

Multiple Parietal “Eye Fields”: Insights from Electrical Microstimulation

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Introduction

Research into the functional role of the parietal lobe of primates began with the pioneering experiments of David Ferrier, who studied the functional consequences of lesions and the effects of electrical stimulation of monkey cortex, including parts of the parietal lobe (Ferrier 1876). Lesions of the angular gyrus surrounding the dorsal end of the superior temporal sulcus disrupted visually guided behavior, a deficit Ferrier erroneously mistook for blindness, leading him to suggest that the angular gyrus was the visual area of the brain. This misinterpretation brought about a fierce dispute with Munk (see Glickstein 1985), who, based on his own lesion work, had correctly identified the visual area with the occipital lobe. Ferrier's bias for a primary visual role of the parietal lobe was also reflected in his narrow interpretation of the effects of electrical stimulation of this part of the brain. Fig. 1 shows a reproduction of figures taken from his work which summarize his observations based on cortical stimulation. Electrical stimulation of sites 13 and 13' on the anterior and the posterior limbs of the angular gyrus, respectively, caused eye movements towards the opposite side, occasionally accompanied by head movements in the same direction. Ferrier interpreted these movements as reflexive reactions to a stimulation-induced visual sensation, also being responsible for the observed contraction of the pupils and “a tendency to closure of the eyelids as if under the stimulus of a strong light.” In spite of his narrow interpretation of the stimulation effects, the observation of these movements was instrumental for the development of the concept of a parietal eye field, contributing to visually guided eye movements. Ferrier had to rely on stimulation techniques which from our present vantage point necessarily must look crude and ill-defined. The use of comparatively large surface electrodes confined to the cortical opercula and the lack of objective and reliable means to control and quantify the currents¹ produced observations that were the result of

¹ The appropriate amount of current was detected by noting that the electrode caused sensory sensations when attached to the investigator's tongue.

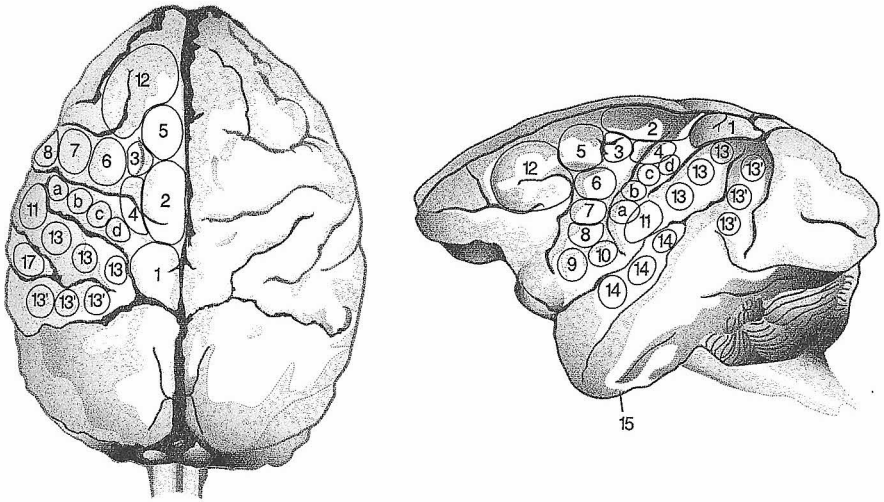


Fig. 1. Ferrier's figure from the first edition of his book *The Function of the Brain* summarizing the effects of electrical stimulation of the monkey cortex. Sites 13 and 13' are on the anterior and posterior limbs of the angular gyrus. Their stimulation evoked eye movements to the contralateral side, occasionally accompanied by head movements in the same directions. Furthermore, pupillary contraction and eyelid closure were observed. These effects were interpreted as reflexive reactions to strong visual sensation, contributing to the view that the angular gyrus was the visual area of the brain. (From Ferrier 1876 with slight modifications)

simultaneous activation of widespread parts of the parietal lobe. The lack of any differences between the various stimulation sites along the angular gyrus directly reflects these limitations.

Areas LIP and MST

More specific stimulation effects both in anatomical and functional terms were only obtained almost 100 years later when surface electrodes were replaced by microelectrodes, allowing for a more localized application of electrical current to patches of parietal cortex. The first stimulation study of the posterior parietal cortex based on microelectrodes was presented by Shibutani et al. (1984), who were able to demonstrate that evoked eye movements were restricted to a part of the posterior parietal cortex they referred to as area 7. Actually, a look at the electrode penetrations reproduced in their original publication makes it clear that most of the effective sites were located on the posterior bank of the intraparietal sulcus, many of them within a cortical area we today refer to as the lateral intraparietal area (LIP) rather than area 7 (Fig. 2). The eye movements evoked

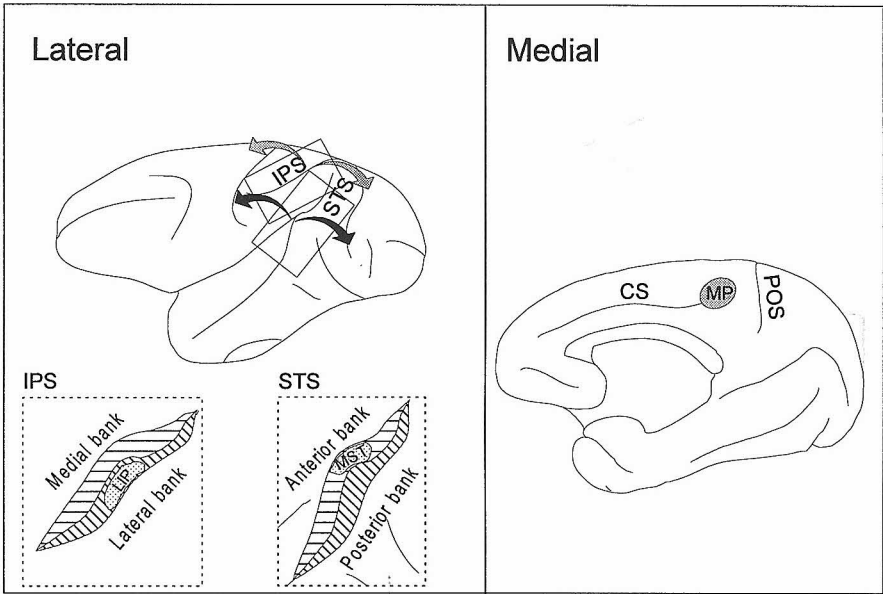


Fig. 2. Views of the lateral and medial aspects of the monkey cortex showing the locations of the lateral intraparietal area (*LIP*), the medial parietal area (*MP*), the *intercalated zone* and the medial superior temporal area (*MST*). *IPS*, intraparietal sulcus; *STS*, superior temporal sulcus; *POS*, parietooccipital sulcus; *CS*, cingulate sulcus

were always fast, resembling saccades, and eye movements as slow as smooth pursuit eye movements were not found although some of their penetrations may have hit pursuit-related medial superior temporal area (*MST*).

Our own experiments (Thier and Andersen 1996) with electrical microstimulation corroborate and extend the conclusions suggested by the Shibutani et al. study. With stimulation currents restricted to 200 μ A or less, saccade-like eye movements could be evoked from the lateral aspect of the posterior parietal cortex (Fig. 3 A) only when the microelectrode hit a small patch of cortex on the posterior bank of the intraparietal sulcus (*IPS*). This stimulation-sensitive region is congruent with area *LIP* as defined on the basis of single-unit recordings and anatomical markers but smaller by roughly a factor of 2 (refer to Fig. 2 for the location of *LIP* and the other areas mentioned). In contrast, no eye movements could be evoked from the posterior parietal operculum, corresponding to area 7a, nor did stimulation at the few sites tested inside the superior temporal sulcus (*STS*), caudal to the *IPS*, evoke any behavioral response.

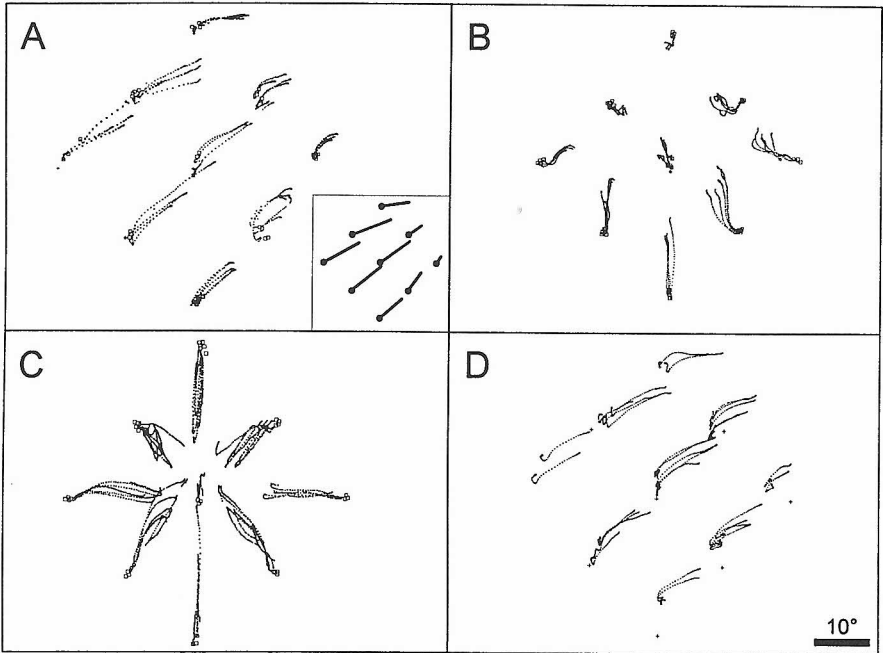


Fig. 3 A-D. *X, Y* plots of saccades evoked from three different parietal areas. The plots start at stimulation onset and end 150 ms later. *Small squares* indicate the initial eye position on each trial before electrical stimulation. **A** Saccades evoked from the *modified vector saccade* representation in the lateral intraparietal area (LIP). Note that varying the initial orbital position affected saccade amplitude, whereas the effect on direction was minor. The *inset* in **A** shows linear approximations of the mean evoked saccades used in some of the later figures. **B** Saccades evoked from the intercalated zone of the IPS, separating the representations of modified vector saccades with an upward and downward component. Stimulation drives the eyes into a head-centered location (goal zone) independent of their orbital position at the time of stimulation onset. **C** Goal-directed saccade evoked from a site in white matter underneath the intercalated zone. **D** Modified vector saccades evoked from the medial parietal area (MP) on the medial aspect of the parietal lobe. (Parts A-C from Thier and Andersen 1996). *Experimental paradigm:* monkeys were rewarded for keeping their line of sight within an eye position window of 5° centered on a memorized location in the frontoparallel plane cued by the presentation of a small fixation spot. If the monkey kept fixation of the spot for 500 ms, the spot was turned off for another 500 ms (gap) and 300 ms after onset of the gap period, electrical microstimulation was applied on half of the trials

The latter finding is in accordance with results presented earlier by Komatsu and Wurtz (1989) who were unable to evoke significant eye movements by stimulating sites in the STS if the eyes fixated a stationary location during stimulation. On the other hand, Komatsu and Wurtz showed that electrical microstimulation with currents as low as 25–50 μA was able to modify the

velocity of ongoing smooth pursuit eye movements, provided the microelectrode stimulated sites within the lateral part of parietal area MST (= MSTl) on the anterior bank of the STS. This finding shows directly that fixation is not simply smooth pursuit at zero velocity. In other words, this result supports the idea of two at least partially independent systems for smooth pursuit eye movements and fixation, respectively. Area LIP contacts the superior colliculus, the key structure in the control of both fixation and saccades (Munoz and Wurtz 1993). It is tempting to speculate that evoked saccades following stimulation of LIP may be the combined result of an activation of collicular saccade representations going hand in hand with a shutdown of the collicular fixation center, vetoing eye movements. The absence of significant evoked smooth pursuit following stimulation of area MST may be the consequence of an inability of MST stimulation to shut the collicular fixation center down. Selective influence of electrical microstimulation on smooth pursuit is in full accordance with the results of single-unit recordings and the effects of lesions, which have suggested that this caudalmost part of the posterior parietal lobe is a key element in circuits organizing slow eye movements such as smooth pursuit (Thier and Erickson 1992; Komatsu and Wurtz 1988; see also Ilg and Thier, this volume) while not contributing to saccades or fixation. The effects of microstimulation therefore suggest the existence of two anatomically and functionally distinct representations for eye movements within the classical parietal eye field on the lateral aspect of the parietal lobe, area LIP, the more rostral one contributing to saccades and area MST, right at the end of the posterior parietal lobe involved in smooth pursuit eye movements. While the stimulation effects obtained for LIP are compatible with a contribution to saccades, they do not rule out an additional contribution to smooth pursuit. We did not test electrical microstimulation of sites in LIP during ongoing smooth pursuit eye movements. An additional contribution to smooth pursuit does not seem to be very likely though, considering the absence of convincing evidence for smooth pursuit-related single-unit activity in LIP.

Areas VIP and MP

Areas MST and LIP are not the only components of the classical parietal eye field of Ferrier electrical microstimulation is able to distinguish. Electrical microstimulation suggests a third eye movement area incorporating a strip of cortex within VIP as defined by Maunsell and Van Essen (1989). This *intercalated zone* has properties very different from those of neighboring cortex. Microstimulation of the *intercalated zone* evokes goal-directed saccades.

Electrical microstimulation suggests the existence of still another representation of saccadic eye movements which is completely confined to the medial aspect of the posterior parietal lobe. We have termed this medial representation of saccades

located close to the end of the cingulate sulcus area MP (for *medial parietal*; Thier and Andersen 1993). MP is probably within area PGm of Pandya and Seltzer (1982) or area 7m of Cavada and Goldman-Rakic (1989, 1993), known to be richly interconnected with area LIP on the lateral aspect (Cavada and Goldman-Rakic 1989, 1993). Electrical microstimulation of sites in MP evokes saccadelike eye movements (Fig. 3D), which at first glance look very similar to those evoked from LIP. Stimulation of both sites in LIP, and MP evokes short-latency (about 30 ms) saccades whose amplitude and direction is largely determined by the location of the site stimulated. However, cortical location is not the only variable influencing the saccade trajectory. The other variable is orbital position at stimulation onset. While the direction of evoked saccades does not depend on orbital position, their amplitude is modified in a characteristic manner (Fig. 3 A, D), as discussed later in this chapter, reflecting a specific representation of space in these areas. MP is not just a redundant duplicate of LIP. A difference between MP and LIP, which sheds first light on the question of why there is a medial parietal eye field in addition to LIP, relates to the distribution of saccade amplitudes. Unlike LIP, which is characterized by a conspicuous emphasis on small amplitudes, the corresponding distribution for MP is much more widespread. Therefore, MP might make a more substantial contribution than LIP to the exploration of the visual periphery. This view is supported by the results of tracing studies, which show that mesial parietal cortex is preferentially connected to the large amplitude saccade representation of the frontal eye field (FEF; Stanton et al. 1995; Schall et al. 1995).

Modified vector saccades, i.e., saccades showing a modification of their amplitude but not of their direction with orbital position, were the dominant type of response to microstimulation in the IPS. However, there was a second type of response found in the IPS characterized by an orbital position dependency not only of the amplitude of the evoked saccades but also of their direction. The modification of saccade amplitude and direction was such as to move the eyes into a particular region in head-centered space (the *goal zone*), largely independent of the starting position of the eyes (Fig. 3 B, C). Two very different interpretations of such *goal-directed* saccades have been suggested. The first one, put forward by Robinson (1972), is that electrical microstimulation mimicks the natural activation of a small group of cells, representing a location in head-centered space. The second one, based on experiments on the caudal superior colliculus of the cat (Roucoux et al. 1980), is that sites which seem to be encoding goal-directed saccades actually encode vector gaze shifts, i.e., shifts based on both eye and head movements. Such vector gaze shifts could be programmed by directly converting a retinal vector into a gaze vector of the same amplitude and direction. The important distinction is that the latter view does not require a nonretinal (i.e., head-centered) representation of the desired location. While stimulation of sites in the intercalated zone may evoke head movements accompanying the evoked saccades, the two do not add up to fixed gaze vectors (Thier and Andersen 1996).

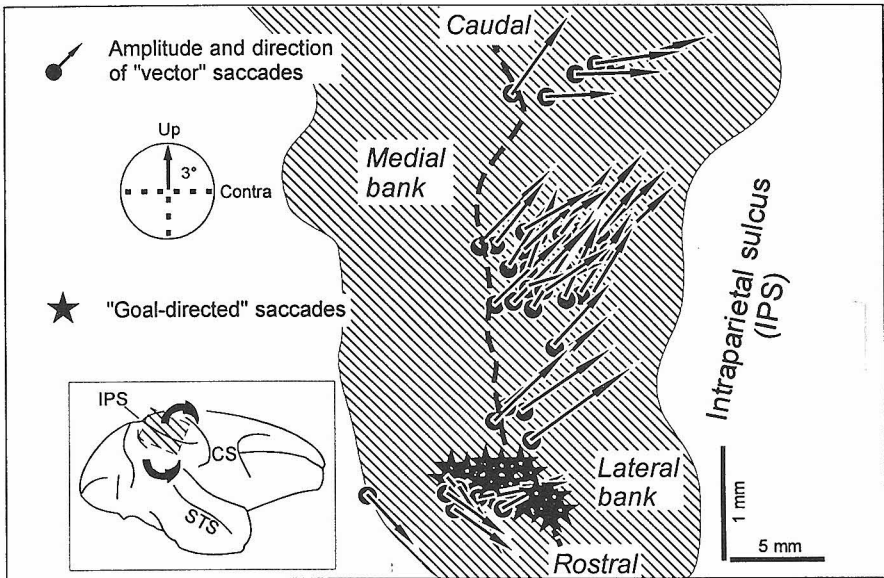


Fig. 4. Flattened reconstruction of the intraparietal sulcus (*IPS*) and its neighboring structures of one of the monkey hemispheres used by Thier and Andersen (1996). The *arrows* indicate the amplitude and the direction of the saccades evoked at a particular site using straight-ahead as a starting position. *Asterisks* indicate sites where goal-directed eye movements were evoked. *STS*, superior temporal sulcus; *CS*, cingulate sulcus. (From Thier and Andersen 1996)

We therefore interpret the occurrence of goal-directed saccades in the intercalated zone as an indication of a localized representation of head-centered space with neighboring groups of cells representing different locations relative to the head (Fig. 4).

Modified Vector Saccades

What is the explanation of the amplitude modification of saccades evoked from area LIP? Again, two qualitatively different interpretations have to be considered. The first one assumes that the group of cells stimulated represents a location on the retina relative to the fovea, defining a vector in retinal coordinates. Activation of this group of cells, either by the occurrence of a visual target at this location or by electrical microstimulation, would elicit the conversion of the retinal vector into a saccade vector of equal amplitude and direction. In the case of

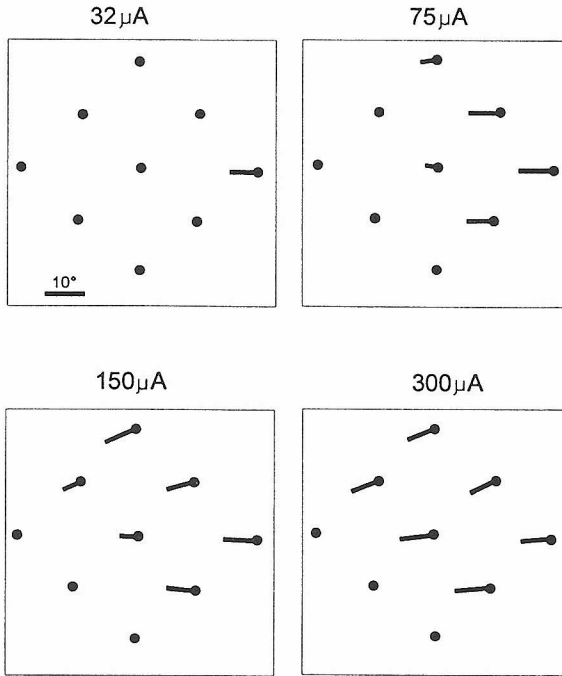


Fig. 5. Stimulation of site in the modified vector saccade representation of the lateral intraparietal area. Thresholds for evoked saccades depend on orbital position

a natural target this would move its image into the fovea. Modification of the amplitudes of evoked saccades could result from downstream mechanisms, such as constraints imposed by orbital mechanics, having the effect that centripetally directed saccades require less muscular effort than centrifugally directed saccades of the same amplitude and direction (Bruce 1990). Alternatively, the modification of the saccade vectors could be a consequence of neural signals related to eye position having a direct effect at the site of stimulation. The eye position-related neural signals required are indeed available. There is ample evidence for LIP cells having access to information on both eye position and retinal location, the two variables needed in order to encode locations relative to the head (Andersen et al. 1990). However, the two variables are usually not combined in such a way as to allow single LIP cells to unambiguously encode locations in head-centered space. Location relative to the head can only be recovered if the compound activity of large groups of cells is considered, suggesting that head-centered space is encoded in the activity of a population of neurons spread out over larger parts of LIP.

There are three reasons which led us prefer the view that the modification of vector saccades is indeed a consequence of an integration of eye position-related information at the level of the site being stimulated. The first one relates to the

pattern of orbital position dependency. Although for most sites tested, the amplitudes of the saccades evoked were decreased when the eyes were shifted in the direction of the saccade, there were also exceptions to this rule. Such exceptions, even if rare, are not compatible with the view that the amplitude modification results from orbital mechanics, which should be the same independent of the site stimulated.

A second finding not compatible with a modification of fixed vector saccades by orbital mechanics is the orbital position dependency of saccade thresholds exemplified in Fig. 5, with smaller thresholds for centripetally directed saccades in most cases. This change of threshold may be expected if eye position-related information is available at the site of stimulation, modifying the state of the cells activated by the artificial stimulus in a gradual fashion. Conversely, it is hard to conceive of a position-dependent mechanical mechanism located downstream of the cortical trigger, modifying the thresholds of the properties of the cortical trigger.

A third argument comes from preliminary results of double stimulation experiments. The rationale of these experiments is outlined on the left side of Fig. 6. We assume that stimulation site 1 represents upward saccades and site 2 rightward saccades. If activation of these sites results in modified vector saccades as a consequence of a local integration of eye position information as suggested in Fig. 6A (= hypothesis 1), the result of simultaneous activation of the two sites will correspond to the vectorial summation of the individual patterns of modified vector saccades. The outcome will be a pattern whose overall direction will be in between the individual ones. Moreover, the resulting pattern, unlike the ones resulting from isolated activation of either site, will show a dependence of saccade direction on orbital position. This orbital position dependency of saccade direction will introduce convergence into the pattern. This is the necessary consequence of the eye position-dependent amplitude modification enhancing the contribution of modified vector sites representing centripetally directed saccades, while conversely reducing the contribution of centrifugally directed saccades. As illustrated in Fig. 6B (= hypothesis 2), no convergence would be introduced into the pattern of saccades evoked by double stimulation if the stimulated sites represented fixed vector saccades with downstream modification of saccade amplitude. Double stimulation will shift the overall direction of evoked saccades to a direction in between the two represented by the two sites, but the direction will remain independent of orbital position. Figure 6C shows the results of one of the few experiments on LIP in which we succeeded in placing one electrode into the representation of upward saccades, while the second electrode was placed into a site representing rightward saccades. Simultaneous stimulation of these two sites resulted in a pattern of evoked saccades whose general direction was to the upper right, and exhibited an increased amount of convergence or centering in full accordance with the idea of a direct influence of eye position-dependent information at the sites of stimulation.

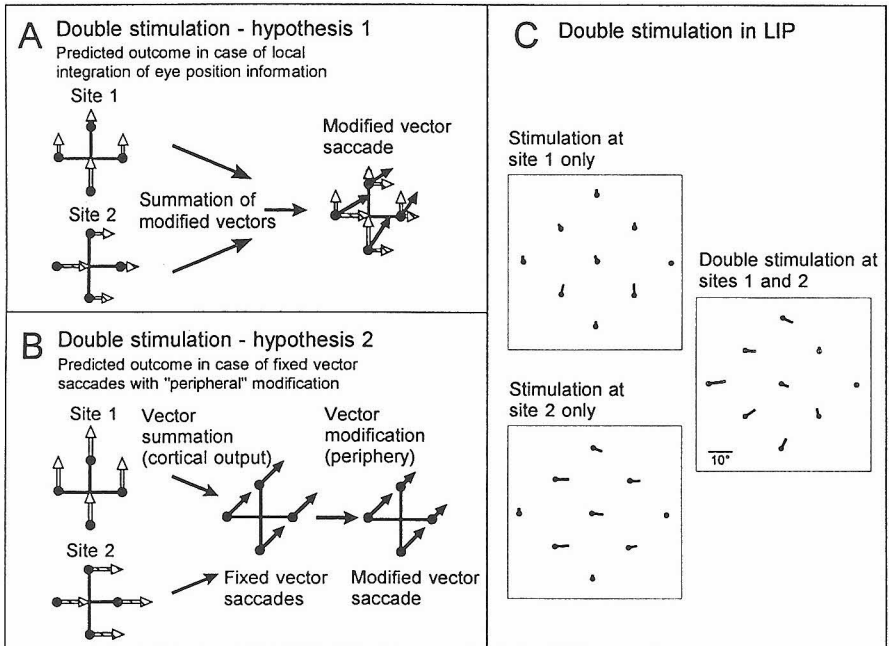


Fig. 6 A-C. Simultaneous electrical microstimulation at two IPS sites clarifies the nature of the orbital position dependency of the amplitude of "modified vector saccades." **A** Modified vector saccades result from an integration of eye position information at the site of stimulation. Double stimulation shifts the direction and induces centering. **B** The cortical sites represent fixed vector saccades whose amplitude is modified by an eye position-dependent mechanism downstream of the site of stimulation. In this case, double stimulation shifts the direction but does not induce centering. **C** Double stimulation of sites in the lateral intraparietal area (*LIP*) results in a pattern of evoked saccades which is fully compatible with hypothesis 1

Studies of parietal single-units have resulted in a good understanding of how eye position information affects the firing of parietal neurons. Typically, saccade-related responses of parietal neurons are modulated by eye position in a monotonic fashion (Andersen et al. 1990). As shown by Zipser and Andersen (1988), the same pattern of modification characterizes the hidden units emerging at the intermediate level of 3-layered network models, whose output layer represents target location relative to the head and whose input layer consists of two sets of units, encoding retinal location and eye position respectively. While the output units encode head centered space in a localized manner, the hidden units (considered models of parietal neurons) encode head-centered space in a distributed fashion. Electrical microstimulation of parietal cortex can be simulated in such networks by fully activating these hidden layer units (Goodmann and Andersen 1989). This results in evoked saccades which show the amplitude

modification by orbital position found in our experiments. In other words, the demonstration of modified vector saccades in LIP is in full accordance with the concept of a distributed representation of head-centered space in this part of the brain.

Possible Functional Relation Between LIP and the Intercalated Zone

Is there a relationship between the distributed representation of head-centered space in LIP and the localized representation in the intercalated zone? A possible answer is suggested by our double stimulation experiment, which has shown that one can increase centering by adding input from sites representing modified vector saccades with sufficiently different directions. As illustrated in Fig. 7, eye movements directed to a goal zone in head-centered coordinates would be expected to occur if the site being stimulated added inputs from sites representing modified vector saccades with several directions more or less equally distributed between 0° and 360° . As already mentioned, centering would be the necessary consequence of the eye position-dependent modification enhancing the contribution of modified vector sites representing centripetally directed saccades, while conversely reducing the contribution of centrifugally directed saccades. Goal zones other than straight ahead could be easily realized by adjusting the size of the contributions of the different directions converging on the same cell or group of cells. The intercalated zone is located right at the border between the representations of upward and downward saccades in the IPS. If local connections were indeed available, the neurons or groups of neurons in the intercalated zone could easily assimilate the inputs required to form a localized representation of head-centered space. However, if sites in the intercalated zone integrated only inputs from the adjoining representations of upward-contralateral and downward-contralateral modified vector saccades, eye movements should always converge in zones located in contralateral head-centered space. Goal zones congruent with the straight ahead location or goal zones in ipsilateral head-centered space, as found in the intercalated zone, would require input reflecting modified vector saccades with an ipsilateral component. Since saccade vectors with this directionality are found in the opposite hemisphere, a specific and testable prediction derived from these considerations is that the intercalated zone should integrate callosal inputs in addition to inputs from the adjoining parietal cortex of the same side.

A distributed representation would be fully sufficient to encode target location relative to the head. Actually, it would have several advantages over a more localized representation such as a much larger resistance of function to a loss of neurons. Why then does the brain take the trouble to implement a second, localized representation of head-centered space in the IPS? A speculative answer to this question is suggested by our observation that stimulation of the intercalated

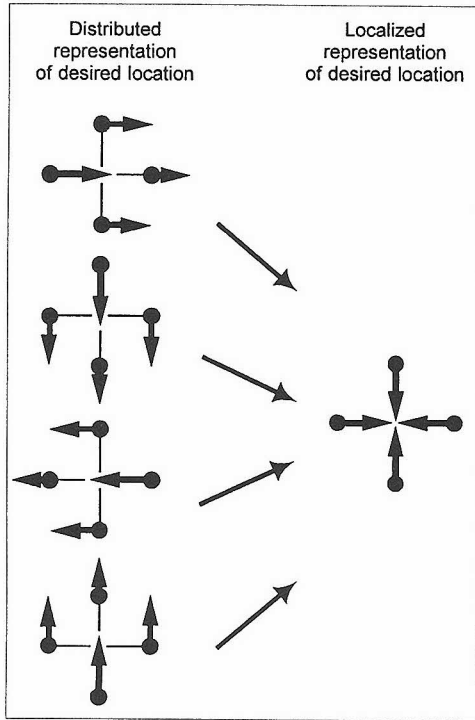


Fig. 7. Scheme suggesting how a localized representation of object location relative to the head might be derived from an earlier, distributed representation of head-centered space. (From Thier and Andersen 1996)

zone evokes combinations of non-eye movements such as movements of the head, shoulders, arms, parts of the face, or the pinnae accompanying the evoked saccades (Thier and Andersen 1996). The intercalated zone could therefore be a first stage contributing to the organization of coordinated movements of different body parts which may require access to multiple spatial representations. Integration of a signal derived from a localized head-centered representation, rather than independent inputs of eye position and retinal position, might help to reduce the complexity of such a system.

Conclusion

Experiments based on electrical microstimulation clearly question the concept of a parietal eye field as inaugurated by the studies of Ferrier. Rather than demonstrating a unitary parietal representation of eye movements, they suggest

that the posterior parietal cortex of monkeys houses at least four distinct areas whose functional architecture suggests specific contributions to goal-directed eye movements. It is plausible from a phylogenetic point of view to find evidence for a parietal eye field specializing in smooth pursuit, namely, area MST, and, on the other hand, to find evidence for distinct areas specifically contributing to saccadic eye movements found in VIP, LIP or MP. Differences in the phylogeny of small and large amplitude saccades may also account for the development of two widely segregated representations for saccades such as LIP and MP. While their role in the organization of eye movements cannot be disputed, it would be a misleading simplification to understand these parietal areas as *eye fields* in the sense of areas making exclusive contributions to eye movements, similar to the well-established brainstem centers for saccades. The demonstration that stimulation of a saccade representation such as the tiny intercalated zone in VIP is able to evoke a complex motor synergy comprising saccades and non-eye movements as well is a good case for contributions of these parietal eye fields beyond eye movements.

The view then that electrical microstimulation is suggesting is that of a network of interdependent parietal modules offering different spatial representations shaped by behavioral context and phylogenetic history. The elements of this parietal network in monkey are small, with the intercalated zone representing an extreme case, having a size which is probably on the order of only 10 mm². This is far beyond the dimensions of the parietal lesions, the study of which is still the major basis of our view of the role of the function of human parietal cortex, and it is probably also still beyond the resolution of the functional imaging techniques available. This is a necessary qualification one should bear in mind before jumping to premature conclusions on similarities of parietal lobe functions in experimental animals and humans.

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