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Behavioural Brain Research 76 (1996) 89–97

BEHAVIOURAL BRAIN RESEARCH

Functional streams in occipito-frontal connections in the monkey

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Received 17 September 1994; accepted 12 December 1994

Abstract

It is known that the prestriate cortical regions that project to area LIP in parietal cortex and to areas TEO and TE in temporal cortex are mostly separated. Two separate streams of information transfer from occipital cortex can thus be distinguished. We wished to determine whether the parietal and temporal streams remain segregated in their projections to frontal cortex. Paired injections of retrograde fluorescent tracers were placed in parietal and temporal cortex, or in the lateral and medial parts of the frontal eye field (FEF). The cortical regions containing retrogradely labeled cells were reconstructed in two-dimensional maps. The results show that temporal cortex mainly projects to lateral FEF (area 45). Parietal cortex sends projections to medial FEF (area 8a) and to lateral FEF, as well as to area 46. Thus, the parietal and temporal streams converge in lateral FEF. Most of the occipital regions projecting to medial FEF are the same as those projecting to parietal cortex, whereas lateral FEF receives afferents from the same occipital regions as those sending projections to temporal cortex. Thus, one can distinguish two interconnected networks. One is associated with the inferotemporal cortex and includes areas of the ventral bank and fundus of the superior temporal sulcus (STS), lateral FEF and ventral prestriate cortex. This network emphasizes central vision, small saccades and form recognition. The other network is linked to cortex of the intraparietal sulcus. It consists of areas of the upper bank and fundus of STS, medial FEF and dorsal prestriate cortex. These areas encode peripheral visual field and are active during large saccades.

Keywords: Double labeling; Retrograde tracer; Visual cortex; Saccade; Frontal eye field

1. Introduction

Since the beginning of the century, a number of clinical studies have established that lesions in human parietal cortex lead to different deficits from lesions in temporal cortex. Temporal lesions are usually associated with various forms of visual agnosia whereas parietal lesions lead to unilateral neglect, difficulties to integrate different parts of a visual scene and deficits in visually guided eye movements [20,36,47]. A similar dissociation between the functional roles of parietal and temporal cortex has also been observed in macaque monkeys with parietal and temporal lesions [49]. Although the evidence gained from more recent lesion studies in monkeys (reviewed by Merigan and Maunsell [41]) is less conclusive than the original study, it is usually accepted that the monkey

Abbreviations: Parietal cortex; Temporal cortex; Functional steam; Monkey; 6D, 6V, 8B, 9 12, 46 are areas of the frontal cortex; 7a is an area of the parietal cortex; 8Ar, 8Ac are areas of frontal cortex corresponding to medial FEF; 45a, 45B are areas of frontal cortex corresponding to lateral FEF; AMT, anterior medial temporal sulcus; AS, arcuate sulcus; CI, cingulate sulcus; CS, central sulcus; DPL, dorsal prelunate area; FB, Fast Blue; FEF, frontal eye field; FST, area of the fundus of the superior temporal sulcus; HRP, horseradish peroxidase; IOS, infero-occipital sulcus; IPa, area of the STS; IT, inferotemporal cortex; LIP, lateral intraparietal area; LS, lunate sulcus; MSTd, dorsal part of area MST; MSTl, lateral part of area MST; MST, medial superior temporal area; MT, medial temporal area; NY, nuclear yellow; OTS, occipito-temporal sulcus; PGa, area of the STS; PITd, dorsal part of PIT, area of the temporal cortex; PMT, posterior medial temporal sulcus; PO, parieto-occipital area; POM, medial branch of parieto-occipital sulcus; PS, principal sulcus; SF, Sylvian fissure; STS, superior temporal sulcus; TAa, area of the STS; TE, area of the inferotemporal cortex; TEa, anterior part of TE; TEm, medial part of TE; TEO, area of the inferotemporal sulcus; TEp, posterior part of TE; TPO, area of the STS; TPt, area of the STS; V1, primary visual area; V2c, part of area V2 representing central visual field; V3A, area of the occipital cortex; V3d, dorsal part of area V3; V3v, ventral part of area V3; V4c, part of V4 representing central visual field; V4p, part of V4 representing peripheral visual field; V4t, area of the occipital cortex between V4 and MT; V4v, ventral part of area V4; VIP, ventral intraparietal area (functional zone of parietal cortex)

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0166-4328/96/$15.00
SSDI 0166-4328(95)00182-4

parietal cortex plays an important role in processing the spatial aspect of visual information, i.e., the relative position of objects with respect to the body, whereas temporal cortex is essential for the visual recognition of objects [67]. More recently, examination of clinical cases has lead to the idea that temporal cortex is essential for the conscious identification of objects grasped by foveal vision, whereas parietal cortex is important for visuomotor coordination [29].

That different aspects of vision are processed in parietal and temporal cortex suggests that segregated messages are transferred through corticocortical connections from the occipital cortex. Visual information relayed in the lateral geniculate nucleus enters cortex through area 17 or V1, from which it is distributed to various extrastriate cortical areas. These areas are densely interconnected and several wiring diagrams of this network have been published [21,25,73]. Because of complexity of these diagrams, it is difficult to identify separate streams leading from V1 to parietal and temporal cortex. Such streams can nonetheless be revealed by placing simultaneous injections of retrograde tracers in temporal and parietal cortex and charting the regions of labeling in occipital cortex [6,43]. Another method that has been used to identify separate streams is to group together cortical areas that are connected to the same targets. This method confirms the results of the double labeling studies and shows that ventral prestriate areas are linked to temporal cortex whereas the dorsal prestriate areas are connected to parietal cortex [72].

Thus, two major streams of connections can be identified in occipital prestriate cortex, the occipito-parietal and the occipito-temporal streams. Temporal and parietal cortex are known to be connected with frontal cortex and in particular with the anterior bank of the arcuate sulcus [9,30,60]. This cortical region broadly corresponds to the frontal eye field (FEF), a zone in which eye movements can be elicited by small intensity electrical stimulation [12,52]. We were interested in determining to what extent the parietal and temporal streams, which are mostly segregated in the occipital lobe, remain segregated in their connections with frontal cortex. We therefore placed injections of tracers in parietal, temporal and frontal cortex and mapped the resulting regions of labeling. Our results show that both streams converge in the lateral FEF which corresponds to areas in the dorsal bank of the lower branch of the arcuate sulcus (areas 45a/b). On the other hand, the medial FEF (corresponding to area 8A) is innervated exclusively by the parietal stream. In addition, our data show that, in most cases, the cortical regions in occipital cortex that are interconnected with parietal and temporal cortex are the same as those linked to medial and lateral FEF. Thus, a network of converging and divergent streams can be recognized in the connections between the occipital, parietal, temporal and frontal cortex in the monkey.

2. Results

In this section, we review some of the results reported earlier [43] and we present new data concerning the connections of the frontal cortex. The experiments were made by injecting different retrograde tracers in various cortical regions and mapping the distributions of labeled neurons on flattened reconstructions of the cortical surface. The methods and, in particular the criteria for the identification of borders between different cortical areas, have been described in detail elsewhere [43,57].

2.1. *Afferents to parietal and inferotemporal cortex*

The first part of the study consisted in charting the cortical regions containing labeled neurons in frontal, occipital, temporal and parietal cortex following paired

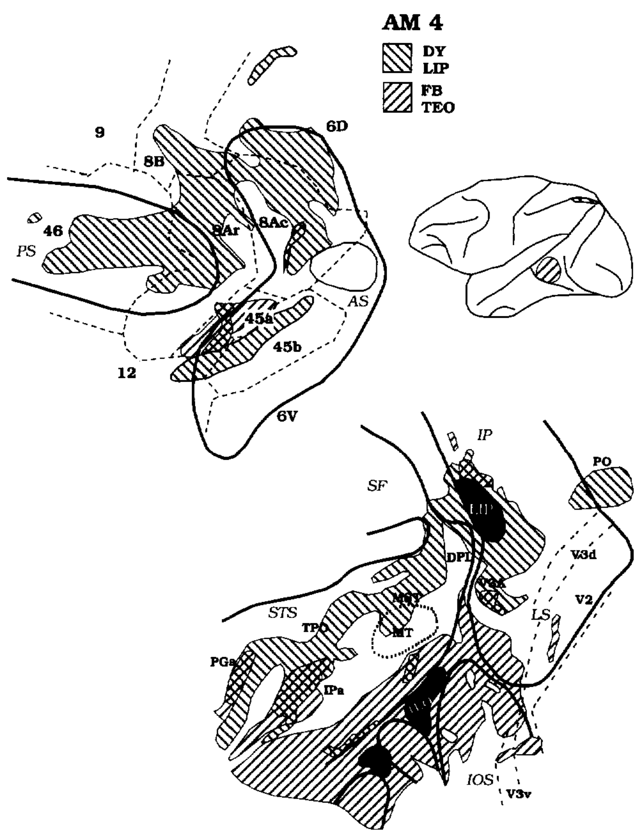

Fig. 1. Labeling observed in flattened reconstructions of frontal (upper left) and occipital cortex (lower map) following injections in LIP and TEO. The injections sites are represented as hatched regions on the lateral view of the cortex and as black regions in the flattened map of occipital cortex. Orientation of the maps : in both posterior and frontal cortex, caudal is to the right, medial is up and lateral is down. Abbreviations in italics correspond to sulci. Other abbreviations correspond to cortical areas.

injections in the parietal and temporal cortex. Fig. 1 illustrates the results of paired injections in the LIP area of the parietal cortex (also called POa in [43]) and in area TEO of the inferotemporal cortex. Flattened reconstructions of the cortical surface in the temporal, parietal and occipital cortex are illustrated in the lower part of the figure. Cells labeled by either injection are mainly segregated on the cortical surface. The neurons projecting to the temporal cortex are located mostly in lateral and ventral prestriate cortex (areas V2, V3v, V4), on the lateral surface of the inferotemporal cortex (areas TEO, TE), and in the lower bank of the superior temporal sulcus (STS). Neurons labeled by the parietal injection, on the other hand, were found in the dorsal prestriate cortex (areas V3A, DPL, PO) and in the fundus and upper bank of STS (areas MT, MST, TPO, IPa, PGa). Only a few regions providing diverging projections to parietal and inferotemporal cortex were found to contain overlapping populations of cells labeled by one or the other dye. These were the prestriate areas V3a and FST, and PGa and IPa in the anterior part of the STS fundus.

The upper part of the figure illustrates the labeling in frontal cortex. Most of the labeling observed after the parietal injection was observed in area 6D, in the medial part of the frontal eye field (FEF; areas 8Ac, 8Ar) and in the principal sulcus (area 46). A smaller region of labeling was also found in the lateral part of the FEF (areas 45a, 45b). In contrast to the extensive labeling due to the parietal injection, only a small region of labeling corresponding to the inferotemporal injection was observed in the lateral part of the FEF (area 45a). The two populations of labeled neurons overlap in area 45a.

Another example of labeling in occipital, parietal, temporal and frontal cortex after injections in parietal and inferotemporal cortex is illustrated in Fig. 2. The injection in parietal cortex was again placed in LIP but was more rostral and deeper in the sulcus, reaching the densely myelinated VIP area. The temporal injection was placed more rostrally on the lateral surface of the inferotemporal cortex, in area TEp.

The labeling due to the parietal injection was located in dorsal areas of the prestriate cortex (areas PO, V3A, DPL, V4d, MT, MST) and in the upper bank of STS (TPO). Most of the labeling related to the temporal injection was in the ventral regions of prestriate cortex (area V4v), in the lateral part of the inferotemporal cortex (area TEO) and in the ventral bank of STS. Cortical regions projecting to both loci were mostly found in the fundus and upper bank of STS (areas FST, PGa, IPa).

In the frontal cortex, the observed labeling was similar to that observed in the preceding case (Fig. 1) with two differences. First, the labeling due to the parietal injection was much more extensive in the arcuate sulcus, particularly in the lower branch (areas 45a and 45b). This is likely to result from the involvement of the ventral part of LIP and of VIP in the parietal injection. The second difference is that the labeling in areas 45a and 45b resulting from the temporal injection was more extensive and additional labeling was observed in areas 46 and 12. This presumably reflects the fact that the temporal injection was placed in a more anterior site than in the preceding case.

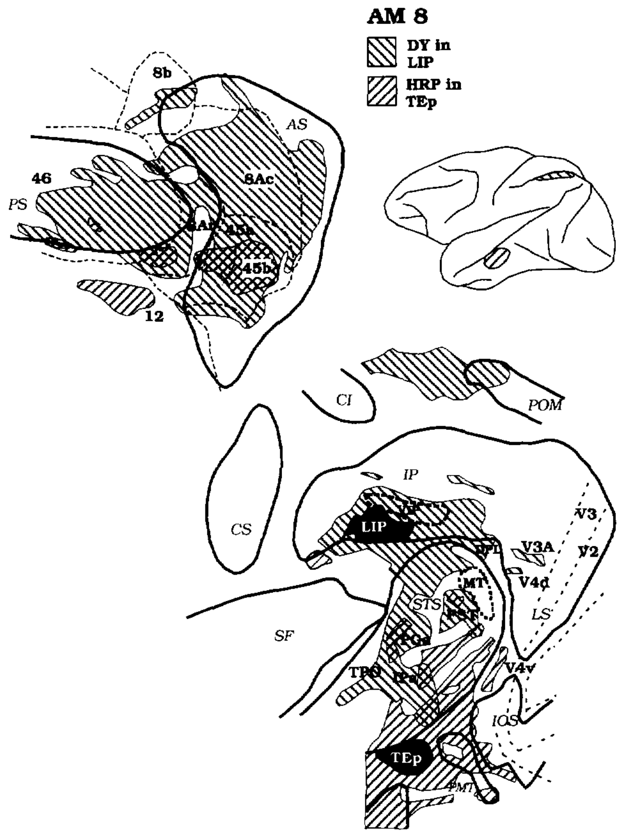

Fig. 2. Labeling observed in flattened reconstructions of frontal (upper left) and occipital cortex (lower map) following injections in LIP and TEp. The injections sites are represented as hatched regions on the lateral view of the cortex and as black regions in the flattened map of occipital cortex. Orientation of the maps : in both posterior and frontal cortex, caudal is to the right, medial is up and lateral is down. Abbreviations in italics correspond to sulci. Other abbreviations correspond to cortical areas.

The results illustrated in Fig. 1 and Fig. 2 show that the cortical territories projecting to parietal and inferotemporal cortex are mostly segregated in parietal, occipital and temporal cortex, with the exception of the fundus of STS which sends diverging projections to both parietal and inferotemporal cortex. In the frontal cortex, the cortex of the intraparietal sulcus (area LIP) is connected most heavily with the upper and lower limbs of the arcuate sulcus and the principal sulcus. In contrast, only the lower limb of the arcuate sulcus appears to be connected to the inferotemporal cortex. Injections of anterograde tracers in parietal and inferotemporal cortex gave rise to similar regions of labeling in frontal cortex

[57]. This shows that the connections between the frontal and parietal/inferotemporal cortex are reciprocal.

The data presented above on the connections of the frontal cortex are particularly interesting in the context of the physiology of eye movements elicited by electrical stimulation of the frontal cortex. It has been shown that stimulation of the medial part of the FEF (area 8A) produces larger saccades than stimulation of the lateral FEF (area 45) [12,52]. In order to identify more precisely the cortical areas sending projections to these two regions of the FEF, we made paired injections of retrograde fluorescent tracers in these sites and reconstructed the cortical regions containing labeled cells in parietal, occipital and inferotemporal cortex.

2.2. *Afferents to medial and lateral FEF*

The results concerning the afferent projections to the medial and lateral parts of the FEF are presented in Fig. 3 and Fig. 4. Fig. 3 illustrates the results of paired injections of horseradish peroxidase (HRP) in areas 45a,

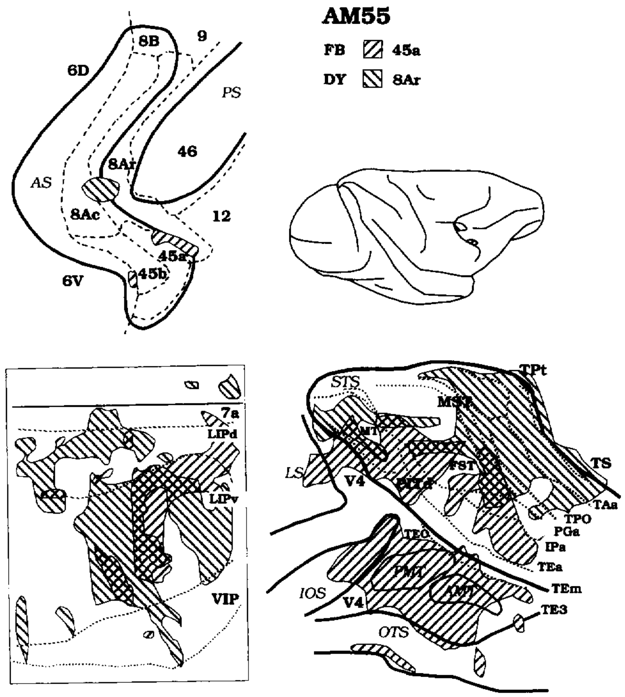

Fig. 4. Labeling observed on flattened reconstructions of the parietal (boxed diagram) and occipital cortex (lower right) following injections in 8ac/r and 45a/b in frontal cortex. Injection sites are represented as hatched regions on the lateral view of the brain and in the flattened reconstruction of frontal cortex (upper left). Orientation of the maps : Caudal is to the left in all cases. In frontal cortex, medial is up and lateral is down; in occipital cortex, ventral is down and lateral is up; in the intraparietal sulcus (boxed diagram), the dorsal part of the sulcus is up, the ventral part is down. The horizontal line at the top of the sulcus corresponds to the apex of the upper lip of the sulcus which was used for the reconstruction.

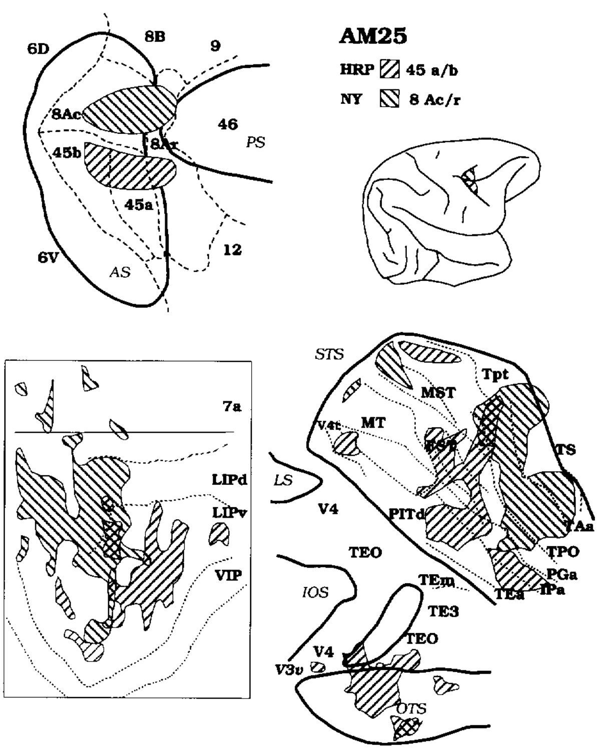

Fig. 3. Labeling observed on flattened reconstructions of the parietal (boxed diagram) and occipital cortex (lower right) following injections in 8ac/r and 45a/b in frontal cortex. Injections sites are represented as hatched regions on the lateral view of the brain and in the flattened reconstruction of frontal cortex (upper left). Orientation of the maps: Caudal is to the left in all cases. In frontal cortex and occipital cortex medial is up and lateral is down; in the intraparietal sulcus (boxed diagram), the dorsal part of the sulcus is up, the ventral part is down. The horizontal line at the top of the sulcus corresponds to the apex of the upper lip of the sulcus which was used for the reconstruction.

45b and the lateral region of area 8Ar, and of Nuclear Yellow (NY) in area 8Ac and the dorsal region of 8Ar.

The labeling in the parietal cortex is illustrated in a flattened reconstruction of the intraparietal sulcus (boxed region in the lower left part of Fig. 3). The populations of retrogradely labelled cells were mostly segregated. Neurons projecting to medial FEF were located in the caudal part of LIPd and LIPv, with a stronger projection from LIPd, whereas the neurons sending projections to lateral FEF were concentrated in the rostral and ventral portions of LIPv. This is in keeping with the observation that a more rostral and deeper injection in the intraparietal sulcus gave rise to a stronger labeling in lateral FEF (Fig. 2) than a more superficial and caudal injection (Fig. 1).

A segregation of the populations of neurons afferent to medial and lateral FEF was also observed in the prestriate cortex. The flattened reconstruction of the occipito-temporal region of the cortex is illustrated in the lower right part of the figure. Afferents to the lateral FEF are mostly located in the ventral part of prestriate and inferotemporal cortex (areas V3v, V4, TEO) and in the ventral bank and fundus of STS (areas V4t, MT, FST, PITd, TEa). Neurons projecting to medial FEF are found in the dorsal region of the STS (TPO, TAa, Tpt). A small amount of mixing of the two populations of labeled cells was observed in the caudal part of PGa.

Another case of paired injections in lateral and medial FEF is illustrated in Fig. 4. This case differs from the preceding one in that the medial FEF injection of DY was more rostral, being placed mostly in area 8Ar instead of 8Ac. The injection of Fast Blue (FB) was located more rostrally in the arcuate sulcus and was mostly contained within area 45a.

Like in Fig. 3, the labeling observed in parietal and occipito-temporal cortex is illustrated in flattened reconstructions in the lower part of the figure. In the parietal cortex (left box), the medial FEF injection led to labeling in the caudal part of LIPd and LIPv, as in the previous case (Fig. 3). In addition, labeling due to the medial FEF injection was also found in the rostral part of LIPv. This difference with the results of the preceding case (Fig. 3), is likely to be due to the involvement of area 8Ar in the injection site. Like in the preceding case, the labeling corresponding to the injection in lateral FEF was mostly observed in the rostral part of LIPv. The two populations of labeled cells in LIPv overlap more extensively than in the preceding case (Fig. 3). This is probably the consequence of the larger cortical surface occupied by cells labeled by the medial FEF injection, itself due to the invasion of area 8Ar by the injection site.

The populations of labeled cells in the occipito-temporal cortex also show a larger amount of overlap, as illustrated in the lower right part of Fig. 4. The labeling corresponding to the lateral FEF injection occupied the lateral part of the inferotemporal cortex (areas V4, TEO, TE3) and the lower bank and fundus of the STS (areas V4t, MT, FST, PITd, TEa). The major difference with the preceding case concerning the labeling due to the lateral FEF injection was the location of labeling on the dorsal instead of the ventral surface of the inferotemporal cortex and the stronger involvement of areas MT, MST and FST. Labeling in MT, V4 and TEO is located in the regions of central visual field representation. It appears therefore that the more rostral region of area 45 receives afferents from the central visual field representation in prestriate cortex.

Cells labeled by the medial FEF injection were again concentrated on the dorsal bank of the STS. Comparison with the preceding case shows a stronger labeling in areas MT, MST and TPt, which are presumably related to the involvement of area 8Ar in the injection site. Because of the larger extent of the labeling due to both FEF injections in the caudal part of STS, a larger zone of overlap between the populations of labeled cells was observed in STS. Areas containing neurons projecting to both medial and lateral FEF were MT, MST, FST, PGa and IPa.

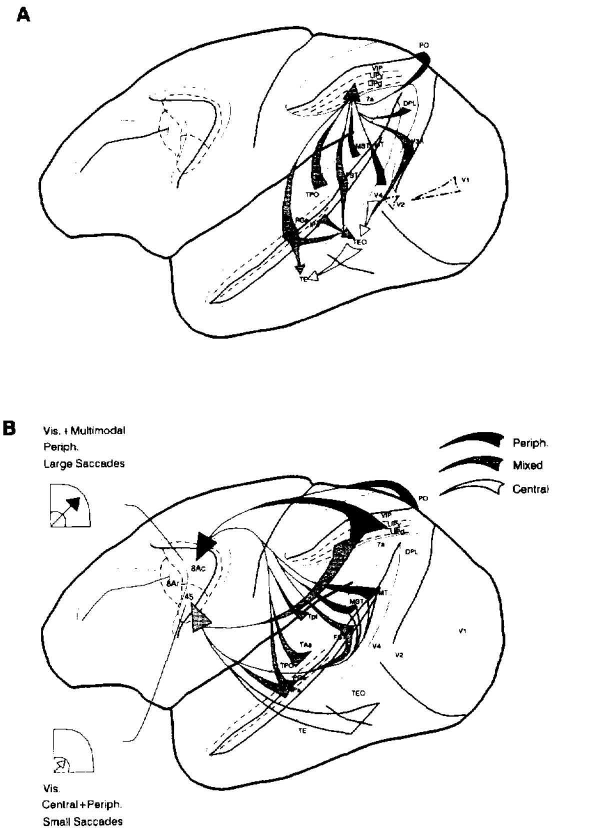

Fig. 5. Schematic representation of the connections afferent to temporal and intraparietal cortex (A) and to lateral and medial FEF (B). White arrows correspond to connections arising in the central representations of retinotopically organized areas. Black arrows correspond to afferents from the peripheral representations of visual areas. Gray arrows correspond to a mixing of central and peripheral representations.

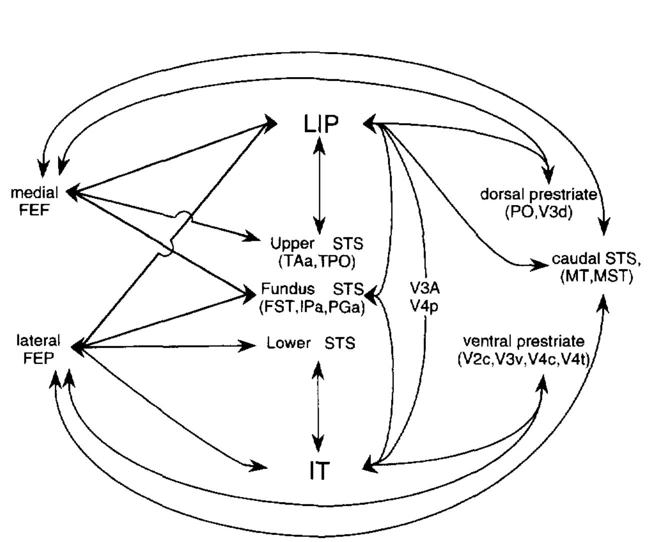

Fig. 6. Network organization of the connections between parietal, inferotemporal and frontal cortex.

3. Discussion

3.1. Summary of anatomical data

Fig. 5 and Fig. 6 summarize the data obtained in the course of these experiments and others reported elsewhere [43,57]. In Fig. 5A are represented the posterior cortical regions sending projections to LIP and TE/TEO. Most areas projecting to inferotemporal cortex are located in ventral prestriate areas, on the lateral surface of the inferotemporal cortex or in the lower bank of the STS. In contrast, most afferents to LIP belong to the dorsal prestriate areas or the dorsal bank of STS. Common information is sent to these two regions from prestriate area V3A and areas IPa and PGa in the fundus of the STS.

The connections with the frontal cortex are illustrated in Fig. 5B. Most of the projections to medial FEF originate from the same areas as those projecting to LIP, which itself is the major source of afferents to medial FEF. Lateral FEF receive its major input from TEO/TE and their prestriate afferents, from rostral LIP and from areas of the posterior STS (MT/MST).

Some areas, such as IPa and PGa of the STS provide common inputs to both parietal and inferotemporal cortex as well as to lateral and medial FEF. Areas MT and MST which are connected principally to parietal cortex also send diverging projections to lateral and medial FEF. These projections arise from different retinotopic regions of these areas. Finally, there is only a partial segregation of afferents to medial and lateral FEF from LIP in parietal cortex.

Thus, the connections between frontal, parietal and inferotemporal cortex appear to be organized as networks of interrelated areas as illustrated in Fig. 6. Three groups of areas can be distinguished. One is associated with the inferotemporal cortex (IT) and includes areas of the ventral bank of STS, the lateral FEF and the ventral prestriate cortex. This network emphasizes central vision, small saccades and form recognition. Another group of areas is associated to areas of the intraparietal sulcus. It consists of areas of the upper bank of STS, the medial FEF and the dorsal prestriate cortical areas. These areas encode peripheral visual field, are associated to large saccades and 'active' vision. Finally, a third group consists of areas connected to members of both groups and located in the fundus of STS.

3.2. Functional interpretation

Paired injections in posterior parietal and inferior temporal cortex resulted in overlapping connections in just a few cortical regions. One zone correspond to areas PGa and IPa of the STS [58]. Neurons in these areas are activated by acoustic and tactile as well as visual stimuli but exhibit little stimulus specificity [10]. Further work is needed to determine how neural activity in this cortical region relates to behavior and perception.

Another zone that was connected with both parietal and temporal visual areas was the inferior limb of the anterior bank of the arcuate sulcus and ventrolateral to the principal sulcus. More can be said about the zone of overlap in frontal cortex because it corresponds to the ventral part of the frontal eye field (FEF) and rostrally adjacent prefrontal cortex. The FEF, in the rostral bank of the arcuate sulcus, represents the final stage of cortical processing before a visually guided saccadic eye movement (reviewed in [13,28,55]. A variety of functional types of neurons have been identified in FEF, including neurons that are visually responsive, others that discharge in relation to saccadic eye movements, others that exhibit both visually-elicited and saccade-related activation, and some that discharge during fixation.

Intracortical electrical stimulation in FEF with currents less than 50 μA elicits saccadic eye movements [12]. Mapping the representation of saccades in FEF with microstimulation has demonstrated that saccade amplitude is laid out in FEF with the shortest saccades represented ventrolaterally and longer saccades dorsomedially [12,52]. This pattern of mapping is consistent with the finding that the receptive fields of visual cells in lateral prearcuate cortex represent the central visual field, and dorsomedial cells, the peripheral visual field [61].

One important finding in our experiments was that the parts of FEF generating saccades of different amplitudes received different constellations of prestriate visual afferents. Visually guided behavior in primates is organized around the fovea of the retina which provides high acuity vision over a very limited part of the visual field (see [16]). To identify an object in the scene, the eyes move in conjugate fashion so that the image of the object falls on the fovea. Saccadic eye movements are rapid shifts of gaze that redirect the visual axis onto a new point in the image. During natural viewing, saccades of less than 10° amplitude, which are by far the most common [5], direct gaze to conspicuous and informative features in the scene (reviewed in [68]; see also [50]).

The pattern of visual inputs to FEF can be interpreted in light of its role in generative purposive saccades. Two recent studies have investigated how neurons in FEF are involved in selecting the target for a saccade. One study trained rhesus monkeys to make saccades to fixate the target in a simple visual search task [56]. The initial visual response of FEF neurons elicited by presentation of the search stimulus array did not discriminate the target from distractors. However, the activation in one population of neurons that had combined visual- and eye movement-related activity evolved to specify target location before the execution of the saccade. The other study recorded the activity of neurons in FEF of monkeys scanning complex natural images [14]. The activation of visually responsive cells during scanning behavior varied according to whether the subsequent saccade was made to a feature in the cells' receptive field.

The afferents to FEF from the prestriate visual areas with selective responses for color, orientation, or direction of motion probably signal feature attributes to be used for selecting the target for eye movements. Thus, the motion selective afferents to FEF from MT and MST must play a role in guiding eye movements based on moving stimuli [26]. The topographic organization of the motion afferents to FEF provides additional information about the kinds of signals available for gaze control in different situations. Specifically, MST has been subdivided into at least two regions on physiological and anatomical grounds. In a dorsomedial zone, referred to as MSTd, neurons have very large visual receptive fields that emphasize the peripheral visual field and respond to large rotating or expanding optic flow stimuli [22,54,62,63,65]. We have found that MSTd projects heavily to medial FEF and less so to lateral FEF (see also [30,35]). The connections between MSTd and medial FEF may be involved in the mutual interaction of gaze control and heading during locomotion. The optic flow field has long been recognized as providing necessary information for heading guidance during locomotion [27]. Only recently, however, have behavioral experiments indicated how precisely such information can be used by observers (e.g., [69]).

Information about optic flow is clearly of use in directing gaze, but recent work also shows that extraretinal information about eye position is needed for the accurate perception of heading based on optic flow [53]. Motion processing is also necessary for generating pursuit tracking eye movements. In ventrolateral MST, referred to as MSTl, cells have smaller receptive fields, responding best to smaller spot stimuli [33]; this zone of MST is particularly involved in the generation of pursuit eye movements [24,34]. MSTl projects to both medial and lateral FEF. Data from single unit, stimulation and ablation experiments indicate that a region near the fundus of the arcuate sulcus, directly posterior to the principal sulcus is necessary for pursuit generation [32,37,40].

Afferents from areas V4, TEO and caudal TE in the inferior temporal cortex innervated lateral, but less so medial FEF. Neurons recorded in caudal inferior temporal cortex are selective for primary stimulus features such as color or orientation whereas neurons recorded in rostral TE are selective for more elaborate stimulus feature combinations such as complex shapes or faces [64]. Thus, the parts of inferior temporal cortex that are selective for stimulus features rather than whole objects project directly to FEF. This pattern of information processing is consistent with the common finding that eye movements are directed to features of objects such as the eyes, nose and mouth of a face [31,71].

Recording studies have found neural signals in ventral stream related to visual stimulus selection [18,42,44–46]. Furthermore, the time course of the evolution of the selective activation in these studies corresponds to the time course of selective activation observed in FEF [56]. Thus, FEF may function for gaze control as a saliency map, registering the location in the image of conspicuous features derived from processing in prestriate areas [66,70].

A major finding of our work and several other anatomical studies is that the lateral bank of the intraparietal sulcus projects to most if not all of the cortex in the rostral bank of the arcuate sulcus [1,11,17,48]. Indeed, Andersen et al. [4] first defined area LIP by its connections with FEF, although the same region in parietal cortex was identified by other criteria by other investigators [39,59]. It is well known that posterior parietal cortex is involved in visually guided behavior (reviewed in [3,19]). The lateral bank of the intraparietal sulcus has been shown by Andersen and his coworkers to be directly involved in saccade production [7,8]. Recent work indicates that LIP may serve to represent the spatial location of objects (e.g., [1]) as well as to update the visual field representation before saccades [23]. Also, the visual responses of cells in posterior parietal cortex are modulated by the attentive state of the animal [15,51]. Visually guided behaviour requires information about spatial location as well as information about object identity. Because posterior parietal cortex is interconnected with parts of FEF generating saccades of all amplitudes, we surmise that the partial processing subserved by parietal cortex must contribute to, or be updated by, saccades of all amplitudes.

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