Electrical Microstimulation Distinguishes Distinct Saccade-Related Areas in the Posterior Parietal Cortex

PETER THIER[1] AND RICHARD A. ANDERSEN[2]
[1]*Neurologische Universitätsklinik, Sektion für Visuelle Sensomotorik, 72076 Tübingen, Germany; and* [2]*Massachusetts Institute of Technology, Cambridge, Massachusetts 02139*

Thier, Peter and Richard A. Andersen. Electrical microstimulation distinguishes distinct saccade-related areas in the posterior parietal cortex. *J. Neurophysiol.* 80: 1713–1735, 1998. Electrical microstimulation (0.1-ms bipolar pulses at 500 Hz, current strength usually between 100 and 200 μA) was used to delineate saccade-related areas in the posterior parietal cortex of monkeys. Stimulation-induced saccades were found to be restricted to the lateral intraparietal area (area LIP) in the intraparietal sulcus (IPS) and a region on the medial aspect of the parietal lobe (area MP, medial parietal area), close to the caudal end of the cingulate sulcus, whereas stimulation of area 7a did not evoke eye movements. Two different types of evoked saccades were observed. Modified vector saccades, whose amplitude was modified by the position of the eyes at stimulation onset were the hallmark of sites in area LIP and area MP. The same sites were characterized by a propensity of single units active in the memory and presaccadic response segments of the memory saccade paradigm. Goal-directed saccades driving the eyes toward a circumscribed region relative to the head were largely restricted to a small strip of cortex on the lateral bank and the floor of the IPS (the intercalated zone), separating the representation of upward and downward directed saccades in LIP. Unlike stimulation in LIP or MP, stimulation in the intercalated zone gave rise to head, pinnae, facial, and shoulder movements accompanying the evoked saccades. We propose that the amplitude modification of vector saccades characterizing LIP and MP may reflect a spatially distributed head-centered coding scheme for saccades. On the other hand, the goal-directed saccades found in the intercalated zone could indicate the use of a spatially much more localized representation of desired location in head-centered space.

INTRODUCTION

Using electrical stimulation under conditions that, from our present vantage point, may look crude and ill-defined, Ferrier (1876) was able to evoke eye movements from a part of the posterior parietal lobe, which since then has been referred to as the parietal eye field. Later electrical stimulation in its more refined form of microstimulation has been able to add further support to the view (Komatsu and Wurtz 1989; Kurylo and Skavenski 1991; Shibutani et al. 1984), suggested by single-unit recordings (Andersen et al. 1990b; Barash et al. 1991a,b; Komatsu and Wurtz 1988; Thier and Erickson 1992) that the parietal eye field consists of at least two partitions, a more caudal one corresponding to parietal area middle superior temporal (MST) in the superior temporal sulcus (STS) responsible for smooth pursuit eye movements, and a more rostral one, responsible for saccades and corresponding to the lateral intraparietal area (area LIP).

A hallmark of saccade-related single-unit responses in area LIP and neighboring parts of the posterior parietal cortex is their consistent modulation by eye position (Andersen et al. 1990b). This finding has been instrumental for the development of the view that these areas encode goals for saccades in head-centered coordinates, engraved in the collective activity of assemblies of saccade-related cells spread out over larger parts of these regions (Zipser and Andersen 1988). This view is incompatible with the conclusions deduced from previous electrical microstimulation studies of the posterior parietal cortex by Shibutani and co-workers (1984) and Kurylo and Skavenski (1991). These authors reported that electrical microstimulation of posterior parietal cortex evoked either vector saccades, or, alternatively, centering or goal-directed saccades. Whereas vector saccades exhibit amplitudes and directions independent of orbital position, goal-directed saccades are characterized by the fact that the eyes are driven toward a common location relative to the head, independent of their starting position. Vector saccades are thought to reflect retinal coding of target location, whereas goal-directed saccades are usually taken to indicate head-centered coding for saccades (Robinson 1972), both being different from the coding scheme suggested by single-unit studies. Hence do we have to reject the concept of spatially distributed nonretinal coding? In our view this would be premature given the open questions left by earlier microstimulation work. First, how does stimulation-sensitive cortex relate to parietal cortex housing saccade-related neurons? Are the two congruent? Furthermore, is there a consistent anatomic segregation of sites whose stimulation evokes vector saccades and those whose stimulation evokes goal-directed saccades. If so, can it be related to the topography of single-unit properties in the posterior parietal cortex? Previous work has not tried to relate the effects of microstimulation to the properties of single units, and only the study by Kurylo and Skavenski (1991) but not the one by Shibutani et al. (1984) suggests an anatomic segregation of goal-directed saccades and vector saccades. Second, how solid is the evidence for stimulation-induced vector saccades? Actually, the view that stimulation of posterior parietal cortex may evoke vector saccades is based on qualitative observations, and one looks in vain for a convincing quantitive demonstration of the vectorlike property of evoked saccades. However, as discussed in detail later, even subtle modifications of the amplitudes and/or directions of evoked saccades depending on orbital position may challenge the conclusion that a retinal coding scheme is being

used. Third, there is a clear alternative to the conclusion that goal-directed saccades reflect head-centered coding. This alternative has been put forward by Roucoux et al. (1980), based on their experiments on the cat caudal superior colliculus. Stimulation of this part of the brain evoked saccades that showed the typical pattern of goal-directed saccades. However, if the head of the animal was unrestrained, the saccades were accompanied by head movements. Moreover, eye and head trajectories summed to give a gaze vector, and the amplitudes and directions of these vectors corresponded to the retinal vectors represented by the sites being stimulated. In other words, a pattern of saccades, seemingly indicating a head-centered representation of saccade targets can at least in this particular preparation be shown to reflect a retinal representation, when the head is free to move. Because the effects of electrical stimulation of the posterior parietal cortex on head movements are unknown, the interpretation of goal-directed saccades remains ambiguous.

Our study of the posterior parietal cortex was designed to find answers to the questions raised. Parts of the work have been presented in short form previously (Thier and Andersen 1993, 1996, 1997).

METHODS

Standard microelectrode techniques were used to examine the properties of single units and the effects of electrical microstimulation at sites located in the posterior parietal cortex of two male rhesus monkeys, performing fixation and saccade tasks. Eye position was measured using the scleral search coil technique (Fuchs and Robinson 1966). All procedures adopted were in accordance with guidelines on the use of animals in research as published by the Society for Neuroscience.

Surgery

Details of the surgical procedure have been described elsewhere (e.g., Barash et al. 1991a). Briefly, under barbiturate anesthesia and sterile surgical conditions, each animal was implanted with an acrylic skullcap for immobilizing the head and an eye coil for recording the eye position (Judge et al. 1980). Following full postoperative recovery the animals were trained on various oculomotor tasks, described in detail below. Once performance on these tasks was satisfactory, a second surgery was performed in which a recording chamber was mounted over a trephine hole, centered at stereotactic coordinate P6/L12 above the intraparietal sulcus (IPS). The recording chamber was oriented such that during experiments the electrodes could be advanced at an angle roughly perpendicular to the outer surface of the cortex.

Electrical microstimulation

Monkeys were rewarded for keeping their line of sight within an eye position window of usually 5° centered on a memorized location in the frontoparallel plane (Fig. 1). This location was initially cued by the presentation of a small (0.1°) fixation spot projected onto the otherwise completely dark tangent screen 57 cm in front of the animal. If the monkey kept fixation of the spot for 500 ms, the spot was turned off for another 500 ms (gap period), and, 200 ms after onset of the gap period, electrical microstimulation was applied on 50% of the trials (the other trials serving as controls). Stimulation trials and controls were randomly interleaved. Because stimulation had the potential to drive the eyes outside the confines of the position window, fixation requirements for reward were abandoned in stimulation trials from stimulation onset until the end of the gap period. Electrical stimuli applied were 500-Hz bipolar pulses (0.1 ms duration). Current size was initially set at 100 μA and, if uneffective, was increased in increments of 25–50 μA to up to 200 μA, rarely up to 400 μA. We add that estimates of the radius of the region activated by stimulation to be found in the literature range in the order of 0.5 mm for currents in the order of 100–200 μA as mostly used in this study (Ranck 1975; Yeomans 1990). On several occasions we tried to determine the threshold for saccades by trying to pinpoint the minimum current required for consistent responses. However, no attempts were made to determine such current thresholds routinely. Train duration was typically 100 ms. Electrical stimuli were delivered through conventional glass-insulated Pt-Ir electrodes. These same electrodes were also used for recording of single-unit activity at the site of stimulation. If stimulation at a given electrode site elicited eye movements from a starting position of the eyes corresponding to straight ahead, stimulation-evoked eye movements for additional starting positions of the eyes were collected either 15 or 30° off the straight-ahead position on the cardinal axes and on the bisecting axes centered on straight ahead (see Fig. 1). Eye position was monitored by sampling the search coil voltages at 500

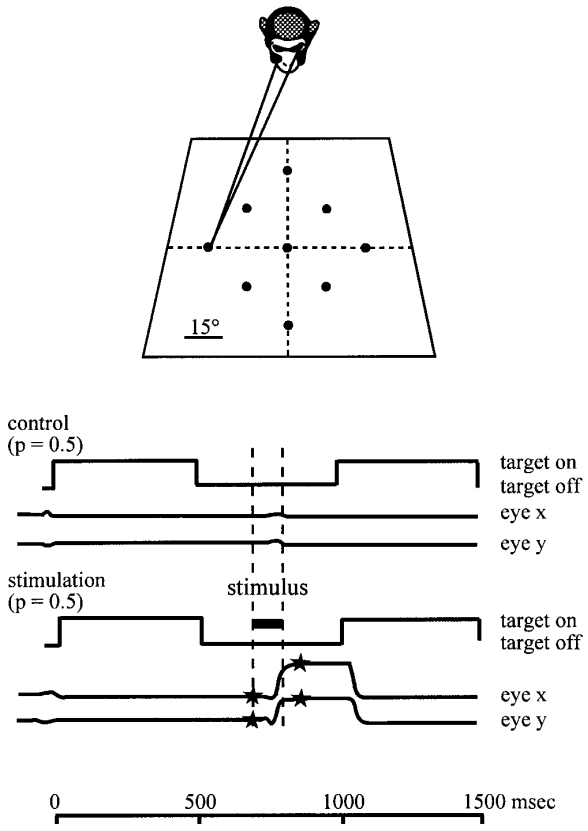


FIG. 1. Experimental paradigm: monkeys were rewarded for keeping their line of sight within an eye position window of usually 5° centered with respect to a memorized location in the frontoparallel plane cued by the presentation of a small (0.1°) fixation spot projected onto the otherwise completely dark tangent screen 57 cm in front of the animal. If the monkey kept fixation of the spot for 500 ms, the spot was turned off for another 500 ms (gap period), and, 200 ms after onset of the gap period, electrical microstimulation was applied on 50% of the trials (the other trials serving as controls). Asterisks at stimulation onset and 50 ms after stimulation end, respectively, mark the 2 time points underlying the calculation of the mean evoked saccade vectors. See METHODS for further details.

Hz per channel. All parietal sites were stimulated while the head was immobilized by way of the implanted head-holder with the front of the head being parallel to the tangent screen. This basic test was supplemented for a subset of sites by varying the static position of the head relative to the trunk (usually: head 15° to the left, straight, 15° to the right) and/or allowing unrestrained movement of the head about the yaw-axis while stimulation was applied.

Analysis of stimulation effects

Eye velocity was computed from the eye-position signal using the two-point central difference algorithm of Bahill et al. (1982). The size and direction of saccades elicited by stimulation was quantified by vectorially subtracting the eye position at stimulation onset from the eye position 50 ms after the end of stimulation. The choice of this latter time point as a measure of saccade endpoint was based on a careful analysis of evoked eye movements, which demonstrated that the eyes usually paused at this time in the newly aquired orbital position before returning to the starting point (see Fig. 1; see also Figs. 2–4). Means and standard deviations of the start and endpoints of evoked saccades for each initial orbital position were calculated based on at least four stimulation trials and corrected by corresponding measures based on a comparable number of control trials. The latter proved to be important to correct for eye drifts and eye-blink–related fast eye movements occasionally occurring during the gap period in both control and stimulation trials. The modification of the amplitude and the direction of the evoked saccade by the starting position of the eyes was quantified by subjecting the mean response vectors connecting the mean start and endpoints to a two-dimensional regression analysis (Sachs 1984), which plotted the x- and the y-component of the evoked response as a function of the x- and y-components of the starting position each. An alternative approach chosen to quantify the eye position dependency of evoked saccades, described in more detail in RESULTS, involved the calculation of the divergence differential operator div$\mathbf{S}$.

Noneye movements such as movements of the pinnae (i.e., the outer ear), facial movements, movements of the shoulder or the arms, etc., were documented and analyzed by taking 8-mm videos, which were later digitized and edited frame by frame running standard image processing PC software. In addition, in a few instances, the dynamics of evoked pinnae movements were studied using the search-coil technique by taping the search coil to the pinnae.

Single-unit recordings

The properties of single units were determined primarily by studying eye position–related and saccade-related responses. For the latter, the saccade-to-a-remembered target or memory-saccade task was used (Hikosaka and Wurtz 1983). Eight hundred milliseconds after the monkey had acquired stable fixation of a central fixation spot, a peripheral target came on for 300 ms. The monkey was required to withhold the saccade toward the target as long as the central fixation spot was on. Because the central fixation spot was turned off only 400 ms after the peripheral target had already disappeared, the monkey had to make a saccade toward a remembered target location in total darkness. After the saccade, the monkey had to keep his eyes in the new position for at least 500 ms. The peripheral target could appear in one of eight positions on a circle centered on the fixation spot having a radius of 15° in most cases, and the positions were separated by 45° starting at 0° (rightward). Both the central fixation cue and the peripheral target were 0.1° diam low-contrast spots. Single-unit responses related to the appearance of the peripheral target (visual response) were quantified by measuring the mean discharge rate between 875 and 1,075 ms after the start of the trial (from 75 ms after onset of the target until 25 ms before its disappearance). The mean discharge rate between 1,300 and 1,500 ms after the start of the trial (from 200 ms after the disappearance of the target until the disappearance of the central fixation spot) will be referred to operationally as the memory response. Responses related to the execution of the saccade were quantified by two measures, the presaccadic response, the mean discharge rate from 200 to 25 ms before the saccade, and the postsaccadic response, the mean discharge rate from 200 to 500 ms after the saccade. The various responses were measured relative to baseline, which was the mean discharge rate between 400 and 700 ms after start of the trial. Circular statistics (Batschelet 1981) were used to determine whether a unit was more active for certain directions than for others. For each of the response components, the angular mean (i.e., the mean direction) and the angular variance were calculated. The response was considered to be directional if the angular mean was significant at the 0.1% level (Rayleigh test) and if the response for the best direction was at least twice as large as the baseline discharge rate. The angular mean was taken as the preferred direction of the unit.

Reconstruction of stimulation sites

In the final weeks of the electrophysiological experiments, locations selected to serve as reference points for the reconstruction were marked by either passing DC current through the electrode tip (+20 μA for 30 s) or by making small deposits (0.1–0.2 μl) of the fluorescent dyes rhodamine and fluorogold, respectively. Such deposits were made by pressure-ejecting the dye from a syringe that was exchanged for the metal electrode used for recording. Following deep anesthesia with pentobarbital sodium, each animal was perfused with a solution of heparinized saline, followed by 4% phosphate-buffered paraformaldehyde. Guide wires were lowered into the brain at selected chamber coordinates immediately after perfusion. After removal from the skull, brains were postfixed in the same fixative used for perfusion for 12 h before being cryoprotected and blocked. The guide wires inserted earlier were used to block the brain in a plane that was parallel to the electrode tracks, roughly corresponding to the coronal plane. The block containing the stimulation and recording sites was sectioned on a freezing microtome at 50 μm. Alternate sections were prepared for cells (cresyl violet), myelin (Gallyas 1979), and fluorescence (unstained). Stimulation sites were reconstructed and transferred onto flattened maps of the posterior parietal cortex. Flattening consisted of linearly unfolding individual sections with respect to layer 4 and thereafter aligning the straightened sections with respect to the IPS. No attempt was made to account for the distortion of the map resulting from an increase of the size of the sections along the rostrocaudal axis.

RESULTS

The eye movements evoked by electrical microstimulation from the posterior parietal cortex were always fast and in most cases rather straight for the larger parts of their trajectories, suggesting their identification as saccades. Figures 2–4 show examples from different parts of the posterior parietal cortex including one dramatic deviation from straightness (Fig. 4, *C* and *D*). Note that in any case small and at times irregular eye movements could precede the main component of the evoked saccades. Some of these small eye movements were much too early, occasionally even preceding stimulation onset, to reflect stimulation effects and may have resulted from

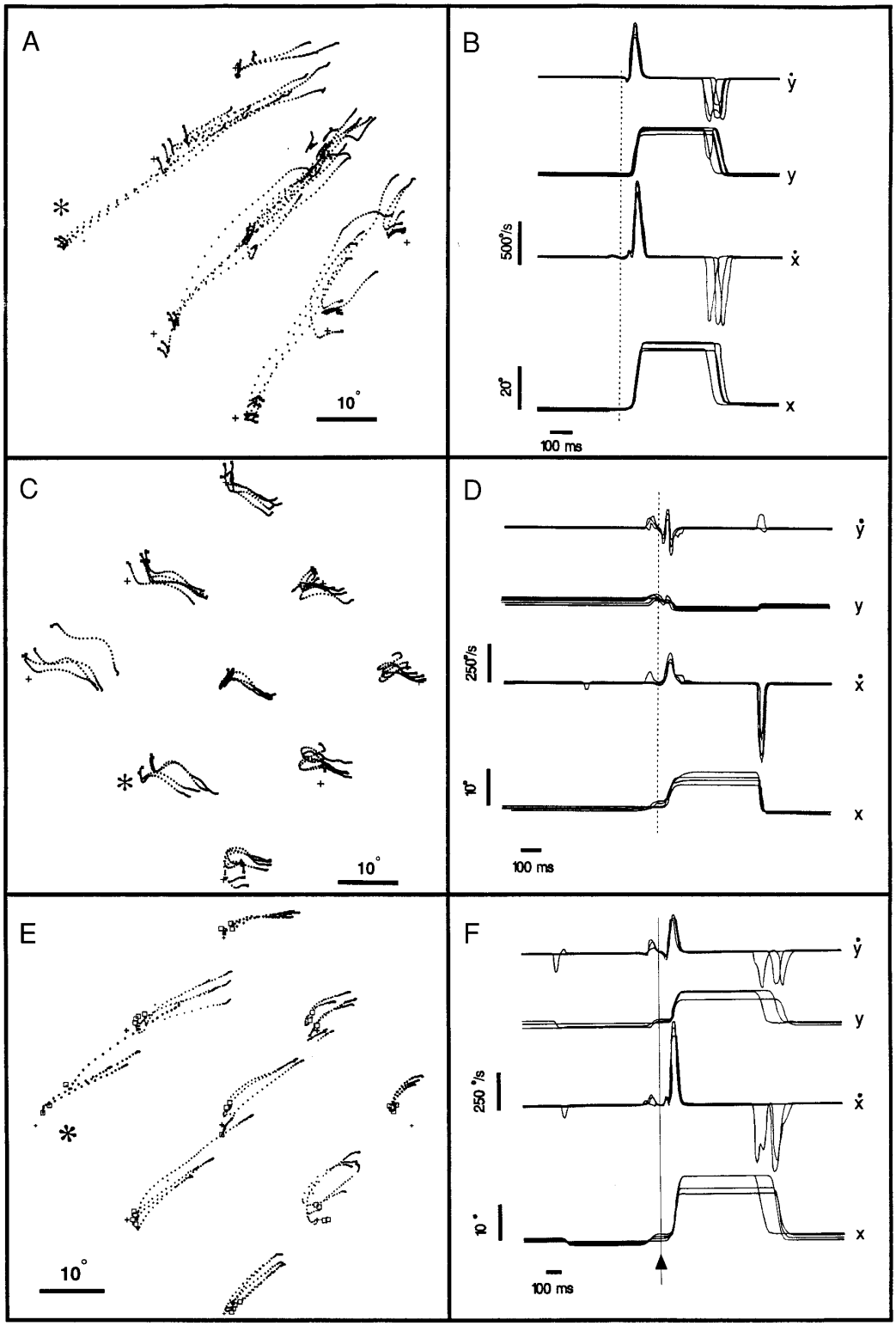


FIG. 2. Representative examples of stimulation-evoked eye movements. *A*, *C*, and *E*: eye movements plotted in an *x*,*y*-format for a time slice starting at stimulation onset (indicated by tiny boxes) and ending 150 ms later (i.e., 50 ms after the end of stimulation). Asterisk in the *x*,*y*-plot marks saccades evoked from a selected orbital starting position, which are plotted as functions of time on the *right*. Note that some of the time plots shown on the *right* are aligned with respect to stimulation onset (vertical dashed line), whereas others are aligned with respect to the onset of evoked saccades (closed line with arrow), determined according to the criteria specified in RESULTS on *Saccade latency and velocity*. *A* and *B*: modified vector saccades evoked by stimulation of site in LIP (current size 200 μA). *C* and *D*: modified vector saccades after stimulation of site in LIP (current size 200 μA). *E* and *F*: modifed vector saccades evoked by stimulation of white matter below LIP (current size 200 μA). *x*, *y*: horizontal and vertical components of eye position, $\dot{x}$, $\dot{y}$: horizontal and vertical components of eye velocity.

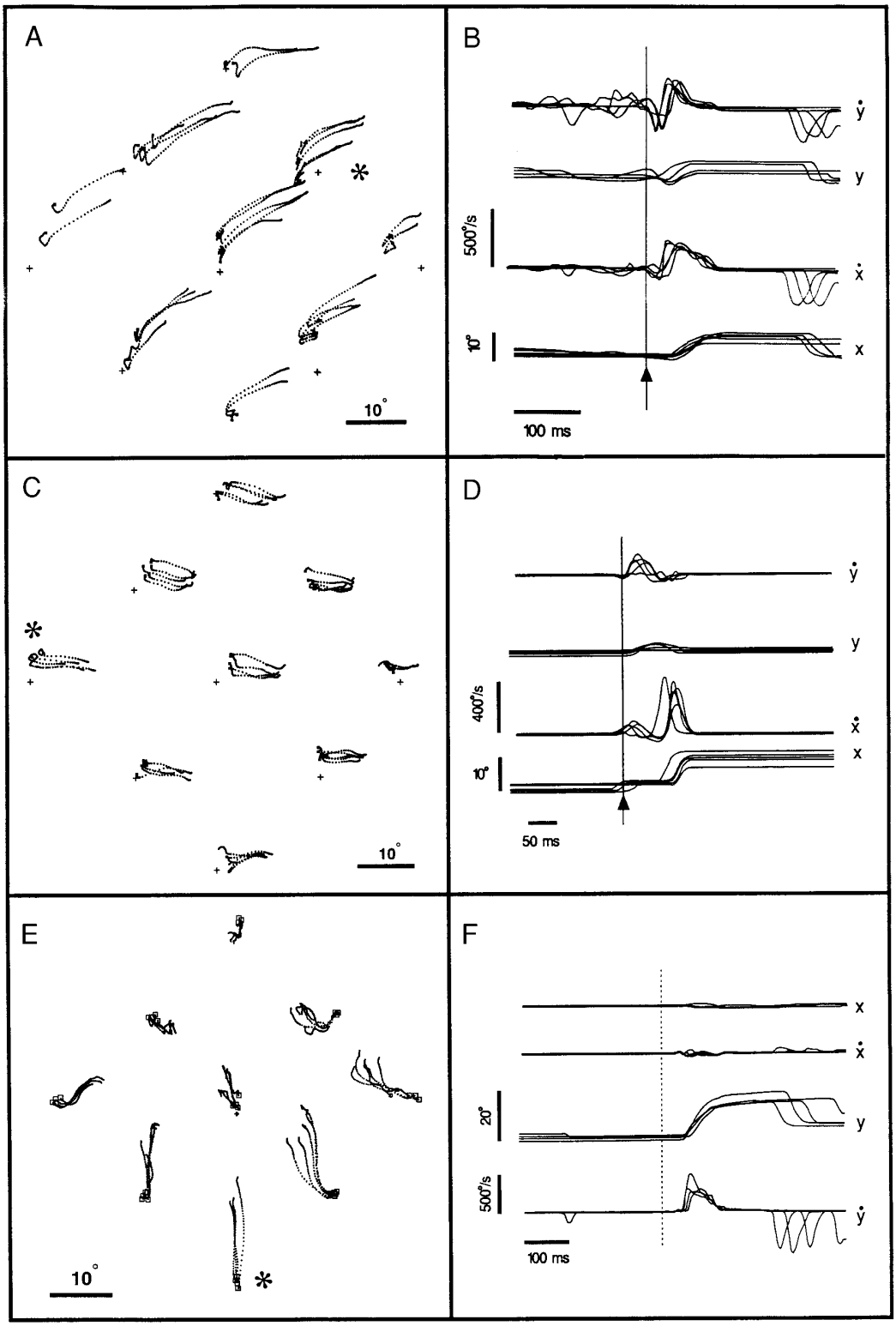


FIG. 3. Same format as in Fig. 2. *A* and *B*: modified vector saccades after stimulation of site on the medial aspect of the parietal lobe (MP; current size 200 μA). *C* and *D*: modified vector saccades after stimulation of other site in MP (current size 200 μA). *E* and *F*: goal-directed saccades after stimulation of site in the intercalated zone (current size 200 μA).

eye blinks. Others, on the other hand, showed a consistent latency relative to stimulation onset, suggesting that they were indeed early components of the stimulation response. The rich diversity of these early responses precluded a standardized approach to quantification. We therefore decided to base the quantitative analysis of evoked eye

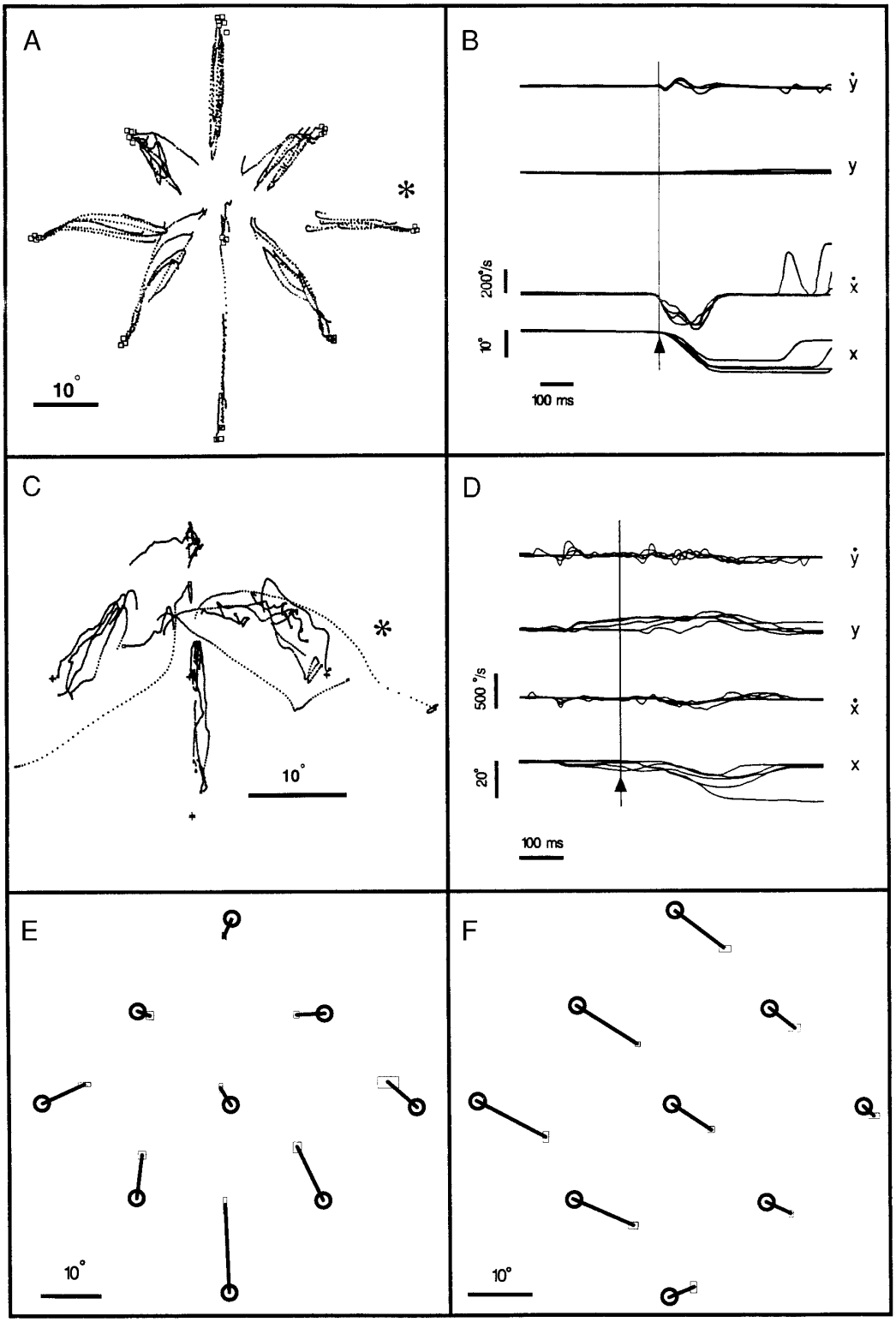


FIG. 4. *A–D*: same format as in Fig. 2. *A* and *B*: goal-directed saccades. White matter underneath intercalated zone (current size 200 μA). *C* and *D*: wavy eye movements. Area 5 (current size 150 μA). *E* and *F*: evoked saccades are approximated by vectors plotting the mean direction and amplitude of the response (see METHODS for details). Open circles in these approximations indicate the starting position of the eye at stimulation onset, whereas the little boxes at the end of the lines give the standard deviations of the end positions. *E*: goal-directed saccades from intercalated zone (based on the responses shown in Fig. 3*E*). *F*: modified vector saccades from area LIP (based on the responses shown in Fig. 2*C*).

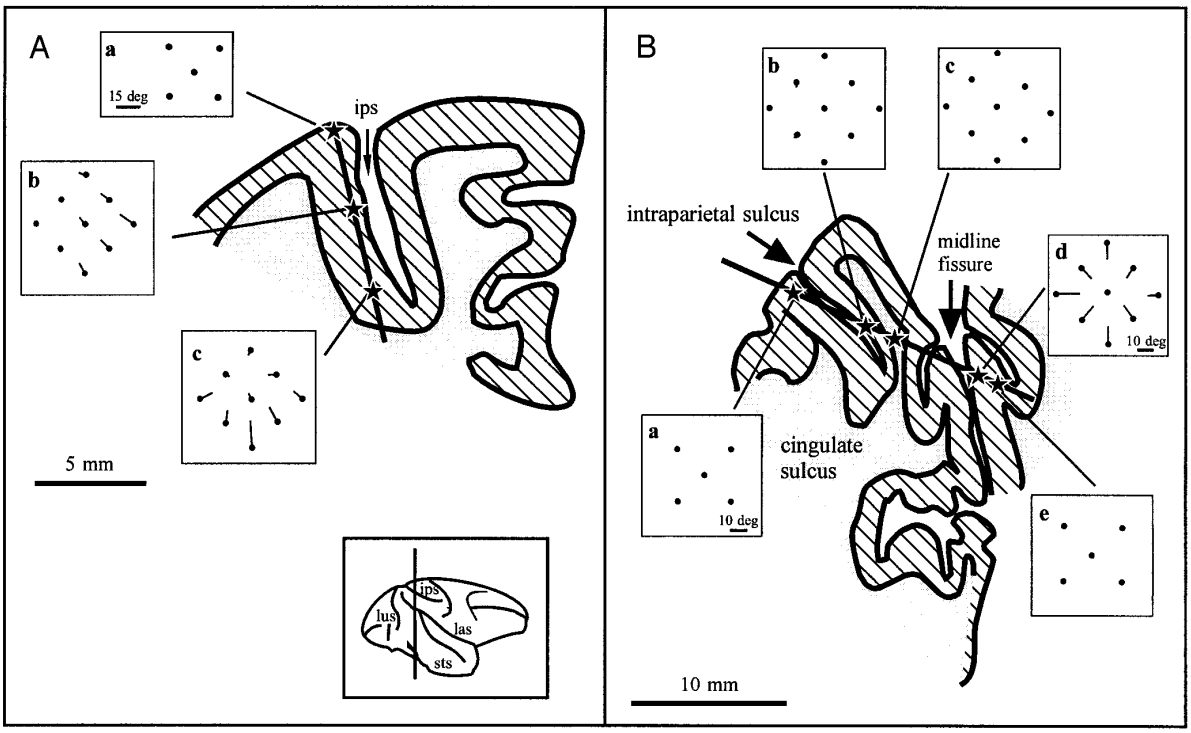


FIG. 5. Plots of 2 coronal sections cut through the posterior parietal cortex (see *inset* on *bottom right* in *A* for orientation) with reconstructed electrode penetrations. *A*: electrode penetration traversing the lateral bank of the intraparietal sulcus (ips). *A–C*: selected sites along the track. The effect of stimulation (current size throughout 200 μA) at these sites on the eyes is indicated by the *x,y*-plots of evoked eye movements shown in the corresponding *insets.* Thick dots in these plots indicate starting positions of the eyes, and straight lines approximate the averaged amplitude and direction of eye movements evoked from this starting position. *B*: electrode penetration traversing the intraparietal sulcus, the cingulate sulcus on the same side, and finally the lower bank of the cingulate sulcus of the other hemisphere. Current size throughout 200 μA. Conventions as in *A.*

movements on linear approximations of the mean evoked eye movements as described in detail in METHODS. That this approach yielded satisfactory results is demonstrated by a comparison of Fig. 4, *E* and *F,* showing such linear approximations, with the corresponding raw *x,y*-plots in Figs. 3*E* and 2*C.* We abstained from attempts to quantify the wavy eye movements of the kind shown in Fig. 4, *C* and *D.*

Topography of stimulation effects

Evoked saccades were restricted to circumscribed regions of the posterior parietal cortex, and the location of the stimulation site within this region determined some of the major features of evoked saccades. The impact of location is exemplified in Fig. 5. Figure 5*A* shows the reconstruction of an electrode penetration through the lateral bank of the IPS. Immediately after the electrode had entered area 7a (*site a* in Fig. 5*A*), electrical stimulation was applied with a current of 200 μA. As shown in the corresponding *inset,* electrical stimulation was not able to displace the eyes significantly. Moreover, it also failed to evoke any other kind of motor response. Saccades were first evoked after the electrode had entered the deeper parts of the lateral bank of the IPS, corresponding to area LIP. Saccades very similar to the ones evoked from *site b* could also be evoked from subsequently tested deeper parts of the track. However, when the electrode approached *site c,* close to the fundus of the IPS, there was a second, qualitative change of the response. As shown in *inset c,* changing the starting position of the eyes here not only influenced the amplitude but also the direction of the evoked saccades, causing convergence of evoked saccades within a region located in the upper-left head-centered quadrant.

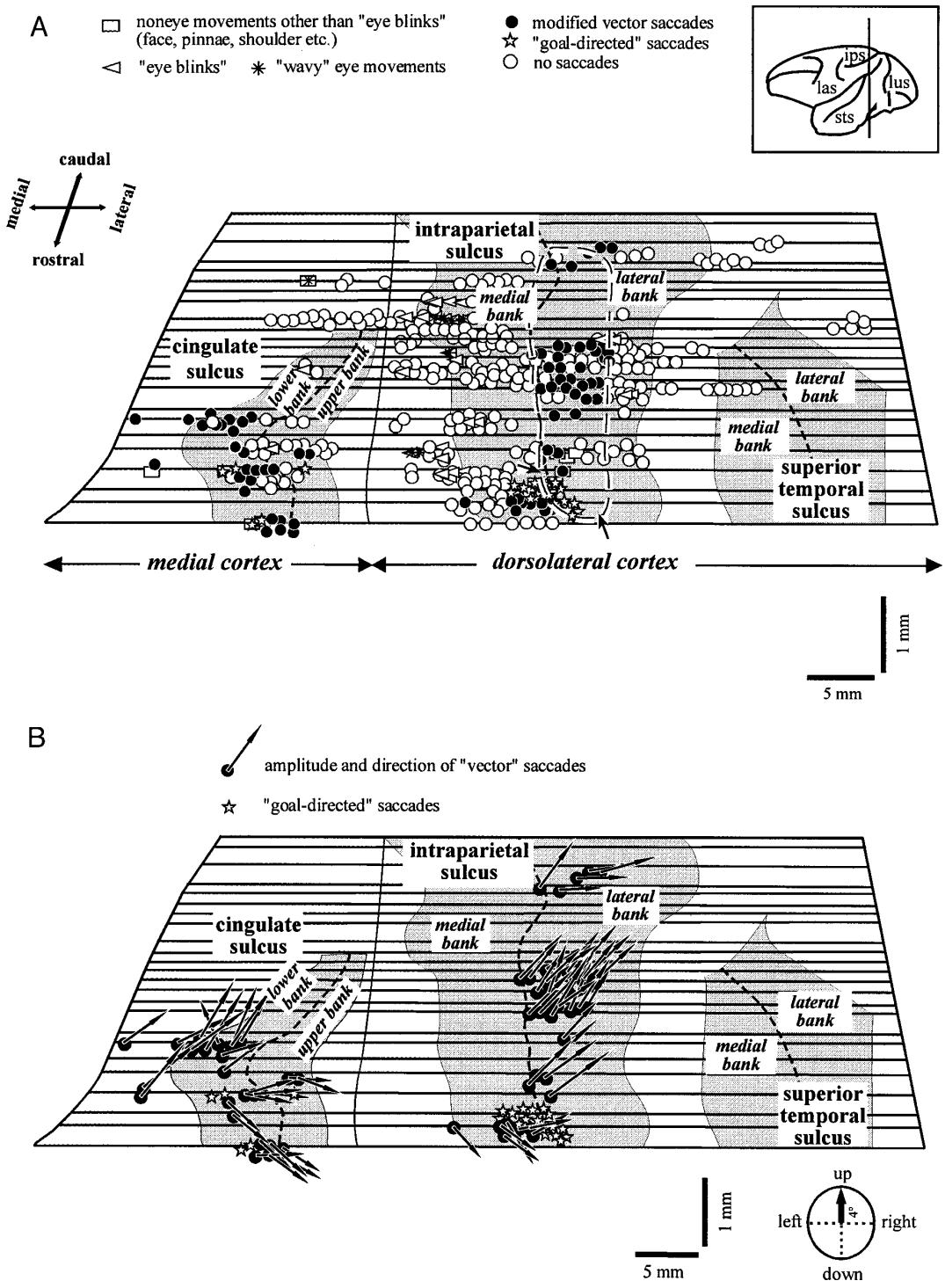
Figure 5*B* shows the reconstruction of a second electrode track that started in area 7a and ended on the medial aspect of the contralateral hemisphere. Again, stimulation of the site in area 7a (*a*) was ineffective. Because the angle of the penetration deviated from the orientation of the wall of the sulcus, the electrode crossed the IPS, missing area LIP, and ran into the medial bank. A stimulation effect was observed for the first site tested after the electrode had crossed the midline fissure and run into cortex below the medial portion of the cingulate sulcus. Stimulation at this site evoked eye movements that, very similar to stimulation of the last site of the first track described, were characterized by a high degree of orbital position dependence of saccade direction.

A comprehensive representation of the topography of the stimulation effects is given in Fig. 6. This figure shows a flattened view of layer IV of the posterior parietal cortex of one of the two monkeys used (*monkey S*), with all the stimulation sites found to be in gray matter projected onto this layer. This figure and the affiliated legend include infor-

mation on the second monkey (*monkey E*), indicating that the topography of stimulation effects was very similar in the two monkeys.

Areas 7a and 5

As already suggested by the individual penetrations discussed earlier, Fig. 6*A* shows that stimulation of sites in area 7a was unable to evoke eye movements (open circles). The only behavioral effects that occasionally resulted from stimulation of sites in area 7a were eye blinks (open triangles). Eye blink sites were also found in a region close to the medial bank of the IPS, probably part of area 5. Eye blinks evoked here were occasionally accompanied by evoked eye movements, characterized by highly wavy trajectories in *x,y*-plots (see Fig. 4, *C* and *D*, for an example). Although their velocity came close to the velocities of natural saccades (Fig. 4*D*), their conspicuous waviness makes



us reluctant to assign them to naturally occurring saccades. The monkeys usually soon stopped participating in the experiment when being stimulated at these sites, suggesting that some kind of aversive quality was attached to the stimulation. This precluded a more thorough analysis of stimulation effects related to such sites. It should be emphasized that stimulation outside the zone of wavy eye movements in area 5 never gave rise to any signs of irritation of the monkey. Even when electrical stimulation evoked the largest amplitude saccades, the monkeys did not demonstrate any discomfort.

IPS: area LIP and the intercalated zone

Stimulation at sites, indicated by filled circles in Fig. 6*A*, which were located on the lateral bank of the IPS and in a circumscribed region on the medial aspect of the parietal lobe yielded modified vector saccades. As exemplified by the *x,y*-plots of eye position shown in Figs. 2, *A, C,* and *E,* and 3, *A* and *C,* evoked saccades were vectorlike with highly reproducible direction and amplitude. Although the direction of such evoked saccades was largely independent of the starting positon of the eyes, their amplitude showed a clear modulation by eye position. Typically, the amplitude of the evoked saccades became smaller, when the starting position of the eyes was moved in the direction of the evoked saccades (Figs. 2, *A, C,* and *E,* and 3*C*). However, there were exceptions to this rule as exemplified in Fig. 3*A.* Instead of becoming larger for peripheral eye positions opposite the preferred saccade direction, as was the case for the overwhelming majority of effective sites, in this particular case and a few more, saccade amplitude was largest for a starting position corresponding to straight ahead. It decreased when the starting position was shifted to either side on an axis given by the direction of saccades evoked. The zone of modified vector saccades on the lateral aspect comprises the lower two-thirds of the lateral bank of the medial IPS with a rostral appendage encroaching on the fundus of the sulcus. Except for this appendage, the location of the zone of modified vector saccades in the IPS is largely congruent with previous descriptions of the location of saccade-related area LIP (Barash et al. 1991a,b; Blatt et al. 1990). The modified vector saccade region

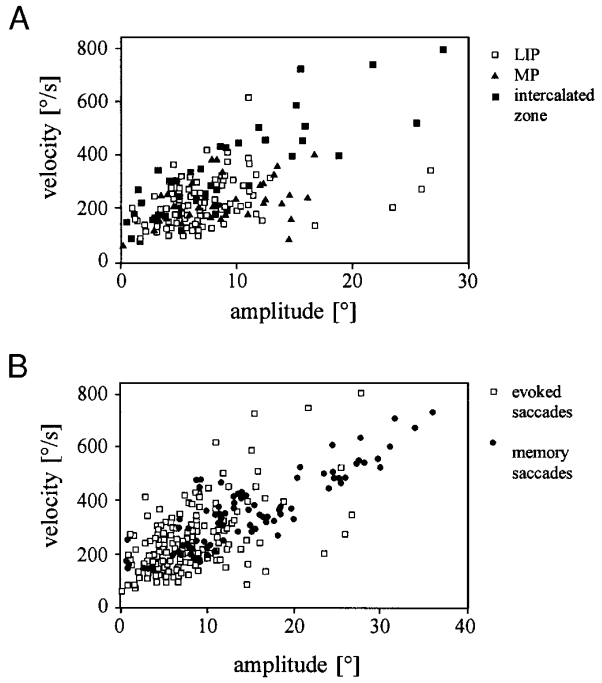


FIG. 7. Plots of saccade velocity as a function of saccade amplitude (main sequence plots). *A*: comparison of the main sequences for saccades evoked from LIP, MP, and the intercalated zone. *B*: comparison of the main sequence of evoked saccades (LIP, MP, and the intercalated zone pooled) with the main sequence of memory saccades made by 1 of the 2 monkeys used.

with downward saccades will be analyzed with the region of upward saccades and referred to as LIP for the sake of simplicity and the necessary qualification of this assignment deferred to the discussion.

Figure 6*B* shows the topography of the directions and amplitudes of evoked modified vector saccades for saccades evoked from straight ahead. As can be seen there, stimulation of sites in the ''appendage'' on the floor of the sulcus gave rise to saccades with a downward component. Conversely, saccades evoked from the larger representation of modified vector saccades on the neighboring lateral bank were without exception characterized by an upward component. The horizontal component of evoked saccades was always directed contralaterally to the side of stimulation, independent of the

FIG. 6. Flattened reconstruction of posterior parietal cortex of *monkey S. A*: summary of the topography of stimulation effects in this monkey. Solid circles, sites whose stimulation evoked modified vector saccades; open stars, sites whose stimulation gave rise to goal-directed saccades; asterisks, sites where ''wavy,'' converging eye movements could be observed; open triangles, sites whose stimulation evoked eye blinks; open rectangles, sites where noneye movements other than eye blinks, namely movements of the face, the pinnae, or the shoulder, were found. Such noneye movements usually supplemented converging eye movements. Open circles, sites whose stimulation did not give rise to any behavioral response. Minimum current strength at nonresponsive sites, 200 μA; identification of responsive sites based on current strength, 100 μA in most cases (range: 25–200 μA). The architecture of stimulation sensitive cortex in the intraparietal sulcus of the 2nd monkey (*E*) was very similar to that of *monkey S.* Closed dashed line approximates the corresponding region in *monkey E* transferred onto the map of *monkey S.* Note that also in *monkey E* most of this region was occupied by upward component modified vector saccades and that the intercalated zone (short arrows) was located close to the anterior end of this region. Area MP in *monkey E* (not shown) had a similar extension but seemed to be displaced posteriorly by ~2 mm. *B*: same flattened reconstruction of posterior parietal cortex of *monkey S* as in *A,* summarizing the topography of the direction and amplitude of modified vector saccades. In addition to sites (solid circles) whose stimulation gave rise to modified vectors saccades, sites (open stars) where converging eye movements were obtained are shown. Vectors plotted for a given site represent the direction and amplitude of the saccade evoked from straight ahead. Note that sites on the lateral aspect of the hemisphere representing converging eye movements are restricted to a narrow strip of cortex, the ''intercalated zone,'' separating the representations of upward and downward saccades in the intraparietal sulcus.

vertical component being upward or downward. Examination of Fig. 6*B* shows that there was hardly any topographical order in the representation of the lengths of vector saccades. The upper and lower field representations of evoked saccades in the IPS were not contiguous. Rather, there was a thin strip of tissue separating them, a fact that has led us to refer to this narrow strip as the intercalated zone. Sites in the intercalated zone have functional properties as revealed by microstimulation, which we found to be qualitatively different from those of the neighboring zones. Stimulation of sites (stars in Fig. 6) in the intercalated zone gave rise to goal-directed saccades. Unlike the modified vector saccades described before, not only the amplitude of the evoked saccades but also their direction was changed by varying the starting position of the eyes at stimulation onset. As shown by the examples in Figs. 3*E* and 4*A*, the modification of the saccade direction and amplitude by eye position was typically such as to drive the eyes toward the same region in head-centered space (''goal zones''), independent of the position of the eyes at stimulation onset. Although individual sites in the intercalated zone could be found to represent very different goal zones, the location of the goal zones did not systematically map onto the intercalated zone (not shown). This negative result is not too surprising, although, taking into account that the intercalated zone is very small, its width probably not exceeding the estimated resolution of the reconstruction of stimulation sites, even if we make the most favorable assumptions. In other words, our results do not necessarily rule out that there is a map of goal zones in the intercalated zone.

In summary, our observations suggest a fractured organization of the IPS with separate representations of evoked saccades directed into the upper and the lower contralateral head-centered space, segregated by a strip of tissue, the intercalated zone, with very different properties.

Medial aspect of posterior parietal cortex: area MP

As seen in Fig. 6*A*, modified vector saccades and goal-directed saccades could not only be evoked from the IPS, but also from a region located on the medial aspect of the parietal lobe, shown in the *left part* of the unfolded maps presented in Fig. 6. To indicate its general location, we refer to this region as area MP for medial parietal area.

A look at the topography of the amplitude and direction of evoked saccades in Fig. 6*B* suggests that MP shares with LIP the segregation into a caudal part representing vector saccades with an upward component and a rostral part representing downward component saccades. There is a tendency for the few sites giving rise to goal-directed saccades to lie close to the boundary between the downward and upward representations, respectively. The much greater dispersion of such sites in MP as compared with LIP could simply reflect the poorer precision of the reconstruction, because MP sites usually fell at the end of penetrations. Finally, note that similar to LIP we did not find much evidence for a topographical order in the representation of the lengths of vector saccades.

Kinematics of evoked saccades

SACCADE LATENCY AND VELOCITY. Our estimates of the onset latencies of evoked saccades were based on a subset of selected trials with the eyes at straight ahead at the time of stimulation onset. The start of an evoked saccade was determined by adopting a velocity criterion. To count as a saccade, eye velocity had to exceed a threshold velocity of 50°/s for at least 25 ms. In such cases, the start of the saccade was defined by going backward in time to the time point at which velocity had reached 10°/s. Altogether, 60 sites were considered (32 in LIP, 18 in MP, and 10 in the intercalated zone; current size between 25 and 200 μA). The average latency based on all sites considered was 30 ms (29.6 ± 12.6, mean $\pm$ SD) without any statistically significant difference between the three areas considered [1-way analysis of variance (ANOVA), $P > 0.05$]. One might have expected that changing the starting position of the eyes would not only modulate the amplitude and (in case of sites in the intercalated zone) the direction of evoked saccades but also the latency of the response. However, this was not the case as

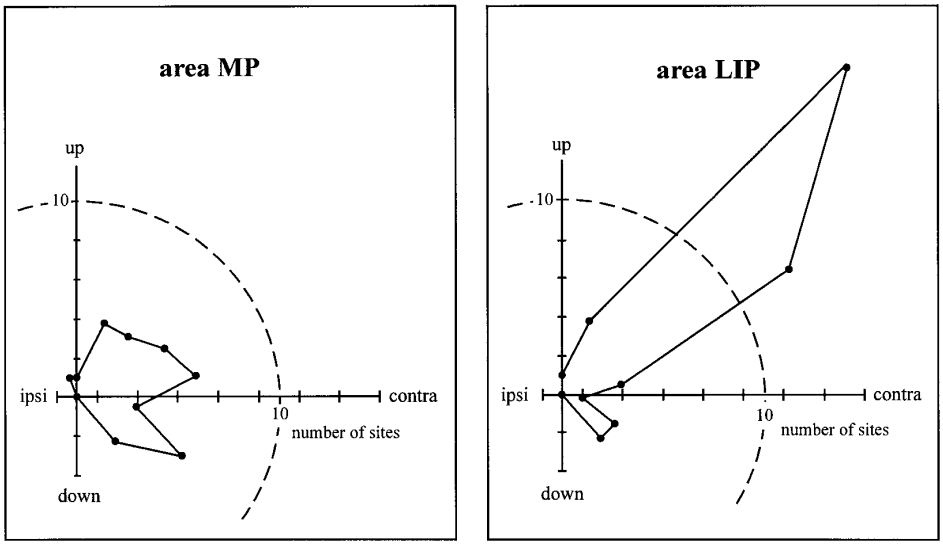


FIG. 8. Polar plots comparing the directions of saccades evoked from LIP and MP. The analysis is based on saccades evoked from straight ahead and considers all sites, for which saccades could be evoked from this orbital position. The circular means are 17.4° for MP and 35.1° for LIP, indicating that sites yielding saccades with an upward component dominated the samples. This dominance of sites representing upward-component saccades was even stronger in LIP as compared with MP as indicated by a significant difference of the circular means (Mardia-Watson-Wheeler-test, $P < 0.001$).

shown by a comparison of the latencies of saccades evoked from straight ahead with the latencies of maximum amplitude saccades (areas LIP and MP pooled, *t*-test, $P > 0.05$).

The velocities of saccades evoked from LIP, MP, and the intercalated zone corresponded to the velocities of memory-guided saccades made by the same monkeys and are slower than visually guided saccades. The former is demonstrated by plots of velocity as a function of saccade amplitude (the so-called main sequence plots) (Bahill et al. 1975) for evoked saccades and memory-guided saccades, respectively, shown in Fig. 7. Figure 7*A* compares the scatter plots of velocity as a function of the amplitude of saccades evoked from LIP, MP, and the intercalated zone respectively, whereas *B* compares evoked saccades, without differentiating between the responsive parietal regions, with memory-guided saccades made by one of the two monkeys used. The main sequences for saccades evoked from LIP, MP, and the intercalated zone, respectively, were not statistically different from each other.

Staircase saccades

One additional difference between the intercalated zone and neighboring stimulation-sensitive cortex was revealed by increasing the standard 100 ms duration of the stimulation train to 500 ms. When such prolonged stimulation was applied in either LIP or MP, we frequently were able to evoke sequences of discrete saccades (staircase saccades), in which individual saccades were separated by intervals of variable duration, in which the eyes did not move (see Fig. 3 in Thier and Andersen 1996, for an example from LIP). Staircase saccades tended to drive the eyes toward the limits of the oculomotor range, and the amplitude of the saccades in the staircase sequence often decreased with increasing order. This is what would be expected if eye position modulated the amplitude of staircase saccades in the same way as it modulated the amplitude of single saccades. By the same token, the direction of the saccades constituting the staircase stayed the same.

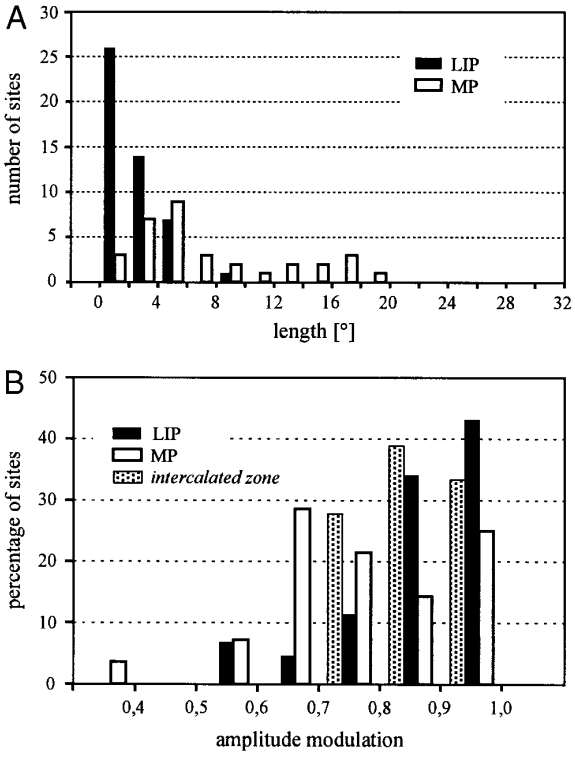


FIG. 9. Histograms comparing the amplitudes of saccades evoked from LIP and MP. *A*: histogram plotting the amplitudes of saccades evoked from straight ahead for sites in LIP and MP, respectively. Refer to the text for further details. *B*: histogram comparing the change of amplitude of evoked saccades by varying the initial orbital position for sites in LIP, MP, and the intercalated zone. The change of amplitude was quantified by dividing the difference between maximal saccade amplitude and minimal saccade amplitude by the maximal saccade amplitude. This ratio will vary between 0 and 1. It will be 0 if saccade amplitude does not change with orbital position, yielding the same values for maximal and minimal saccade amplitude. Conversely, the ratio will take up the maximal value 1 in cases the minimal amplitude becomes 0.

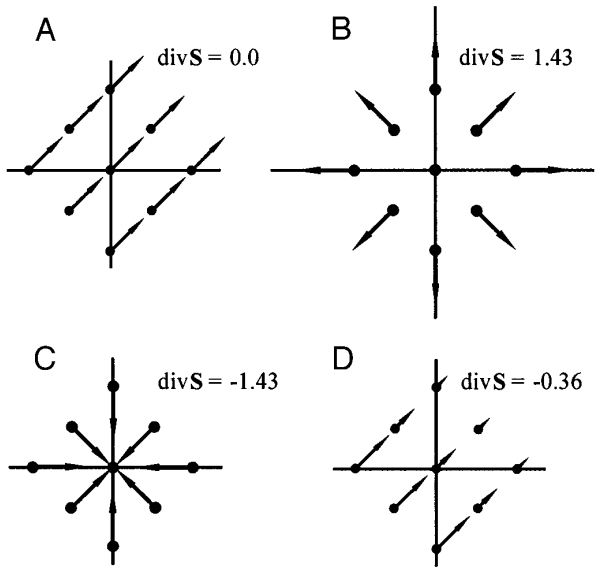


FIG. 10. Divergence operator was used to quantify the magnitude of the change of direction of evoked saccades, brought about by varying the initial orbital position. *A–D*: 4 different hypothetical 2-dimensional vector fields, which try to give a flavor of the basic properties of the divergence operator. Although the divergence operator is not insensitive to changes of vector length (*D*), changes of direction (*B*) have a much stronger impact. See the text for further details.

Prolonged stimulation of sites in the intercalated zone did not evoke staircase saccades. Rather single saccades were evoked, which drove the eyes into more or less distinct regions in the frontal plane. Once the eyes had arrived inside the confines of these goal zones, continuing stimulation elicited slow unsystematic drifting eye movements rather than further saccades. Very similar results were obtained for the few sites in MP whose stimulation with standard stimuli elicited goal-directed saccades.

Preferred directions

We have noted earlier that much more space in the IPS is devoted to evoked saccades with an upward component than to saccades with a downward component (Thier and Andersen 1996). A comparable imbalance does not seem to hold for MP. This is shown in a quantitative manner in Fig. 8, which compares the distributions of the directions of

saccades evoked from LIP with those evoked from MP. The distributions are based on saccades evoked from straight ahead. The marked overrepresentation of sites with upward directed saccades in LIP is reflected by a peak in the LIP distribution comprising the bins 0–20° and 20–40° and a circular mean of the directions of evoked saccades of 35.1°. On the other hand, the distribution of the directions of saccades evoked from MP sites is much more widespread, without a distinctive peak and a circular mean, which at 17.4° is significantly closer to the horizontal meridian than the circular mean for LIP (Mardia-Watson-Wheeler-test, $P < 0.001$) (compare Batschelet 1981).

Saccade amplitude

Figure 9A compares the distributions of the amplitudes of saccades evoked from straight ahead for areas LIP and MP. Similar to saccade direction, saccade amplitudes are also represented more unevenly in LIP as compared with MP. As shown in Fig. 9*A*, LIP is characterized by a clearcut overrepresentation of sites whose stimulation gave rise to comparatively small amplitude saccades. On the other hand, stimulation of many sites in MP resulted in fairly large amplitude saccades and correspondingly, the distribution of saccade amplitudes obtained for MP differs significantly from the one derived for LIP (Wald-Wolfowitz-runs test, $P \leq 0.045$). The fact that the amplitude distribution for saccades evoked from LIP peaks at only 2° (compare Fig. 9*A*) seems to suggest that LIP specializes in small amplitude saccades. This view would be misleading, however, because, as mentioned before, shifting the starting position against the direction of the evoked saccade usually enlarged the amplitude of saccades considerably. We will examine the degree of amplitude modulation by orbital position in more detail next.

Quantitative analysis of orbital position effects

MODULATION OF SACCADE AMPLITUDE BY INITIAL ORBITAL POSITION. To quantify the modulation of saccade amplitude by varying the starting position of the eye at the time of stimulation onset, we divided the difference between the maximal and the minimal saccade amplitude by the maximal saccade amplitude. This ratio will vary between 0 and 1. It will be 0 if saccade amplitude does not change with orbital position, yielding the same values for maximal and minimal saccade amplitude. Conversely, the ratio will take up the maximal value 1 in case the minimal amplitude becomes 0. Figure 9*B* shows the distribution of this amplitude modulation ratio for MP, LIP, and the intercalated zone. The high degree of dependency on initial orbital position in all 3 regions is emphasized by the fact that the majority of sites were characterized by modulation ratios between 0.8 and 1.0, whereas only 1 site in MP displayed a smaller modulation index of ~0.4. Although the distribution for MP was shifted somewhat relatively to the ones for LIP and the intercalated zone toward smaller modulation indices, this shift did not reach statistical significance (Kruskal-Wallis nonparametric ANOVA, $P > 0.05$).

Current size, needed to reliably evoke saccades from LIP, MP, and the intercalated zone varied between 25 and 150 μA, depending on the particular site and also the starting position of the eyes at stimulation onset. Although we did not attempt to study the thresholds for evoked saccades in detail, we encountered many sites in LIP and MP, whose stimulation at a given current size evoked saccades only if the starting position of the eyes had been shifted against the direction of the evoked saccade. Starting positions located at the opposite side were usually rendered effective only after the stimulation current had been raised further.

DEGREE OF CENTERING OF SACCADES. We had initially assigned evoked saccades to either the modified vector saccade group or the ''goal-directed'' saccade group qualitatively by eye. Although this approach is probably appropriate in cases of clear-cut examples of either response type, there were examples of orbital position dependency that did not allow for a satisfactory assignment by eye. We therefore devised two objective methods to quantify the degree of centering or goal directedness of evoked saccades.

Formally, the linear approximations of evoked saccades can be considered as two-dimensional vectors $\mathbf{S} = (s_x, s_y)$, which are functions of two-dimensional space, thus forming a vector field. Two-dimensional space in this case is defined by the x and y components of the initial orbital position of the eyes (e_x, e_y) at the time of stimulation onset. The divergence differential operator $\mathrm{div}\mathbf{S} = \delta s_x/\delta e_x + \delta s_y/\delta e_y$, when applied to this vector field, derives a scalar that quantifies the amount of vergence in the vector field. The examples shown in Fig. 10 try to illustrate the major properties of this operator. Figure 10*A* depicts a vector field, made up of saccades of constant length and direction. The divergence operator is zero in this case. It becomes positive in the case of a highly divergent vector field (Fig. 10*B*), in which the individual vectors point away from a common central source. Conversely, in the case of a highly convergent vector field (Fig. 10*C*), similar to some of the patterns obtained from sites in or close to the intercalated zone, the operator becomes negative. Although the size and sign of the operator is largely determined by the amount of vergence present in the vector field, it is not invariant to changes in the lengths of the vectors. This is exemplified by the vector field shown in Fig. 10*D*, which resembles the patterns of modified vector saccades found in LIP and most of MP. Although nonzero and negative in this case, the operator remains much smaller than in the case of patterns containing substantial vergence. In conclusion, we would expect to find a quantitative rather than a qualitative difference between the values, the divergence operator adopts for sites in LIP as compared with sites in the intercalated zone. Figure 11*A* shows that this is actually the case. This figure compares the distributions of the divergence operator for stimulation sites in LIP, MP, and the intercalated zone. The distribution of div**S** for the intercalated zone is displaced significantly toward more negative values relative to the distributions for LIP and MP, the latter two not being statistically different (see legend to Fig. 11*A* for details on the statistics). Because the amount of amplitude modification was the same for the intercalated zone and LIP (Kruskall-Wallis analysis, $P > 0.05$) and lower in MP than in the intercalated zone (Kruskall-Wallis analysis, $P < 0.02$), this result indicates a significantly larger degree of centering in the intercalated zone than in both LIP and MP.

The second objective approach we chose to determine the validity of the subjective differentiation into the intercalated zone and neighboring LIP was based on a two-dimensional linear regression analysis. This analysis expressed the x and y components of the linear approximation of the evoked saccade obtained for a given orbital position (s_x, s_y) as the linear combination of the x and y components of the initial orbital positions of the eyes (e_x, e_y). We then derived from the pair of linear equations $s_x = f(e_x, e_y)$ and $s_y = f(e_x, e_y)$ the orbital position at which both s_x and s_y will become zero. In the case of goal-directed eye movements, this orbital position would obviously correspond to the location of the ''goal'' in head-centered coordinates. In the case of modified vector saccades without any convergence, however, s_x and s_y will be reduced and finally become zero solely as a consequence of amplitude modification. Figure 11*B* is a plot of the calculated orbital positions for which the affiliated eye movements would become zero (''zeroing positions''). Although most of the zeroing positions calculated for sites taken from the intercalated zone fell within the oculomotor range (stippled line), the vast majority of zeroing positions calculated for sites taken from LIP lay clearly outside. The much more eccentric locations of the zeroing positions for sites taken from LIP simply reflect the fact that the modification of the saccade amplitude within the confines of the oculomotor range does not zero the amplitude of evoked saccade.

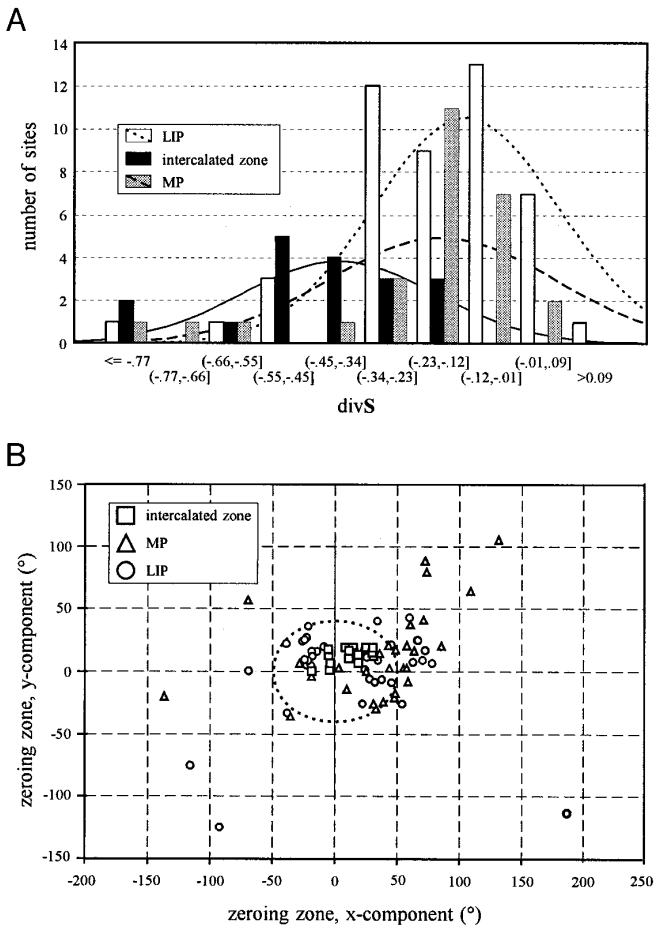


FIG. 11. Quantitative analysis of the degree of centering of evoked saccades. *A*: comparison of the distributions of the divergence operator div**S** for sites in area LIP, MP, and the intercalated zone. The distribution of div**S** for the intercalated zone is displaced significantly toward more negative values relative to the distributions for LIP and MP (Kruskall-Wallis analysis, $P < 0.00001$), the latter not being statistically different (Kruskall-Wallis analysis: comparison of intercalated zone, LIP, MP: $P = 0.00001$; intercalated zone vs. LIP or MP: $P < 0.000001$; LIP vs. MP: $P = 0.42$). *B*: plot of locations of starting positions of the eyes at which electrical stimulation would be rendered ineffective (zeroing positions). See text for details on the approach underlying the calculation of these locations. The dashed ellipsoid is an approximation of the primate oculomotor range. Note that unlike the goal zones calculated for MP and LIP, those derived for stimulation sites in the intercalated zone are confined to the oculomotor range.

In summary, the quantitative analysis based on two different aproaches indicates that our subjective differentiation of sites with and without goal directedness was quite reliable. We therefore conclude that irrespective of some overlap, saccades evoked from the intercalated zone and neighboring LIP are qualitatively different.

Noneye movements evoked by electrical microstimulation

Stimulation of virtually every site in the intercalated zone gave rise to noneye movements. Noneye movements could also be evoked at the few sites in MP whose stimulation gave rise to goal-directed saccades. Conversely, noneye movements were absent from modified vector saccade sites in MP and LIP. Noneye movements evoked from the intercalated zone and from the goal-directed saccade sites in MP were very similar. The full pattern of noneye movements consisted of transient contractions of varying parts of the face (Fig. 12, *2c* and *2d*), pinnae movements (Figs. 12, *1*, and 13), brief contractions of the shoulder girdle and the proximal parts of either arm that could cause jerks of the arms and the hands (Fig. 12, *2a* and *2b*), and fast head movements (Fig. 14*A*). Isolated movements of the more distal parts of the arm were absent, and also leg movements were never observed. The specific shape of the pattern depended on the site being stimulated. While the full pattern was found only at a minority of sites, stimulation at most others elicited parts of the full pattern, for instance head and shoulder movements without pinnae or facial movements or vice versa. Similar to the evoked saccades, also the noneye movements evoked were of short latency and high velocity.

Although most of our results related to noneye movements were based on visual inspection and occasional video taping of the stimulation effects, we have been able to study pinnae and head movements evoked from a few of the sites in the intercalated zone, using quantitative methods. Pinnae movements were recorded using search coils taped to the pinnae, and head movements were measured using a precision potentiometer attached to a special head holder, restricting head movements to the yaw axis. As can be seen in Fig. 13, stimulation-evoked pinnae movements did not start much after the stimulation-evoked eye movements, only ~40 ms after stimulation onset. As shown in Fig. 14*A*, the same held true for the stimulation-evoked head movements, which started ~50 ms after stimulation onset. Both the amplitude and the direction of the stimulation-evoked head movements depended on the starting position of the head.

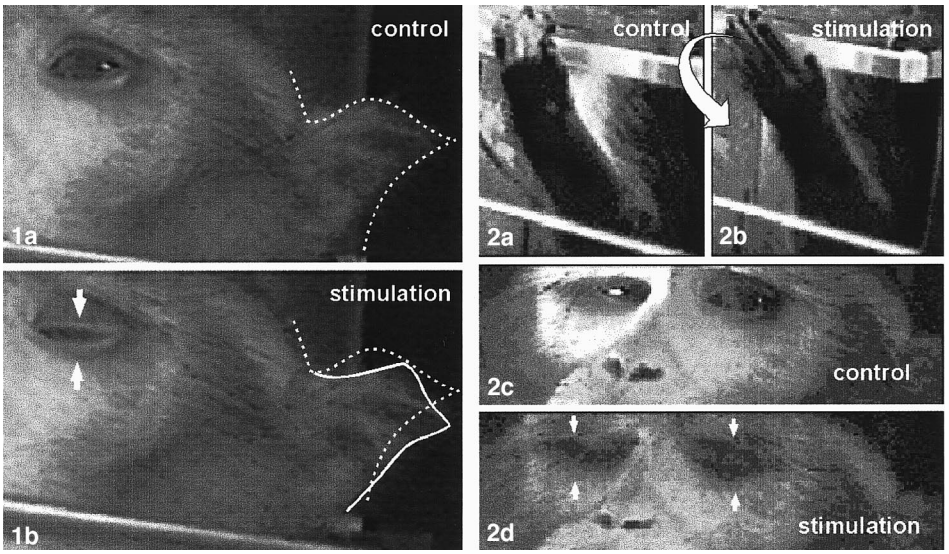


FIG. 12. Video frames showing examples of noneye movements evoked by sites in the intercalated zone. *1*: 2 subsequent frames exemplifying that stimulation elicited eye closure and pinnae movements (see also Fig. 18 for the latter). *2*: examples of eye closure accompanied by a brisk movement of the whole arm, including the shoulder girdle (*a* and *c* and *b* and *d*, respectively, are based on the same, subsequent video frames). Note that the noneye movements shown were in any case accompanied by evoked saccades. Refer to METHODS for details on the stimulation parameters. Stimulation current throughout 250 μA.

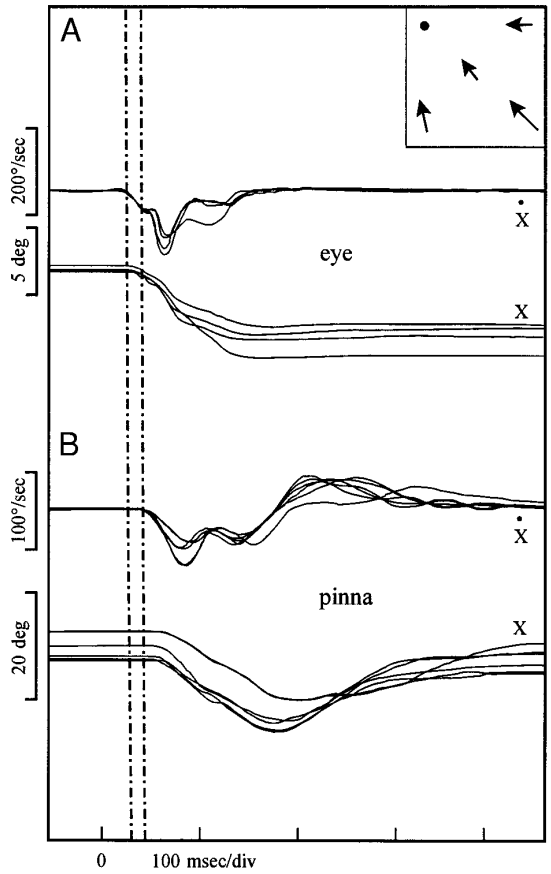


FIG. 13. Pinnae movements (*B*) accompanying eye movements (*A*) evoked by stimulation of a site in the intercalated zone. Stimulation current 200 μA. The time course of evoked pinnae movements was studied by taping a search coil to 1 of the 2 pinnae. *A, inset*: size and direction of evoked saccades (linear approximations, see METHODS for details) for a reduced set of 5 initial orbital positions (the 5 innermost shown in Fig. 1) characterizing this particular site. Stimulation starts at 0. The 1st dashed line marks the onset of the evoked eye movement; the 2nd one the onset of the pinnae movement.

In the example shown in Fig. 14*A*, evoked head movements were directed to the right if the head was initially on the left and conversely, evoked head movements were directed to the left, if the head started from a position on the right. However, if the head was initially turned straight ahead, the stimulus was rendered largely ineffective. Figure 14*B* plots the size and direction of stimulation-evoked head movements as a function of the initial position of the head relative to the trunk. The data could be fitted by a linear regression ($P < 0.001$, solid line). In accordance with the aforementioned qualitative observation, the regression predicted that the amplitude of the evoked head movement would become zero if the head is turned straight ahead initially. A comparably detailed analysis was possible for three other sites in the intercalated zone spanning a distance of ~3.5 mm. In every case, the regression lines crossed the *y*-axis at an initial head position corresponding to straight ahead (*y*-intercepts for the 3 sites not significantly different from 0).

Observations on the influence of head position on evoked saccades

We studied the effects of static head position on the metrics of evoked saccades by comparing the pattern of evoked saccades obtained from a restricted set of four initial orbital positions for three static head positions, corresponding to straight ahead, head rotated to the left and to the right (relative to the trunk). Figure 15 compares the results obtained for four sites in LIP for the two extreme static head positions (head 15° left vs. head 15° right). Evoked eye movements presented in this figure are plotted in head-centered coordinates, and the patterns derived for the two opposite static head positions (left vs. right) are superimposed for comparison. As can be seen, the patterns are virtually identical, suggesting that differences in head position relative to the trunk do not affect the size and direction of evoked saccades. Figure 16 shows a site from the intercalated zone for comparison. Obviously, changing the position of the head relative to the trunk (20° left, straight ahead, 20° right) influences the metrics of the evoked eye movements considerably. The

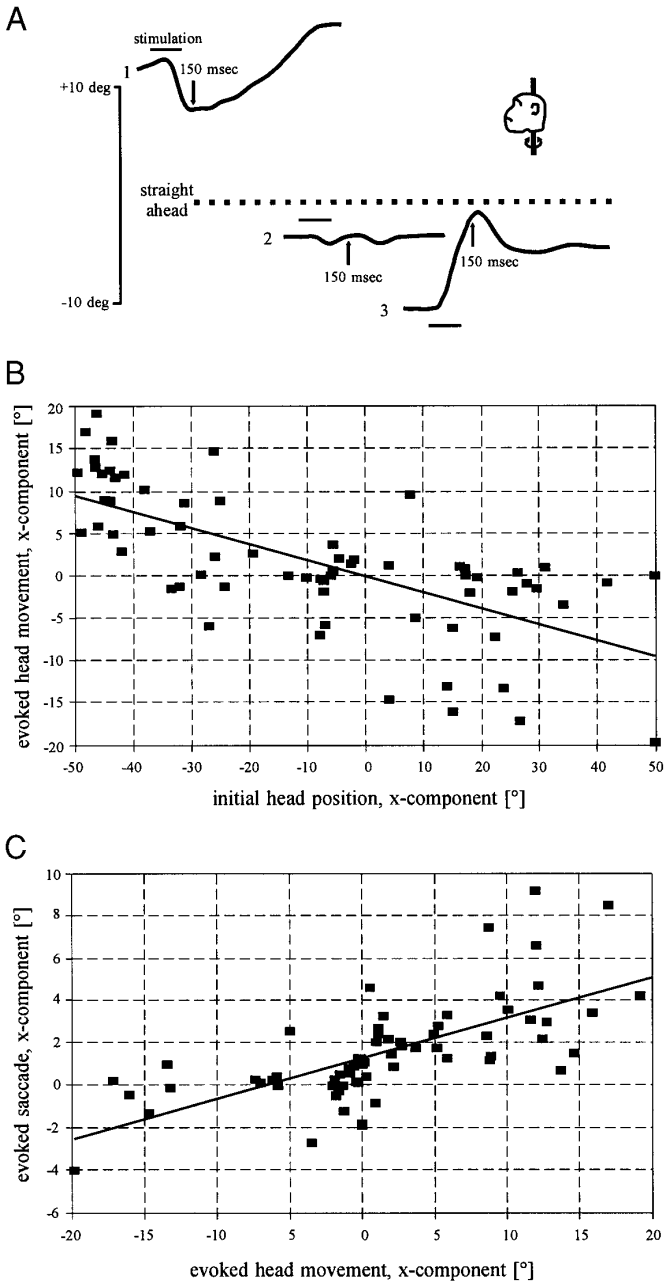


FIG. 14. Electrical microstimulation in a monkey whose head was free to move about the yaw axis (see *inset* in *A*). Stimulation current 400 μA. *A*: head movements evoked by stimulation of site in the intercalated zone. Note the dependence of the amplitude and direction of the evoked head movement on the location of the head relative to the trunk at stimulation onset. When the head was turned to the right (1), stimulation evoked a head movement to the left. However, when the head was initially turned to the left, the direction of the evoked head movement was to the right (3). Finally, when the head was turned straight relative to the trunk (2), no comparable head movement was evoked. *B*: plot of the size and direction of the evoked head movement as a function of the initial head position for this site. *C*: plot of the size and direction of the *x*-component of the evoked eye movement as a function of the size and direction of the *x*-component of the evoked head movement for the same site, demonstrating that evoked eye and head movement do not add up to a constant evoked gaze shift.

three patterns of eye movements plotted in head-centered coordinates related to the three positions of the head relative to the trunk no longer coincide. Shifting the head to the right displaced the goal zone to the right, and, conversely, shifting the head to the left moved the goal zone to the left. Similar results characterized the two other sites from the intercalated zone in which we tested the effects of static head position. These findings are at odds with the possibility that sites in the intercalated zone represent fixed gaze saccades with varying contributions of the head and the eyes. In the case of a representation of gaze vectors, we would have expected to find that moving the head to the right should move the centering zone of the eyes to the left rather than to the right. One might argue that the normal summation of the eye and head movement contributions to the putative gaze shift represented by the site studied might be altered by the fact that the head was only statically displaced, rather than allowed to respond to the stimulus as well. However, a reexamination of the relationship of eye and head movements in those instances in which the head was allowed to move freely about the yaw axis suggests that our initial conclusion is valid. Figure 14*C* plots the *x*-component of the evoked saccade as a function of the *x*-component of the evoked head movement with the starting position of the head varied between ±50° (compare Fig. 14, *A* and *B*). As can be seen,

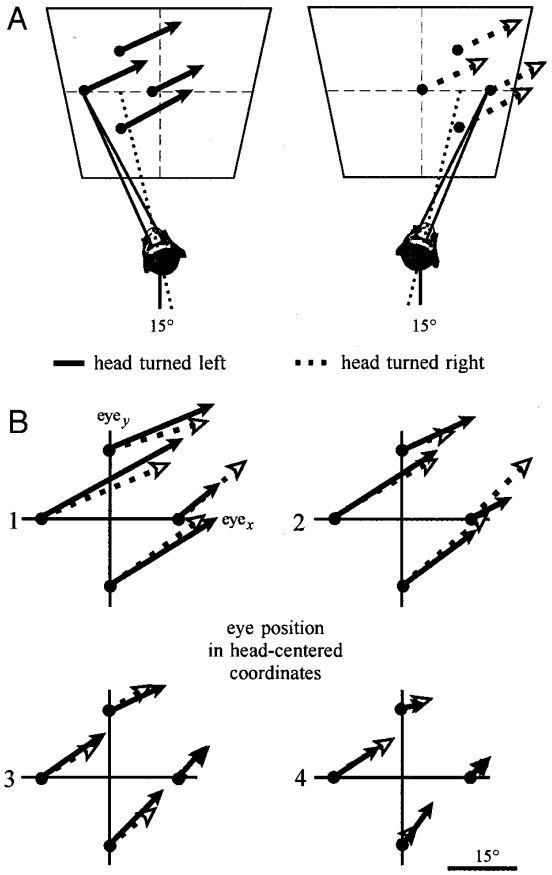


FIG. 15. Saccades evoked from sites in LIP do not depend on the static position of the head related to the trunk. *A*: paradigm: saccades were evoked with the monkey's head, which in any case was fixed, being turned either 15° to the left or 15° to the right. *B1–B4*: examples based on 4 individual stimulation sites. Each shows plots of the linear approximations of evoked saccades for the 5 innermost initial orbital positions shown in Fig. 1 for the 2 different static head positions.

rather than adding up to a constant gaze shift, the *x*-component of the evoked saccade increased, when the *x*-component of the evoked head movement became larger (linear regression, $P < 0.001$).

Single units

For many sites stimulated, we were able to isolate single units and to determine their properties. Saccade-related responses were the hallmark of single units recorded from LIP, MP, and 7a. On the other hand, units located in the intercalated zone were not activated by the standard memory saccade paradigm. We did not test the possibility that units from this part of the IPS would respond to the presentation of a saccade target within the confines of the goal zone as defined by microstimulation. Figure 17 shows the example of a unit from area MP, tested with the memory saccade paradigm. Its location is shown in the *inset* to Fig. 18 (*site A*). The unit started to discharge soon after the visual target had appeared below the central fixation point. The discharge continued after the target had been turned off and blended into activity before and during the execution of the saccade. The plots of mean discharge rate as a function of direction (direction tuning curves) for the visual, the memory, and the presaccadic response components depicted in Fig. 18*A* shows that the preferred directions of these three response components were similarly aligned with downward and, moreover, were very similar in terms of the spike rates. As first shown by Barash et al. (1991a), strong memory and saccade-related responses are a feature distinguishing many LIP units from those found in neighboring area 7a. The example presented before suggests that units from area MP might share this feature with LIP units. That this is indeed the case is demonstrated by Fig. 19, which compares the population means of the visual, the memory, the presaccadic, and the postsaccadic responses for areas LIP, MP, and 7a. Although both LIP and MP units are characterized by strong visual, memory, and presaccadic activity, area 7a units are distinguished by strong visual and postsaccadic discharge and a virtual absence of memory and presaccadic responses.

A relationship between unit preferred direction and the directions of evoked saccades in saccade-related cells is suggested by the two examples shown in Fig. 18, comparing the direction tuning curves of two units from neighboring sites in MP with the directions of saccades evoked from these sites. Stimulation at *site A* evoked saccades to the lower right, and the unit (same as the one shown in Fig. 17) was activated maximally by downward saccades with a small right component. Stimulation of *site B* evoked saccades to the upper right, and the unit recorded from this site preferred saccades toward the upper right. The notion of a relationship between the preferred directions of single units in MP and LIP with the directions of microstimulation evoked saccades is supported by highly significant circular-circular correlations between the directions of evoked saccades and the preferred directions of the visual as well as the memory response components of single units with significant memory responses ($n = 21$; MP and LIP pooled; $P < 0.01$) recorded from the same sites. The circular-circular correlations are illustrated in Fig. 20. The close relationship between unit preferred directions and directions of evoked saccades is also expressed by the fact that the distributions of the differences of directions of evoked saccades and the preferred directions of the visual and the memory responses are centered on zero (Fig. 20, *A* and *B*, *bottom*).

DISCUSSION

The major finding of the present study is that electrical microstimulation is able to delineate distinct eye movement–related regions in the posterior parietal cortex with well-defined functional properties. We will first try to relate the parcellation of the posterior parietal cortex suggested by microstimulation to the well-established parcellation based on anatomy and single-unit recordings. We will then try to answer the question whether the properties of the stimulation effects may help us to extend our understanding of information processing for saccades and specifically if they are able to shed light on the coordinate frames used for the representation of saccade targets. With respect to the latter, we will concentrate on the implications of the eye position–dependent modulation of saccade amplitude and direction.

Topography of stimulation effects in the IPS

Eye movements were evoked from two widely separated parts of the posterior parietal cortex, one encompassing a

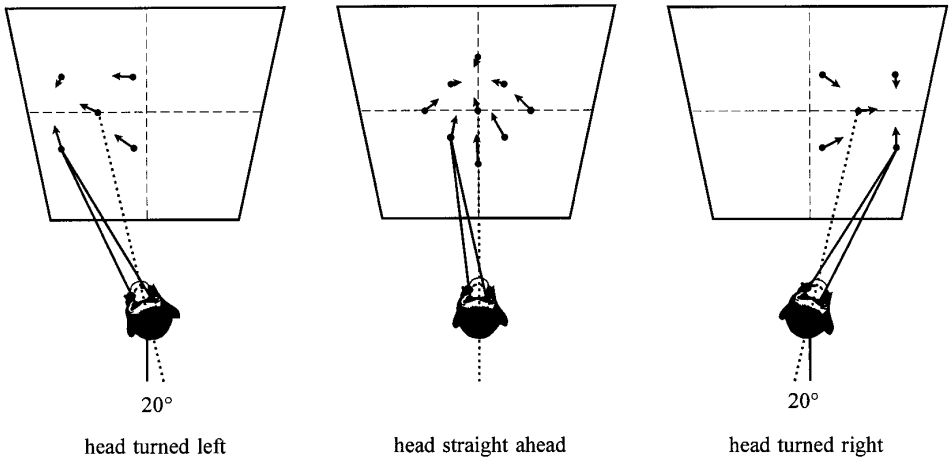


FIG. 16. Saccades evoked from the intercalated zone depend on the static position of the head relative to the trunk. Paradigm: saccades were evoked with the monkey's head, which in any case was fixed, being turned either 20° to the left, 20° to the right, or straight relative to the trunk.

strip of cortex on the lateral bank and the fundus of the IPS and the other one confined to mesial parietal cortex close to the caudal end of the cingulate sulcus. In neither case did we try to relate the topography of the stimulation effects to cytoarchitectonic or myeloarchitectonic boundaries. Despite the absence of such information, we are confident that an identification of the topography of the stimulation effects, at least with respect to the parts of the IPS explored, with previous parcellations of this part of the brain is possible. One helpful criterion is the use of topographical landmarks such as cortical sulci. However, the most useful criterion is the physiological properties of single cells. We were able to record from single units at the same sites that later were microstimulated. This comparison demonstrated that evoked saccades whose amplitude was modulated by eye position were confined to those parts of the IPS, characterized by a comparatively high density of saccade-related cells with strong activity in the memory period of the saccades-to-remembered targets task (memory saccade cells). Does that mean that the modified vector saccade zone in the IPS and area LIP as previously defined are identical? We would not go that far for the following reasons. The modified vector saccade zone in both monkeys used was considerably smaller than previous designations of area LIP. LIP was originally singled out as that part of the posterior parietal cortex having strong connections to sacccade centers, including the frontal

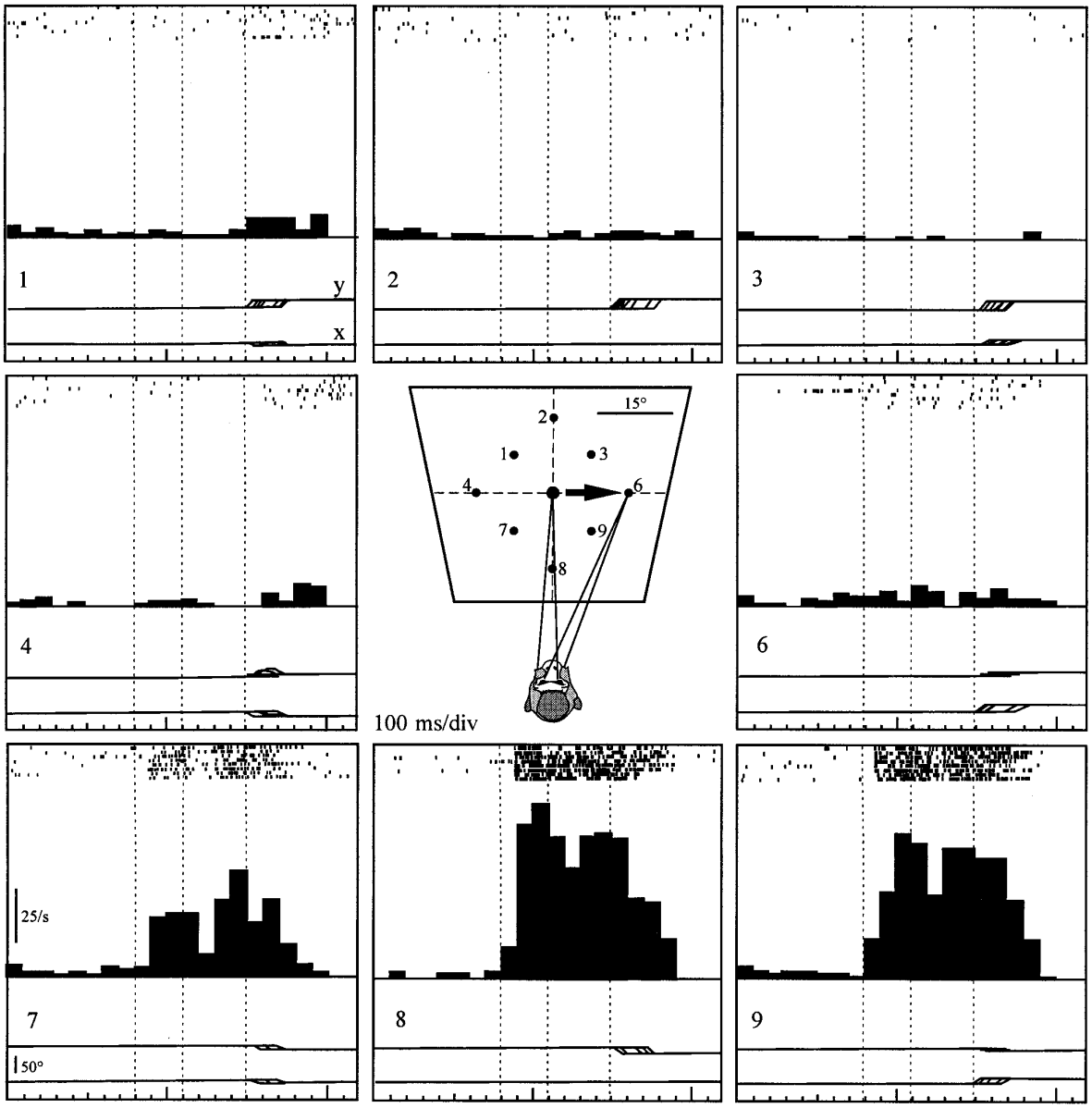


FIG. 17. Responses of a single unit from area MP in the memory saccade task in 8 directions (amplitude 15°). Shown in each panel, from the *top*, are the spike rasters, where each horizontal trace represents one trial, and each tick marks the occurrence of a spike, the resulting histogram and the horizontal (x) and vertical eye position (y) traces of the various trials superimposed. Vertical dotted lines denote, from the *left*, the onset and the offset of the target, and the offset of the central fixation spot. Trials are aligned on the sensory events.

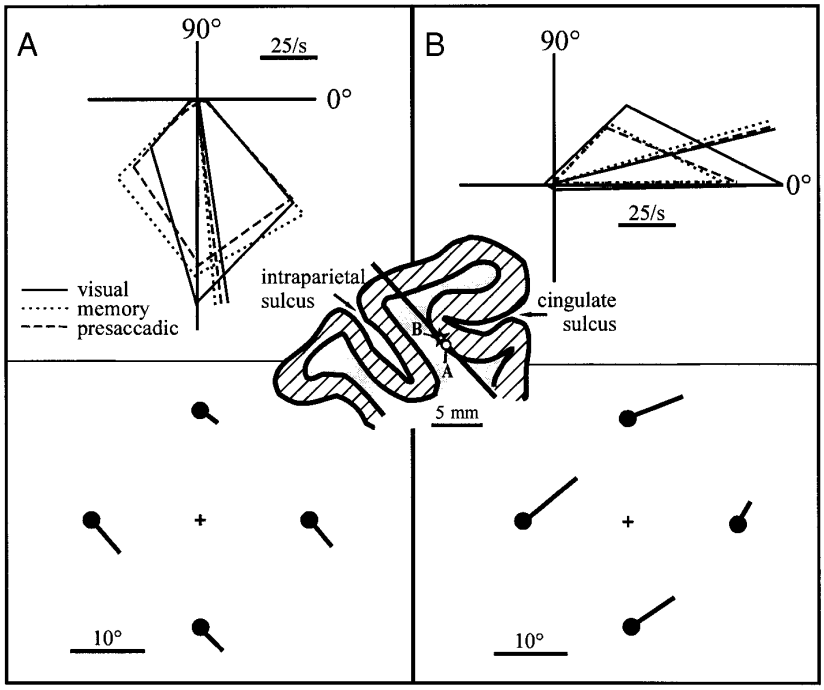


FIG. 18. Comparison of preferred directions of 2 single MP units with the directions of evoked saccades (stimulation current 150 μA). *Middle inset*: location of the recording sites. The unit whose directional tuning is shown in *B* corresponds to the one shown in Fig. 17*1*.

eye fields (FEF) and the superior colliculus (SC) (Andersen et al. 1985). According to previous anatomic and electrophysiological work, area LIP has two parts, a larger ventral part, corresponding to the densely myelinated region on the posterior aspect of the lateral bank of the IPS and a much smaller dorsal part, encompassing the adjoining 1–2 mm of nonmyelinated cortex on the lateral bank of the IPS (Andersen et al. 1990a; Blatt et al. 1990). The myelinated zone is ~10 mm long in the anterior-posterior dimension of the sulcus and 3–4 mm wide in the dorsoventral axis (Blatt et al. 1990; Ungerleider and Desimone 1986). Although the dorsoventral extension of the stimulation-sensitive upward saccade zone in the IPS seems to correspond to that of area LIP, its anterior-posterior dimension is much smaller.

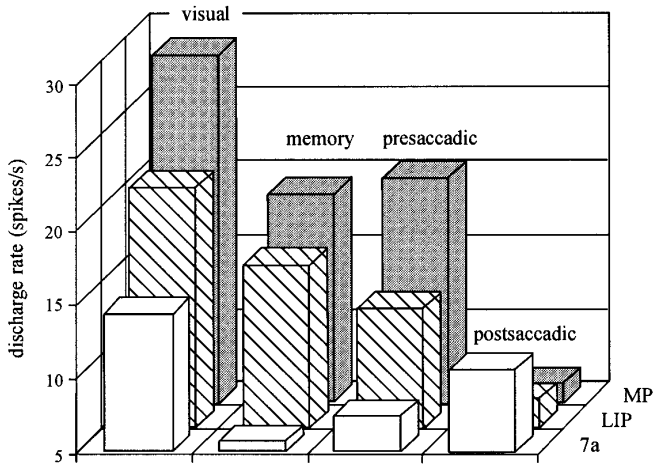


FIG. 19. Histogram comparing mean visual, memory, presaccadic, and postsaccadic activity for single units recorded from areas 7a (n = 32), LIP (n = 35), and MP (n = 40). Confer to METHODS for a definition of the response components.

Another finding preventing the immediate identification of the stimulation-sensitive zone with area LIP is the topography of the stimulation effects in the IPS, which does not correspond to the complex topography of visual receptive-field locations in area LIP seen in recordings from anesthetized cynomologus monkeys (Blatt et al. 1990). However, there is no inevitable contradiction. Not all the cells available within a region of cortex are necessarily responsible for the shaping of the microstimulation effect, and the topography of the subpopulation relevant may be much simpler than the topography of the overall population. Actually, as will be discussed later, there is indeed evidence that the stimulation effects are mediated by the subpopulation of memory saccade cells whose topography seems to reflect the simple topography of the stimulation effect at least roughly. Even if there were significant differences between neighboring cells, e.g., in terms of their preferred directions, electrical microstimulation would tend to iron them out. The reason is that the currents needed are so large that they will always activate a large group of neighboring cells and the saccade evoked will probably represent the averaged activity of these cells. The direction of the evoked saccade in this scenario will reflect the directional bias in the group of cells activated. Actually, a bias for the upper visual field has been seen in recording experiments from area LIP (Li and Andersen 1994) and may account for the dominance of upward evoked saccades in the larger, caudal part of the stimulation-sensitive zone. Such an averaging may also account for the small amplitude of saccades evoked from LIP. Area LIP visual receptive fields (Barash et al. 1991b; Blatt et al. 1990) and memory and movement fields (Barash et al. 1991b) are often centered at considerably peripheral locations, certainly locations much more peripheral than suggested by the small amplitude evoked saccades. A direct example of this phenomenon is seen in Figs. 17 and 18*A*, where a cell in area

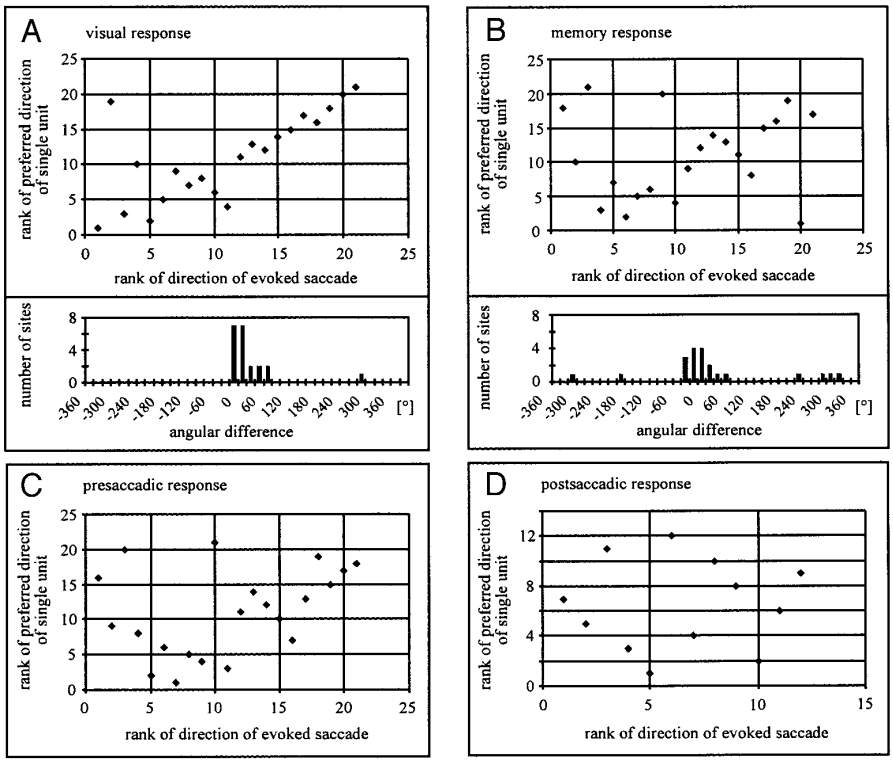


FIG. 20. Relationship between the preferred directions of the visual, the memory, the presaccadic and the postsaccadic response components of single units and the directions of saccades evoked from the same sites. Refer to the text for the definition of the response components. *A*: visual response. *Top panel*: plot of circular-circular correlation (Batschelet 1981). *Bottom panel*: distribution of angular differences between preferred direction of visual response component and direction of evoked saccade. *B*: memory response. Format of presentation as in *A*. The circular-circular correlations in *A* and *B* are significant, $P < 0.01$. *C* and *D*: circular-circular correlations (nonsignificant, $P > 0.05$) for the presaccadic and the postsaccadic responses.

MP has robust neural activity at 15° eccentricity, but microstimulation-evoked saccades at this location (for the optimal eye position) are only ~5°. Thus the large current required to reach threshold for evoking saccades from the posterior parietal cortex may engage a large population of cells with different preferred directions and amplitudes, and only the vector average of the cells stimulated is seen in the response.

In conclusion, we suggest that the region of upward evoked saccades corresponds to a low-threshold core within previously described area LIP. Such a low-threshold core would be expected if saccade-related units within this core had a more direct connection to the saccade effectors than those outside. Such an organization is probably the explanation of the organization of the FEF, characterized by a low-threshold core zone for evoked saccades, being much smaller than the region of arcuate cortex with saccade-related single-unit activity (Bruce et al. 1985). The intercalated zone and the downward evoked saccade zone in the IPS are rostral and ventral to area LIP. These latter zones could be considered to comprise a continuation of LIP that had previously not been explored. A reason for adding them to LIP is that they represent a low-threshold region for evoking saccades. The anatomic position of these two zones anterior to previously described LIP and within the fundus of the IPS suggests that they may share territory with previously described area VIP (Colby et al. 1988, 1993; Duhamel et al. 1997).

Whereas stimulation of the IPS outside the intercalated zone gave rise to vector saccades whose amplitude was modified by the starting position of the eyes, the hallmark of the intercalated zone was goal-directed saccades, typically accompanied by a rather stereotype pattern of noneye movements that included head movements. Although both Shibutani et al. (1984) and Kurylo and Skavenski (1991) mention goal-directed patterns of evoked eye movements, both studies missed the highly conspicuous organization of this part of the IPS. Although some of the penetrations made by Shibutani et al. (1984) may have touched our intercalated zone, several observations communicated by Kurylo and Skavenski (1991) clearly indicate that their goal-directed movements could not have arisen from this part of the IPS. First, the goal-directed movements they obtained were in most cases accompanied by blinking but not by the other noneye movements characterizing the intercalated zone. We found eye movements with blinking but without other kinds of noneye movements only on the upper medial bank of the IPS and in cortex rostral to it, cortex identified as part of area 5. The eye movements evoked from this part of the parietal lobe, although reminiscent of goal-directed eye movements, were much less predictable than the goal-directed eye movements evoked from the IPS. Second, although we could evoke saccades from the intercalated zone very reliably with latencies on the order of 30 ms, Kurylo and Skavenski (1991) gave a mean latency of ~160 ms for their goal-directed saccades. These latency data are not only different from our own data but also from those of Shibutani et al. (1984), who reported latencies between 25 and 50 ms for most sites stimulated, including the ones giving rise to goal-directed saccades.

Area MP, a second, medial, parietal eye field

Probably the most unexpected result of the present study was the demonstration of a region fully confined to the medial aspect of the parietal lobe, whose stimulation

gave rise to saccadelike eye movements that in many respects resembled those evoked from LIP. We have termed this region, located close to and partially within the caudal end of the cingulate sulcus, the medial parietal area (area MP). In view of its general location close to the end of the cingulate sulcus, we think that MP is probably largely congruent with area PGm as defined by Pandya and Seltzer (1982) on the basis of cytoarchitectonic criteria or area 7m as defined by Cavada and Goldman-Rakic (1989, 1993) on the basis of both its cytoarchitecture and connectivity. Its more caudal part might also overlap with the medial dorsal parietal area MDP of Colby et al. (1988). MDP is a part of the mesial parietal cortex, located dorsally and anteriorly to area PO, which is labeled retrogradely by injection of PO. The comparison between MP and 7m/MDP is complicated by the fact that probably not all of MP was mapped in our experiments. Although cortex in the IPS was densely explored with electrical microstimulation, the number of sites explored on the medial aspect was much smaller, furthermore thinning out considerably toward more eccentric parts of MP. In other words, it seems likely that the full extent of MP is larger than suggested by our results. At any rate, it is clear that MP and 7m overlap and that MP therefore may share some of the connectivity of 7m. Area 7m is reciprocally connected with area LIP (Andersen et al. 1990a; Blatt et al. 1990; Cavada and Goldman-Rakic 1989). In view of this connectivity, an obvious concern is that stimulation of sites in MP might have retrogradely activated cell groups in LIP. In other words, stimulation effects we attributed to MP might actually be mediated by LIP. However, this does not seem to be very likely for two reasons. First, area MP houses saccade-related neurons with properties similar to those of area LIP, obviously offering a direct substrate for the electrical stimulus. Second, if area MP stimulation would take effect by retrograde activation of cells in LIP, one would not expect to find differences between areas LIP and MP regarding the stimulation effects. However, area MP lacked the conspicuous overrepresentation of small-amplitude evoked saccades directed into the upper parts of the hemifield found for area LIP. A final concern relates to the similarity in the caudal to rostral topography of upward, goal-directed, and downward saccade sites in the IPS and MP, which might suggest that evoked saccade sites in LIP were mistakenly assigned to the medial parietal cortex. However, we think this is unlikely in view of the large distances involved.

Both area LIP and mesial parietal cortex encompassing the region we refer to as area MP have been shown to be reciprocally connected to the FEF (Andersen et al. 1985; Blatt et al. 1990; Schall et al. 1995; Stanton et al. 1995). As shown by Schall et al. (1995) and Stanton et al. (1995) the pattern of connections seems to maintain a high degree of topographical specificity. Although mesial parietal cortex is preferentially connected to the large amplitude representation of the FEF, area LIP, on the other hand, is connected to both the large and the small amplitude representation of the FEF. Generally speaking, our stimulation data are in line with the view suggested by anatomy that mesial parietal cortex emphasizes large amplitude saccades much more than LIP. However, our stimulation data also indicate that MP is not confined to large amplitude saccades and, conversely, microstimulation failed to reveal a representation of large amplitude saccades in LIP. Irrespective of these inconsistencies, it seems a reasonable working hypothesis to start with that MP, unlike LIP, might emphasize the saccadic exploration of the visual periphery.

A recent study by Ferraina and co-workers (1997) has demonstrated the existence of single-unit activity related to hand and gaze associated behavioral variables during visually guided reaching. These neurons were found in a part of area 7m that seems to overlap with our area MP. The absence of evoked hand movements might suggest that the reaching-related part of 7m is different from saccade-related area MP. However, there is an alternative interpretation, compatible with the possibility of overlap. The absence of evoked hand movements from area MP might be a consequence of connections to the hand effector structures being less direct than the ones to the eye movement effectors. In view of the lack of reliable anatomic criteria and the dissimilarity of the functional tests applied in the two studies, it must be left to future work to decide whether area MP is indeed involved in hand movements in addition to eye movements.

Absence of evoked saccades from area 7a

We were unable to evoke saccades from the dorsal parietal operculum between the STS and the IPS, for which the designation area 7a is usually reserved nowadays. At first glance, the absence of evoked saccades from area 7a seems to contradict the older physiological literature, which equated the parietal eye field with area 7a or PG, not least in view of the effects of electrical stimulation (Keating et al. 1983; Kurylo and Skavenski 1991; Shibutani et al. 1984). However, the seeming contradiction disappears if one considers the change in terminology that has taken place. Classical cytoarchitectonic parcellations did not differentiate between the dorsal parietal operculum and adjacent cortex in the IPS and referred to both collectively as area 7a or PG (Vogt and Vogt 1919; von Bonin and Bailey 1947), and this lack of differentiation pertains to the older physiological literature. Some of the earlier stimulation experiments used stimulation techniques unsuited to confine currents to restricted parts of cortex, therefore rendering them unable to differentiate between opercular and nonopercular cortex inferior parietal cortex. Others, using more subtle techniques, did not show the anatomic reconstruction of the actual sites of stimulation. However, if delivered, as in the report by Shibutani et al. (1984), it becomes clear from looking at the electrode penetrations presented (see their Fig. 1) that there is no conflict with our findings. Most of their saccade-evoking sites were in or close to the lateral bank of the IPS, corresponding to cortex we nowadays would probably have referred to as area LIP rather than as area 7a. On the other hand, stimulation of the dorsal parietal operculum between the IPS and the STS led to isolated eye blinks, an observation that again is in accordance with our own results.

Relationship between the sensitivity to microstimulation and the properties of single units

Saccade-related responses can be found in large parts of the posterior parietal lobe including areas LIP, VIP, 7a, and PO (Andersen et al. 1990b; Barash et al. 1991a,b; Duhamel et al. 1992, 1997; Gnadt and Andersen 1988; Hyvärinen and Poranen 1974; Lynch et al. 1977; Mountcastle et al. 1974). However, only area LIP has been shown to house a large number of cells, active in the memory period of the saccades-to-remembered-target paradigm (Barash et al. 1991a,b). As demonstrated by the present report, single units in area MP share this property with cells in area LIP. It could be mere coincidence that the same two parietal areas whose stimulation evokes saccades house memory saccade cells. Alternatively, there could be a causal relationship between the presence of memory saccade cells and the sensitivity to stimulation. Although not fully conclusive, two of our observations support the latter view. First, we found a significant correlation between the preferred directions of memory saccade cells and the directions of stimulation-evoked saccades. Second, we found that the velocity of evoked saccades matched the velocity of memory-guided saccades, the latter known to be slower than that of visually guided saccades (Becker and Fuchs 1969; Skavenski and Steinman 1970; White and Sparks 1986).

Eye position–dependent modulation of saccade amplitude and direction

We have suggested previously (Andersen and Thier 1996) that the modification of vector saccades in cortex surrounding the intercalated zone in the IPS results from a neural signal related to eye position, having a direct effect at the site of stimulation, rather than from constraints imposed by orbital mechanics. We favored this view, among others, because of the fact that the existence of this eye position signal has been amply demonstrated by single-unit work (Andersen et al. 1990b). The analysis of network models has suggested that such single units may be interpreted as elements of neuronal assemblies establishing a spatially distributed representation of desired location in head-centered coordinates (Zipser and Andersen 1988). The simulation of electrical microstimulation in these models (Goodman and Andersen 1989) yields modified vector saccades similar to the ones observed in our experiments, a finding that gives further support to the idea of assembly coding of head-centered space in this part of posterior parietal cortex. As yet, we do not know whether eye position modulates saccade-related discharges in area MP as well. However, the fact that the eye position–dependent modulation of evoked saccades is the same in LIP and MP suggests that MP might use a similar coordinate system for the representation of space.

Several studies have demonstrated goal-directed saccades outside the posterior parietal cortex. Places in which goal-directed saccades were observed include the caudal superior colliculus of the cat (Guitton et al. 1980; McIlwain 1986; Roucoux et al. 1980), the dorsomedial frontal cortex (Bon and Lucchetti 1992; Mann et al. 1988; Mitz and Wise 1987; Schall 1991; Schlag and Schlag-Rey 1987; Tehovnik and Lee 1993; however, see Russo and Bruce 1993 for an opposing view) of the monkey, the posterior parietal cortex (Kurylo and Skavenski 1991; Shibutani et al. 1984), and the cat cerebellum (Ohtsuka et al. 1987). As pointed out in the INTRODUCTION, the studies on the superior colliculus (SC) of the cat are particularly interesting because they have suggested an interpretation of ''goal-directedness'' incompatible with the idea of head-centered coding for saccades put forward by Robinson (1972). Stimulation at sites that gave rise to the typical pattern of goal-directed eye saccades when the animal's head was restrained elicited vector gaze shifts when the head was free to move. This finding suggested the possibility that the site stimulated encoded a retinal vector, describing target location relative to the fovea, which would translate into a gaze vector of fixed length and direction. We could indeed evoke head movements in addition to goal-directed eye movements from a few sites in the intercalated zone. However, our observations demonstrate that the specific interpretation of goal-directedness appropriate for the caudal SC of the cat does not seem to hold for the intercalated zone. The decisive finding is that evoked head movements and eye movements did not add up to fixed gaze vectors independent of the starting position of the eyes relative to the head. Also incompatible with the notion of a simple representation of gaze error in the intercalated zone is our observation, again based on a limited number of stimulation sites, that the head movements evoked depended on the starting position of the head relative to the trunk, having the effect of centering the head relative to the trunk. This finding could be understood if individual cells or small groups of cells represented target location for saccades relative to the head and simultaneously target location for head movements relative to the trunk. Duhamel et al. (1997) have recently described cells with head-centered receptive fields in area VIP. This finding is intriguing in view of the possible congruence of the intercalated zone with parts of VIP. It will therefore be interesting to define the location of these cells in relation to the intercalated zone and to clarify whether they may also encode location for head movements relative to the trunk. We have hypothesized previously (Thier and Andersen 1996) that the localized representation of desired location for eye movements in the intercalated zone could be derived from the distributed representation of target location for saccades characterizing neighboring stimulation sensitive cortex by a specific, simple pattern of anatomic connections. Our finding that evoked head movements and the varying combinations of accompanying evoked movements such as movements of the shoulders, arms, parts of the face, or the pinnae were confined to the intercalated zone suggests that this tiny part of the IPS must have anatomic connections not shared by the remainder of LIP. Unlike the remainder of LIP, the intercalated zone could be involved in the early stages of the organization of complex, coordinated movements involving many body parts.

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Present address of R. A. Andersen: California Institute of Technology, Pasadena, CA 91125.

Address for reprint requests: P. Thier, Neurologische Universitätsklinik, Sektion für Visuelle Sensomotorik, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany.

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