

The Sources of Visual Information to the Primate Frontal Lobe: A Novel Role for the Superior Parietal Lobule

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Reaching movements are performed in order to bring the hand to targets of interest. It is widely believed that the distributed cortical network underlying visual reaching transforms the information concerning the spatial location of the target into an appropriate motor command. Modern views decompose this process into sequences of coordinate transformations between informational domains. The set of cortical areas and pathways by which the information on target location is relayed from the visual areas of the occipital lobe to the motor areas of the frontal lobe have, so far, been poorly understood. Recent data from different fields of neuroscience offer the basis for a new definition of the cortical system subserving reaching and, at the same time, for a reconsideration of the nature of the underlying visuo-motor transformation.

We live and move within a complex three-dimensional world anchored to objects that we identify and locate in space by using vision. The way visual information is used to guide arm movements toward objects of interest has been a problem of perennial interest in neuroscience. This problem can be decomposed into two related questions, the first of which concerns the anatomical substrata whereby visual information reach the motor apparatus. The second relates to the form of this information when it becomes available to the motor centers; that is, to the transformations from visual to motor coordinates believed to occur at the interfaces between vision and movement. At the present time, both of these questions remain, for the most part, unanswered. However, in the last 10 years, apparently unrelated studies have offered vast material that have significantly changed traditional views on this subject.

In this article we will review studies concerning the cortical pathways by which visual information can influence the areas of the distributed cortical system (Mountcastle, 1978) that underlie visual reaching, in an attempt to offer a comprehensive overview of this subject. The organization of these pathways strongly influences the functional processes by which visual information is used in the composition of motor commands.

From Psychophysics to Neuroanatomy

Marc Jeannerod (see Jeannerod et al., 1992, for a review) has suggested that the process of reaching to visual targets can be decomposed into transport and grasp components. The former is based on information concerning the spatial locations of objects of interest, while the latter is influenced by the intrinsic properties of objects, such as size, shape, weight, texture, etc. These different aspects of visually guided reaching seem to be processed by parallel, independent neural channels (Jeannerod, 1981; Paillard, 1982; Jeannerod et al., 1995). It is believed that different visual streams underlie these two visuomotor channels (Paillard, 1982; Jeannerod et al., 1992), with peripheral vision contributing mainly to the transport phase of reaching and central vision subserving the delicate manipulatory component. Psychophysical studies directly addressing this question, while emphasizing the role of

peripheral vision in both transport and manipulation components of reaching, have basically confirmed this view (Sivak and MacKenzie, 1990).

Recent advances in the study of the organization of the visually related cortices in macaques have identified a series of extrastriate visual areas that may provide keys to understanding how vision is used in reaching. We will focus on the demands placed on the visual system during the transport phase of reaching, the organization of visually related areas in the parietal lobe likely to carry out these visual functions, and the projections of these parietal areas to the motor centers of the frontal lobe controlling arm movement.

It is widely believed that the visual system is composed of multiple parallel channels (Trevarthen, 1968; Schneider, 1969), which subserve different aspects of visual experience (for reviews, see Maunsell and Newsome, 1987; De Yoe and Van Essen, 1988; Martin, 1988; Van Essen et al., 1992). Although the degree of segregation, and therefore of parallelism, of these pathways has recently been questioned (Merigan and Maunsell, 1993), visual processing has been divided into a "ventral stream" devoted to the fine analysis of the visual scene and the perception of form, color, and object features, and a "dorsal stream" concerned with coding the spatial characteristics of visual experience and motion analysis (Ungerleider and Mishkin, 1982). The central node of the ventral stream is the inferotemporal cortex, while that of the dorsal stream is the posterior parietal cortex (see Motter and Mountcastle, 1981, for a discussion). In a recent reexamination of this issue, Goodale and Milner (1992) have argued that the role of these two different channels is better understood when more emphasis is placed on output rather than on input channels. Accordingly, they suggested that the dorsal stream is mainly concerned with the spatial analyses relevant to composition of commands for different forms of visuomotor behavior.

At the time that the posterior parietal cortex became a focus of physiological study, its involvement in different forms of visuomotor behavior was unequivocally established (Hyvärinen and Poranen, 1974; Mountcastle et al., 1975). In the influential view of Mountcastle and his colleagues (1975), the parietal lobe was regarded as the central node of a distributed system suitable for supplying the frontal lobe with a holistic representation of visuomotor operations within the extrapersonal space. This idea rested on the existence of populations of neurons in both areas 5 and 7 (see also MacKay, 1992), which were active with reaching movements to visual targets, independently of the specific parameters of movement. In area 7, populations of neurons related to visual fixation, visual tracking, and saccade generation (Mountcastle et al., 1975; Lynch et al., 1977; Sakata et al., 1980) were also described. Later, when the dynamic properties of light-sensitive cells in area 7a were studied in a detailed quantitative fashion, two important observations were made. Motter and Mountcastle (1981) described light-sensitive neurons tuned to stimulus motion and direction. Characterized by an opponent vector

organization, the direction of neuronal tuning was either toward the center or toward the periphery of the visual field. These populations were well-suited to monitor the motion of objects, and therefore the trajectory of the hand as well, in the visual field when the eyes fixate the target. In this same cortical area, Andersen and Mountcastle (1983) described the profound influence of an extraretinal signal concerning the angle of gaze on the light-sensitivity of neurons, thus providing the basis for a mechanism of coding target location in a craniocentric frame of reference (Andersen et al., 1985b; Zipser and Andersen, 1988; Mazzoni et al., 1991). This observation was of interest, because for successful target location and reaching, extraretinal signals are also necessary. These signals can be used to provide information concerning the positions of the eyes relative to the head. Recently, it has been shown that parietal neurons are influenced also by head position signals (Brothie et al., 1995), which could be used to code the head position relative to the body. Such information is required for encoding target location in a body-centered reference frame, since the retinal image of an object of interest is not, in general, sufficient to define its position with respect to the body.

A Bridge between Neurophysiology and Neuropsychology

That the visual information represented in the parietal lobe is used during visually guided reaching has been suggested from human neuropsychological studies of patients suffering parietal lesions (see Critchley, 1953). This idea that the parietal lobe supplies the frontal lobe with the visual information necessary not only for visually guided eye movements, but also for visually guided arm reaching derives mainly from the observation that humans (see De Renzi, 1982, for a review) and monkeys (Denny-Brown and Chambers, 1958; Bates and Ettlinger, 1960; Ettlinger and Kalsbeck, 1962; Moffet et al., 1967; Hartje and Ettlinger, 1973; Ratcliff et al., 1977; Faugier-Grimaud et al., 1978; LaMotte and Acuña, 1978; Stein, 1978; Deuel and Regan, 1985) with parietal lesions display a severe misreaching that consists of an inaccuracy in the direction of movement of the limb toward a visual target. In this respect, it is interesting that Balint (1909) interpreted "optic ataxia," first described in a patient with bilateral parietal lesions and free of visual, somatosensory, or motor deficits, as the result of a defective control of movement by vision, due to the lack of visual input to the motor areas. Holmes (1918), instead, included the reaching disorder within the broader frame of "visual disorientation."

Optic ataxia is now recognized as a specific entity (Garcin et al., 1967; Rondot et al., 1977; Perenin and Vighetto, 1988). In their report of "10 cases of pure optic ataxia," Perenin and Vighetto (1988) have examined patients with unilateral parietal lesions and free of significant visual, oculomotor, and motor disorders. In these patients the defective control of reaching includes not only the transport component of the movement, but also the shaping of the hand necessary for grasping. A hemispheric asymmetry was observed: in right-damaged patients, reaching was affected with either hand in the contralateral visual field ("visual field effect"), while left-damaged patients, in addition, showed a significant "hand effect," as reaching with the right hand was inaccurate in both right and left visual fields. Most of these patients had lesions centered around the intraparietal sulcus and in the superior parietal lobule (SPL). Unilateral involvement of the SPL has been described in cases of optic ataxia by other authors (Ratcliff and Davies-Jones, 1972; Levine et al., 1978; Auerbach and Alexander, 1981). The "ataxie optique" of Garcin et al. (1967) and the "defective visual localization" described by Ratcliff and Davies-Jones (1972) are disturbances of reaching in the contralateral peripheral visual field. Lesions causing unilateral ne-

glect involve mainly the inferior parietal lobule (IPL; Vallar and Perani, 1986), allowing a dissociation between optic ataxia and neglect.

Similar disorders result from lesions of the SPL in monkeys. Attempts to produce misreaching by leukotomy of the white matter underlying the parietal lobe, thus interrupting the occipitofrontal flow of information via corticocortical pathways, were, however, unsuccessful (Myers et al., 1962). In that same study, simultaneous ablations of the occipital lobe (ipsilateral to the performing arm) and the sensorimotor cortex (contralateral to the performing arm) also failed to produce misreaching toward targets in the intact visual half-field, after a recovery period. The results of the Myers et al. study are consistent with subsequent studies that have shown recovery of proximal movements following removal of the motor cortex (Denny-Brown, 1966; Deuel, 1977). These data suggest that, with time, other brain regions can assume the role of the frontal lobe motor centers. Given that the leukotomized monkeys in the Myers et al. (1962) study were allowed time to recover before the behavioral testing, it is not surprising that the interruption of the afferent pathways to the frontal lobe did not affect performance.

Using a more demanding behavioral task, Haaxma and Kuypers (1975) undertook similar experiments. The task now involved fractionated finger movements and thus required the participation of the primary motor cortex. The same type of leukotomy as used by Myers et al. (1962) resulted in behavioral deficits. Haaxma and Kuypers concluded that it is "likely that intrahemispheric cortical fibers to the frontal lobe play a role in the visual guidance of relatively independent hand and finger movements." Together, these data indicate that while the parietofrontal connection is not necessary for the generation of reaching movements in the pathological case, such a pathway may be required for the visual control of movement in the intact animal. In this experiment (Haaxma and Kuypers, 1975) the deficit was restricted only to the control of finger movements and did not involve the transport component, possibly because of the bilateral control exerted by descending motor pathways on the proximal musculature, which is responsible for the initial phase of reaching (Brinkman and Kuypers, 1973).

The transport component of reaching is, however, clearly affected by posterior parietal lesions, as noted previously. Thus, in monkeys, lesions of the parietal lobe at the cortical level mimic the clinical picture observed in humans better than do lesions aimed at disrupting the occipitofrontal connections.

The anatomical substrata underlying visually guided arm movements as will be outlined in this article involve a different and more distributed cortical system than that probably injured by the experimental lesions so far performed. This, together with potential plastic changes occurring after the lesions, may, at least in part, explain the inconsistencies existing in the literature on the paucity and short duration of the effects often observed.

Attempts to identify whether the deficiency in reaching observed in parietal animals was due to damage of the SPL or IPL alone have produced so far conflicting and rather inconclusive results (Moffet et al., 1967; Faugier-Grimaud et al., 1978; Stein, 1978). However, the ablation of the SPL produces profound effects on the performance of a conditional motor task (Halsband and Passingham, 1992).

From these studies it has become clear that the visual information represented in the parietal cortex is used during visually guided reaching. How this information could be relayed to the frontal motor centers controlling reaching and the differential roles of the SPL and IPL in reaching, however, remained to be determined.

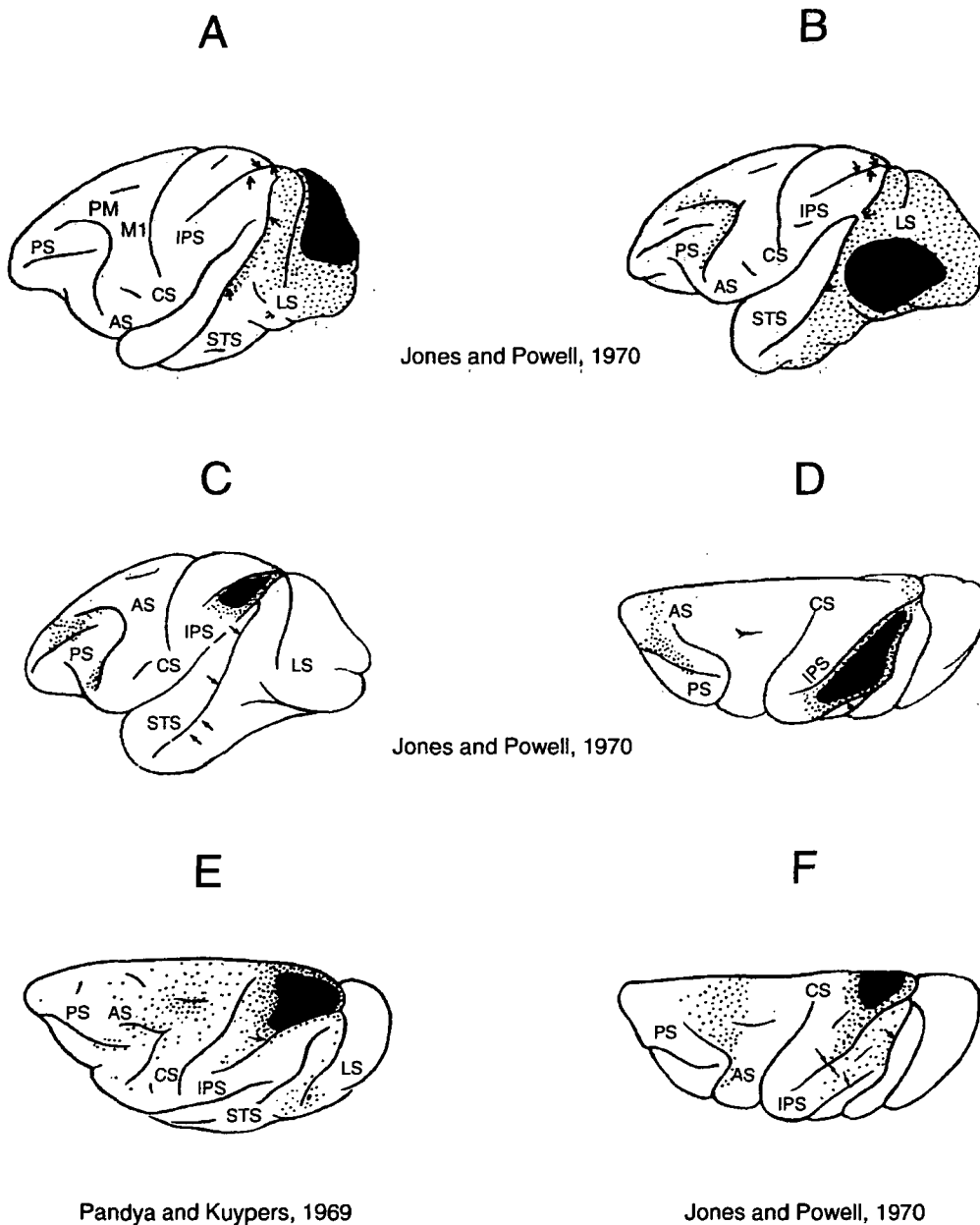


Figure 1. Distribution of degeneration in the ipsilateral hemisphere after lesions involving area 17 (A), parts of area 17, 18, and 19 (B), area 7 (C–D), and area 5 (E–F). Lesions are shown in black, terminal degeneration by stippling. Small arrows point toward terminal degeneration in the banks of sulci. LS, IPS, STS, CS, AS, and PS indicate lunate, intraparietal, superior temporal, central, arcuate, and principal sulci, respectively. M1, primary motor cortex; PM, dorsal premotor fields. (Reproduced with modifications from Jones and Powell, 1970, and Pandya and Kuypers, 1969, by permission of Oxford University Press and Elsevier Science Ltd.)

The Cortical Network for Reaching and the "Parietal Paradox"

It has been known since the first modern studies on corticocortical connectivity, that there are no direct projections between visual cortex and either the dorsal premotor fields or the primary motor cortex (M1; Pandya and Kuypers, 1969; Jones and Powell, 1970; Fig. 1A,B). The striate cortex was shown to project to the peristriate belt, and this, in turn, to the caudal part of the IPL (Fig. 1A). As a consequence, the IPL was regarded as a potential intermediate link between visual and motor cortical areas. However, these same studies (Pandya and Kuypers, 1969; Jones and Powell, 1970) showed that the frontal projections of the IPL were addressed not to motor or premotor cortices, but to prefrontal cortex (Fig. 1C,D), as later confirmed in more detail by many other studies (see Petrides and Pandya, 1984; Schwartz and Goldman-Rakic, 1984; Andersen et al., 1985a; Cavada and Goldman-Rakic, 1989b). Massive parietal projections to dorsal premotor fields were instead shown to originate from area 5 in the SPL (Fig. 1E,F), a cortical

region devoid of any visual input (Pandya and Kuypers, 1969; Jones and Powell, 1970; Fig. 1A,B).

Since the time of these early studies, both parietal and frontal lobes have been divided into numerous anatomical and functional areas (Fig. 2). A reconsideration of the entire issue seems warranted in light of this subsequent parcellation. The IPL includes areas 7a and 7b in its exposed lateral surface; areas LIP (lateral intraparietal area, Andersen et al., 1985a; Blatt et al., 1990), and VIP (ventral intraparietal area, Maunsell and Van Essen, 1983; Colby et al., 1993) in the lateral bank and fundus, respectively, of the intraparietal sulcus (IPS), and AIP (anterior intraparietal area; see Sakata et al., 1995) in the rostral part of the lateral bank of the IPS.

Area 7b receives corticocortical fibers mainly from a variety of somatosensory-related areas (Cavada and Goldman-Rakic, 1989a) and projects to a variety of prefrontal and frontal areas, including ventral premotor cortex (Petrides and Pandya, 1984; Matelli et al., 1986; Cavada and Goldman-Rakic, 1989a,b)

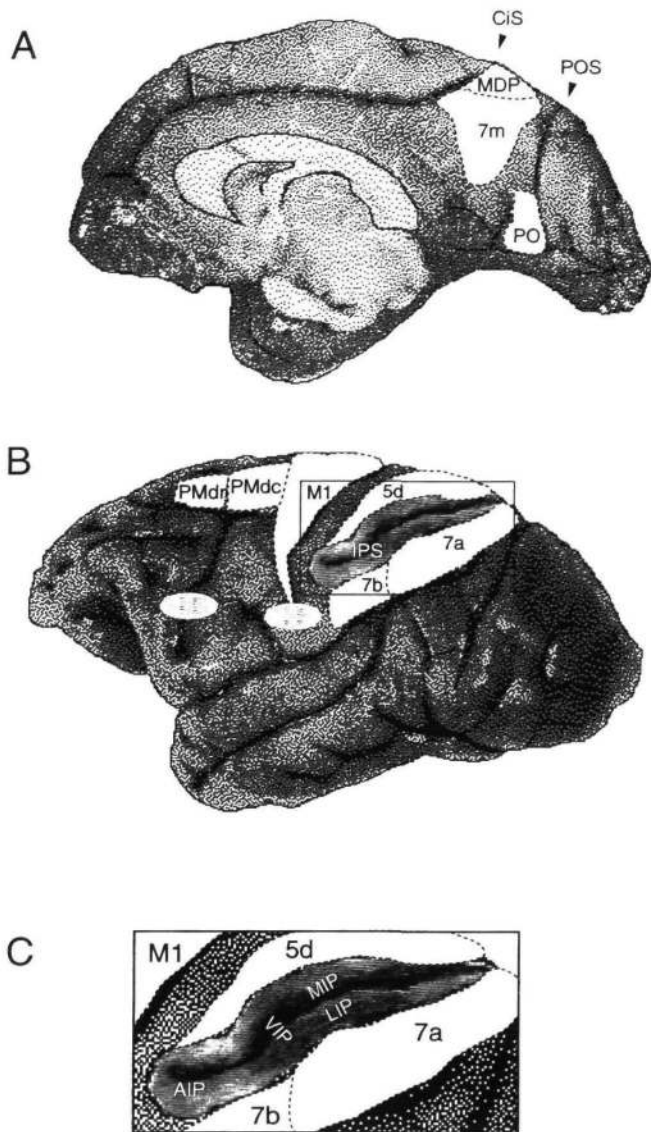


Figure 2. Brain figurines illustrating the locations and approximate boundaries of cortical areas, as discussed in the text. On the mesial aspect of the hemisphere (A), PO, parietooccipital visual area; MDP, medial dorsal parietal area; POS, parietooccipital sulcus; CIs, cingulate sulcus. On the lateral aspect of the hemisphere (B), M1 indicates primary motor cortex; PMdr and PMdc rostral and caudal parts of dorsal premotor cortex, respectively; 5d, the dorsal surface of area 5. In this figurine and in the inset (C) centered on the parietal lobe, the intraparietal sulcus (IPS) is shown as "opened" to display the lateral intraparietal area (LIP) and the medial intraparietal area (MIP), located in the lateral and medial banks of the IPS, respectively; the ventral intraparietal area (VIP) is located in the region surrounding the bottom of the sulcus, the anterior intraparietal area (AIP), in the rostral part of the lateral bank of the IPS. Conventions and symbols as in Figure 1.

and supplementary motor cortex (SMA; Cavada and Goldman-Rakic, 1989a,b). Area 7a, on the other hand, receives visual input (Cavada and Goldman-Rakic, 1989a) mainly from areas V2, PO (parietooccipital area; Covey et al., 1982; Gattass et al., 1985; Colby et al., 1988), superior temporal sulcus, and dorsal prelunate gyrus (DP). Multiple visually related areas project to LIP (Cavada and Goldman-Rakic, 1989a; Blatt et al., 1990; Baizer et al., 1991) and VIP (Baizer et al., 1991) including the peripheral field representation of V2, V3, V4, the dorsal parietooccipital areas V3A, PO, and DP. In addition, many motion-sensitive areas project to LIP (Cavada and Goldman-Rakic,

1989a; Blatt et al., 1990; Baizer et al., 1991) and VIP (Maunsell and Van Essen, 1983; Baizer et al., 1991).

The frontal lobe (Fig. 2), on its lateral aspect, contains M1 and numerous premotor fields (Matelli et al., 1985; Barbas and Pandya, 1987). Among these, the dorsal premotor cortex (PMd; Weinrich and Wise, 1982; He et al., 1993) is of particular interest to us, since it is involved in coding arm reaching (Caminiti et al., 1991) and possesses significant projections to the spinal cord (He et al., 1993). It can be divided into a rostral (PMdr) and caudal (PMdc) parts (Barbas and Pandya, 1987). None of the studies mentioned above on the connectivity of the parietal lobe has identified a projection from the visually related part of the IPL to the arm-representations of either PMd or M1, as determined by physiological studies (see Johnson, 1992, for a review). Area 5 was shown to be directly connected not only with premotor but also with motor cortex (Strick and Kim, 1978; Jones et al., 1978). However, none of the connectivity studies based on the parcellations of the SPL proposed in the late 1970s and early 1980s was able to show the existence of any visual inputs to these areas (Jones et al., 1978; Pandya and Seltzer, 1982). Thus, students of the mechanisms by which visual information guides reaching movements were faced with an apparent "paradox" occurring in the parietal lobe. The precentral motor areas possessed access to the "blind" area 5, but were "prohibited" access to the visually recipient area 7. The significance of the anatomical link provided by area 7m between the visually recipient IPL and the movement-related area 5 was difficult to evaluate at the time it was reported (Pandya and Seltzer, 1982), given the lack of any physiological study of 7m. Thus, the source of visual input to the precentral frontal areas still remained to be defined.

A Novel Role for the Superior Parietal Lobule

The SPL had traditionally been regarded as a somatosensory association area (Duffy and Burchfiel, 1971; Sakata et al., 1973). In addition, a potential role of the SPL in the control of movement was suggested by the anatomical and physiological studies reviewed above. In recent years, a variety of anatomical, physiological, and metabolic mapping studies have suggested that, in addition to its role in somesthesia and motor control, the SPL may be involved in certain forms of visual information processing. Posterior portions of the SPL are activated during visual reaching, as shown by 2-DG metabolic mapping experiments (Macko and Mishkin, 1985; Savaki et al., 1993). In animals in which the hemisphere contralateral to the reaching arm was surgically deprived from visual input by sectioning the forebrain commissures, certain regions of the SPL in the medial bank of the intraparietal sulcus (IPS) were metabolically depressed relative to the same regions in intact monkeys (Savaki et al., 1993). These regions overlapped portions of the intermediate and deep parts of area 5, area MIP (Fig. 2), as recently labeled by Colby et al. (1988), and VIP, a cortical area involved in the analysis of visual motion (Colby et al., 1993) and recently shown to be connected with MIP, MDP, LIP, and PO (Lewis and Van Essen, 1994). A similar pattern of metabolic activity was found in area MDP (Fig. 2; medial dorsal parietal area; Colby et al., 1988). In these studies, the metabolically active "visual" areas include the most caudal parts of the SPL and extends anteriorly in both the deep part of the medial bank of the IPS and on the medial wall of the hemisphere.

Neurophysiological studies have noted significant differences in the functional properties of neurons within the SPL (Seal et al., 1983; Crammond and Kalaska, 1989; Burbaud et al., 1991; Colby and Duhamel, 1991), indicating that neuronal activity in the dorsal exposed part of area 5 and around the crown of the dorsal bank of the IPS is more somatosensory

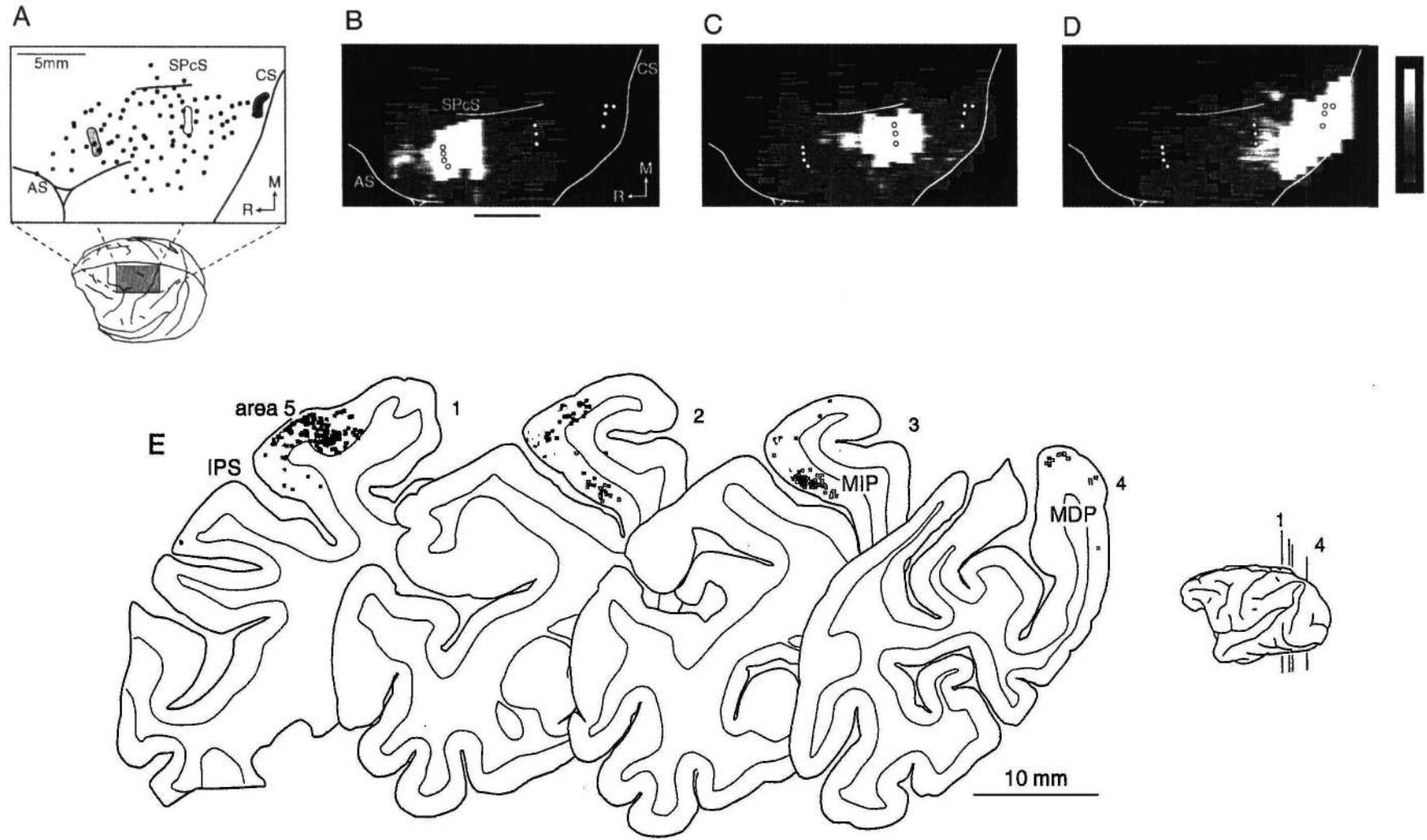


Figure 3. A, Location of successful recording penetrations (black dots) in the frontal lobe. The colored areas indicate locations of tracer injections: rhodamine labeled latex microspheres (red), cholera toxin B-subunit conjugated to colloidal gold (yellow), fluorescein-labeled latex microspheres (green). SPcS indicates superior precentral sulcus. Other conventions as in Figures 1 and 2. B–D, Flattened maps of labeled cell density in the frontal lobe after tracer injections, as shown in A. Cell density is expressed on a color scale (right; white represents maximal cell density). Calibration bar is 5 mm. E, Series of coronal sections through the parietal lobe of a macaque monkey. Colors in each section indicate location of neurons retrogradely labeled by the tracers injected in the frontal cortex. Levels of sections (1–4) are indicated in the brain figurines. (Reproduced with modifications from Johnson et al., 1996, by permission of Oxford University Press.)

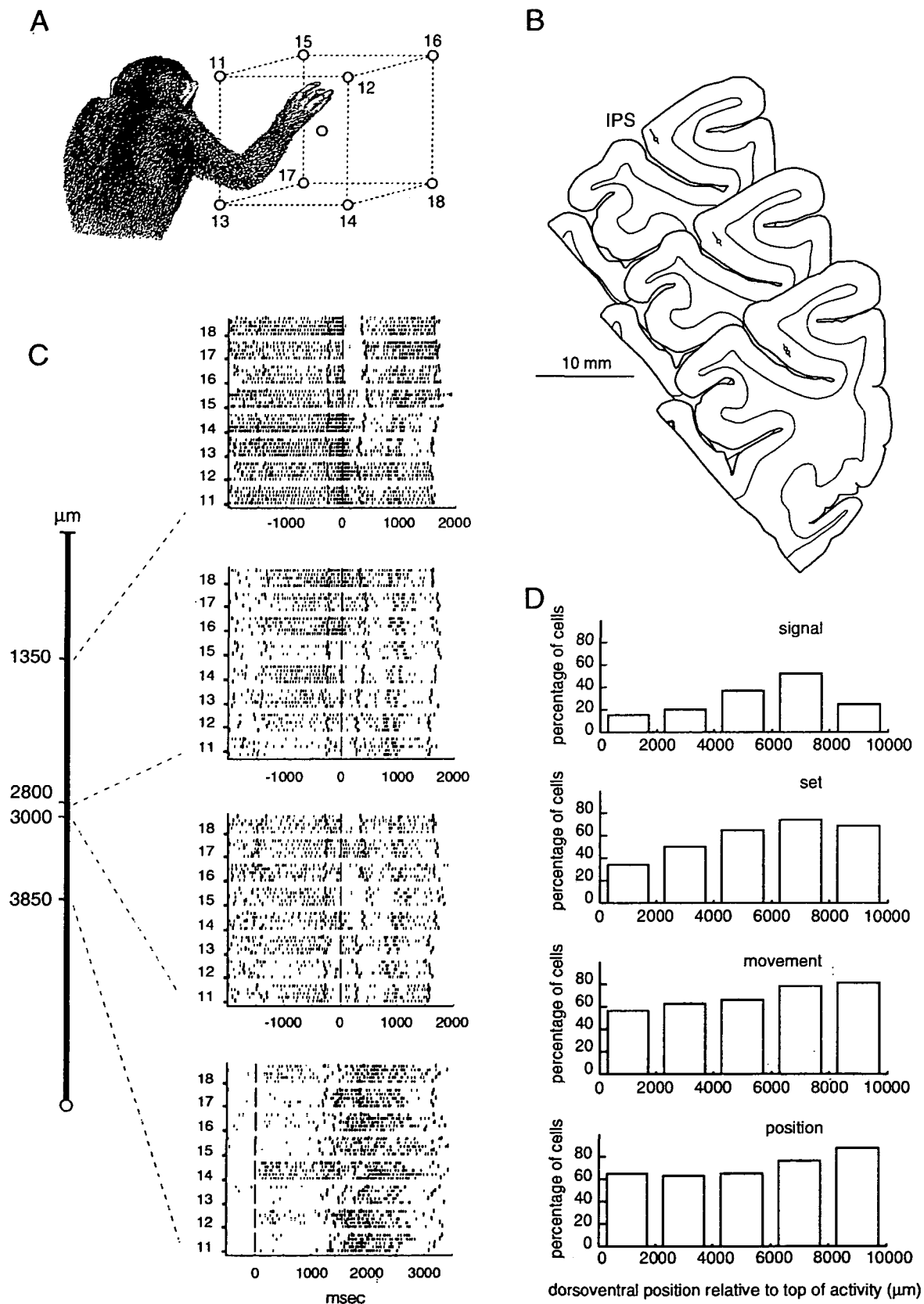


Figure 4. Trends of functional properties in the tangential domain of the superior parietal lobule. **A**, Monkeys were trained to perform an instructed-delay directional reaching task in a behavioral apparatus where movements were made in eight different directions (11–18) starting from a common central (unnumbered) origin. *Circles* represent the locations of LED/pushbuttons situated at the ends of metal rods protruding from a rear panel. In a typical trial, the central button was first illuminated, and the animal was required to push it for a variable period of time (1000–1500 msec). Then, one of the peripheral targets was illuminated green (instruction signal, IS). The animal was required to continue holding the center button for a variable instructed-delay time (600–2500 msec, IDT) until the green light turned to red. This served as a “go signal” for the animal to reach toward that pushbutton,

in nature, while at deeper locations within the bank of the sulcus (area MIP, Colby et al., 1988; area PEa, Pandya and Seltzer, 1982) cell activity is more tuned to motor and visual functions.

Anatomical studies, for their part, are changing the established dogma that the only parietal regions receiving visual information are those located in the IPL. Recent tracing experiments have shown that area PO (Covey et al., 1982; Gattass et al., 1985; Colby et al., 1988), a cortical region located deeply in the medial wall of the hemisphere (Fig. 2), in the rostral bank of the parietooccipital sulcus, receives direct projections from V1, V2, V3, V4, and the medial temporal visual area MT (Colby et al., 1988). MIP and MDP project to PO (Colby et al., 1988), while PO and MDP project to MIP (Blatt et al., 1990). Other studies (Cavada and Goldman-Rakic, 1989a) have shown that 7m is reciprocally linked to area PO. Furthermore, 7m projects to PMd and SMA (Cavada and Goldman-Rakic, 1989b). Therefore, area PO provides visual information to MIP, 7m, MDP, and probably to SMA as well. In addition, area 7m receives a dense projection from areas 7a and LIP (Cavada and Goldman-Rakic, 1989a) in the IPL and projects, within the SPL, to dorsal area 5 and to MIP (Pandya and Seltzer, 1982; Cavada and Goldman-Rakic, 1989), thus offering a link for a cross talk between SPL and IPL.

It is interesting that area PO seems to be the only visual area of the macaque cerebral cortex that does not possess an expanded representation of foveal vision (Covey et al., 1982; Colby et al., 1988; Galletti et al., 1991). The quasi-uniform representation of the visual field, and resulting relative emphasis on the visual periphery, together with the set of functional properties of neurons in area PO (Galletti et al., 1991, 1993, 1995), for instance, the motion-sensitivity, their tuning to saccadic eye movements, the influence of the angle of gaze on their visual responsiveness, and mainly the existence of a mechanism capable of encoding target location in spatial coordinates, suggest a role of this area in the types of analyses of the visual scene necessary for the spatial localization of targets of interest.

A Multilayered Cortical Network

In view of these newly recognized visual relations and the functional heterogeneity of the SPL, we have recently compared the spatial pattern of the ipsilateral association parietofrontal connections with the functional properties of neurons in their areas of origin and termination (Johnson et al., 1993, 1996). The goals were (1) to decide whether or not the visually recipient parietal areas MIP, MDP, and 7m projected to physiologically defined arm regions of the frontal lobe, and (2) to relate the pattern of parietofrontal connectivity with the functional properties of neurons in these cortices, in an attempt to offer a picture of the flow of information set in motion within this network by the presentation of a visual stimulus serving as the target for a reaching movement.

An instructed-delay directional reaching task was used to

characterize the arm-related zones of both frontal (PMd and M1) and parietal (dorsal area 5 and MIP) cortices. This task dissociates in time the early events concerned with the visuospatial signals about target location from the latest ones leading to movement onset, and allows the identification of 4 main neuronal activity types: signal-, set-, movement-, and position-related activities (see also Weinrich and Wise, 1982). When neuronal activity concerned with these different behavioral epochs was correlated with the tangential position of individual cells, a rostral-caudal gradient of properties emerged in the frontal lobe arm zones. The dominant activity type changed gradually from signal-related activity (expression of the input of visual information about target location), to set-related activity (probably reflecting to the combination of visual information on target location and somatic information about arm posture), to movement- and arm position-related activity.

Injections of different retrograde tracers (Fig. 3A) within this frontal functional trend (Johnson et al., 1993; 1996), while revealing the primarily local nature of the intrinsic connectivity of the frontal lobe arm representations across PMd and M1, have shown an orderly pattern of parietal projection to the frontal lobe regions involved in reaching (Johnson et al., 1993; 1996; Fig. 3). Dorsal area 5 projects mainly to M1, and to a lesser extent, to PMdc; MIP, MDP, and 7m project to the PMdc/M1 border and to PMdc, with the heaviest projection coming from MIP. Additional projections from MIP, MDP, and 7m are addressed to PMdr (Tanné et al., 1995), rostrally to the reaching-related zone of PMd.

Physiological recordings within the arm-related regions of the SPL (Fig. 4), containing the cells of origin of the projections to the frontal lobe, revealed a gradient of functional properties similar to that observed in the frontal cortex (Johnson et al., 1996). Neurons modulated by active static position of the arm in space and/or during movement were distributed uniformly in the dorsoventral tangential domain of the dorsal bank of the IPS, across dorsal area 5 and MIP, while signal- and set-related activities were more common in area MIP. As was observed for the intrinsic connectivity within the frontal lobe, at the larger scale of parietofrontal connectivity, the association projections tended to relate regions sharing similar activity types in a gradient-like fashion.

From these studies, area MIP, but also MDP and 7m, emerge as the intermediate parietal links in the corticocortical network underlying visually guided reaching (Fig. 5). Within this network the visually derived information concerning target location and the somatic information concerning the position of the arm in space, can be used for the generation of the appropriate motor output. This is possible due to the gradient-architecture of the network and the types of functional properties of its constituent elements.

The other essential feature of this network rests in its multilayered structure, involving both parietal and frontal cortices. The distribution of functional properties across the arm-

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within defined reaction (120-250 msec) and movement (1000 msec) time limits, and to press it for a specified target-holding time (THT, 150-1500 msec). Different targets were then presented in a randomized block design. *B*, Histological reconstruction of a typical microelectrode penetration within the rostral bank of the IPS. *C*, Activity types encountered by recording from cells at different cortical tangential locations within the sulcus. Signal-related activity, occurring in the first 300 msec of the IDT; set-related activity defined as the remainder of the IDT; movement-related activity defined as the 400 msec epoch centered on the movement onset, and position-related activity occurring during THT. Five replications of neuronal activity were collected for each movement direction (11-18). Rasters from cells recorded at depths of 1350, 2800, and 3000 μm are aligned to movement onset, those recorded from the cell at 3850 μm to presentation of the IS. *D*, Population analysis displaying the percentages of parietal neurons with significant directional modulation ($p < 0.01$, ANOVA) as a function of dorsoventral location in the rostral bank of the intraparietal sulcus. Percentages were calculated for 2 mm wide dorsoventral bins along each penetration relative to the top of neural activity. Percentages were calculated for each of the four prototypical activity types identified. From these histograms it can be seen that while movement- and position-related activity are distributed relatively uniformly across the tangential domain of the medial bank of the intraparietal sulcus, signal- and set-related activity are more frequently encountered in the cortex of the intermediate and deep part of the sulcus, corresponding to area MIP. (Reproduced with modification from Johnson et al., 1996, by permission of Oxford University Press.)

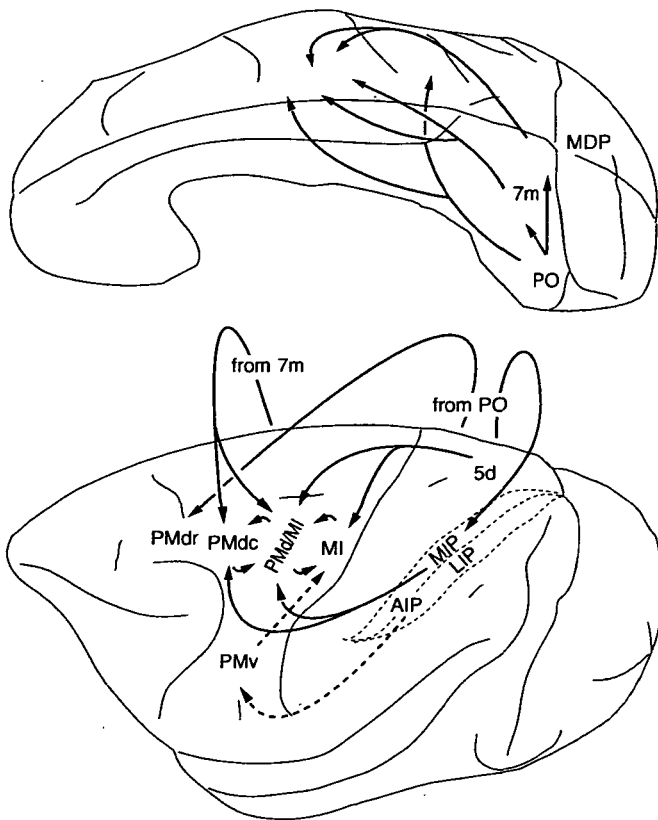


Figure 5. Tentative chart of the organization of the parietofrontal network for reaching and grasping (broken lines), as discussed in the text. Mesial and lateral schematic views of the origins and terminations of main ipsilateral corticocortical pathways. Note that most of these connections are reciprocal, although not shown in this figure. *PMv* indicates ventral premotor cortex. Other conventions and symbols as in Figures 1 and 2.

related regions of the frontal cortex and their pattern of association and intrinsic connectivity support a model where information throughout the entire visual to motor continuum is processed in a parallel fashion, with further local computations occurring within the frontal cortical areas, once the information concerning target location becomes available to them.

Coding of Reaching in the Cerebral Cortex

The study of the internal models of movement in the cerebral cortex and of their transformation across cortical areas is crucial to any theory of motor control. In the last 15 years, systematic analyses concerning coding of reaching in the cerebral cortex have led to the discovery that in motor (Georgopoulos et al., 1982, 1986; Schwartz et al., 1988), premotor (Caminiti et al., 1991), and posterior parietal area 5 (Kalaska et al., 1983) reaching is encoded in the activity of populations of neurons, probably combining visually derived information concerning target location with somatic information about the orientation of the arm in space, in a body-centered coordinate system (Caminiti et al., 1990, 1991). Furthermore, it has been recently shown (Lacquaniti et al., 1995) that in dorsal area 5 neuronal activity encodes information about arm position and movement in a body-centered reference frame whose coordinates define the azimuth, elevation, and distance of the hand in space. Different subpopulations of reach neurons encode the individual spatial coordinates, which remain largely segregated up to the level of the motor mechanism of the frontal lobe (Lacquaniti et al., in preparation).

These results, together with those presented in the previ-

ous section, bring into question the notion that the combinations of different types of information that underlie reaching occur within the exclusive domain of the "association" cortex of the parietal lobe. Instead, they point toward a more distributed and parallel coding mechanism within a parieto-frontal network, where different information remain for the most largely independent.

Concluding Remarks

The potential network described in this review offers a basis for the reinterpretation of a vast amount of experimental and clinical data, allowing further refinements and predictions concerning the mechanisms underlying visually guided arm reaching. The bridge between anatomy and physiology, basic science, and clinical observations, however, is still tenuous.

Physiological data available on the cortical areas of the distributed network of the SPL and of the frontal lobe are not yet sufficient to offer a picture of the mechanisms underlying reaching that fulfill all the necessary theoretical requirements. In spite of this, it is now known that mechanisms similar to those described in the IPL concerning the transformations from target to head- and body-centered coordinates exist in the SPL and the frontal lobe as well. Recent data show, in fact, that eye-position signals influence the activity of neurons in PO (Galletti et al., 1991, 1993, 1995) and PMd (Boussaoud, 1995). Since MIP receives association inputs from PO and projects to PMd, it can be predicted that eye-position signals will influence neural activity in MIP as well. Furthermore, although limited in number, populations of neurons exist in PO explicitly coding target location in spatial coordinates (Galletti et al., 1993). This pathway can therefore be considered as a medial system, within the dorsal stream, devoted mainly to the control of the transport phase of reaching and "parallel" to a lateral system devoted to hand manipulation and grasping mechanisms (see Jeannerod et al., 1995, for a review). Area AIP in the IPL, due to its set of connections with the ventral premotor cortex (see Petrides and Pandya, 1984; Matelli et al., 1986; Rizzolatti et al., 1987; Cavada and Goldman-Rakic, 1988), can be the central node of this lateral system.

In the finale of this overview, the questions left unanswered overpower the solutions offered. If the medial system within the dorsal stream is considered as a substratum whereby the coordination of eye, head, and arm movements subserving reaching occurs, its interplay with the lateral system for the coordination of transport and manipulation components of reaching within the dorsal stream remain to be elucidated. Whichever the nature of this interplay will be, a cross talk between the medial and lateral system can be provided by area 7m, due to its connections with area 7a (Cavada and Goldman-Rakic, 1989a). This link could be of crucial importance because it offers to the information embedded in the activity of a large class of reaching-related neurons of area 7a a route to the motor apparatus of the frontal lobe (see Mountcastle, 1985, for a review). Similarly, area VIP can serve as a bridge between the motion-sensitive areas of middle temporal cortex and those reaching-related zones of the superior parietal lobule, such as MIP, projecting to PMd. If so, VIP could very well be involved in the visual monitoring of hand trajectory in space, as has been proposed for area 7a.

Difficult, yet stimulating, work is guaranteed for many years to come.

Notes

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