Parietal control of hand action

Hideo Sakata and Masato Taira

Nihon University, Tokyo, Japan

Recent advances suggest that neurons of the anterior intraparietal area play a critical role in the visual guidance of hand action. The parietal cortex appears to process in-coming binocular visual signals of the three-dimensional features of objects and matches these signals with the motor signals, which come from the ventral premotor cortex, that will be required for hand manipulation of the object.

Current Opinion in Neurobiology 1994, **4**:847–856

Introduction

The prehensile hand and binocular stereopsis are two major functional features of primates [1]. From an evolutionary point of view, prototypes of these features emerged in tarsiers [2], developed further with the emergence of the opposable thumb and conjugate eye movement in macaque monkeys, and culminated in tool-using and tool-making in man [3]. The accurate visual guidance of hand movement facilitated by binocular vision ensures the high precision and skillful manipulation required for these tasks. But where are these functions integrated in the brain?

Human patients with parieto-occipital lesions show deficits in reaching and/or grasping, using tools, imitating gestures and drawings, and/or constructing block designs. The disorders characterized by these symptoms are called optic ataxia [4–6], ideational apraxia [7], ideomotor apraxia [8] and constructional apraxia [9•], respectively. All of these symptoms are disorders of visually guided hand action and are often associated with disturbances of visuospatial perception and attention [10,11••], as well as eye movement disorders [4,5]. Parietal lesions in monkeys also cause deficits in reaching and/or grasping [12,13] and skilled movements of the hand [14].

The cortical neurons related to the natural hand actions of reaching and grasping were first recorded in the parietal cortex by Mountcastle *et al.* [15] and Hyvaerinen and Poranen [16], long before similar types of neurons were recorded in the motor cortex [17] and premotor cortex [18,19]. However, quantitative analysis of the activity of these neurons was confined to the cells related to reaching [15,20]. Recently, we studied in detail the functional properties of the parietal neurons that are specifically related to hand movement [21,22]. Many of these neurons receive both visual and motor signals, and probably play a crucial role in visual guidance of skilled hand movement.

In this article, we review the recent investigations of goal-directed hand actions carried out using various approaches (see also [23] for review), and propose a hypothesis of how the visual information about the spatial characteristics of objects is processed in the parietal cortex to allow for matching of hand actions with a wide variety of objects.

Neuropsychological background

The first indication that the parietal cortex is involved in the visual control of hand movement was the clinical symptoms manifested by lesions of the parieto-occipital, as reported by Balint [4].

One of the disorders of Balint's syndrome [4], optic ataxia, has been described as misreaching [5,24]. As patients groped for an object with overextended fingers, the abnormal grasping was attributed to a strategy for compensating for the reaching deficit and increasing the probability of contact of the hand with the object.

Recently, Jeannerod [25] found in patients with parieto-occipital lesions a remarkable disturbance of the formation of finger grip before reaching the target objects, which he called 'preshaping'. Perenin and Vighetto [6] found a disturbance of the adjustment of hand orientation to that of the target in patients with optic ataxia. More recently, Jeannerod *et al.* [26••] found a patient with bilateral posterior parietal lesions who manifested a bilateral deficit in grasping without having a deficit in reaching. The patient had both abnormal preshaping with overextended grip and an inability to adjust hand orientation. The dissociation of the deficits in reaching and grasping suggested that separate regions may exist for the control of reaching and grasping.

The disturbance of visually guided grasping may be dissociated from that of visuospatial perception, as suggested

---

Abbreviations

AIP—anterior intraparietal; **IPS**—intraparietal sulcus; **LGB**—lateral geniculate body; **LIP**—lateral intraparietal;
M—magnocellular; **MRI**—magnetic resonance imaging; **MST**—medial superior temporal; **MT**—mediotemporal area;
P—parvocellular; **PET**—positron emission tomography; **PIP**—posterior intraparietal; **PO**—parietal–occipital;
rCBF—regional cerebral blood flow; **STS**—superior temporal sulcus; **VIP**—ventral intraparietal.

by the report of Goodale *et al.* [27] about a patient with carbon monoxide poisoning who manifested severe visual agnosia of objects but showed perfect matching of the orientation and the grip size of the hand to the targets. In contrast, Goodale *et al.* [28••] reported a case of optic ataxia in which the patient showed difficulty in grasping objects but was able to discriminate differences in shape. They suggested that separate visual cortical pathways exist for the perception of object shape and for the control of action of object grasping [29].

There is also an important dissociation of functional deficits in reaching for objects in the peripheral visual field from that in reaching for objects in the central visual field. Patients with a lesion in the superior parietal lobule misreach for objects in the contralateral visual field but do not appear to have a deficit in reaching in the central visual field [30,31]. A similar type of misreaching was found by Rondot *et al.* [32] in patients with surgical disconnection of the parieto-occipital junction. On the other hand, a classic symptom of optic ataxia resulting from bilateral lesions of the angular gyrus and combined with oculomotor disorder is misreaching when using central vision [5]. Pierrot-Deseilligny *et al.* [33] reported the case of a patient with a lesion in the bilateral inferior parietal lobules who showed misreaching when using central vision as well as when using peripheral vision.

Patients with parietal lesions may have deficits in more complex skilled hand actions than simple reaching and grasping, as revealed by the symptoms of apraxia. The two major types of apraxia, as defined by Liepmann [34], are ideational and ideomotor apraxia. Patients with ideational apraxia commit errors in the use of tools, for example, they brush their teeth with a spoon or stir the contents of a glass with a bottle-opener [7], although they can recognize and name the tools. The deficit may be result from a loss of knowledge of tool function [35], or the inability to match the hand action with the structure and function of the objects.

On the other hand, ideomotor apraxia manifests as a deficit in presenting or imitating gestures, and is often observed in patients with a lesion in the left parietal cortex [36]. Ideomotor apraxia appears to result from a deficit in the ability to match the action of the hand and arm to the visual image of the movement and posture of the hand and arm of the examiner.

A third type of apraxia, as defined by Kleist [37], is constructional apraxia, which manifests as an inability to draw pictures, assemble block designs, etc. Although Kleist localized the causative lesion of this symptom in the posterior parietal area of the left hemisphere, patients with right hemisphere lesions also show visuoconstructive disabilities, as shown in the illustrative cases described by Hecaen *et al.* [38]. It is well known that a split-brain patient studied by Sperry *et al.* [39] showed much better constructional performance with his left hand than his right. A number of studies led to the suggestion that the right hemisphere supplies a perceptual component and the left hemisphere an executive component to the visuoconstructional task (see [40] for review). Thus, the constructional apraxia may be secondary to a deficit of spatial perception, especially in the case of right parieto-occipital lesions [41].

Therefore, it is not possible, on the basis of clinical observations, to exclude visuospatial perception from the functions attributed to the dorsal pathway and the posterior parietal cortex, as suggested by Goodale and Milner [29]. Alternatively, it may be suggested that the perceptual function of the parietal cortex is action-oriented [42] and that a link exists between perceptual and motor systems within the parietal cortex.

The deficits of perceptions resulting from parieto-occipital lesions described below are relevant to the visual guidance of hand action. Loss of stereoscopic vision resulting from parieto-occipital lesion was first reported by Holmes and Horrax [43]. Carmon and Bechtoldt [44] tested patients using a modified Julesz random-dot stereogram and found marked deficits in performance in patients with right hemisphere lesion. Right hemisphere dominance in stereopsis was confirmed by several authors [45–48]. Rothstein and Sacks [49] found deficits in stereopsis in patients with lesions of the parietal lobe; however, the impairment was greater in patients with lesions of the left parietal cortex. It is highly likely that the parietal cortex is involved in stereopsis, although Ptito *et al.* [50] reported that global stereopsis, but not local stereopsis, was impaired after anterior temporal lobectomy. It is clear from our daily experiences that a deficit in stereopsis may cause disturbance of precise skilled hand action, such as threading of a needle.

Inability to judge the orientation of lines or vertical and horizontal axes has been associated with right parieto-occiptal lesions [51–53]. However, Mehta *et al.* [54] found that the contribution of the left hemisphere was greater in the task of matching line orientation than that of the right hemisphere. Recently, Von Cramon and Kerkhoff [11••] found impairment of elementary visuospatial perception, including length and distance estimation, in patients with parieto-occipital lesions. These functions are also important in visual guidance of hand action.

Finally, the selective deficit of visual size perception has been attributed to lesions of the parietal cortex [55], although recently, cases of micropsia in patients with lesions of the occipitotemporal pre-stiate cortex have also been reported [56•].

Lesion experiments in monkeys

It is difficult to replicate the disturbances of hand action of human patients with parieto-occipital lesions by inducing experimental lesions in monkeys, especially in the case of apraxia. Thus, most of the early studies of parietal lesions in monkeys have focused on the deficits in visually guided reaching [57,58]. However, it is significant that misreaching occurred only with the contralateral arm in both visual fields and therefore could be dissociated from more general visual disorientation, including eye-movement disorders.

In more recent detailed studies of parietal lesions, misreaching was associated with disturbance of preshaping [12] or improper orientation of the contralateral hand or fingers [13]. In an experiment of a parietal leukotomy that damaged the inferior parietal lobule, Haaxma and Kuypers [14] observed a deficit in the type of visual guidance of hand and finger movement where opposition of thumb and index finger are needed.

Performance of other spatial tasks, such as landmark discrimination [59], the stylus maze task [60], or follow the route of a bent wire [61] or a patterned string [62], was impaired by parieto-occipital lesions. In contrast to lesions of the inferotemporal cortex, parietal lesions did not cause a deficit of form or object discrimination [59,63], with the notable exception of discrimination of a square versus a diamond [64], which is actually the discrimination of the orientation of the same shape. Recently we induced deficits of preshaping by means of a functional block of the anterior intraparietal area (AIP), on the posterior bank of the rostral intraparietal sulcus [65••], where we recorded those neurons that were related to the hand manipulation task, as will be described in the following section of this review. Fig. 1 shows an example of the loss of preshaping after muscimol injection into area AIP. Before injection, when a monkey prepares to grasp and pull a small plate buried in a groove, it extends the index finger, flexes the 2nd to 5th fingers and inserts the index finger smoothly into the groove (Fig. 1a,i). However, after the injection, it extends all of the fingers so that the fingers hit the side plate (Fig. 1a,ii). Even when it manages to insert the index finger, it is not able to oppose the thumb against the index finger. The lower diagrams (Fig. 1c,d) show the sites of injections, with the sites of recordings of the hand-manipulation-related neurons that were recorded in the posterior bank of the rostral intraparietal sulcus (area AIP) that was directly posterior to the hand area of the primary somatosensory area.

Anatomical background

It is now generally accepted that two cortical visual pathways exist [66,67]. The occipitotemporal pathway, or 'ventral stream', is crucial for visual identification of objects, whereas the occipitoparietal pathway, or 'dorsal stream', is crucial for the perception of the spatial position and movement of objects, as well as for the visual guidance of hand movements toward objects in space [68•].

The segregation of visual pathways begins at the level of the retina, and continues through the lateral geniculate body (LGB). Large M ganglion cells project to the magnocellular (M) layers of LGB and small P cells project to the parvocellular (P) layers [69]. The former is called the M system and the latter the P system. The M system is concerned with movement and depth, whereas the P system is concerned with shape and color [70,71]. It is important to note that M layers of the primate LGB contain X-type cells, which exhibit sustained discharge, as well as Y-type cells, which exhibit transient discharge [72]. M system neurons project through layer 4B of cortical area V1 directly, or by way of a thick band of area V2, to area V5 (MT) and V3 complex.

Most of the cells of V5 are sensitive to moving stimuli and are directionally selective, and seem to play a crucial role in motion vision. On the other hand, many of the cells of the thick band of V2 are sensitive to binocular disparity [73] and many cells of V3 and V3A are binocularly driven and disparity sensitive [74,75]. It is thus likely that the V3 complex plays a critical role in stereopsis [76].

V3 complex cells project to area PO (V6) of the superior parietal lobule [77], area LIP [78] and PIP (DJ Felleman, A Burkhalter, DC Van Essen, Soc Neurosci Abstr 1987, 13:626) in the lateral bank and fundus of the intraparietal sulcus (IPS). These areas may be involved in the coding of spatial position and/or stereopsis, whereas areas MST and VIP, which receive strong projections from MT [79,80], are involved in motion analysis.

Corticocortical connections between the parietal cortex and frontal cortex are important in relation to the control of hand action. Area LIP has strong interconnections with the frontal eye field [78,81] and the superior colliculus, and plays an important role in saccadic eye movement. In contrast, the more rostral part of the posterior bank of IPS, which we called anterior intraparietal (AIP) area, is reciprocally connected with inferior area 6 of the premotor cortex [82]. This is a region where we induced deficits of visually guided hand movement by functional blockage with muscimol injection [65••]. Inferior area 6 has connections also with area 7b where the somatosensory input converges with visual input. Thus, the inferior parietal lobule is connected not directly with the primary motor cortex but indirectly through the connection of the premotor areas to the motor cortex [82,83].

Neurophysiological studies of hand action

The cortical neurons related to the visually guided hand actions of reaching and grasping objects were first recorded in the posterior parietal association cortex of alert monkeys by Mountcastle *et al.* [15] and Hyvaerinen and Poranen [16]. They classified two types of movement-related neurons. One type was the reach (or projection) neurons that were related to the proximal movement of reaching toward the target position. The other type was hand manipulation neurons that were related to the distal movement of hand and fingers, for example, digging out a food morsel covered by fingers. Georgopoulos *et al.* [17] trained a monkey to point to a target in different positions and found that many neurons of the primary motor cortex were activated during this task and were selective in the di-

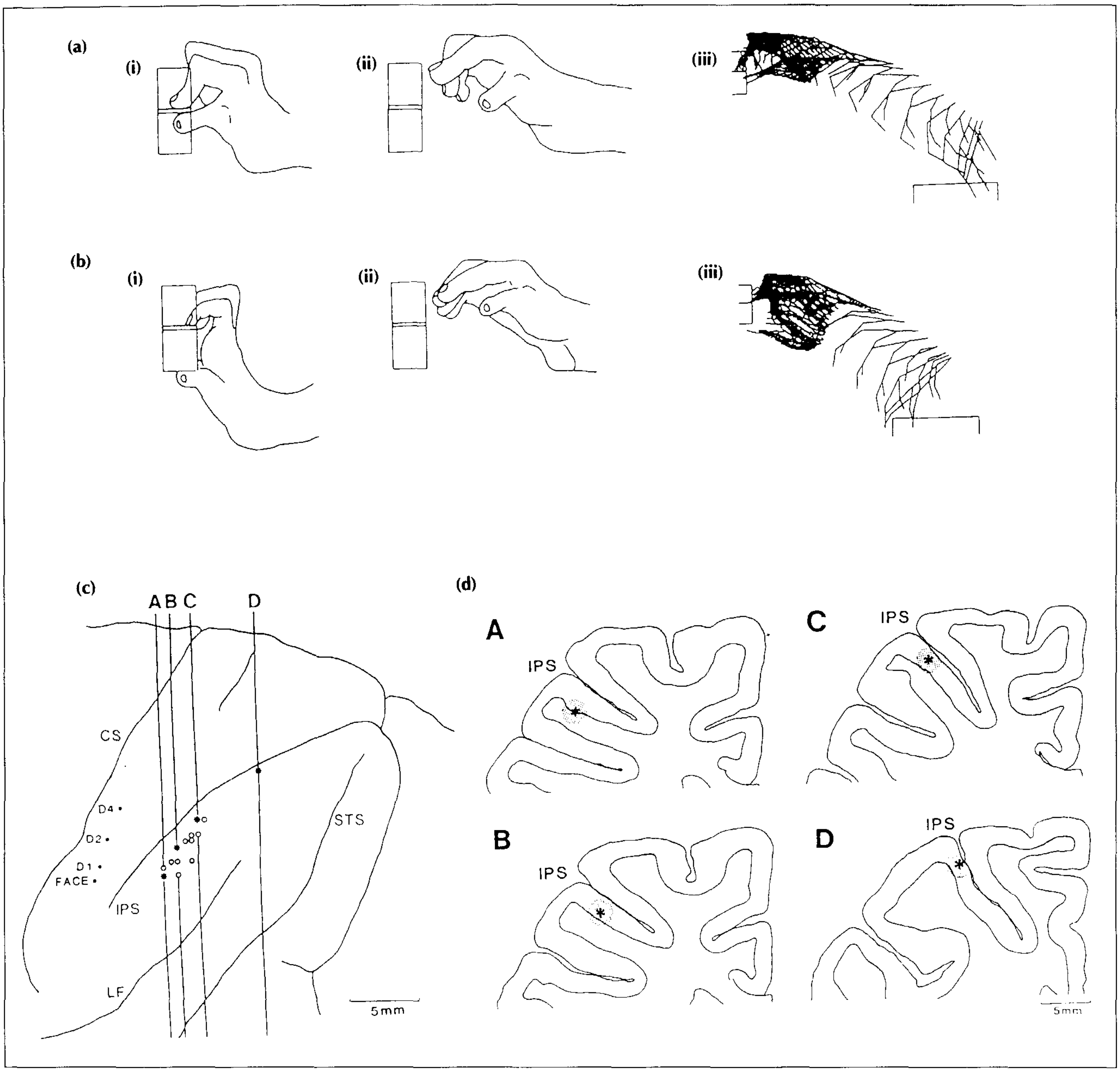

Fig. 1. Deficit in hand preshaping after functional inactivation of area AIP of monkey parietal cortex. **(a)** and **(b)** Preshaping and grasping of a small plate in a groove. **(a)** Single-frame images redrawn from (i,ii) video and (iii) stick diagram of a typical control trial. (ii) During the preshaping phase, the monkey extends the index finger and simultaneously flexes the last three fingers. (i) Grasping is achieved by opposing the pulpar surface of thumb and index finger. **(b)** Single-frame images redrawn from (i,ii) video and (iii) stick diagram of a successful test trial after muscimol microinjection into site B (see (c) and (d) below). (ii) During the preshaping, the animal does not flex the last three fingers, and (i) even when it is able to insert the index finger into the groove, index–thumb opposition cannot be accomplished. **(c)** and **(d)** Four anatomical locations (A–D) of single-unit recordings and muscimol microinjection sites. **(c)** Enlarged lateral view of the left parietal cortex of the monkey. Filled dots indicate the location of four recording sites in primary somatosensory area (S1). Letters indicate the body parts in which tactile receptive field were located: D1, thumb; D2, index finger; D4, fourth finger. Open circles indicate the sites where hand manipulation-related neurons were recorded. Asterisks indicate the muscimol microinjection sites. **(d)** Selected coronal sections showing the microinjection sites. Shaded areas represent the local diffusion of muscimol. The sections are taken at the level indicated by vertical bars on (c) the brain drawing. Abbreviations: CS, central sulcus; LF, lateral fissure.

rection of movement. Kalaska *et al.* [20] recorded a similar type of reach neurons in area 5 (superior parietal lobule). The distribution of onset time for area 5 neurons lagged behind the corresponding distribution of motor cortical cells by about 60 ms, suggesting that area 5 neurons receive an efference copy of the motor cortex output. Their function may be to monitor command signals and correct errors. Recently, Kalaska *et al.* [84] studied the activity of area 5 neurons with a load on the manipulandum in different directions, and found that the directional tuning of their activity was insensitive to the application of load, suggesting that they encode the kinematics but not the dynamics of the arm. On the other hand, MacKay [85] recorded reach-related neurons in area 7a and found that the majority of them showed spatial preference and many of them showed visual responses, suggesting that they monitor the visual movement of the hand and arm to correct errors.

Recently, we studied the parietal neurons related to hand manipulation tasks [21,22]. Many of these hand manipulation neurons were highly selective and were preferentially activated during the manipulation of one of four different objects. In order to exclude visual input, we trained the monkey to perform the task in the dark and also to fixate on the object without grasping it. Thus, the hand manipulation neurons were classified into three types: 'motor dominant', 'visual and motor', or 'visual dominant'. More recently, we made a systematic study of the correspondence of visual and motor components with regard to the object, and found that the highly selective neurons showed the same preference of object for manipulation and fixation [86••]. These neurons were localized in the rostral part of the posterolateral bank of the intraparietal sulcus, which we designated area AIP [65••].

As mentioned in the anatomical background section, area F5 of the ventral premotor cortex and area AIP of the inferior parietal lobule are tightly interconnected [82]. Rizzolatti *et al.* [18] recorded in area F5 many neurons related to the distal hand movement that they designated as 'grasping-with-the-hand neurons'. They were quite similar to the parietal hand-manipulation neurons with respect to their selectivity in the pattern of hand movement. They distinguished three main groups of neurons — 'precision grip neurons', 'finger prehension neurons' and 'whole hand prehension neurons' — which may correspond to the highly selective 'motor dominant' neurons of area AIP. Thus, it is highly likely that the 'motor dominant' cells receive an efference copy from the premotor area F5 cells. On the other hand, the 'visual dominant' cells probably receive visual signals of the spatial characteristics of an object from cells within the parietal cortex. These two signals are integrated in 'visual and motor' cells, which may send positive feedback signals to the premotor cortex. We have presented this idea of parietal premotor interaction as a conceptual diagram in a recent paper (see [86••]).

Hand manipulation neurons are selective not only for the shape of an object but also for the orientation of the object, especially in the case of a lever switch or a small knob in a groove. Recently, we found a group of visual neurons in the caudal part of the lateral bank of IPS, roughly corresponding to area PIP, that were selective for the three-dimensional orientation of the longitudinal axis of objects (M Kusunoki *et al.*, Soc Neurosci Abstr 1993, 23:770). Most of these orientation-selective neurons were binocularly driven and may be involved in stereopsis. Thus, it is highly likely that visual signals encoding three-dimensional shape are processed in the parietal cortex rather than the inferotemporal cortex. The output of that processing may be sent to area AIP for matching of the hand grip to the three-dimensional object.

Fig. 2 shows an example of the response of axis orientation-selective neurons that prefer a diagonal axis tilted to the right and toward the animal. In order to discriminate such a three-dimensional orientation it is necessary to compute the gradient of binocular disparity [87]. The parietal association cortex is the most likely area for such a complicated processing. In fact, there are various types of visual neurons in the parietal cortex that represent position and other spatial characteristics. Recently, Galletti *et al.* [88••] found neurons of area V6 (PO) that encode spatial locations in body-centered coordinates. Such neurons are suitable for visual guidance of reaching in the peripheral visual field. Area PO sends projections to the dorsal premotor area [89•], where Caminiti *et al.* [90] recorded reach neurons with three-dimensional directional selectivity. In area 7a there are many visual fixation neurons that code three-dimensional position of a fixation point, including egocentric distance [91], and the visual receptive fields of at least some of them are near the fovea. These neurons are suitable for guidance of reaching with central vision, although no corticocortical pathway is known to connect area 7a directly to the premotor cortex.

Recently, Graziano and Gross [92•] found bimodal, visual and tactile, neurons that were shown to be involved in the representation of extrapersonal space. Of particular interest were the neurons having a visual receptive field close to the hand; this receptive field was found to move as the animal changed the position of its hand. They found such bimodal neurons in the putamen initially; however, the bimodal response may be generated in areas VIP and 7b of the parietal cortex [93••]. The bimodal neurons were also found in the inferior area 6; thus, these neurons probably contribute to the control of hand movement.

Finally, di Pelegrino *et al.* [94] found that neurons in the rostral part of inferior premotor cortex discharged when the monkey observed meaningful hand movements performed by the experimenters as well as during the same movement by the animal. This is similar to but different from the case of neurons of the superior temporal sulcus (STS), which responded to the sight of hand action [95], as STS neurons were not activated by the animal's own movements. It is highly likely that similar neurons may be present in the parietal cortex that contribute to the imitation of body action, which are impaired in patients with ideomotor apraxia.

Psychophysical studies of human prehension

To obtain information about object size, shape and distance, binocular vision is very important. Servos *et al.* [96] examined the contribution of binocular vision to the control of grasping. They found that when the grasping movements were executed under monocular conditions, the subjects underestimated the object distance and size (showing longer movement duration, lower peak velocity, longer deceleration phase and smaller grip size). They suggested that binocular vision might make a sig-

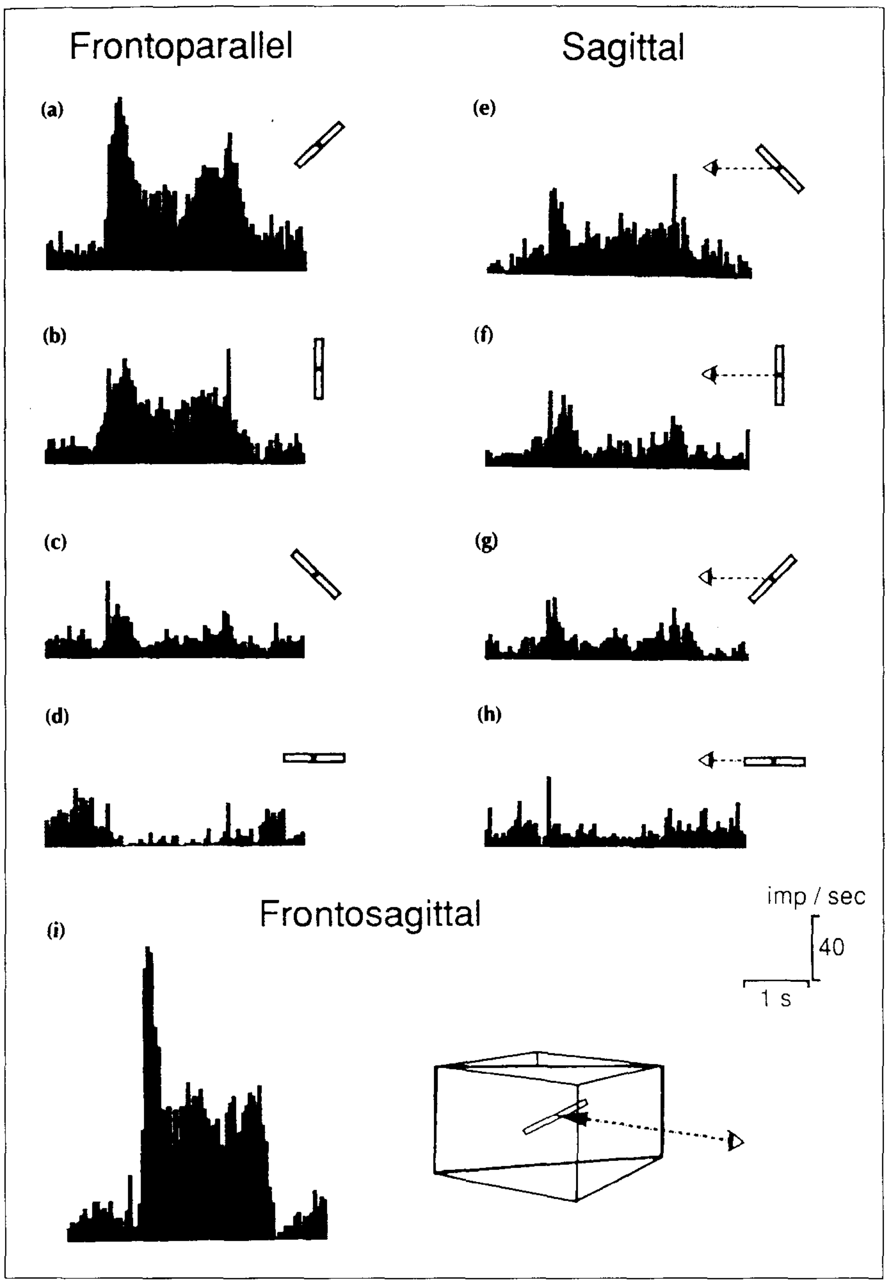

Fig. 2. An example of the response of axis orientation-selective neurons of the inferior parietal lobule of the monkey. **(a–d)** Responses to the luminous bar in varied orientations in the frontal plane at 45-degree steps. **(e–h)** Responses to the bar in varied orientations in the sagittal plane at 45-degree steps. **(i)** The best response to the bar tilted 45-degrees to the right and forward.

nificant contribution to prehensile movement. There is an alternative interpretation, which is that these differences reflect a motor strategy that the subjects used to compensate for the lack of fine tuning of the movement during its execution. The study of Jakobson and Goodale [97], however, showed that this was unlikely. They studied responses under open-and closed-visual conditions using the same set-up and found no differences between the two conditions with respect to the movement duration, peak velocity and length of acceleration phase. These results suggest that the initial binocular view of the object and hand before movement onset determines the kinematics irrespective of visual feedback.

In a recent study, Servos and Goodale [98•] confirmed the importance of binocular vision in prehension movements in tests using goggles with a liquid-crystal shutter controlling the view of each eye. They used four viewing conditions. In one condition, binocular vision was used throughout the execution of the grasping movement. In the second, the initial binocular viewing conditions were switched to monocular viewing conditions immediately after initiation of the movement. In the third condition, monocular vision was used throughout the movement; and in the fourth, monocular viewing conditions were switched to binocular viewing conditions immediately after movement onset. An interesting finding was that the maximum grip aperture, which occurred two-thirds of the way through the reach movement at a point at which on-line visual information could have an effect, was only affected by the initial viewing condition. Another important finding was that the time allotted for the object contact was longer in the case of initial monocular viewing than initial binocular viewing. These results suggest that the initial binocular view provides important information about the size, shape and distance of an object for smooth and accurate execution of prehension movements and that binocular vision is an important source of feedback information.

Human brain imaging studies

An early rCBF study of human subjects showed that the parietal cortex was activated by finger movement during the maze task [99]. Recent advances in brain imaging techniques allow us to obtain substantial amounts of information of the localization of higher functions in the human brain. However, studies concerning hand and arm movement have been relatively few, with most of them focused on the frontal motor areas. Some researchers have reported that the parietal cortex is activated during finger and arm movement. Colebatch *et al.* [100] reported that a shoulder movement caused a significant increase in rCBF in Brodmann areas 5 and 40, but finger movement did not. This may be due to the fact that the movement was restricted within the personal space and did not involve reaching toward external objects. Other studies suggest that the parietal cortex is more highly involved in the selection of movement [101], the preparation for reaching [102], the integration of special attributes [103] and the learning of motor sequence [104•], than in the control of movement itself.

Neurophysiological and neuropsychological data suggest that the different areas in the parietal cortex may have specific roles for controlling both reaching and grasping movements. Grafton *et al.* [105•] examined the within-arm somatotopy in various cortical areas using a visuomotor tracking task in which the subject continuously followed the randomly moving target with the index finger, thumb, wrist, forearm, elbow and eyes. They found the foci of activity in the motor cortex, supplementary motor cortex and cingulate cortex, but not in the parietal cortex. These results also contradict the neurophysiological data of Grafton *et al.* [103] who found activation during the visually guided finger movements in the superior parietal lobule but not in the inferior parietal lobule. The most recent PET study by Decety *et al.* [106••] showed that the focus of activity during imagining of the grasping of objects with the subject's own hand was in area 40 of the inferior parietal lobule as well as in the premotor (area 6) and prefrontal (area 46) areas. Moreover, it appears to be critical that they presented graspable objects of various shapes and orientations in a three-dimensional display.

Conclusion

Recent neuropsychological studies suggest that the lesions of the parietal cortex may cause not only misreaching but also the disturbance of visually guided grasping, and that the latter may be dissociated from the former. Moreover, reaching using peripheral vision in contrast to central vision may be affected separately as a result of lesions of the superior parietal lobule, whereas the latter is affected as a result of lesions of the inferior parietal lobule. It has also been suggested that disturbances of the visuospatial perception caused by parietal lesions, which include binocular stereopsis and the judgment of line orientation, length and distance, may be associated with disorders of visually guided hand actions, such as tool using, drawing and block construction.

Recent anatomical studies suggest that there may be a third major visual pathway, which projects to the parietal cortex via the V3–V3A complex, and is probably concerned with stereopsis. On the other hand, the corticocortial connection between the inferior parietal lobule and the ventral premotor area may support the visual guidance of hand actions, whereas the interconnection of the superior parietal lobule and the dorsal premotor area may support visual reaching.

Recent neurophysiological studies of behaving monkeys demonstrated that the neurons in the rostral part of the posterior bank of the intraparietal sulcus, which was designated the AIP area, are specifically related with the visually guided hand actions and play an important role in matching the pattern of hand action with the spatial characteristics of the object. More recently, we obtained new evidence that the visual neurons of the lateral bank of the caudal intraparietal sulcus are coding axis orientation and other three-dimensional features of objects with binocular stereopsis. These binocular neurons may provide visual information to area AIP to guide the hand actions. Recent psychophysical experiments also confirmed the importance of binocular vision for reaching and grasping.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Napier JR, Napeir RH: *A handbook of living primates.* London: Academic Press; 1967.
2. Polyak S: *The vertebrate visual system.* Chicago: Chicago University Press; 1957.
3. Napier JR: *Hands.* Princeton: Princeton University Press; 1980.
4. Balint R: **Die seelenlahmung des "schauens".** *Monatsschr fur Psych und Neurol* 1909, **25**:51–81.
5. Hecaen H, de Ajuriaguerra J: **Balint's syndrome (psychic paralysis of visual fixation) and its minor forms.** *Brain* 1954, 77:373–400.
6. Perenin MT, Vighetto A: **Optic ataxia: a specific disruption in visuomotor mechanism. I: Different aspects of the deficit in reaching for objects.** *Brain* 1988, **111**:643–674.
7. De Renzi E, Lucchelli F: **Ideational apraxia.** *Brain* 1988, **111**:1173–1185.
8. Heilman KM, Rothi LJG: **Apraxia.** In *Clinical neuropsychology.* Edited by Heilman KM, Valenstein E. New York: Oxford University Press; 1985:131–150.

9. Carlesimo GA, Fadda L, Caltagirone C: **Basic mechanisms of**
• **constructional apraxia in unilateral brain-damaged patients: role of visuo-perceptual and executive disorders.** *J Clin Exp Neuropsychol* 1993, **15**:342–358.

An attempt to investigate basic mechanisms of constructional apraxia by assessing the relationship of the performance on drawing tasks with that on elementary tasks. In normal subjects, the efficiency in model perception is most related to drawing performance. Right-brain-damaged patients have impaired manipulo-spatial ability, as assessed by visual tracking with a pencil. As for left-brain-damaged patients, left-handed patients show greater impairment in drawing than right-handed ones.

10. Newcombe F, Ratcliff G: **Disorders of visuospatial analysis.** In *Handbook of neuropsychology* vol 2. Edited by Boller F, Grafman J. Amsterdam: Elsevier; 1989:333–356.

11. Von Cramon DY, Kerkhoff G: **On the cerebral organization of**
•• **elementary visuo-spatial perception.** In *Functional organization of the human visual cortex.* Edited by Gulyas B, Ottoson D, Roland PE. Oxford: Pergamon Press; 1993:211–231.

The authors tested 67 patients with focal parietal lesions (confirmed with MRI), and found that patients had impaired perception of basic visuospatial functions, including discrimination of horizontal and vertical axes, length, distance, orientation and position. Impaired perception of axes and angles was more closely associated with anterior parietal damage, whereas impaired perception of position and distance was more closely associated with posterior parietal damage.

12. Faugier-Grimaud S, Frenois C, Stein DG: **Effects of posterior parietal lesions on visually guided behavior in monkeys.** *Neuropsychology* 1978, **16**:151–168.

13. LaMotte RH, Acuna C: **Defects in accuracy of reaching after removal of posterior parietal cortex in monkeys.** *Brain Res* 1978, **139**:309–326.

14. Haaxma R, Kuypers HGJM: **Intrahemispheric cortical connections and visual guidance of hand and finger movements in the rhesus monkey.** *Brain* 1975, **98**:239–260.

15. Mountcastle VB, Lynch JC, Georgopoulos AP, Sakata H, Acuna C: **Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space.** *J Neurophysiol* 1975, **38**:871–908.

16. Hyvaerinen J, Poranen A: **Function of the parietal associative area 7 as revealed from cellular discharge in alert monkeys.** *Brain* 1974, **97**:673–692.

17. Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT: **On the relations between the direction of two-dimensional arm movement and cell discharge in primate motor cortex.** *J Neurosci* 1982, **2**:1527–1537.

18. Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M: **Functional organization of inferior area 6 in the macaque monkey. II: Area F5 and the control of distal movements.** *Exp Brain Res* 1988, **71**:491–507.

19. Gentilucci M, Fogassi L, Luppino G, Matelli M, Rizzolatti G: **Functional organization of inferior area 6 in the macaque monkey.** *Exp Brain Res* 1988, **71**:475–490.

20. Kalaska JF, Caminiti R, Georgopoulos AP: **Cortical mechanisms related to the direction of two-dimensional arm movements: relation in parietal area 5 and comparison with motor cortex.** *Exp Brain Res* 1983, **51**:247–260.

21. Taira M, Mine S, Georgopoulos AP, Murata A, Sakata H: **Parietal cortex neurons of the monkey related to the visual guidance of hand movement.** *Exp Brain Res* 1990, **83**:29–36.

22. Sakata H, Taira M, Mine S, Murata A: **Hand-movement-related neurons of the posterior parietal cortex of the monkey: their role in the visual guidance of hand movements.** In *Control of arm movement in space. Experimenal Brain Research Series 22.* Edited by Caminiti R, Johnson PB, Burnod Y. Berlin: Springer-Verlag; 1992:185–198.

23. Jeannerod M: *The neural and behavioral organization of goal-directed movements.* Oxford: Oxford University Press; 1988.

24. Damasio AR, Benton AL: **Impairment of hand movements under visual guidance.** *Neurology* 1979, **29**:170–174.

25. Jeannerod M: **The formation of finger grip during prehension. A cortically mediated visuomotor pattern.** *Behav Brain Res* 1986, **19**:99–116.

26. Jeannerod M, Decety J, Michel F: **Impairment of grasping**
•• **movements following a bilateral posterior parietal lesion.** *Neuropsychologia* 1994, **32**:369–380.

A patient with bilateral posterior parietal lesions showed a bilateral deficit in grasping cylindrical dowels but showed no deficit in reaching toward their location. The major deficit was the lack of preshaping and precision grip without any disorder of size perception.

27. Goodale MA, Milner AD, Jakobson LS, Carey DP: **A neurological dissociation between perceiving objects and grasping them.** *Nature* 1991, **349**:154–156.

28. Goodale MA, Meenan JP, Bulthoff HH, Nicolle DA, Murphy KJ,
•• Racicot CI: **Separate neural pathways for the visual analysis of object shape in perception and prehension.** *Curr Biol* 1994, **4**:604–610.

A comparison was made of a patient with optic ataxia, caused by bilateral parieto-occipital lesions, to a patient with visual agnosia, caused by carbon monoxide poisoining. The former chose unstable grasp points to pick up irregularly shaped objects, although the patient was deemed normal in terms of orientation matching and shape discrimination. The latter, in contrast, chose stable grasp points but could not didscriminate shape and orientation of the objects.

29. Goodale MA, Milner AD: **Separate visual pathway for perception and action.** *Trends Neurosci* 1992, **15**:20–25.

30. Ratcliff G, Davies-Jones GAB: **Defective visual localization in focal brain wounds.** *Brain* 1972, **95**:49–60.

31. Auerbach SH, Alexander MP: **Pure agraphia and unilateral optic ataxia associated with a left superior parietal lobule lesion.** *J Neurol Neurosurg Psychiat* 1981, **44**:430–432.

32. Rondot P, De Recondo J, Ribadeau-Dumas JL: **Visuomotor ataxia.** *Brain* 1977, **100**:355–376.

33. Pierrot-Deseilligny CH, Gray F, Brunet P: **Infarcts of both inferior parietal lobules with impairment of visually guided eye movements, peripheral visual inattention and optic ataxia.** *Brain* 1986, **109**:81–97.

34. Liepmann H: **Apraxie.** *Ergebnisse der Gesamten Medizin* 1920, **1**:516–543.

35. Ochipa C, Rothi LJG, Heilman KM: **Ideational apraxia: a deficit in tool selection and use.** *Ann Neurol* 1989, **25**:190–193.

36. Kolb B, Milner B: **Performance of complex arm and facial movements after focal brain lesions.** *Neuropsychologia* 1981, **19**:491–504.

37. Kleist K: **Kriegsverletzungen des gehirns in ihrer bedeutung fur die hirn lokalization und hirnpathologie.** In *Handbuch der arztlichen erfahrung in weltkriege,* vol 4. Edited by von Schjerning O. Leipzig:Barth; 1923.

38. Hecaen H, Penfield W, Bertrand C, Malmo R: **The syndrome of apractognosia due to lesions of the minor cerebral hemisphere.** *Arch Neurol Psychiat* 1956, **75**:400–434.

39. Sperry RW, Gazzaniga MS, Bogen JE: **Observations on visual perception after disconnection of the cerebral hemisphere in man.** *Brain* 1965, **88**:221–236.

40. Warrington EK: **Constructional apraxia.** In *Handbook of clinical neurology. Vol 4. Disorders of Speech, Perception and Symbolic Behavior.* Edited by Vinken PJ, Bruyn GW. Amersterdam: North-Holland; 1969:67–83.

41. Kritchevisky M: **The elementary spatial functions of the brain.** In *Spatial cognition.* Edited by Stiles-Davis J, Kritchevisky M, Bellugi U. Laurence Erlbaum: Hillsdale, New Jersey; 1988:111–140.

42. Arbib M: *Metaphorical brain. 2, Neural networks and beyond.* New York: John Wiley; 1989.

43. Holmes G, Horrax G: **Disturbances of spatial orientation and visual attention, with loss of stereoscopic vision.** *Arch Neurol Psychiat* 1919, **1**:385–407.

44. Carmon A, Bechtoldt HP: **Dominance of the right cerebral hemisphere for stereopsis.** *Neuropsychologia* 1969, 7:29–39.

45. Benton AL, Hecaen H: **Stereoscopic vision in patients with unilateral cerebral disease.** *Neurology* 1970, **20**:1084–1088.

46. Danta G, Hilton RC, O'Boyle DJ: **Hemisphere function and binocular depth perception.** *Brain* 1978, **101**:569–589.

47. Hamsher K: **Stereopsis and unilateral brain disease.** *Invest Ophthalmol* 1978, **17**:336–343.

48. Ross JE: **Disturbance of stereoscopic vision in patients with unilateral stroke.** *Behav Brain Res* 1983, 7:99–112.

49. Rothstein TB, Sacks JG: **Defective stereopsis in lesions of the parietal lobe.** *Am J Ophthalmol* 1972, **73**:281–284.

50. Ptito A, Zatorre RJ, Larson WL, Tosoni C: **Stereopsis after unilateral anterior temporal lobectomy.** *Brain* 1991, **114**:1323–1333.

51. McFie J, Piercy MF, Zangwill OL: **Visual-spatial agnosia associated with lesions of the right cerebral hemisphere.** *Brain* 1950, 73:167–190.

52. De Renzi E, Faglioni P, Scotti G: **Judgement of spatial orientation in patients with focal brain damage.** *J Neurol Neurosurg Psychiatry* 1971, **34**:489–495.

53. Benton AL, Varney NR, Hamsher K: **Visuospatial judgement: a clinical test.** *Arch Neurol* 1978, **35**:364–367.

54. Mehta Z, Newcombe F, Damasio H: **A left hemisphere contribution to visuospatial processing.** *Cortex* 1987, **23**:447–461.

55. Wyke M: **Alterations of size constancy associated with brain lesions in man.** *J Neurol Neurosurg Psychiat* 1960, **23**:253–261.

56. Cohen L, Gray F, Meyrignac C, Dehaene S, Dego J-D: **Selective**
• **deficit of visual size perception: two cases of hemimicropsia.** *J Neurol Neurosurg Psychiat* 1994, **57**:73–78.

Two cases of hemimicropsia were reported. There was a perceived reduction of the size of objects when they were presented in the hemifield contralateral to the lesion in the occipital cortex.

57. Bates JAV, Ettlinger G: **Posterior biparietal ablations in the monkey.** *Arch Neurol* 1960, **3**:177–192.

58. Ettlinger G, Kalsbeck JE: **Change in tactile discrimination and in visual reaching after successive and simultaneous bilateral posterior parietal ablations in the monkey.** *J Neurol Neurosurg Psychiat* 1962, **25**:256–268.

59. Pohl W: **Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys.** *J Comp Physiol Psychol* 1973, **82**:227–239.

60. Milner AD, Ockleford EM, Dewar W: **Visuo-spatial performance following posterior parietal and lateral frontal lesions in stumptailed macaques.** *Cortex* 1977, **13**:350–360.

61. Petrides M, Iversen SD: **Restricted posterior parietal lesions in the rhesus monkey and performance on visuospatial tasks.** *Brain Res* 1979, **161**:63–77.

62. Ungerleider LG, Brody BA: **Extrapersonal spatial orientation: the role of posterior parietal, anterior frontal, and inferotemporal cortex.** *Exp Neurol* 1977, **56**:265–280.

63. Ockleford EM, Milner AD, Dewar W, Sneddon IA: **Form perception in stumptail macaques following posterior parietal and lateral frontal lesion.** *Cortex* 1977, **13**:350–360.

64. Mendoza JE, Thomas RK: **Effects of posterior parietal and frontal neocortical lesions in the squirrel monkey.** *J Comp Physiol Psychol* 1975, **89**:170–182.

65. Gallese V, Murata A, Kaseda M, Niki N, Sakata H: **Deficit of**
•• **hand preshaping after muscimol injection in monkey parietal cortex.** *Neuroreport* 1994, **5**:1525–1529.

Local inactivation of the anterior part of the lateral bank of the intraparietal sulcus (area AIP), where the neurons related to hand manipulation were recorded, and found to cause a selective deficit in the preshaping of the hand to grasp the object without misreaching. The results suggest that area AIP plays a crucial role in the visual guidance of hand movements.

66. Ungerleider LG, Mishkin M: **Two cortical visual systems.** In *Analysis of visual behavior.* Edited by Ingle DJ, Goodale MA, Mansfield RJW. Cambridge, Massachusetts: MIT Press; 1982:549–586.

67. Mishkin M, Ungerleider LG, Macko KA: **Object vision and spatial vision: two cortical pathways.** *Trends Neurosci* 1983, 5:414–417.

68. Ungerleider LG, Haxby JV: **'What' and 'where' in the human**
• **brain.** *Curr Opin Neurobiol* 1994, **4**:157–165.

This review deals with two functionally specialized visual pathways, a 'ventral stream' for object vision and 'dorsal stream' for spatial vision. Evidence of the effects of focal brain lesions and PET–rCBF studies in human cortex were reviewed together with evidence showing the hierarchical organization of face processing in the ventral stream.

69. Perry VH, Oehler R, Cowey A: **Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey.** *Neuroscience* 1984, **12**:1101–1123.

70. De Yoe EA, Van Essen DC: **Concurrent processing streams in monkey visual cortex.** *Trends Neurosci* 1988, **11**:219–226.

71. Zeki S, Shipp S: **The functional logic of cortical connections.** *Nature* 1988, **335**:311–317.

72. Kaplan E, Shapley RM: **X and Y cells in the lateral geniculate nucleus of macaque monkeys.** *J Physiol (Lond)* 1982, **330**:125–143.

73. Hubel DH, Livingstone MS: **Segregation of form, color and stereopsis in primate area 18.** *J Neurosci* 1987, 7:3378–3415.

74. Zeki SM: **The third visual complex of rhesus monkey prestriate cortex.** *J Physiol (Lond)* 1978, **277**:245–272.

75. Felleman DJ, Van Essen DC: **Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex.** *J Neurophysiol* 1987, **57**:889–920.

76. Zeki S: **The motion pathways of the visual cortex.** In *Vision: coding and efficiency.* Edited by Blakemore C. Cambridge, UK: Cambridge University Press; 1990:321–345.

77. Colby CL, Gatlass R, Olson CR, Gross CG: **Topographic organization of cortical afferents to extrastriate visual area PO in macaque: a dual tracer study.** *J Comp Neurol* 1988, **269**:392–413.

78. Andersen RA, Asanuma C, Essick G, Siegel RM: **Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule.** *J Comp Neurol* 1990, **296**:65–113.

79. Ungerleider LG, Desimone R: **Cortical connections of visual area MT in the macaque.** *J Comp Neurol* 1986, **248**:190–222.

80. Boussaoud D, Ungerleider LG, Desimone R: **Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque.** *J Comp Neurol* 1990, **296**:462–495.

81. Barbas H, Mesulum MM: **Organization of afferent input to subdivisions of area 8 in the rhesus monkey.** *J Comp Neurol* 1981, **200**:407–431.

82. Matelli M, Camarda R, Glickstein M, Rizzolatti G: **Afferent and efferent projections of the inferior area 6 in the macaque monkey.** *J Comp Neurol* 1986, **251**:281–298.

83. Muakkassa KF, Strick PL: **Frontal lobe inputs to primate motor cortex: evidence of four somatotopically organized premotor areas.** *Brain Res* 1979, **177**:176–182.

84. Kalaska JF, Cohen DAD, Prud'homme M, Hyde ML: **Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics.** *Exp Brain Res* 1990, **80**:351–364.

85. MacKay WA: **Properties of reach-related neuronal activity in cortical area 7a.** *J Neurophysiol* 1992, **67**:1335–1345.

86. Sakata H, Taira M, Murata A, Mine S: **Neural mechanisms of**
•• **visual guidance of hand action in the parietal cortex of the monkey.** *Cereb Cortex* 1994, in press.

The authors present a systematic study of the functional properties of hand manipulation task-related neurons in the posterior bank of the intraparietal sulcus using four kinds of objects for manipulation. Activity profiles of these neurons across objects were analyzed during object manipulation and object fixation tasks, in the light as well as in the dark. Cells were classified as being 'motor dominant', 'visual dominant' or 'visual and motor' types. Visual components were classified as being 'object' or 'non-object' types. Most of the highly selective neurons preferred the same object for manipulation and fixation.

87. Marr D: *Vision*. Edited by Freeman WH. New York: Congany; 1982.

88. •• Galletti C, Battaglini PP, Fattori P: **Parietal neurons encoding spatial locations in craniotopic coordinates.** *Exp Brain Res* 1993, **96**:221–229.

The authors report that the neurons of area V6 or PO of the superior parietal lobule respond to the visual stimulation of the same spatial location regardless of eye position and therefore directly encode visual space in head-centered instead of retinotopic coordinates.

89. • Johnson PB, Ferraina S, Caminiti R: **Cortical network for visual reaching.** *Exp Brain Res* 1993, **97**:361–365.

Retrograde tracers were injected into the cortical regions of the frontal areas where the neurons related to reaching movements were recorded. The most rostral part defined as dorsal premotor area (PMd) was found to receive projections from areas medial intraparietal (MIP) and 7m, which were connected with area PO, suggesting that the premotor area received visual input from the superior parietal lobule.

90. Caminiti R, Johnson PB, Galli C, Ferraina, Burnod Y: **Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets.** *J Neurosci* 1991, **11**:1182–1197.

91. Sakata H, Shibutani H, Kawano K: **Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey.** *J Neurophysiol* 1980, **43**:1654–1672.

92. • Graziano MSA, Gross CG: **A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields.** *Exp Brain Res* 1993, **97**:96–109.

The bimodal, visual and somatosensory neurons in the putamen responded to visual stimuli near their tactile receptive field. These bimodal properties provide a map of the visual space that immediately surrounds the monkey and may function to guide movements in the animal's immediate vicinity.

93. •• Graziano MSA, Gross CG: **The representation of extrapersonal space: a possible role for bimodal, visual-tactile neurons.** In *The cognitive neurosciences*. Edited by Gazzaniga MS. Cambridge, Massachusetts: MIT Press; 1994.

The authors propose that extrapersonal space is represented in the brain by bimodal, visual-tactile neurons in the inferior area 6 and area 7b of the parietal lobe, as well as the putamen. For many neurons with tactile receptive fields on the arm or hand, the visual receptive fields moved when the arm was moved.

94. di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G: **Understanding motor events: a neurophysiological study.** *Exp Brain Res* 1992, **91**:176–180.

95. Perrett DI, Harries MH, Bevan R, Thomas R, Benson PJ, Mistlin AJ, Chitty AJ, Hietanen JK, Ortega JE: **Frameworks of analysis for the neural representation of animate objects and actions.** *J Exp Biol* 1989, **146**:87–113.

96. Servos P, Goodale MA, Jakobson LS: **The role of binocular vision in prehension: a kinematics analysis.** *Vis Res* 1992, **32**:1513–1521.

97. Jakobson LS, Goodale MA: **Factors affecting higher-order movement planning: a kinematics analysis of human prehension.** *Exp Brain Res* 1991, **86**:199–208.

98. • Servos P, Goodale MA: **Binocular vision and the on-line control of human prehension.** *Exp Brain Res* 1994, **98**:119–127.

This study involves a very interesting experiment using goggles with liquid-crystal shutters. This paper clearly shows that binocular vision is important for both planning and on-line control of visually guided reaching and grasping movements.

99. Roland PE, Skinhöj E, Lassen NA, Larsen N: **Different cortical areas in man in the organization of voluntary movements in extrapersonal space.** *J Neurophysiol* 1980, **43**:137–150.

100. Colebatch JG, Deiber MP, Passingham RE, Friston KJ, Franckowiak RSJ: **Regional cerebral blood flow during voluntary arm and hand movements in human subjects.** *J Neurophysiol* 1991, **65**:1392–1401.

101. Deiber M-P, Passingham RE, Colebatch JG, Friston KJ, Nixon PD, Franckowiak RSJ: **Cortical areas and the selection of movement: a study with positron emission tomography.** *Exp Brain Res* 1991, **84**:393–402.

102. Decety J, Kawashima R, Gulyás B, Roland PE: **Preparation for reaching: a PET study of the participating structures in the human.** *Neuroreport* 1992, **3**:761–764.

103. Grafton ST, Mazziotta JC, Woods RP, Phelps ME: **Human functional anatomy of visually guided finger movements.** *Brain* 1992, **115**:565–587.

104. • Jenkins IH, Brooks DJ, Nixon PD, Frackowiak RSJ, Passingham RE: **Motor sequence learning: a study with positron emission tomography.** *J Neurosci* 1994, **14**:3775–3790.

Cortical areas that have important contributions to the learning of sequence of keypresses were examined by PET. Activation of the parietal association cortex was found while performing a learned sequence, but was significantly increased during new learning.

105. • Grafton ST, Woods RP, Mazziotta JC: **Within-arm somatotopy in human motor areas determined by positron emission tomography imaging of cerebral blood flow.** *Exp Brain Res* 1993, **95**:172–176.

In this study, human subjects performed visuomotor tracking tasks with their fingers, wrist, elbow, shoulder and eyes. The authors found that there was an overlapping somatotopic distribution of responses in the motor cortex, supplementary motor cortex and the cingulate cortex.

106. •• Decety J, Perani D, Jeannerod M, Bettinardi V, Tadary B, Woods R, Mazziotla JC, Fazio F: **Mapping motor representations with positron emission tomography.** *Nature* 1994, **371**:600–602.

The authors used PET to study the brain activity of normal subjects during passive observation of the movements of a 'virtual' hand grasping the objects and while imagining the grasping of objects with their own hand. During movement observation, activation was mainly found in the prestriate cortex (area 19) and occipitotemporal junction (area 37). In contrast, during motor imagery, the inferior parietal lobule (area 40), as well as premotor (area 6) and prefrontal (area 46) areas were activated.

H Sakata and M Taira, Department of Physiology, Nihon University, School of Medicine, Oyaguchi Kamimachi 30-1, Itabashiku, Tokyo, 173 Japan.