# Parietal cortex: from sight to action
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Recent findings have altered radically our thinking about the functional role of the parietal cortex. According to this view, the parietal lobe consists of a multiplicity of areas with specific connections to the frontal lobe. These areas, together with the frontal areas to which they are connected, mediate distinct sensorimotor transformations related to the control of hand, arm, eye or head movements. Space perception is not unitary, but derives from the joint activity of the fronto-parietal circuits that control actions requiring space computation.

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**Abbreviations**

| | |
|---|---|
| 3D | three-dimensional |
| AIP | anterior intraparietal (area) |
| IPL | inferior parietal lobule |
| IPS | intraparietal sulcus |
| LIP | lateral intraparietal (area) |
| MDP | medial dorsal parietal (area) |
| MIP | medial intraparietal (area) |
| MST | medial superior temporal (area) |
| MT | middle temporal visual (area) |
| PIP | posterior intraparietal (area) |
| PO | parieto-occipital (area) |
| RF | receptive field |
| SPL | superior parietal lobule |
| VIP | ventral intraparietal (area) |

## Introduction

The parietal lobe of primates consists of three main sectors: the postcentral gyrus, the superior parietal lobule (SPL) and the inferior parietal lobule (IPL). Together, the two lobules (SPL and IPL) form the posterior parietal lobe, classically seen as a large association region in which different types of sensory information converged to provide space perception and a general schema of the body [1,2]. At the time, space perception was seen as unitary and independent of action systems. Modern data have challenged this view. The posterior parietal lobe is now thought to consist of a mosaic of areas, each receiving specific sensory information and transforming it into information appropriate for action [3,4], with no identifiable 'space area'. Rather, space perception appears to be a secondary result of the activity of a series of sensorimotor circuits, each of which encodes the spatial location of an object according to its own motor purposes and transforms it into a potential action [4,5,6•].

The main aim of the present review is to focus on recent data concerning the functional properties of 'visual' parietal areas related to the organization of hand, arm and head movements. Oculomotor circuits will not be considered.

## Inferior parietal lobule

Figure 1 depicts the main areas of the parietal lobe and agranular frontal cortex. Among the inferior parietal areas, two areas have recently attracted particular attention: areas AIP (anterior intraparietal) and VIP (ventral intraparietal). We will discuss their properties in particular detail.

**Figure 1**
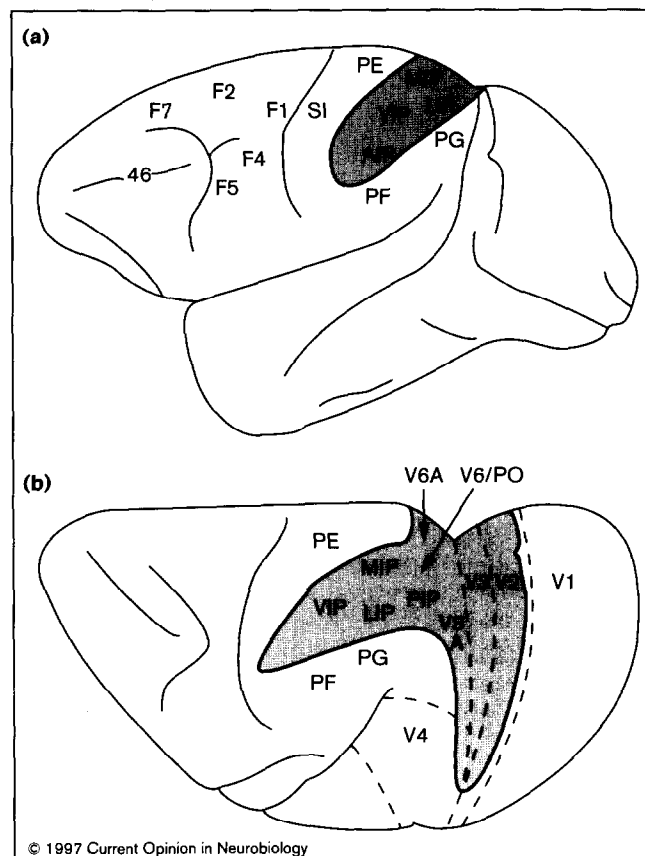


Lateral and dorsal view of macaque monkey cerebral cortex, highlighting the main areas of the parietal lobe and of the agranular frontal cortex. (a) Frontal and parietal areas of the macaque monkey. The intraparietal sulcus is opened (shaded gray) to show areas located in its medial and lateral banks. Frontal agranular cortical areas are classified according to Matelli et al. [51]. (b) Occipital and posterior parietal areas. Lunate, intraparietal and parieto-occipital sulci are opened (shaded gray) to show the location of different areas within the sulcal cortex, including areas V6/PO and V6A. Modified from Colby et al. [41].

## Area AIP and related areas

Neurons that discharge in response to the presentation of specific three-dimensional (3D) objects and/or during

grasping movements directed towards these objects were described several years ago by Sakata and co-workers [7,8]. These neurons are concentrated in area AIP, a specific sector of the lateral bank of the intraparietal sulcus (IPS) in front of the lateral intraparietal (LIP) area [9].

Recently, Sakata and co-workers ([10••]; M Kusunoki, Y Tanaka, H Ohtsuka, K Ishiyama, H Sakata, *Soc Neurosci Abstr* 1993, 19:770) described neurons that most probably represent a stage between occipital visual processing and area AIP. They identified two sets of neurons: one set that selectively discharges in response to long and thin 3D bars (axis-orientation-selective neurons) and another set that discharges in response to 3D flat stimuli (surface-orientation-selective neurons). Both sets of neurons are sensitive to binocular disparity. These neurons are located predominantly in the caudal part of the lateral bank of the IPS, posterior to area LIP and anterior to area V3A [10••].

Injections of neural tracers in area AIP, after electrophysiological characterization, have demonstrated that its main target is area F5 (M Matelli, G Luppino, A Murata, H Sakata, *Soc Neurosci Abstr* 1994, 20:404.4), which is characterized by neurons responding to 3D stimuli [11] and coding goal-related hand actions [12]. Areas AIP and F5 appear to be part of a visuomotor circuit specific for the organization of grasping movements [13].

This view was tested recently by studying the effects of reversible independent inactivation of these two areas in the monkey ([14•]; see also [15]). The main effect was a disruption of preshaping of the hand during grasping. The deficit consisted in a mismatch between the 3D features of the object to be grasped and the posturing of finger movements. When the monkey was successful in grasping the object, the grip was very often achieved only after several corrections that relied on tactile exploration of the target. The deficits following inactivation of either area AIP or area F5 were very similar.

In spite of the similarity of the deficits following inactivation of areas AIP and F5, the role they play in grasping movements is probably different. On the basis of the functional properties of the two areas [13] and theoretical considerations ([16]; AH Fagg, MI Arbib, unpublished data), we have developed a model [14•] whereby area AIP provides multiple descriptions of a 3D object, thus 'proposing' several grasping possibilities to area F5 — for example, a cup can be grasped on the handle or on its upper border. Area F5 then selects the most appropriate type of grip on the basis of contextual information (e.g. purpose of the action, spatial relation with other objects, etc.). Furthermore, F5 fragments the selected grip into different phases, such as aperture and closure, and simultaneously keeps active the set of AIP neurons that also encode the selected grip.

Our grasping model predicts that AIP neurons have a short-term memory of the object to be grasped. This possibility was tested in a behavioral paradigm that allowed a dissociation between the memory of the object and the type of grip employed [17••]. The results showed that both 'visual-dominant' and 'visual-and-motor' AIP neurons [9] are endowed with a mechanism for remembering objects (or some of their features) [17••].

### Area VIP and related areas

Area VIP occupies the fundus of the IPS along its middle third (Figure 1). It extends up from the fundus onto both the lateral and the medial banks of the sulcus [18]. Area VIP receives a rich visual projection from the middle temporal visual area (MT) [19,20]. Other visual inputs come from the medial superior temporal area (MST), the fundus of superior temporal area (FST) and the parieto-occipital area (PO). In addition, several cortical sources (e.g. area PE and area PF) provide area VIP with somatic information.

The functional properties of VIP neurons have been investigated by Colby *et al.* [18] and Duhamel *et al.* ([21•]; F Bremmer, J-R Duhamel, S Ben Hamed, W Graf, *Soc Neurosci Abstr* 1996, 22:666.8). They have described two main classes of VIP neurons: purely visual neurons and bimodal (visual and tactile) neurons. Purely visual VIP neurons are strongly selective for the direction and speed of the stimuli. Some respond preferentially to expanding or contracting stimuli. Their receptive fields (RFs) are typically large. Bimodal neurons respond independently to visual and tactile stimulation. Tactile RFs are located predominantly on the face. Tactile and visual RFs are aligned in a congruent manner, with the central visual field having its tactile counterpart on the nose and mouth area and the peripheral visual field on the side of the head or body. Directional selectivity is the same in both modalities [21•]. A special type of bimodal VIP neurons is formed by cells that respond to visual stimuli located proximal to the tactile field. Some of these neurons are activated only when 3D objects move towards or, more rarely, away from the animal [18].

In some VIP neurons, the visual RF changes position with gaze shift; in others (about 30%), the visual RF remains in the same spatial position with respect to the head in spite of gaze shift (F Bremmer, J-R Duhamel, S Ben Hamed, W Graf, *Soc Neurosci Abstr* 1996, 22:666.8). The independence of RF position from gaze direction characterizes also those VIP neurons that respond to stimuli moved in the sagittal plane. The fact that VIP neurons code in nonretinal coordinates and the characteristics of their RFs suggest that VIP neurons play a role in acquiring visual targets for somatic movements, most probably those of the head [6•].

These findings are of great interest because they demonstrate that in the IPL, target location may be coded in

two ways: by using a retinocentric code, as described in the oculomotor area LIP (see [22]), and by using a nonretinotopic code, as shown in area VIP [18]. A similar dichotomy between oculomotor and somatomotor areas has been observed in the frontal lobe. RFs are coded in retinocentric coordinates in frontal eye fields (FEFs) [23], whereas they are coded in spatial coordinates in area F4 [24,25,26••,27]. Furthermore, bimodal neurons with tactile and visual RFs are present extensively in area F4 [26••,28–31]. Some of them have tactile RFs on the face and visual RFs around it. Others have tactile RFs on the body, the arms and the hands, and the visual RFs located around the tactile ones. In contrast to area VIP, purely visual neurons are rare in area F4 [32].

The tight link between areas VIP and F4 was confirmed by anatomical studies. Matelli *et al.* (M Matelli, G Luppino, A Murata, H Sakata, *Soc Neurosci Abstr* 1994, 20:404.4) found that an injection limited to area F4 labeled extensively neurons in area VIP. The region of projection, however, from the frontal lobe to area VIP is larger than area F4, as it also extends upwards into the posterior bank of the superior arcuate sulcus in lateral F7 (JW Lewis, DC Van Essen, *Soc Neurosci Abstr* 1996, 22:160.4).

Iriki *et al.* [33••] have recently published a fascinating experiment showing that the parietal bimodal visuotactile system is involved also in acquiring visual information for arm reaching. They recorded neurons from the fundus and medial bank of the IPS. Some neurons had tactile RFs on the hand and forearm (distal neurons), whereas others on the shoulder and face (proximal neurons). Visual RFs were located around the tactile ones and were independent of gaze. When the hand moved, the visual RFs moved with it. Most interestingly, the visual RFs expanded when the animal was trained to use a tool to interact with objects. This expansion, which involved both proximal and distal neurons, was not related to tool holding but to the monkey's 'intention' to use it.

Other areas that should be involved in visuomotor transformations for head, face and arm movements are areas PF, PG, and a newly discovered small region in the depth of the IPS, just rostral to area LIP [34], possibly belonging to it. However, with the exception of a short report by Graziano *et al.* (SA Graziano, CG Gross, T Fernandez, *Soc Neurosci Abstr* 1996, 22:160.5) on PF bimodal neurons with tactile RFs located on the arm, there are no new reports on areas PF and PG. These authors found that in PF, unlike in F4, the visual RFs (that are very large) did not move when the arm moved.

Very recently, Snyder *et al.* [35••] explored area LIP and a region immediately medial and posterior to it using a behavioral test that allowed them to differentiate arm-related activity from eye-related activity. They found that, when appropriately tested, almost all the neurons showed an activity preceding either eye saccades or reaching movements.

## Superior parietal lobule

Unlike the IPL, the SPL is essentially related to the elaboration of somatosensory information. The anatomical dichotomy between the IPL (in large part visual) and the SPL (mostly somatosensory) fits well their physiological properties ([36–38]; see also [39,40•]). However, recent data have shown that the posterior part and some of the mesial parts of the SPL receive visual information (see below). Here, we will review the properties of the visual sectors of the SPL and, in particular, the areas forming the anterior bank of the parieto-occipital sulcus.

### Areas of the anterior bank of the parieto-occipital sulcus

There is converging evidence that the anterior bank of the parieto-occipital sulcus is formed by two areas: V6/PO, which occupies its most ventral part, and V6A, which is located more dorsally [41,42••]. V6/PO is a purely visual area. It receives retinotopically organized input from areas V1, V2, V3, V4 and MT [41]. In each of these areas, the projection to area V6 arises from the representation of the periphery of the visual field. The study of single neurons of V6 showed that its neurons have functional properties typical of the visual areas, being either orientation selective or direction selective, or both [41,43]. All V6 neurons have visual RFs organized in retinotopic coordinates, many of them being modulated by the position of the eye [43].

Area V6A, in addition to having visual neurons functionally indistinguishable from those of V6/PO, is characterized by the presence of visual-unresponsive (nonvisual) neurons and of neurons with complex visual properties [42••]. Particularly interesting, among the latter, are neurons whose RF locations do not change in space with gaze shifts. Therefore, these neurons, referred to as 'real position cells' [44], appear to encode space in nonretinotopic coordinates, similar to neurons in the VIP–F4 circuit.

More recently, Galletti *et al.* [45•] discovered that many of the so-called nonvisual neurons in area V6A discharge during arm movements; their discharge is time-locked to the onset of arm movement and often is direction selective. These 'arm movement' neurons are also driven by passive somatic stimulation.

From these data it is clear that areas V6/PO and V6A are markedly different. The former is a visual area that provides a relatively direct route from the occipital lobe visual field periphery to the parietal lobe. Its output terminates in various areas of the IPS, including areas VIP, LIP and MIP (medial intraparietal). Its hierarchical level in the visual pathways appears to be similar to that of areas MT and V4 [41]. In contrast, area V6A appears to be functionally similar to parietal areas, showing nonretinotopic RFs and motor properties. A detailed study

contrasting the output of V6/PO with that of V6A is lacking. Shipp and Zeki (S Shipp, S Zeki, *Eur J Neurosci* 1995, suppl 8:32.24), however, have described a direct route from area V6A to the dorsal premotor cortex.

### Other superior parietal lobule areas

Recently, it was shown independently by Boussaoud [46] and Caminiti [47] and their co-workers that injections of retrograde neural tracers in the dorsal premotor cortex along its rostro-caudal extension mark different parts of the SPL. Posterior injections label area PE, whereas rostral injections label areas MIP, PGm, V6A and MDP (medial dorsal parietal). These data, which fit very well the organization of the visual afferents to the SPL (see above), were confirmed by the observation that the number of neurons that increase their activity at the presentation of a stimulus (signal-related neurons) is high in the rostral part of the dorsal premotor cortex and low caudally, whereas, conversely, movement-related neurons follow an opposite gradient [40•].

Very little is known about area MIP and the other areas that may convey information to the dorsal premotor neurons. Colby and Duhamel [6•,48] reported that, moving from the upper part of the medial bank of the IPS to its depth, purely somatosensory, bimodal (visual and somatosensory) and purely visual neurons were progressively encountered. Johnson *et al.* [40•] found that in SPL, as in the dorsal premotor cortex, there is a gradient in the percentage of signal-related and movement-related neurons, the latter being more frequent in area PE and the former in area MIP.

## Conclusions

### Reaching and grasping circuits: what can one conclude?

We know much more about grasping mechanisms than about those subserving reaching. Although this may seem surprising, in fact it is not. Grasping implies a transformation of a real thing (an object) into a movement. Reaching implies the transformation of an abstract construct (space) into a movement. The understanding of how we get this construct is difficult, per se, and, in addition, hindered by the historical primacy of vision in the neurosciences. In the newborn, space does not appear to be unitary but is formed by many spaces, each of which is related to a different motor activity [49]. Visual information is later matched on these motor spaces. Furthermore, in the early stages of development, visual space has a limited depth, being restricted essentially to personal and peripersonal space [49]. Therefore, space is initially motor; later, it becomes linked to teleception. From this perspective, the functional properties of premotor neurons of area F4 represent the initial step (and the outcome) of the active interaction of an individual with its body. From this interaction, a 'motor space' (which includes space sectors around the different body parts) is formed. This 'motor space' is then coupled with sectors of visual space. According to this view, the visual RFs of VIP neurons

should reflect this inverse transformation from movement to space.

Confirming the developmental studies, clinical evidence also indicates that reaching is not unitary. Patients with optic ataxia are able to perform correctly movements directed towards the body but not away from it, suggesting that movements away and towards the body are mediated by different circuits. It is interesting to note that typically in optic ataxia, reaching is impaired mostly for targets in the periphery of vision. Furthermore, in these patients, misreaching is commonly detected only when the patients cannot see their hand. As optic ataxia is caused by lesions of the SPL (see [3,50]), these data suggest that the SPL system is particularly important for the control of the arm during the transport phase, especially when it is performed without foveation. Consistent with this view are the physiological data reviewed above that the nodal visual point of the SPL system is area V6/PO, in which the visual periphery and not the fovea is represented. This visual information, together with the proprioceptive information typical of the SPL, should be used to monitor and control arm position during the transport phase.

### Space versus action

Is visual information reaching the parietal lobe used for action or for space perception? In agreement with Milner and Goodale [3], the data reviewed here clearly point out that the parietal lobe is involved also in visuomotor transformations that do not require an analysis of space, such as in object grasping. Furthermore, clinical observations that patients with SPL lesions show optic ataxia but no deficit in space perception [50] suggest that even some visuomotor transformations requiring space analysis do not necessarily intervene in space perception. Unlike Milner and Goodale [3], we do not think, however, that these considerations are sufficient to rule out a specific role of the parietal lobe in space perception. Our proposal is that the IPL — with its circuits that acquire visual information and transform it into eye, head and arm movements — represents the anatomical substrate at the basis of space perception. Clinical data showing that lesions of the IPL produce spatial neglect [50] support this contention.

## Acknowledgements

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in which the monkey had to fixate on a peripheral point and reach for an-
other peripheral point located in the opposite visual hemifield (dissociation
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