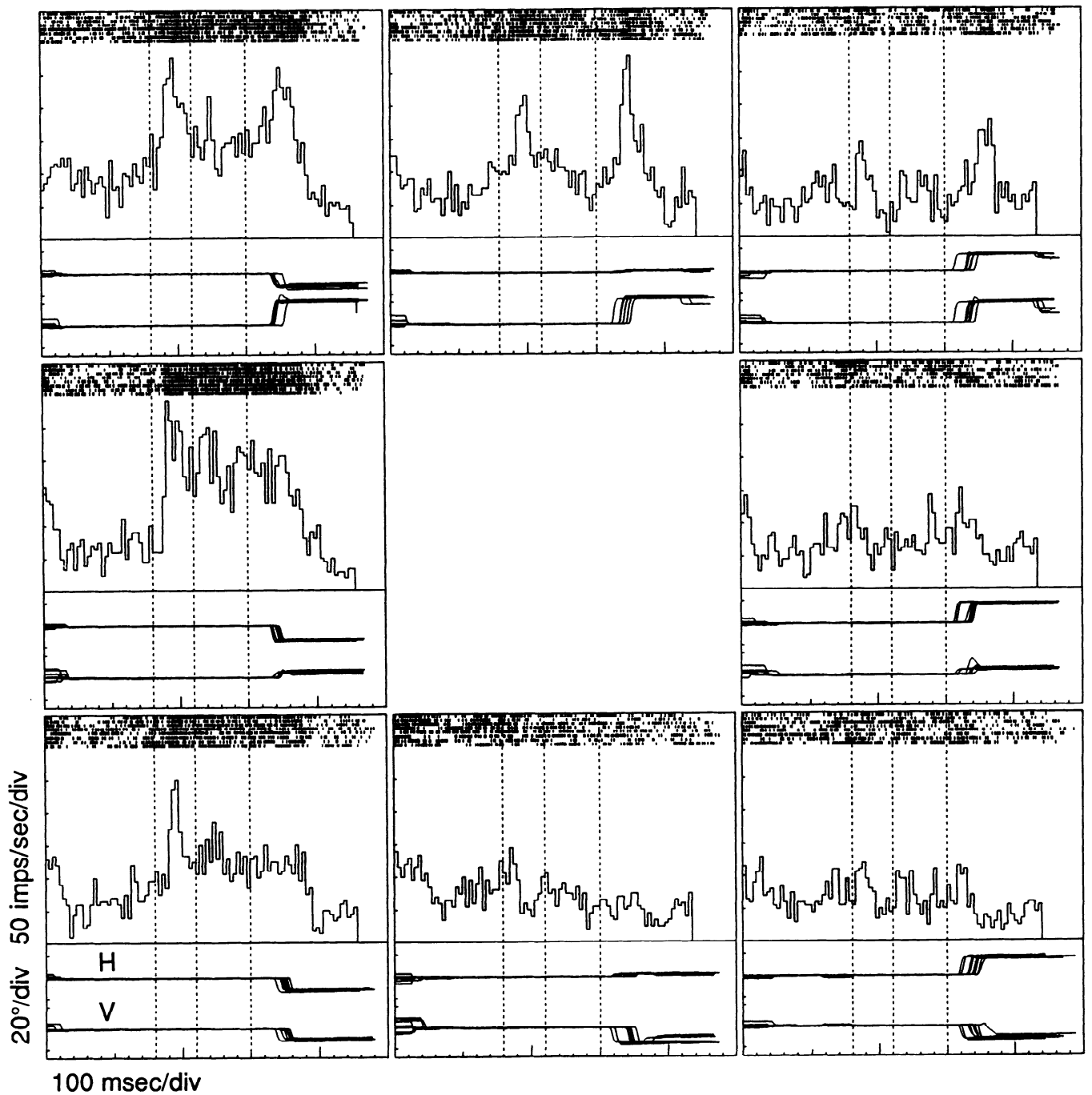

FIG. 1. Activity of an area LIP neuron for delayed saccades made in 8 directions, 45° apart. Each panel illustrates the trials made in the direction the panel occupies relative to the center of the figure. Shown in each panel, from the *top*, are the spike rasters, where each horizontal trace represents a trial, and each tick within a line marks the time of occurrence of a spike; the resulting histogram; and the horizontal and vertical eye-position traces of the various trials, superimposed. Vertical dotted lines denote, from the *left*, the onset and offset of the target, and the offset of fixation spot. Trials are aligned on the sensory events (note variable saccadic latencies).

neuron's rate of activity in the period to which the tuning curve relates. Examples of direction-tuning curves are given in Figs. 2 and 4.

The width of a direction-tuning curve was defined as the angle over which the net activity was at least 50% its maximum. In more detail, the following procedure was applied: the points of the tuning curve were connected with linear segments (see Fig. 2). A threshold rate was defined as $r_{thr} = bck + 0.5 \cdot (r_{max} - bck)$ where $r_{max} = \max \{r_1, \ldots, r_8\}$, and bck is the average background rate. The width of the direction-tuning curve was defined as the length of the unit circle sector(s) $\{\alpha | -180° \leq \alpha \leq 180°$ and $r(\alpha) \geq r_{thr}\}$.

Parametric curve fitting has been used in cortical physiology to evaluate tuning-curve width (and preferred direction), applying various families of curves (e.g., Bruce and Goldberg 1985; Georgopolous et al. 1982). Because the tuning curves we obtained had highly variable shapes (see, for instance, Figs. 2 and 4), we favored a relatively model-free approach.

The following algorithm was used to evaluate the preferred direction of a polar tuning curve (e.g., Fig. 2). To every line through the origin in direction α, we set $S(\alpha) = \sum d^2(r_i, \theta_i, \alpha)$. Here $S(\alpha)$ is the sum of squared distances from the ith point in the graph (r_i, θ_i), $i = 1, \ldots, 8$ to the line $d(r_i, \theta_i, \alpha) = r_i^2 \cdot \sin^2(\theta_i - \alpha)$. Because α is orientation, i.e., $S(180 + \alpha) = S(\alpha)$, we can assume $0° \leq \alpha \leq 180°$. We determined the α for which $S(\alpha)$ was minimal. To decide between α and $180 + \alpha$, we formed the sum $S_p(\alpha) = \sum p(r_i, \theta_i, \alpha)$ of the (signed) projections of the points of the graph on direction α: $p(r_i, \theta_i, \alpha) = r_i \cdot \cos(\theta_i - \alpha)$. The preferred direction was defined as α if $S_p(\alpha) \geq 0$, otherwise $180 + \alpha$.

The reason we have implemented this algorithm rather than the more conventional center of mass (cf. Batschelet 1981) was that some direction-tuning curves were bimodal: in addition to the preferred direction α, there was activity above background also in direction $180 + \alpha$. In such a situation the vector sum strongly fluctuates and does not reflect the cell's directionality, whereas our estimation of α remains robust. Note that bimodal direction-tuning curves were not typical but occurred often enough to merit introducing this algorithm.

Statistically the estimation of α is unbiased by the fact that we always sample the same set of eight directions; e.g., given the random eight points (r_i, θ_i), $i = 1, \ldots, 8$ where $\theta_i = 45° \cdot i$, the estimated α's will be uniformly distributed and not tend to cluster close to the sampled directions $45° i$.

Direction tuning of inhibitory responses

To estimate the "preferred direction" of inhibitory responses, the same procedure as in excitatory responses was applied, not to the spike rate, but, instead, to the inverse of the spike rate, or to the ratio background/spike rate. Care was taken to avoid extreme val-

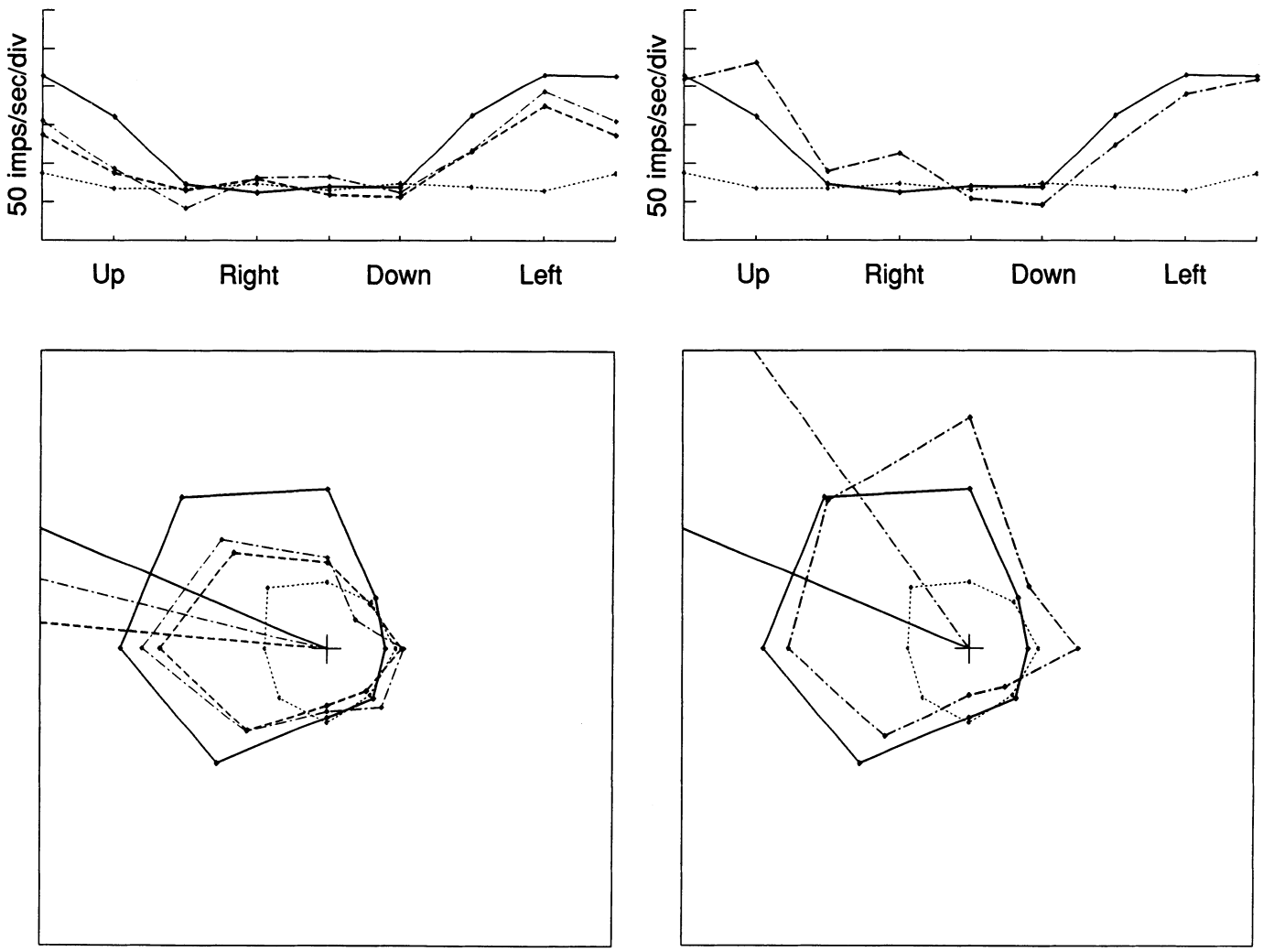

FIG. 2. Direction-tuning curves of each phase of the activity, obtained for the area LIP neuron illustrated in Fig. 2. Data are plotted twice, in rectangular coordinates (*top*) and in polar coordinates (*bottom*). Straight lines radiating from the center of each polar plot represent the calculated best direction for each time slice of activity. Plotted phases are background (· · ·), LS (——), M (– – –), Pre-S (– · – · – in *left panels*), S-Co (– · – · – in *right panels*).

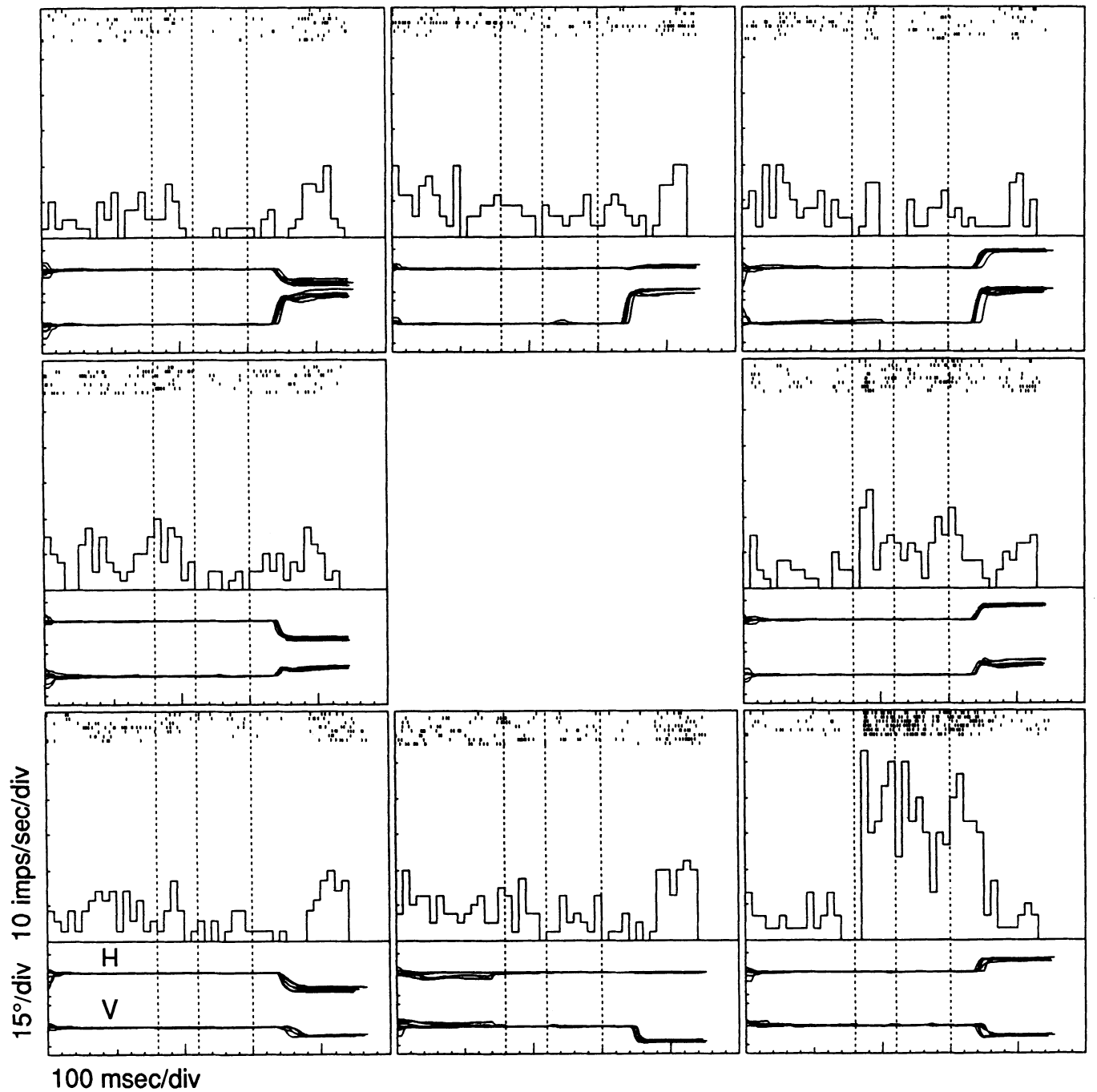

FIG. 3. Activity of another area LIP neuron in delayed saccades made in 8 directions, 45° apart. These plots are in a similar format as Fig. 1. This neuron shows a narrower tuning than the neuron in Fig. 1.

ues, resulting from spike rates very close to zero. This substitution produced reasonable estimates for the directionality but was too crude for estimating other parameters (such as width).

RESULTS

Visual and movement fields

Most LIP neurons are not active in all delayed saccades, but only in trials directed to certain parts of space. Figures 1 and 3 illustrate two LIP neurons active when a saccade is made (Fig. 1) in an up-and-right, up, up-and-left, left, or left-and-down direction, and (Fig. 3) in a right-and-down direction. If neurons are to contribute to spatial processing, their activity cannot be the same in all locations. Clearly, the LIP neurons depicted in Figs. 1 and 3 satisfy this requirement.

The three phases of activity described in the companion paper, LS, delay-period M, and S, can be discerned in Fig. 1 in five of the eight directions investigated. However, the relative intensities of each phase vary from one direction to another; for instance, the memory activity is almost as strong as LS or S-Co in leftward saccades but is barely above background in the upward direction. The direction tuning of these phases is similar, but not identical.

Figure 2 illustrates direction-tuning curves obtained for each phase of activity from the data plotted in Fig. 1. The *bottom* of Fig. 2 are polar graphs, i.e., the distance to each point in the graph from the origin is proportional to the average spike rate measured for saccades whose direction was the same as the direction of the point on the graph. Two curves in Fig. 2, Pre-S and S-Co, cannot be directly compared with Fig. 1. In these phases an interval is marked in each trial with respect to the beginning of the saccade (described in detail in METHODS). The latency of the saccade varies from trial to trial. Hence, to directly convey the direction-tuning curves for Pre-S and S-Co, the trials in Fig. 1 must be shifted so that they are all aligned on the beginning of the saccade. The preferred direction for each tuning curve is indicated by the straight line emanating from the origin (see METHODS for the procedure of computation).

The direction tuning of the neuron depicted in Fig. 2 is very broad: in the S-Co phase, this neuron responds over a range of more than 180°; the LS tuning curve is almost as broad; the M and Pre-S tuning curves are narrower. Note that the direction-tuning curves, in all phases of the activity, are approximately aligned. More specifically, the M and Pre-S tuning curves overlap each other almost precisely. The LS tuning curve is also similar in preferred directions to M and Pre-S (9 and 17° difference, respectively). The S-Co tuning curve, however, is different, particularly in the upward direction; and the S-Co preferred direction is less well aligned with those of LS, M, and Pre-S (31, 48, and 40° difference, respectively).

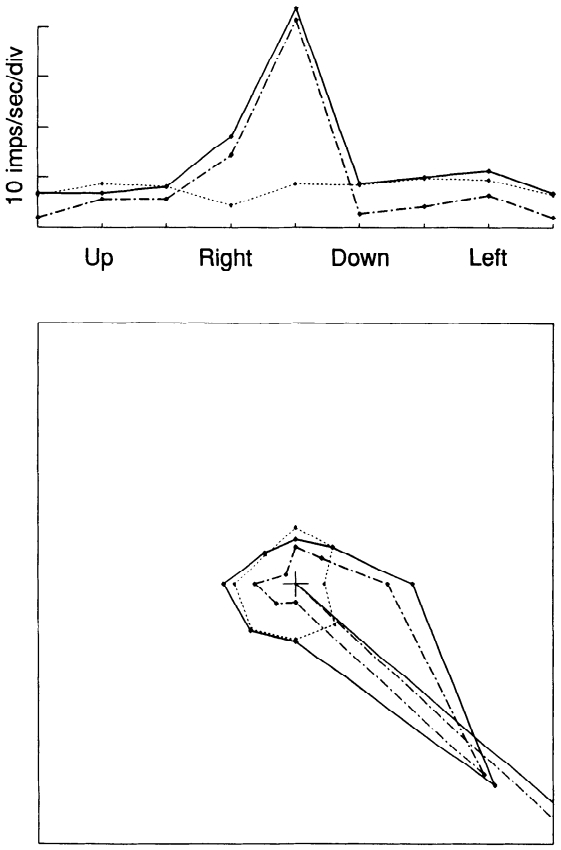

FIG. 4. Direction-tuning curves of each phase of the activity, obtained for the area LIP neuron illustrated in Fig. 3, and plotted in the same format as Fig. 2.

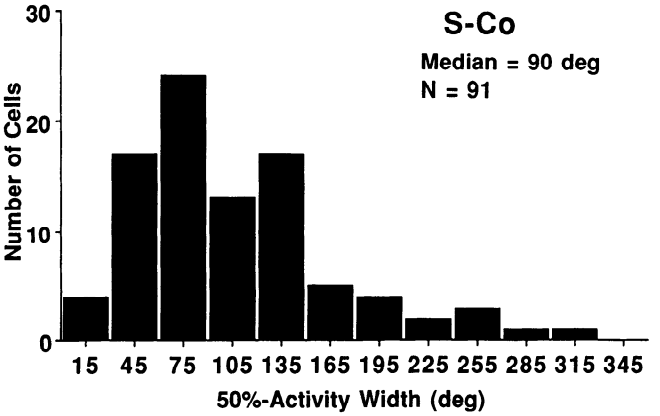

FIG. 5. Distribution of the width of the S-Co activity tuning curves. Width was calculated for 91 area LIP neurons with clear excitatory S-Co activity. The median width is 90°.

Figure 4 shows direction-tuning curves of the neuron of Fig. 3. This neuron is clearly different from the one depicted in Figs. 1 and 2. The direction tuning of this neuron is much narrower, spanning primarily one direction, and the preferred direction is nearly the same for LS, M, and S-Co, thus resulting in an almost perfect alignment.

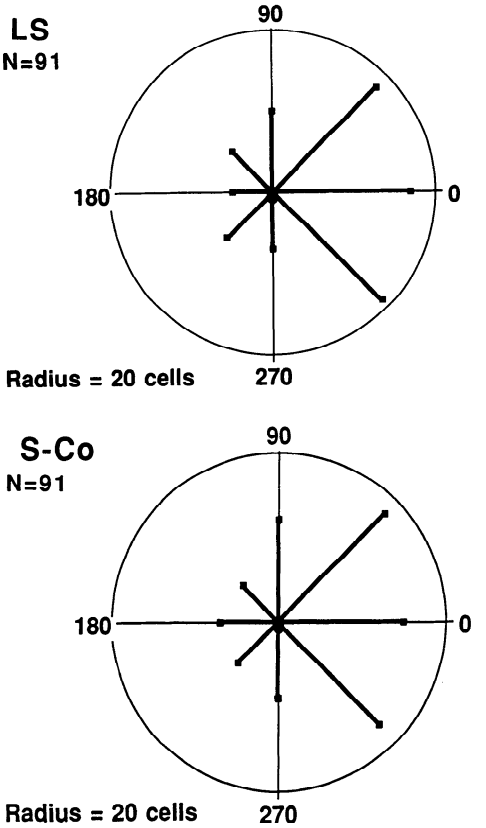

FIG. 6. Distribution of the preferred directions of the LS activity (*top*) and the S-Co activity (*bottom*) of the area LIP neurons with excitatory activity in the respective phases. Each neuron was placed in a 45° wide bin, centered around 1 of the 8 cardinal directions. Number of neurons with a given preferred direction is indicated by the radius of the line in that direction. Zero degrees denotes horizontal contralateral, 90° denotes the up direction.

Distribution of widths of tuning curves

The width of a tuning curve was defined as the angle over which the net activity was at least 50% its maximum (see METHODS for details). Figure 5 displays the distribution of widths for the S-Co phase. Included in this distribution are 91 LIP neurons with clear excitatory activity (S-Co activity index 2.0 or greater) (see METHODS of the companion paper, Barash et al. 1991). Observed width values ranged widely, from 26 to 313°. One-quarter of the units were broad, with width greater than 130°. For instance, the width of the S-Co phase in the unit displayed in Figs. 1 and 2 was 142°. One-quarter of the units were narrow, having width <69°; e.g., the width of the Pre-S activity of the unit of Figs. 3 and 4 was 47° wide. The remaining half of the units had width between 69 and 130°; the sample median was 90°, and mean ± SD was 105 ± 68. Therefore a typical S-Co field spans roughly one quadrant.

The width distributions of the other phases were likewise calculated. The distributions were similar to the S-Co activity. The medians of the M and Pre-S periods were slightly smaller (75 and 69°, respectively), and of the Post-S period slightly larger (103°).

The width of a phase, as defined here (see METHODS), is normalized to the neuron's maximal level of activity in the phase under consideration. An alternative normalization would be to the overall maximal activity of the neuron, in any phase. The maximal activity in M and Pre-S is somewhat lower than in LS and S-Co (Barash et al. 1991). Hence widths defined by this alternative normalization would be somewhat narrower for M and Pre-S.

The eight-target paradigm we employed allowed a sampling resolution of 45°. Therefore very narrow units could be underrepresented because of sample aliasing. The excellent alignment found for narrow units may suggest, however, that such aliasing does not often occur.

Distribution of preferred directions

A preferred direction was calculated for each tuning curve (i.e., for each neuron, in each phase with clear excitatory activity). Figures 2 and 4 show examples of tuning curves and the preferred directions assigned to them.

Figure 6 shows histograms of the preferred directions for the LS and S-Co phases. Only neurons with clear excitatory activity in LS (*top*) or S-Co (*bottom*) were included in the histograms. The shapes of the two histograms are very similar. Virtually all directions are represented; however, most of the neurons [71% (65/91) in the LS phase, 69% (63/91) in the S-Co phase] point in contralateral directions. In the other phases, likewise, all directions were represented, but most neurons were contralateral: 62% (45/73) in M, 69% (49/71) in Pre-S, and 56% (43/77) for Post-S.

We calculated preferred directions also for inhibitory responses. Clear inhibitory responses were required for inclusion in the analysis. (A clear inhibitory response was de-

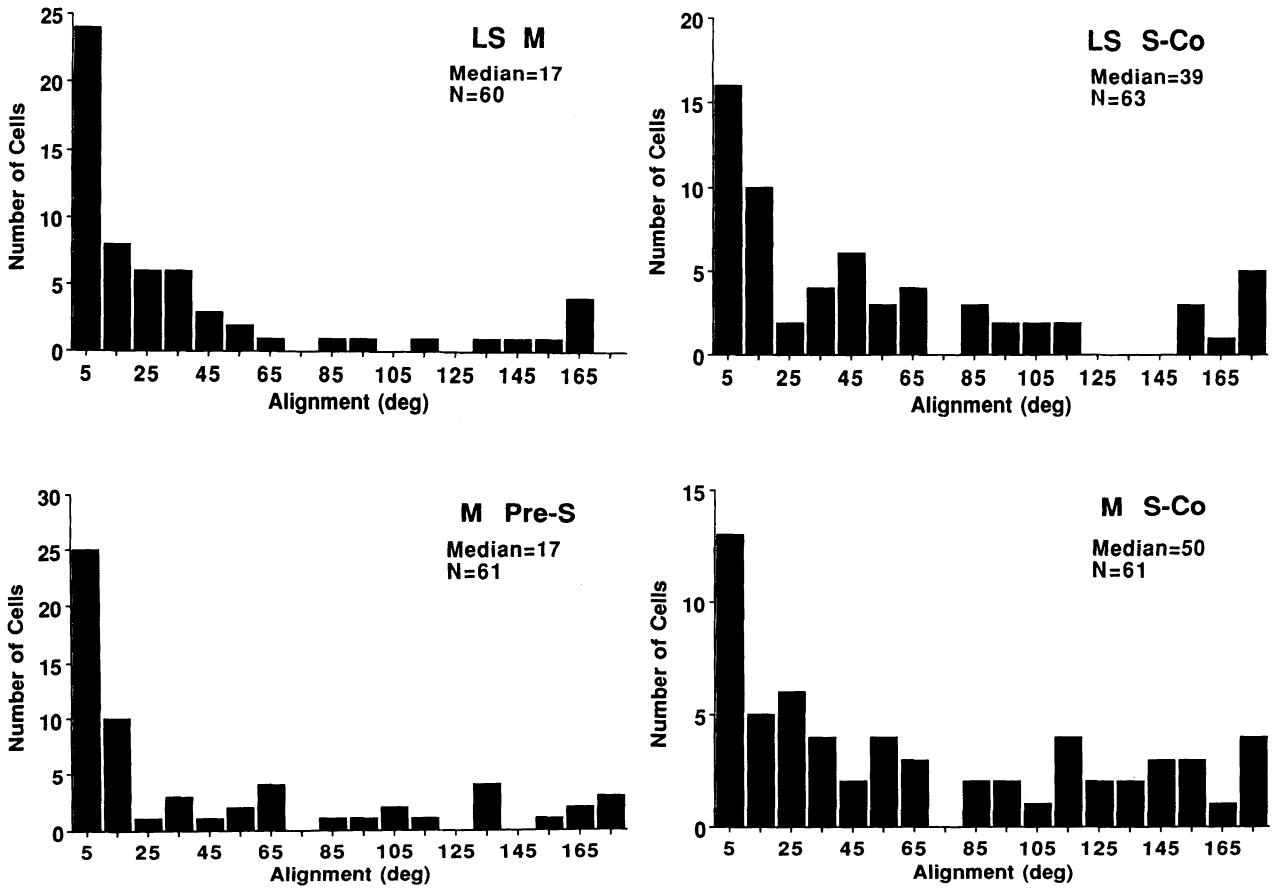

FIG. 7. Distributions of the alignments between phases of activity in LIP neurons. The alignment of 2 phases in the activity of an individual neuron is defined as the difference between the preferred directions of these 2 phases.

fined as activity index −2.0 or lower; see METHODS of companion paper.) During LS and M, most inhibitory responses were directed toward the contralateral hemifield: 73% (11/15) for LS and 71% (12/17) for M. However, around the time of the saccade, this trend reversed, and most inhibitory responses showed ipsilateral preferred directions: Pre-S, 46% (11/24) contralateral; S-Co, only 33% (7/21) contralateral; Post-S, 38% (9/24) contralateral. Therefore the S activity, but not the LS, acts like a "push-pull" mechanism.

Some neurons showed, in some phases, excitation in opposite directions ("bimodal tuning"). Usually the response in the opposite direction was weaker than the response in the preferred direction.

Alignments of the preferred directions of different activity phases

We define the alignment of two activity phases in one neuron as the angle between the preferred directions (the smaller angle, in the range 0–180°). Figure 7 shows distributions of alignments for several pairs of phases. Only neurons whose activity in both relevant phases was clearly excitatory were included in the analysis.

Figure 7 shows that the directions of LS, M, Pre-S, and S-Co, are (at least roughly) aligned. However, these phases break down into two groups. The alignments of the first three phases, LS, M, and Pre-S, are very good: the median alignment of LS and M was 19°, $n = 61$; for LS and Pre-S, 22°, $n = 56$; for M and Pre-S, 14°, $n = 52$. However, the alignments of each of these three periods with S-Co is less accurate: the median alignment of LS and S-Co was 40°, $n = 68$; M and S-Co had median 31°, $n = 56$; Pre-S and S-Co, median 28°, $n = 60$. For an example of this trend, note that the preferred LS, M, and Pre-S directions of the neuron illustrated in Figs. 1 and 2 match each other better than the preferred direction of S-Co.

The less precise alignment between LS, M, and Pre-S with S-Co is not the result of a "drift" in the direction of the activity that accumulates with the passage of time: although the Pre-S and S-Co phases are much closer in time than LS to S-Co, the alignment of Pre-S with S-Co is worse than that of Pre-S with LS.

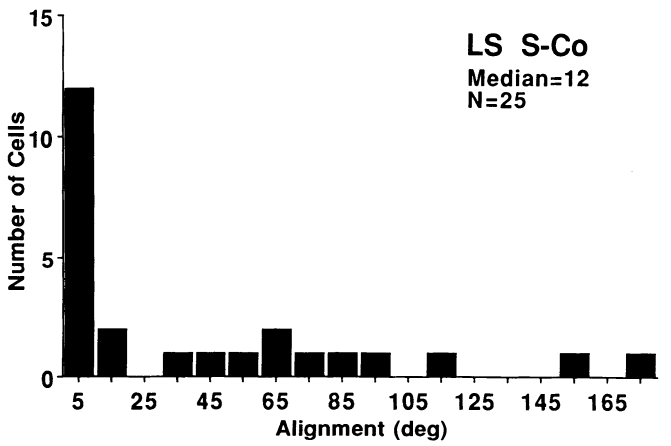

FIG. 8. Distributions of the alignments between the LS- and S-Co–preferred directions in individual area LIP neurons with both clear excitatory activity and narrow tuning (width ≤90°) in both LS and S-Co phases.

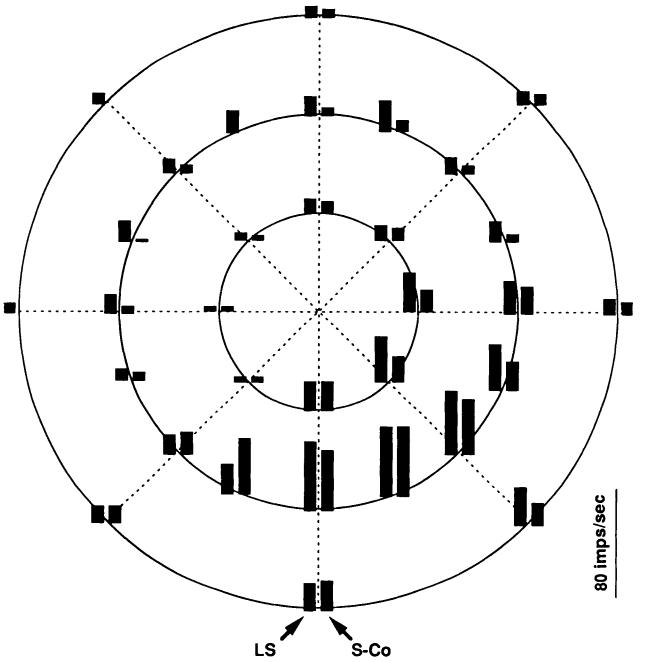

FIG. 9. Activity of an area LIP neuron in M saccades made to 32 targets. Targets are arranged on 3 concentric circles of 7.5, 15, and 22.5° radii, in the 8 standard directions (45° multiples). On the 15° circles, targets are placed 22.5° apart. The intensity of the LS and S-Co activities (left and right bars, respectively) are sketched. The calibration bar at the *bottom right* represents 80 imp/s.

A small group of neurons [14% (9/63)], with clear excitatory activity in both LS and S-Co, had opposite preferred directions in these two phases. These neurons can be seen as a discrete group in Fig. 7.

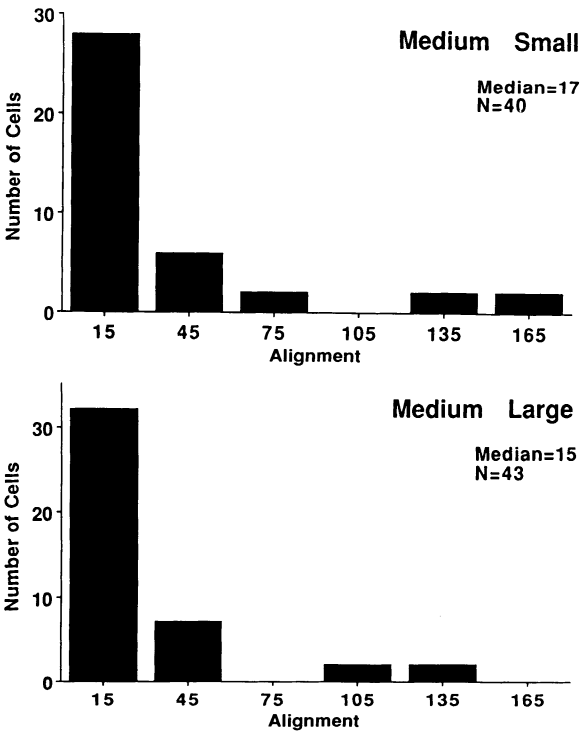

FIG. 10. Alignments of the preferred LS directions in circles of different eccentricities.

Units with narrow fields

when the sample is confined to neurons in which the matched phases not only have clear excitatory activity (that is, activity indexes ≥2.0), but also narrow direction tuning. We call a direction tuning "narrow" if its width is, at most, 90°. Our motivation for this selection is that neurons with extremely broad fields may be less suitable for spatial processing than neurons with somewhat narrower fields.

The alignments of LS, M, and Pre-S in this smaller sample are even tighter than in the total sample. For LS and M the median alignment is 6°; the sample contains 46% (28/61) of the total number of units with excitatory activity in both periods. For LS and Pre-S the median is 10°, and the sample size 46% (26/56). For M and Pre-S the median is 8°, sample size 48% (25/52).

The main finding here is that the discrepancy between the preferred directions of LS, M, and Pre-S, on the one hand, and the preferred direction of S-Co on the other hand, all but disappears. Figure 8 displays the histogram of

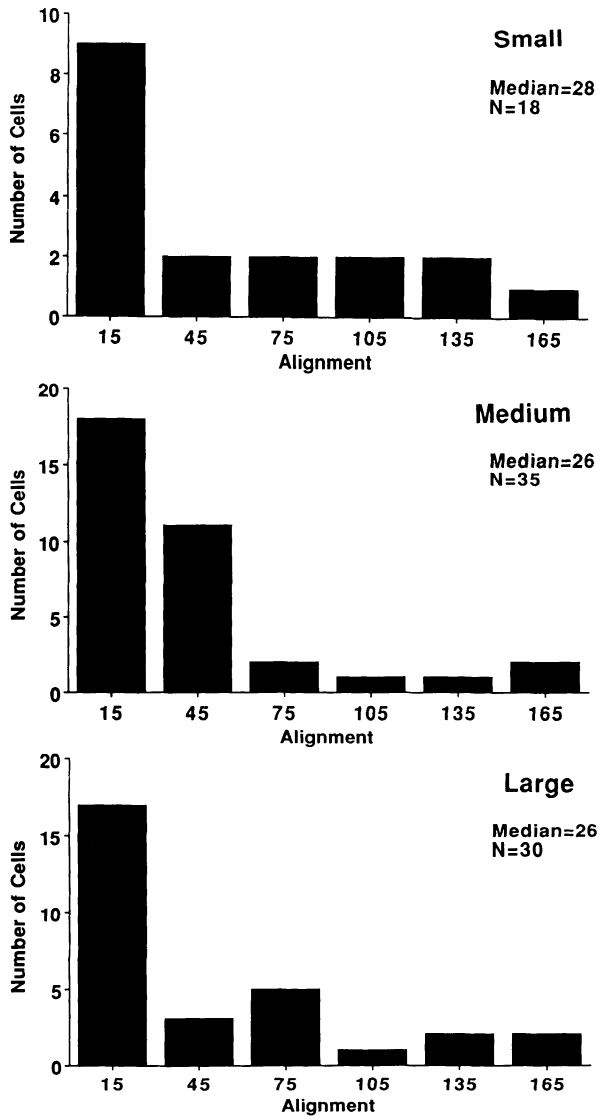

FIG. 11. Alignments of the preferred LS and S-Co directions, calculated separately for circles of 3 different eccentricities.

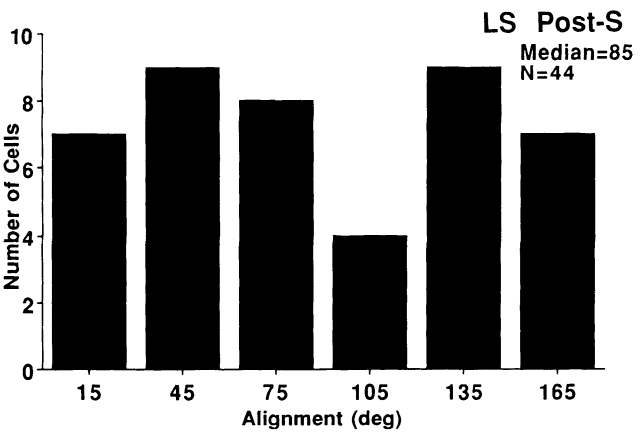

FIG. 12. Distributions of the alignments between the LS- and Post-S–preferred directions in individual area LIP neurons with clear excitatory activity in both phases.

alignments for neurons with excitatory activity and narrow fields in both LS and S-Co. The histogram shows a much better alignment of these phases as compared with Fig. 7. The median alignment is 12° (vs. 40° in Fig. 7). Figure 8 is based on a sample whose size is 37% (25/68) of that in Fig. 7.

The results of the present section are illustrated on a single-neuron level in Figs. 1 and 3: Fig. 1 depicts a neuron with wider fields, but less precise alignments, than the neuron of Fig. 3.

Direction-tuning curve reflects the response field

We have extensively mapped the response fields of an additional group of 82 neurons. Memory-guided saccades were made to 32 target locations, in 4 blocks of trials. Three blocks contained targets positioned, respectively, on small, medium, and large circles. The radii of these circles were usually 7.5, 15, and 22.5°, respectively; but sometimes the small circle was 5°, and the large circle 25°. In all these circles, targets were placed in the eight standard directions (integral multiples of 45°). On the fourth block of trials, targets were placed on a circle of 15° radius, rotated 22.5° with respect to the standard directions.

Figure 9 illustrates the intensity of the LS and S-Co responses of one neuron at these 32 target locations. Both LS and S-Co activities prefer the down-and-right direction. The preferred directions are similar in all three circles.

Neither the average intensity of activity in area LIP nor fraction of LIP neurons showing clear excitatory responses varied with eccentricity. In each phase both parameters were similar in each of the three eccentricities tested. The results were similar to those presented in Figs. 4 and 6 of the companion paper.

For each of the four blocks of trials of each neuron, we have calculated a direction-tuning curve and assigned to it a preferred direction. Each block was analyzed separately, with the use of the same algorithms as in the rest of this study. For each phase, we then calculated the alignment of the preferred directions derived from the different eccentricities.

The main result is that the preferred directions are largely invariant of saccade size. More specifically, similar esti-

mates for preferred directions were obtained for each of the three target circles. Figure 10 illustrates the results for the LS phase. Forty neurons showed excitatory responses (that is, activity index at least 2.0) in both small and medium-sized circles. The median alignment is 17°. Forty-three neurons showed excitatory responses in both medium and large circles. The medium alignment in this case is 15°. Good alignment for the different eccentricities was observed also in the other phases.

Figure 11 shows that alignments between different phases also do not depend on target eccentricity. The figure presents the alignments of the LS and S-Co phases, calculated separately for each eccentricity. The distributions are similar, as are their median values (26–28°). Hence the results presented in this paper are not a peculiarity of the target eccentricities we used.

We also compared the preferred directions calculated separately from the two blocks of trials with targets on a 15° radius circle: one block with the standard directions, the other block with targets rotated by 22.5° with respect to the

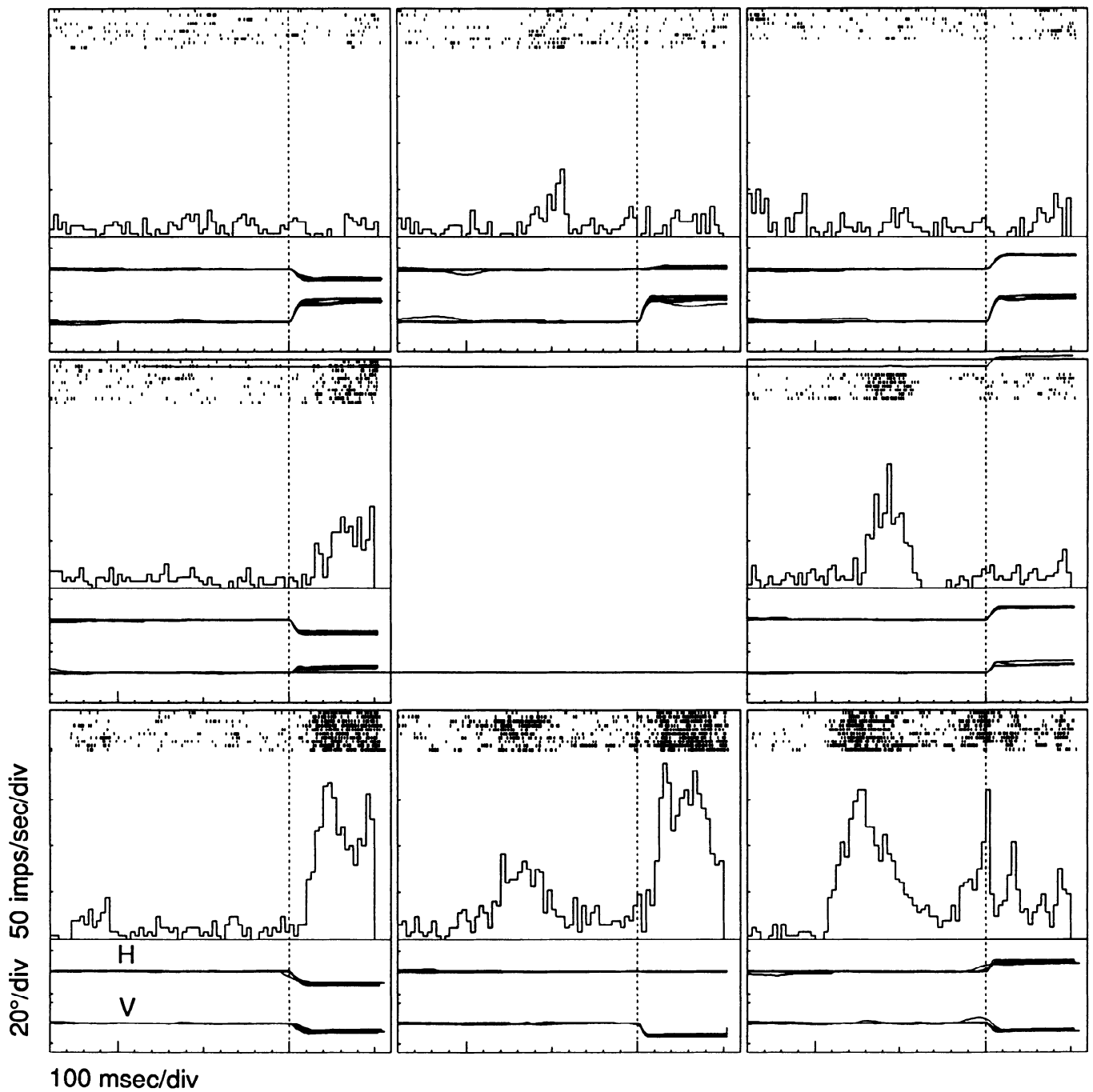

FIG. 13. Activity of an area LIP neuron in which the Post-S activity is poorly aligned with the LS activity and is probably primarily an eye-position signal. Data are in the same format as in Fig. 1, except that the trials are aligned on the onset of the saccade (denoted by the vertical dotted lines).

standard. In the example of Fig. 9, both blocks of trials, to standard and rotated directions, gave quite close estimates for the neuron's preferred directions. The LS phase, for example, is −67° in the standard block, and −86° in the block of rotated targets. On the population level the preferred directions of both blocks were, similarly, generally aligned. For instance, in the LS phase, 44 neurons were active in both blocks, and the median "alignment" was 17°; in other phases the estimates of difference of preferred directions were also similar. Hence eight targets are generally sufficient to capture the neuron's preferred direction, at least in the level of precision applied in this paper.

Alignments of the Post-S phase

Figure 12 shows the alignment of the LS and Post-S phases. The histogram is clearly flat, leading to the conclusion that, over the whole population, LS- and Post-S–preferred directions are uncorrelated. Figure 13 shows a neuron whose activity from the LS to S-Co phases is strictly tuned to the down-and-right direction. The alignment of the LS- and S-Co–preferred directions in this neuron is almost perfect (1°). Nevertheless, the pronounced Post-S activity of this neuron is directed down and down-and-left, resulting in an LS to Post-S difference of preferred direc-

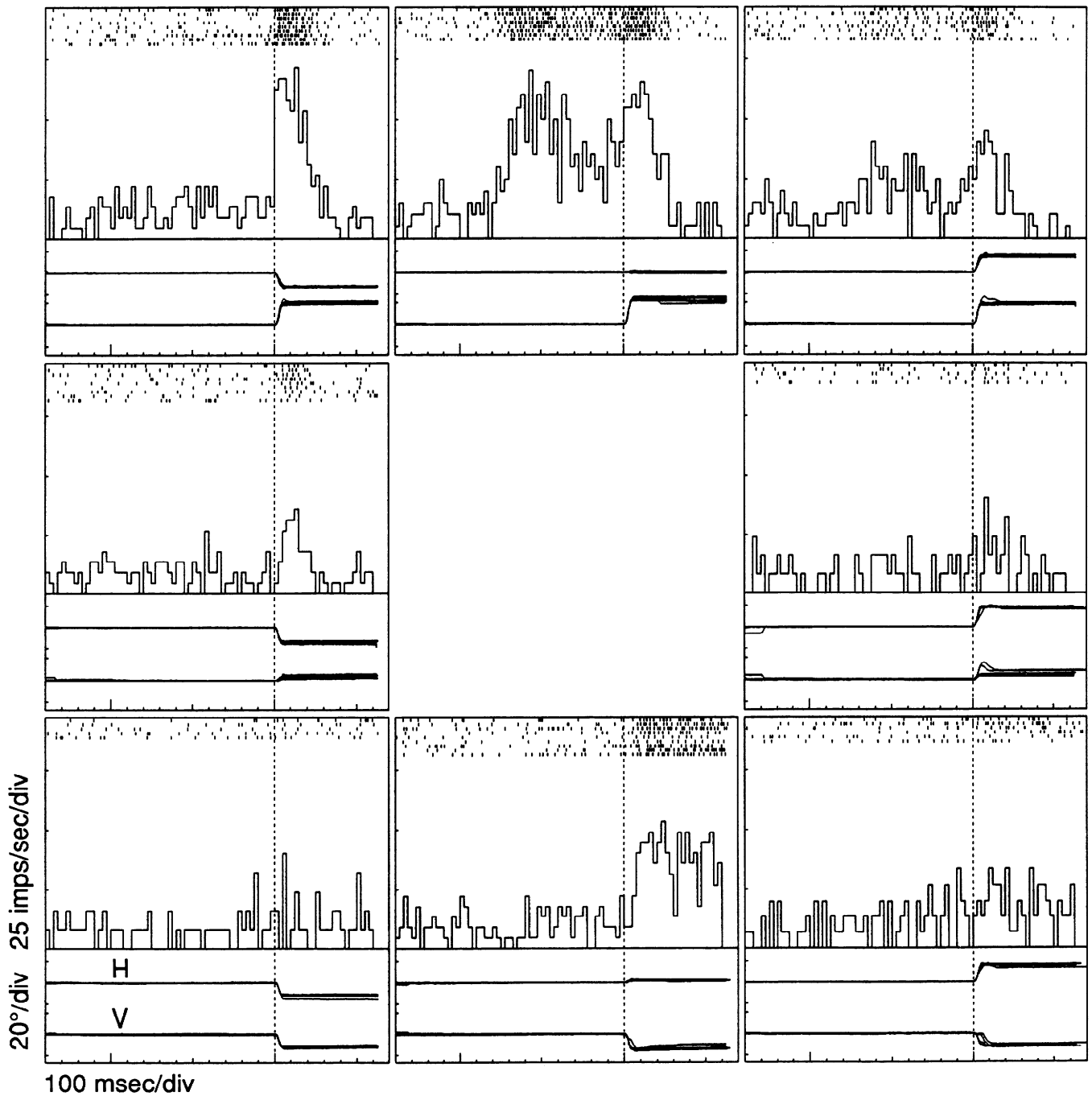

FIG. 14. Activity of an area LIP neuron in which there is sustained Post-S activity in a direction opposite to the LS activity. Data are in the same format as in Fig. 13.

tions of 63°. The Post-S activity of this neuron is a static eye-position signal; this was confirmed in another run (not shown), in which the monkey had to fixate, for 2 s, each of the nine stimulus positions of Fig. 13. When fixating the down-and-left or down positions, this neuron emitted a sustained discharge. We conclude that the flat distribution of LS and Post-S alignments depicted in Fig. 12 may result from several processes occurring simultaneously in the Post-S period, related not only to the completed eye movement, but also to the eye position, and probably, in some neurons, also to the subsequent eye movement, as will now be described.

Figure 14 shows an example of a neuron with nearly opposite Pre-S and Post-S directions. The increase in the activity after down-going saccades occurs at about the same time as the decrease that follows upward saccades. We suggest that in some such neurons the Post-S activity represents the intention of the monkey to saccade back to the fixation point; hence in Fig. 14 the Post-S activity is in the direction opposite to the LS, M, and Pre-S activity. We investigated this hypothesis in this and other neurons, specifically, with the use of the "back-saccade" paradigm discussed below.

The S activity of many neurons is perisaccadic, that is, although starting before or simultaneously with the saccade, the burst continues well after the saccade is completed (see companion paper, Barash et al. 1991). Strong S activity, outlasting the saccade, can be seen in Fig. 14, in directions up, and up-and-left. Clearly, such long S activity can contribute to Post-S spike counts. Our choice of Post-S interval, starting 200 ms after the beginning of the saccade, was meant to reduce the contribution of such slowly decaying S activity. Nevertheless, these spikes do occur after the saccade, and they constitute a process that is aligned in direction with the Pre-S activity. This process is, of course, very different from the one occurring in the down direction, illustrating, again, the complexity of the Post-S activity.

Note that, because we recorded neither eye position nor neuronal activity during the intertrial interval (from ~500 ms after the end of the saccade to the target until the beginning of the next trial), understanding the nature of the Post-S activity requires further work. Post-S activity may reflect a variety of processes, including eye-position signals and intention to saccade back to the fixation point in anticipation of the next trial.

Activity related to the intended movement

We used the double-saccade and back-saccade paradigms (Hallet and Lightstone 1976; Mays and Sparks 1980) to investigate whether LIP neurons code in "motor coordinates": do these neurons become active if a saccade is planned into their motor field even if no visual target falls within their receptive field?

A detailed description of the double-saccade paradigm is provided in METHODS. In short, the initial fixation spot is replaced by a brief presentation of two peripheral targets, one after the other; the monkey must saccade first to the location of the first target, and then directly to the location of the second target. Although no explicit delay is required, the targets are extinguished during the latency of the first saccade, and thus both movements are made in complete darkness. The second saccade is made in a direction in which no retinal stimulation occurred; hence some transformation of coordinates must occur.

Figure 15 illustrates the LS and S-Co fields of the neuron whose activity in the double-saccade paradigm is illustrated in Fig. 16. This neuron has vigorous S activity, but almost no LS activity (also no M activity). The S-Co activity spans mainly the right-to-down quadrant, but some excitatory response is evoked in all directions (the S-Co tuning width is 120°).

Figure 16 illustrates the activity of the same neuron in the double-saccade task. Two pairs of saccade directions are displayed: rightward and upward saccades (Fig. 16, *A* and *B*), and downward and leftward saccades (Fig. 16, *C* and *D*). Within each pair, one direction is preferred (that is, it is in the S-Co field), and the other direction is nonpreferred. The preferred directions are those of the first saccade (Fig. 16, *A* and *C*) or the second (Fig. 16, *B* and *D*).

The key result is that in each of the four panels of Fig. 16, the activity is clearly related to the movement in the preferred directions. This is consistent with a motor coordinate frame.

We have tested 25 neurons in the double-saccade paradigms; 11 neurons showed activity clearly consistent with the hypothesis that the M and S responses are in motor coordinates. Only one neuron clearly did not code in motor coordinates. Although the remaining neurons were consistent with motor coordinates, the data were difficult to inter-

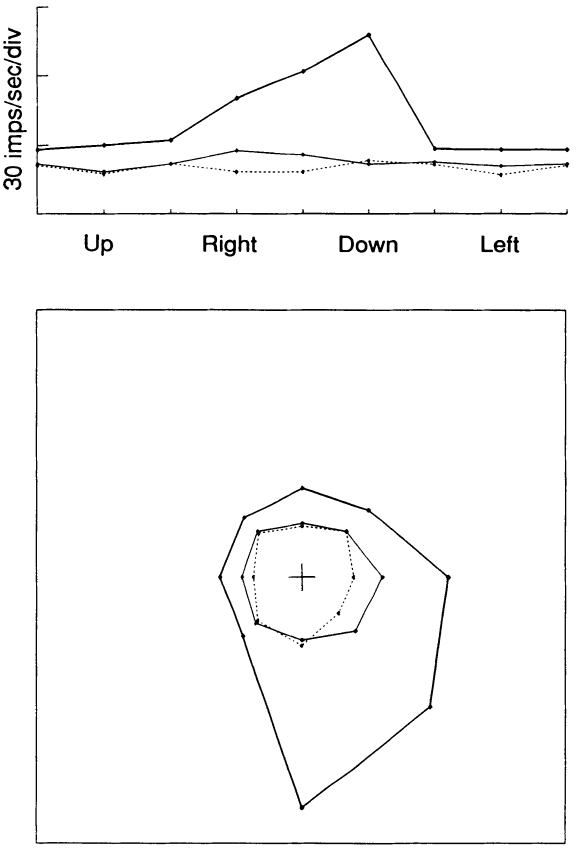

FIG. 15. Direction-tuning curves of an area LIP neuron that is mainly saccade-related, with little LS or M activity. Data are plotted twice, in rectangular coordinates (*top*) and in polar coordinates (*bottom*). Plotted phases are background (· · ·), LS (thin), and S-Co (thick trace).

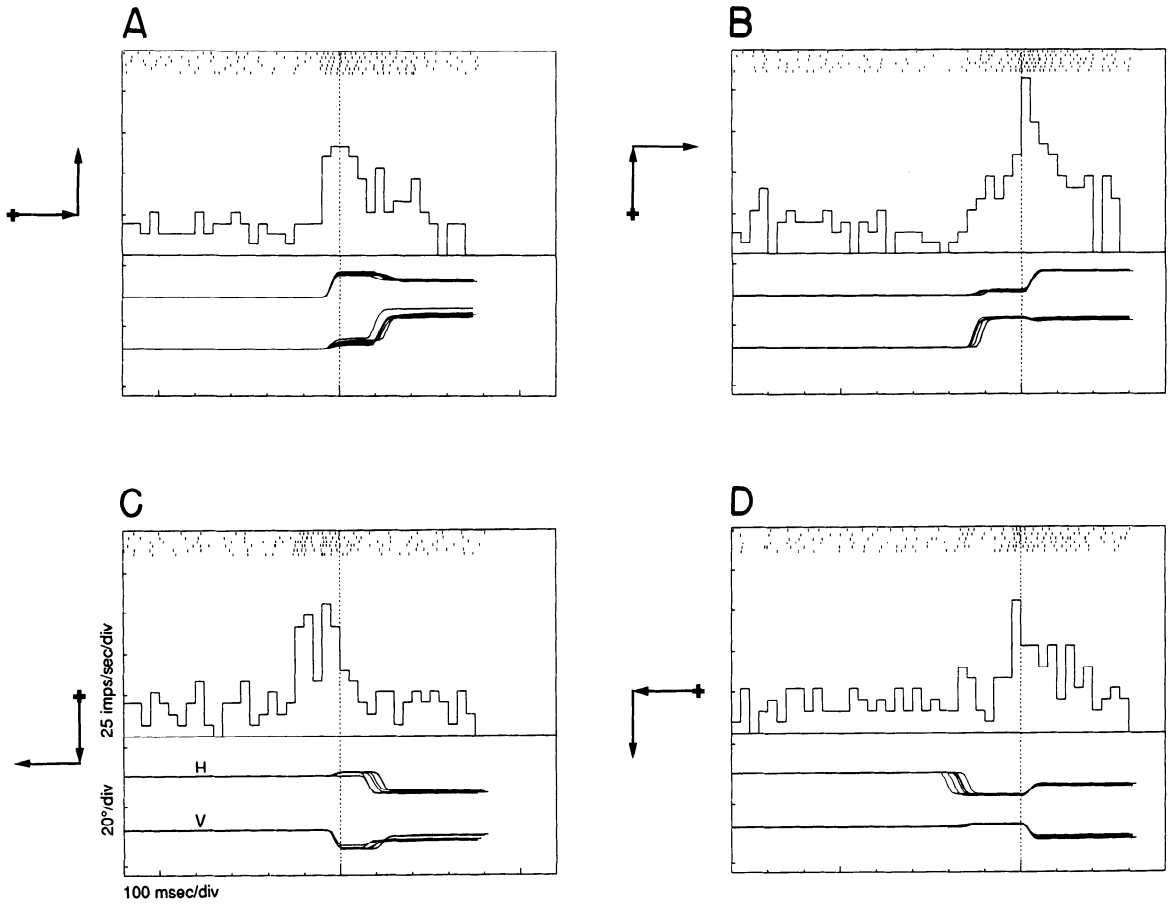

FIG. 16. Activity of the same LIP neuron as in Fig. 15, when tested in the double-saccade paradigm. *A* and *C*: the neuron is active for the 1st (retinotopic) saccade. *B* and *D*: it is active for the 2nd saccade. The neuron clearly is active when the forthcoming saccade is in its preferred direction. Note that in *B* and *D* the retinal location of the 2nd stimulus is outside the neuron's motor field, and yet it is still active for the 2nd saccade. This is consistent with the neuron coding in a motor and not a retinotopic coordinate frame. Vertical dotted lines represent end of 1st saccade (*A* and *C*) and beginning of 2nd saccade (*B* and *D*). Shown in each panel are the spike raster and histogram, and the horizontal and vertical eye-position traces.

pret. Several factors complicate the interpretation of the double-saccade paradigm in the remaining neurons. The main factor is that many neurons have wide tuning curves and are thus active for both saccades. Therefore, to get clear-cut results, we employed the back-saccade paradigm.

Figure 17, *A* and *B*, sketches the back-saccade paradigm (again, a detailed description is provided in METHODS). The initial fixation spot is replaced by a brief presentation of a peripheral target; the monkey must first saccade to the location of this target, and then saccade back to the initial fixation position. Although no explicit delay is required, the target is extinguished during the period before the first saccade, and thus both movements are made in complete darkness. The essential point is that no retinal stimulation occurs in this trial in the direction of the second saccade.

Figure 17 illustrates the activity of an LIP neuron in the back-saccade paradigm. The response of the same neuron to the delayed-saccade task was displayed in Fig. 14. Figure 14 shows that this neuron has visual, M, and S activity in the upward direction, whereas postsaccadically the neuron is active after saccades in the downward direction. Figure 17, *C–E*, depicts a back-saccade sequence in which the target is in the upward direction, that is, in the response field of the neuron. In this case the target is followed by a discharge, which continues through the upward saccade. About 200 ms after the end of the first saccade, the activity declines, in anticipation of the downward saccade, and remains low until the completion of the trial.

Figure 17, *F–H*, shows that a target in the downward direction evokes a very different pattern of activity. The presentation of the target is followed by a subtle inhibition (Fig. 17*F*), and the activity remains low until the first saccade (Fig. 17*G*). As soon as the downward saccade is completed, however, the level of activity becomes elevated (Fig. 17*G*) and is sustained until after the second, upward saccade (Fig. 17*H*). Because no visual stimulus was presented in the upward direction in this trial, the sustained activity is not visual; it is related to the intention to make a movement into the motor field. Hence this neuron codes in a motor coordinate frame.

The back-saccade experiment illustrated in Fig. 17 offers a clue to the nature of the Post-S activity of the neuron depicted in Fig. 14. We suggested (in the section on Post-S activity) that the Post-S activity of this neuron may be related to a saccade made in the intertrial interval, returning to the fixation point in anticipation of the start of the next

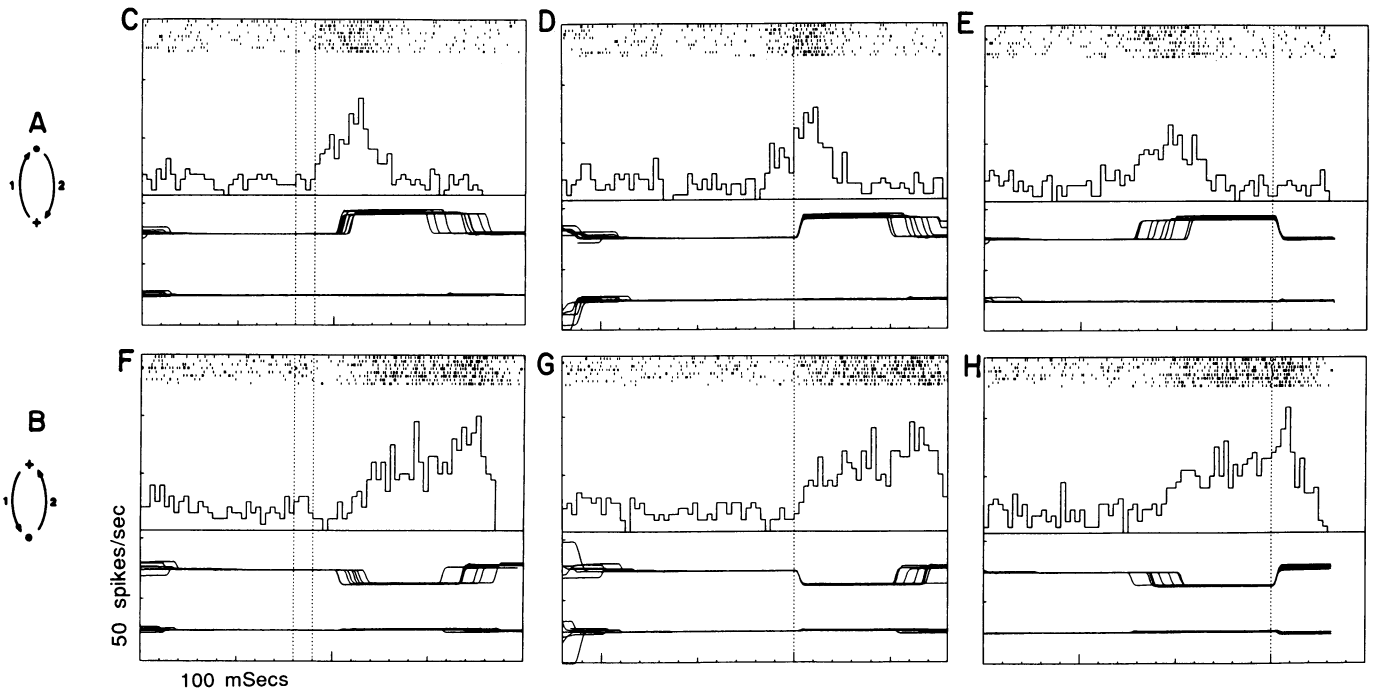

FIG. 17. Back-saccade paradigm. *A* and *B*: scheme of the 2 saccades in the task. The 1st saccade is to the (single) target, the 2nd saccade is made in the dark back to the location of the original fixation point. *C–H*: activity in the back-saccade task of the same LIP neuron as in Fig. 14. The preferred direction of this neuron, for the LS, M, and S phases, is upward. Hence, in the *top row*, the visual stimulation and the 1st movement are in the preferred direction, and the 2nd movement is in the opposite, nonpreferred direction. In the *bottom row* the visual stimulation and the 1st saccade are in the nonpreferred direction, but the 2nd saccade is in the preferred direction. *C* and *F* are aligned on the sensory stimuli. First dotted vertical line denotes offset of fixation spot and simultaneous onset of target. Second dotted line represents target offset. *D* and *G* are aligned on the beginning of the 1st saccade, and the dotted line denotes the time the 1st saccade begins. *E* and *H* are aligned on the beginning of the 2nd saccade, and the dotted line denotes the time the 2nd saccade begins. Shown in each panel, from the *top*, are the spike rasters, where each horizontal trace represents a trial, and each tick within a line marks the time of occurrence of a spike; the resulting histogram; and the horizontal and vertical eye-position traces of the various trials, superimposed.

trial. Some support for this conjecture is presented in Fig. 17. In the back-saccade task the animal is required to look back to the fixation point during the trial. If the trial was truncated after the first saccade, the cell would have Pre-S activity for upward saccades and Post-S activity for downward saccades. Hence it would show the same pattern of activity that was found for the single saccade task illustrated in Fig. 14.

We tested 11 neurons with the use of the back-saccade paradigm. Five neurons had activity clearly related to the intended movement in these trials. Three neurons had weak activity consistent with the intended movement. Three neurons were hard to interpret (e.g., too large response fields). None of these neurons had activity clearly inconsistent with the direction of the intended movement.

DISCUSSION

Three major properties of LIP single-neuron activity were described in the present paper. The first was spatial tuning: each phase of activity was found to have direction tuning. The second was alignment: in the same neuron, the preferred directions of LS, M, Pre-S, and S-Co periods were usually aligned. The third property we described was coding in motor coordinates: neurons become active in anticipation of saccades planned into their motor field even if there is no visual stimulation in their receptive field.

Direction tuning: alignment

Direction tuning in LIP neurons is broad: the median width at 50% maximal activity is ~90°. Similar widths were reported in the frontal eye fields (FEF): Bruce and Goldberg (1985) calculated a parameter T_d, where $2T_d$ is roughly the width at 60% maximum activity. Their average value of $2T_d$ was 91° for Pre-S neurons. Note, however, that some neurons with a very narrow direction tuning could have been misrepresented by aliasing, caused by the 45° sampling bin we used.

For model neural networks two types of spatial coding schemes have been suggested. In local coding schemes each unit has a small response field, and each point in space is coded by one unit. Hinton et al. (1986) suggested that a more efficient spatial tuning scheme would have units with large response fields, with each point of space represented by a set of units ("coarse coding"). The argument for coarse coding holds also for biological systems. In the superior colliculus there is experimental evidence for the existence of a coarse-coding scheme (Lee et al. 1988). In area 7a there are large visual receptive fields, and coarse coding of visual location has been postulated (Andersen 1986; Zipser and Andersen 1988). Hence it is reasonable to assume that in LIP, too, precise population-level coding of the saccade target is achieved by coarse coding on the single-neuron level.

In view of the broad directional tuning, it is significant that there is such good alignment between LS, M, and Pre-S, and between these three and S-Co if the sample is confined to the "narrowly tuned" cells. Thus an accurate linkage of visual and motor-related direction representations exists in a large subpopulation of neurons in area LIP.

Together, these findings corroborate the hypothesis that LIP is involved in spatial aspects of sensorimotor processing.

Post-S activity

This study was not designed to examine the Post-S activity; in particular, we usually recorded the neural activity and eye position only for 500 ms after the saccade, during which the eye remained stationary. We did not monitor (or impose any requirements on) the behavior of the animal during the subsequent 500- to 1,500-ms intertrial interval. However, we did analyze carefully the activity in the first 500 ms after the saccade and feel that several interesting points can be made.

The Post-S activity in LIP is strong. It may have important functions and should not be considered a priori as "noise" that accompanies the Pre-S activity. This is better illustrated in area 7a, in which there is strong activity only during the Post-S phase (see companion paper, Barash et al. 1991).

The Post-S activity in some neurons represents a tonic eye-position signal (see Fig. 13) (Andersen et al. 1990). In some neurons, the Post-S activity mirrors Pre-S activity in the opposite direction (Fig. 14). For some of these neurons, the Post-S activity may reflect the intention of the monkey to saccade, at the end of the trial, back to the fixation point; note that this return saccade is in the neuron's preferred direction. The results of the back-saccade task in some neurons support this proposal.

Bruce and Goldberg (1985) reported a similar pattern of activity in some FEF neurons. Bruce (1988) has suggested an alternative explanation for this pattern of opposite directions; the Post-S activity is presumed to represent an efferent copy, which is subtracted from the Pre-S activity to yield a retinotopic representation invariant of eye position. However, three factors seem inconsistent with the application of such a proposal to area LIP. First, eye position strongly modulates the visual and S representations in area LIP, which would interfere with the proposed subtraction scheme (see Andersen et al. 1990). Second, the neurons having opposite Pre-S and Post-S directions are only a minority in area LIP. More commonly, the discharge occurs during all phases of the saccade, and the Pre-S and Post-S–preferred directions are not opposite. Third, the inhibition Bruce and Goldberg (1985) report at (or immediately after) the saccade is not conspicuous in LIP, at least for delayed saccades.

Motor coordinates

The double- and back-saccade paradigms used in these experiments suggest that S (and M) activity in LIP cells is not coded in retinal coordinates. Cells fire for saccades in their preferred directions regardless of whether a visual stimulus has or has not fallen in their receptive fields.

Further, cells fire in relation to saccades made in a particular oculocentric direction, regardless of where the eye is in the orbit. They do not code for saccades to given locations in craniotopic space. [However, most LIP cells' activity is modulated by eye position, and we suggest that the population activity in LIP could encode saccades to locations in head-centered space (see Andersen et al. 1990).]

Neurons exhibit M and Pre-S activity before the saccade in their preferred direction; if this is the second in a sequence of movements, cells become active only after the first saccade is complete. Together with the data obtained with the use of a novel "change of plan" paradigm (Barash et al. 1989), this suggests that LIP encodes the forthcoming intended saccade. M and Pre-S activity do not occur until it is appropriate for the monkey's behavior.

Although activity can be induced in LIP neurons without receptive-field stimulation, it is clear that this activity, although related to the planned movement, is modulated by other factors, in particular, orbital position.

Overview of the neural activity in area LIP

The following general points can be made about the activity of area LIP neurons based primarily on this and the preceding paper. First, in the delayed saccade, LIP neurons show three phases of activity (LS, M, S). These phases may or may not occur in individual neurons; most neurons show activity in more than one phase. Second, most LIP neurons with S activity are presaccadic. In contrast, in neighboring area 7a the Pre-S neurons are a minority. Third, the activity is spatially tuned. Tuning is wide, typically 90° width at one-half the maximal rate. Fourth, the preferred directions of the different phases of the same neuron, up to and including the saccade, are approximately aligned. The alignment is good between the Pre-S phases (LS, M, Pre-S), and somewhat less precise between each of these and S-Co. Fifth, in neurons with relatively narrow tuning in LS and S-Co, the alignment of the preferred directions of all phases, from LS through S-Co, is much more accurate. Sixth, Post-S activity, although strong, is not aligned with the previous phases and probably reflects several different processes. Seventh, activity is related to the intended saccade: it can be evoked without visual stimulation in the retinal receptive field if the next planned saccade is directed into the movement field. Finally, activity in all phases (LS, M, S) is modulated by eye position. The activity can be described as a gain field, dependent on eye position, that multiplies "canonical" direction and movement fields, both invariant of eye position. Gain fields are typically planar. The gradients of the grain fields of the different phases in the same neuron are typically aligned. They are also aligned with the preferred LS, M, and S directions (Andersen et al. 1990).

These findings support the suggestions that area LIP is involved in representation of space, visual localization, visuomotor transformations, and the planning of saccades.

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