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Neural coding of 3D features of objects for hand action in the parietal cortex of the monkey

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In our previous studies of hand manipulation task-related neurons, we found many neurons of the parietal association cortex which responded to the sight of three-dimensional (3D) objects. Most of the task-related neurons in the AIP area (the lateral bank of the anterior intraparietal sulcus) were visually responsive and half of them responded to objects for manipulation. Most of these neurons were selective for the 3D features of the objects. More recently, we have found binocular visual neurons in the lateral bank of the caudal intraparietal sulcus (c-IPS area) that preferentially respond to a luminous bar or plate at a particular orientation in space. We studied the responses of axis-orientation selective (AOS) neurons and surface-orientation selective (SOS) neurons in this area with stimuli presented on a 3D computer graphics display. The AOS neurons showed a stronger response to elongated stimuli and showed tuning to the orientation of the longitudinal axis. Many of them preferred a tilted stimulus in depth and appeared to be sensitive to orientation disparity and/or width disparity. The SOS neurons showed a stronger response to a flat than to an elongated stimulus and showed tuning to the 3D orientation of the surface. Their responses increased with the width or length of the stimulus. A considerable number of SOS neurons responded to a square in a random dot stereogram and were tuned to orientation in depth, suggesting their sensitivity to the gradient of disparity. We also found several SOS neurons that responded to a square with tilted or slanted contours, suggesting their sensitivity to orientation disparity and/or width disparity. Area c-IPS is likely to send visual signals of the 3D features of an object to area AIP for the visual guidance of hand actions.

Keywords: parietal cortex; 3D features; axis-orientation; selective (AOS) neuron; surface; orientation

1. INTRODUCTION

Binocular stereopsis is one of the principal characteristics of primates, and is essential for the visual guidance of skilled hand movements. It was Charles Wheatstone who invented the stereoscope and discovered the psychophysical mechanisms of stereopsis. He said in his paper in the *Philosophical Transactions* in 1838 'the mind perceives an object of three dimensions by means of the dissimilar pictures projected by it on the two retinae'. He demonstrated with his mirror stereoscope, that if the two perspective projections of the same solid object are presented simultaneously to each eye, the observer will perceive a figure in three dimensions. He stated that 'the determination of the points which appear single seems to depend on previous knowledge of the form we are regarding'.

This hypothesis was challenged by Bela Julesz (1971) with his random dot stereogram. He demonstrated beyond any doubt that the detection of binocular disparity happens at an early stage of visual information processing before the process of form perception. David Marr (1982) proposed in his comprehensive theory of vision that surface orientation, a necessary form of information the representation of 3D shape, can be computed from changes of binocular disparity. Figure 1 shows how a slanted surface produces a gradual change of disparity.

However, the disparity gradient is not the only cue for surface orientation in depth. There are several kinds of disparities on inclined or slanted surfaces other than horizontal positional disparity included in the random dot stereogram (for a review, see Howard & Rogers 1995). Among these, orientation disparities and width disparities are the most important. It is interesting that the original figures of line drawings for the stereoscope by Wheatstone (1838) contained these two disparities for inclination and slant. Figure 2 shows how an inclined line produces an orientation disparity and a slanted line produces width disparity.

Neurophysiological studies of the mechanisms of binocular stereopsis have been limited to the striate cortex (V1) (Barlow *et al.* 1967; Nikara *et al.* 1968; Poggio & Fischer 1977) and adjacent prestriate cortical areas, thick cytochrome oxidase stripes of V2 (Hubel & Livingstone 1987), V3 and V3A (Zeki 1978; Poggio *et al.* 1988). Neurons in these areas were sensitive to simple horizontal positional disparity. Therefore, their activity did not correspond directly to the perception of the 3D features of objects. Our recent studies of the manipulation-related neurons in the anterior part of the lateral bank of the intraparietal sulcus (IPS) (AIP area) of alert monkeys have demonstrated that many of them were visually sensitive to the shape, orientation or size of geometric objects for manipulation (Sakata *et al.* 1995; Murata *et al.* 1996).

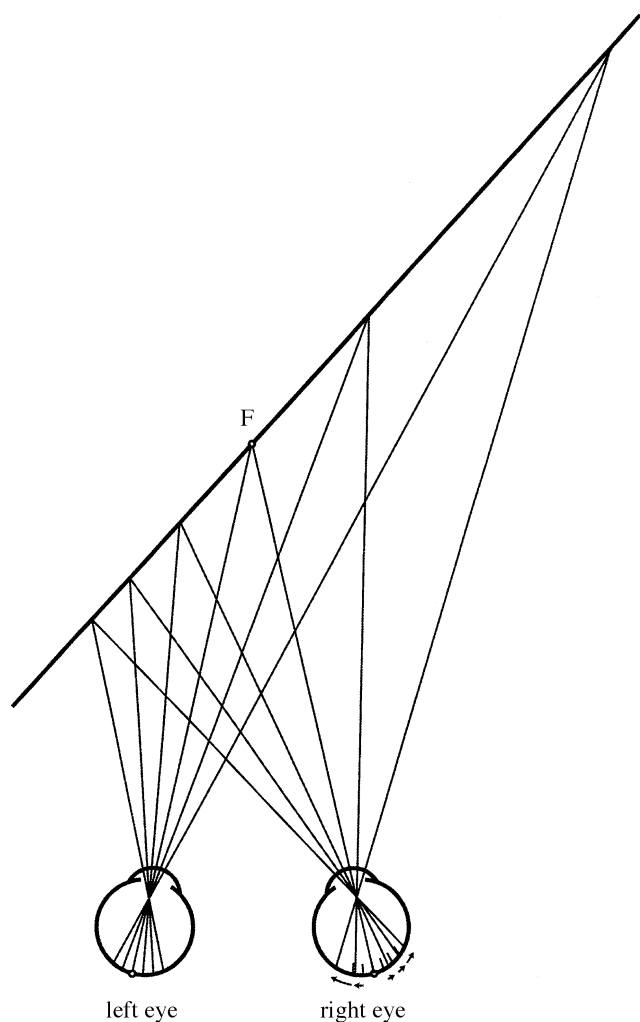


Figure 1. Diagram to show the gradient of disparity produced by a slanted surface. A total of six points on the surface are projected on the retina of the left eye at equal intervals and, in the right eye, the difference between the corresponding points indicated with tics and the projected points increases gradually from the fovea to the periphery as indicated by the small arrows.

These findings suggested the possibility that some visual neurons in the posterior parietal cortex may be specialized to code the 3D features of objects in a way that is useful for the visual guidance of hand action (Sakata *et al.* 1997a). In our search for such visual neurons in the parietal cortex we found binocular visual neurons in the lateral bank of the caudal intraparietal sulcus (c-IPS area) that preferentially respond to a bar, plate or solid object at a particular orientation in space. We studied the visual properties of c-IPS neurons by using a 3D computer graphics display (Kusunoki *et al.* 1996; Shikata *et al.* 1996; Tsutsui *et al.* 1997). The results suggest that the c-IPS area is a higher centre of stereopsis for the extraction of spatial features of objects from sets of binocular disparity signals. It may also incorporate monocular signals for shape discrimination.

2. VISUAL RESPONSES OF HAND MANIPULATION-RELATED NEURONS

The cortical neurons that are involved in visually guided hand movement were first recorded in the inferior

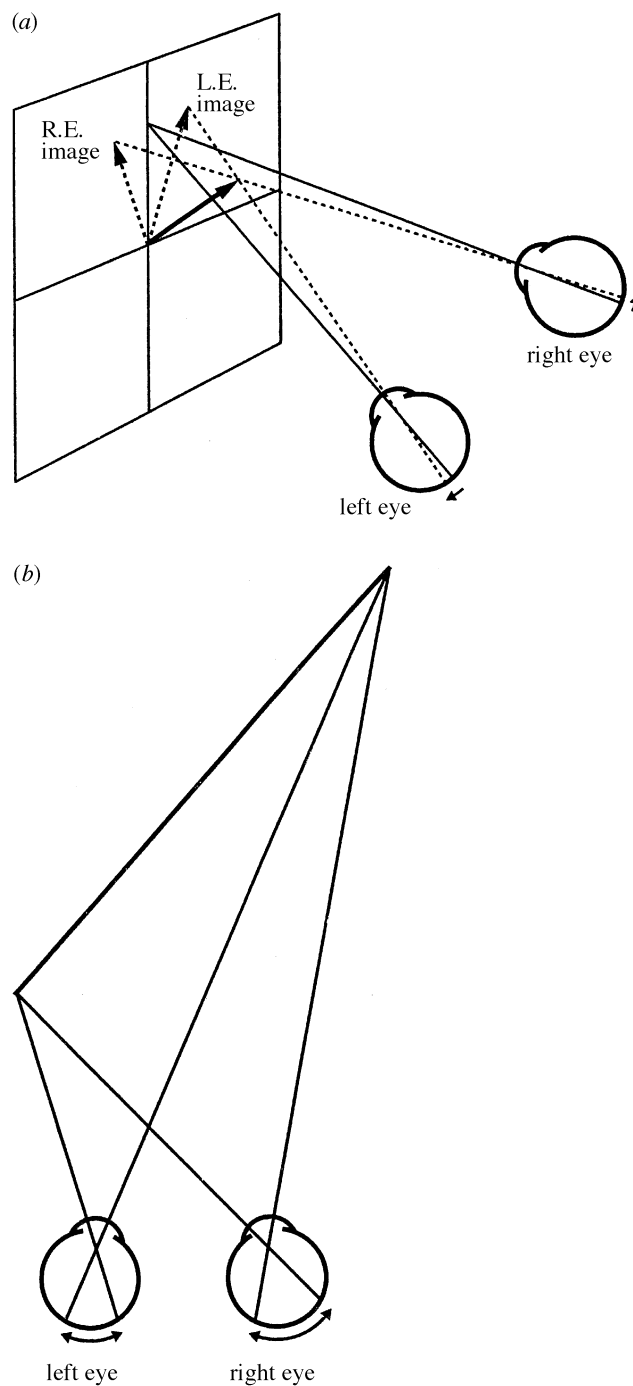


Figure 2. (a) Diagram to show orientation disparity owing to forward tilting. The image of the tilted arrow in the right eye is tilted on the screen toward the left (contralateral) side (right eye arrow with broken line) and that in the left eye is tilted toward the right side (left eye arrow with broken line). Crossed disparity of the tip of the arrow is indicated with a small arrow on the back of each eye. (b) Diagram to show the width disparity due to the slant of the line in the horizontal plane. The retinal image of the slanted line is longer in the right eye than in the left eye.

parietal lobe by Mountcastle *et al.* (1975) and Hyvärinen & Poranen (1974). They designated these neurons as 'hand manipulation' neurons. More recently, neurons that are involved in hand movement were found to be concentrated in the AIP area (Sakata *et al.* 1995). This area is strongly interconnected with area F5 of the inferior

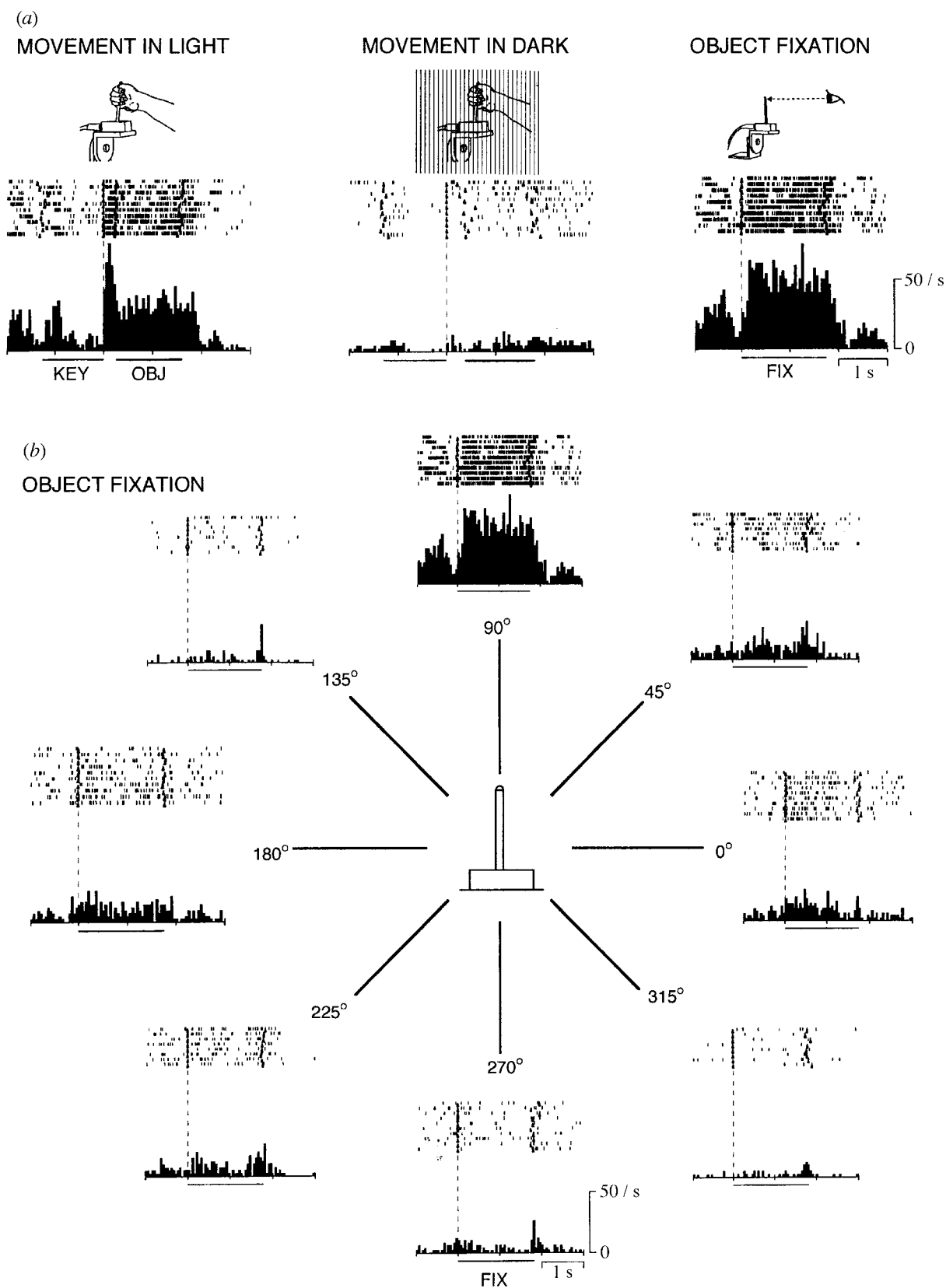


Figure 3. (a) Activity of an object-type visual-dominant neuron in area AIP, during manipulation of the pull lever in the light and in the dark as well as during object fixation, shown with rasters and histograms. The cell was not activated during manipulation in the dark. (b) Activity of the same neuron during fixation of the lever in various orientations, recorded at intervals of 45° in the frontal plane.

(ventral) premotor cortex (Matelli *et al.* 1986), in which Rizzolatti *et al.* (1988) recorded 'grasping-with-the-hand neurons'. We recorded the activity of neurons in this area from monkeys that had been trained to manipulate

various types of switch (Taira *et al.* 1990; Sakata *et al.* 1995). Many of these hand manipulation task-related neurons were highly selective and were preferentially activated during the manipulation of one of four routinely

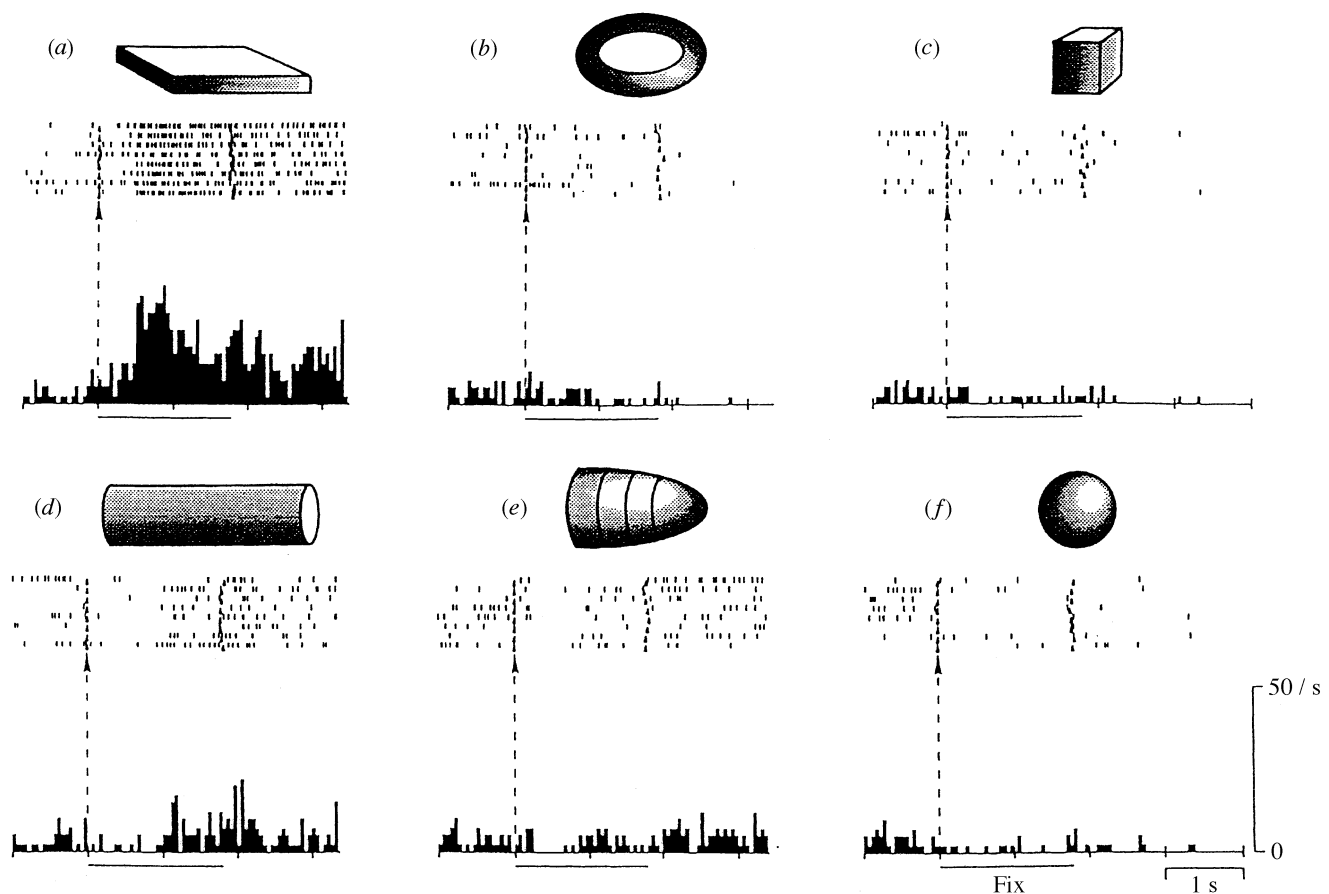


Figure 4. Activity profile of an object-type visual-dominant neuron during object fixation (*Fix*) in the light for six objects of simple geometric shape: (a) square plate, (b) ring, (c) cube, (d) cylinder, (e) cone and (f) sphere (from Murata *et al.* 1996).

used objects (push button, pull lever, pull knob and pull knob in groove).

The task-related neurons were classified into three groups according to the difference between the level of neuronal activity during manipulation of the objects in light and that during manipulation of objects in the dark: 'motor-dominant' neurons, 'visual-and-motor' neurons and 'visual-dominant' neurons. Many of the latter two types of visually responsive neurons were activated by the sight of objects during fixation without grasping (object type), although other neurons were not activated during object fixation (non-object type).

(a) *Orientation selectivity of visual-dominant neurons*

About one-quarter of the cells were found to be highly selective; the activity of these cells for a particular object was significantly stronger than that for any other objects. The activity profile of one highly selective 'visual-dominant' neuron is shown in figure 3. This cell was most strongly activated during manipulation of the pull lever in the light (figure 3*a*, left). However, no significant activation occurred during manipulation in the dark (figure 3*a*, centre). The cell was fully active during fixation of the lever in the light (figure 3*a*, right). The sustained activity during manipulation of the pull lever was smaller than that during object fixation, probably owing to the occlusion of the object by the grasping hand. Most of the cells that showed a stronger response to the pull lever

showed selectivity in the orientation of the axis of the lever. This cell showed a stronger response to the upright vertical lever and was sharply tuned to this orientation; the lever in any other orientation did not activate the cell (figure 3*b*). However, it was not clear in this series of experiments whether or not the visual-dominant neurons were discriminating the 3D shape of the manipulanda because these objects were selected primarily in terms of the pattern of hand movement.

(b) *Selectivity for the 3D shape of objects*

In more recent experiments on hand manipulation task-related neurons (Murata *et al.* 1996) we used six different objects of simple geometric shape: sphere, cone, cylinder, cube, ring and square plate. We used three sets of six shapes at different sizes: small, medium and large. These objects were connected to micro-switches and set in six sectors of a turntable which presented them in a random order one at a time. As the objects were painted white, they stood out against the black background. The animal was required to grasp and pull the object to turn the microswitch on or fixate on the spot reflected on a half mirror that was superimposed on the object. More than one-quarter of the hand manipulation task-related neurons (32 out of 112) were highly selective for one particular object. The activity profile of one highly selective object-type visual-dominant neuron during the object fixation task is shown in figure 4. This cell showed the strongest response to the

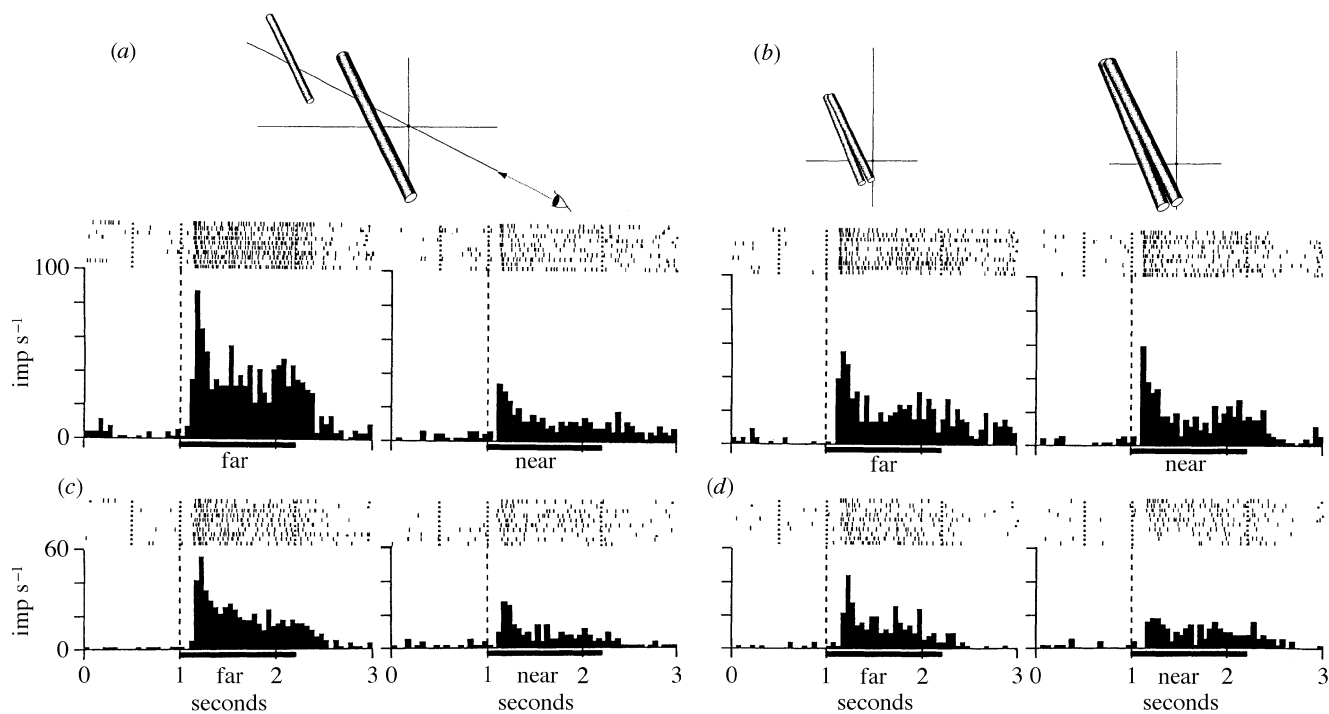


Figure 5. Comparison of the responses of an AOS neuron to binocular and monocular stimulation and the effect of removal of the polarized glasses. (a) Response to the best stimulus: a diagonal cylinder (20 cm \times 2 cm) tilted 22° backward and 22° leftward at the distance of +50 cm from the screen (150 cm from the eye) compared with the response to the same stimulus at a distance of 50 cm from the eye. (b) Response to the same set of stimuli without polarized glasses. (c, d) Responses to the monocular stimuli of the same parameters.

view of the square plate among the six objects. The square plate and circular ring were the most commonly preferred objects, and many of the cells that preferred these two objects showed selectivity to the orientation of the plate or ring. We also found moderately selective neurons that responded to two or more objects equally well (55 out of 112). Some of these moderately selective neurons showed preference for a certain category of geometric shapes such as round objects (sphere, cone and cylinder), angular objects (cube and square plate), or flat objects (plate and ring). By using a cluster analysis of the response profiles across the six objects, cone, sphere and cylinder were grouped in the same category, and plate, ring and cube were grouped in another category in which plate and ring were the closest. These results suggested that the visually responsive neurons in area AIP may represent spatial characteristics of objects for manipulation, and at least some of these neurons may be involved with recognition of the 3D shape of an object, categorized into a limited number of simple geometric shapes. However, it is not clear where and how the visual signals are processed in the cortical visual pathways to encode 3D shapes.

3. AXIS-ORIENTATION SELECTIVE NEURONS

Discrimination of axis-orientation in egocentric space or a viewer-centred coordinate system is important for the manipulation of objects to match the hand orientation with that of the object and may be dissociated from visual axis perception (Perenin & Vighetto 1988; Goodale *et al.* 1991; Milner *et al.* 1991). Indeed, we found that most of

the cells that preferred the pull lever were selective for the axis-orientation of the metal rod (see figure 3). During further investigation, we found a group of neurons in the lateral bank of the caudal part of the intraparietal sulcus (c-IPS area) that showed selectivity to the orientation of a luminous bar (Kusunoki *et al.* 1993; Sakata & Taira 1994). We recorded the axis orientation selective (AOS) neurons that preferred either vertical, horizontal or sagittal bars or bars tilted to the left or to the right in the frontal plane, tilted either forward or backward in the sagittal plane, and one that responded most strongly to a diagonal bar in between the two planes. It was clear that these neurons had orientation selectivity in 3D space in a viewer-centred coordinate system. The discharge rate of AOS neurons increased monotonically with increasing length of the stimulus. Most of these AOS neurons were binocular visual neurons that responded much less strongly under monocular viewing conditions.

Therefore, in more recent experiments (Kusunoki *et al.* 1996) we used a 3D computer graphics display to present stimuli with binocular disparity at various orientations, sizes and positions. A back-projection stereoscopic display with a screen size of 105 cm \times 150 cm was used. Polarizing filters were set in front of the projector and a pair of images with horizontal disparity were presented alternatively (refresh rate: 60 Hz each). The monkey, wearing polarized glasses, fixated on a small spot in the centre of the screen placed at a distance of 100 cm. Figure 5 shows an example of an AOS neuron that responded strongly to the diagonal cylinder on the stereoscopic display. An initial survey of orientation tuning for this

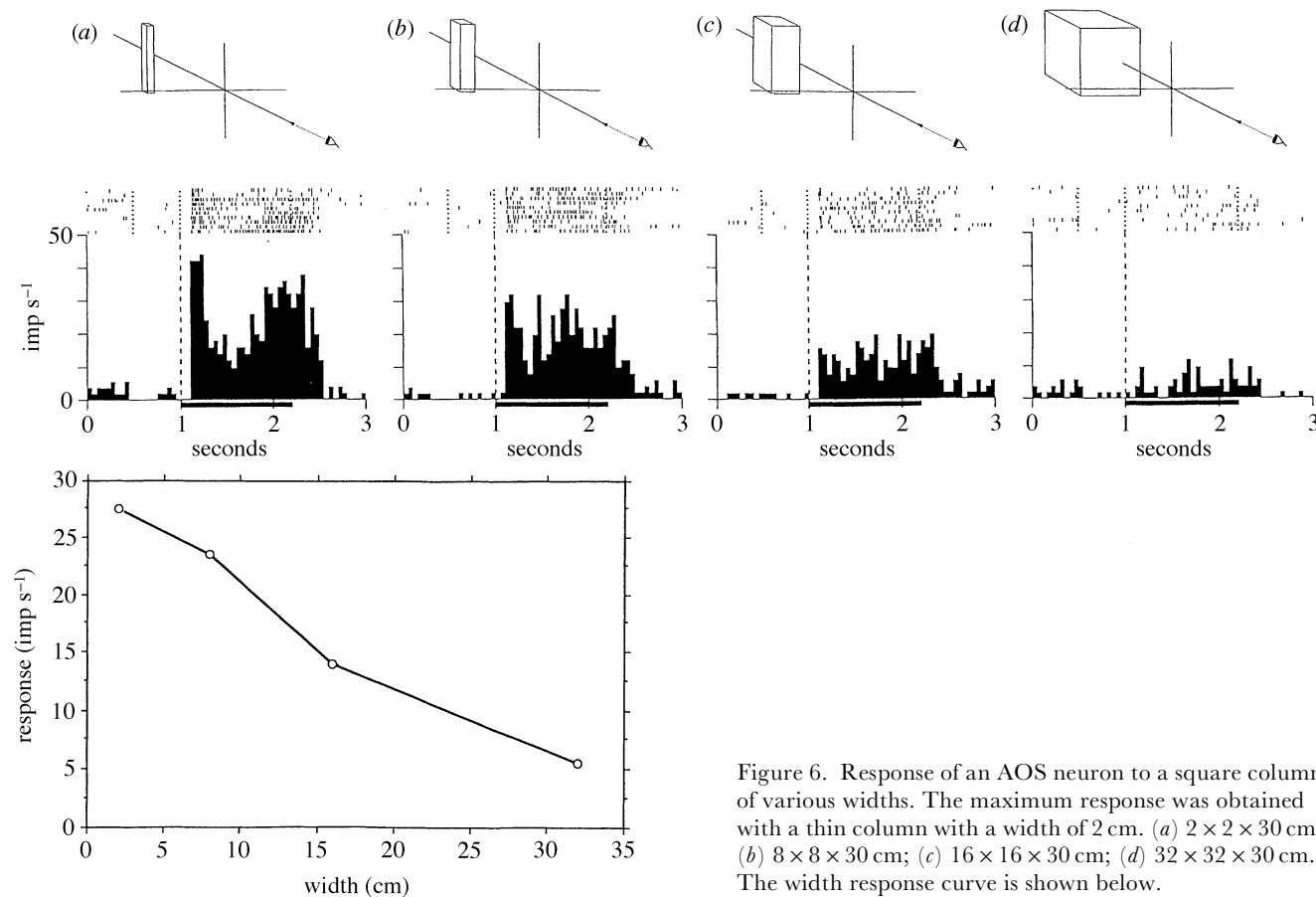


Figure 6. Response of an AOS neuron to a square column of various widths. The maximum response was obtained with a thin column with a width of 2 cm. (a) $2 \times 2 \times 30$ cm; (b) $8 \times 8 \times 30$ cm; (c) $16 \times 16 \times 30$ cm; (d) $32 \times 32 \times 30$ cm. The width response curve is shown below.

neuron showed that the preferred orientation was between vertical and 45° backward in the sagittal plane, and between vertical and 45° in the frontal plane. Thus, the best orientation as tilted 22° backward and 22° leftward, and a far stimulus (50 cm from the screen) was better than a near stimulus (figure 5a). When the polarized glasses were removed and double images were seen, the response to the best stimulus was reduced and the difference due to the distance (far compared with near) was lost (figure 5b). Response to the monocular stimulus either to the left or the right eye was smaller than that to the binocular stimulus (figure 5c).

We examined the effect of a change of thickness on the response of the same AOS neuron to a square column in vertical orientation. The response to the square column decreased as the thickness of the column increased and no response was obtained when the width was equal to the length (figure 6). Thus, the width response curve showed a monotonic decreasing function within the range of 2–32 cm (figure 6, lower graph). This is a general feature of AOS neurons, although the response reached a plateau with intermediate thickness of 10 cm in some AOS neurons. We also examined the effect of changing the length of the stimulus on the responses of AOS neurons. The discharge rate of the AOS neurons increased monotonically with increasing length of the stimulus. In some neurons the maximum response was obtained with a length as long as 70 cm or more on the screen at 57 cm from the eyes (subtending 50° or more).

These results suggest that AOS neurons represent the orientation of the longitudinal axes of objects in 3D

space. The most likely cue for orientation of a line in the sagittal plane is orientation disparity as initially demonstrated by Wheatstone (1838) (see figure 2a). Blakemore *et al.* (1972) reported that some neurons in the cat striate cortex showed a slight difference in preferred orientation between the two eyes. Hänný and co-workers (1980) also reported a few neurons in the monkey striate cortex that showed tuning to orientation disparity. In the present study, the AOS neurons that showed orientation tuning in the sagittal plane reduced their response drastically when the polarized glasses were removed or the stimulus was presented binocularly with zero disparity, suggesting their sensitivity to orientation disparity. The most likely cue for the slant of the axis in the horizontal plane is width disparity (Howard & Rogers 1995). Although we have not found, so far, any AOS neurons that were tuned to a slanted axis in the horizontal plane, a few neurons showed tuning to a diagonal axis, suggesting their sensitivity to width disparity as well as orientation disparity.

In human patients with parietal lobe lesions, a considerable shift of the vertical and horizontal axes toward the contralesional side was reported by Bender & Jung (1948). McFie and colleagues (1950) described a similar symptom in several patients with a right occipitoparietal lesion. Similar deficits in the perception of line orientation owing to a parietal lobe lesion were reported recently by von Cramon & Kerkhoff (1993). De Renzi and co-workers (1971) reported that patients with right parieto-occipital lesions showed significantly larger errors than the other brain-damaged groups in

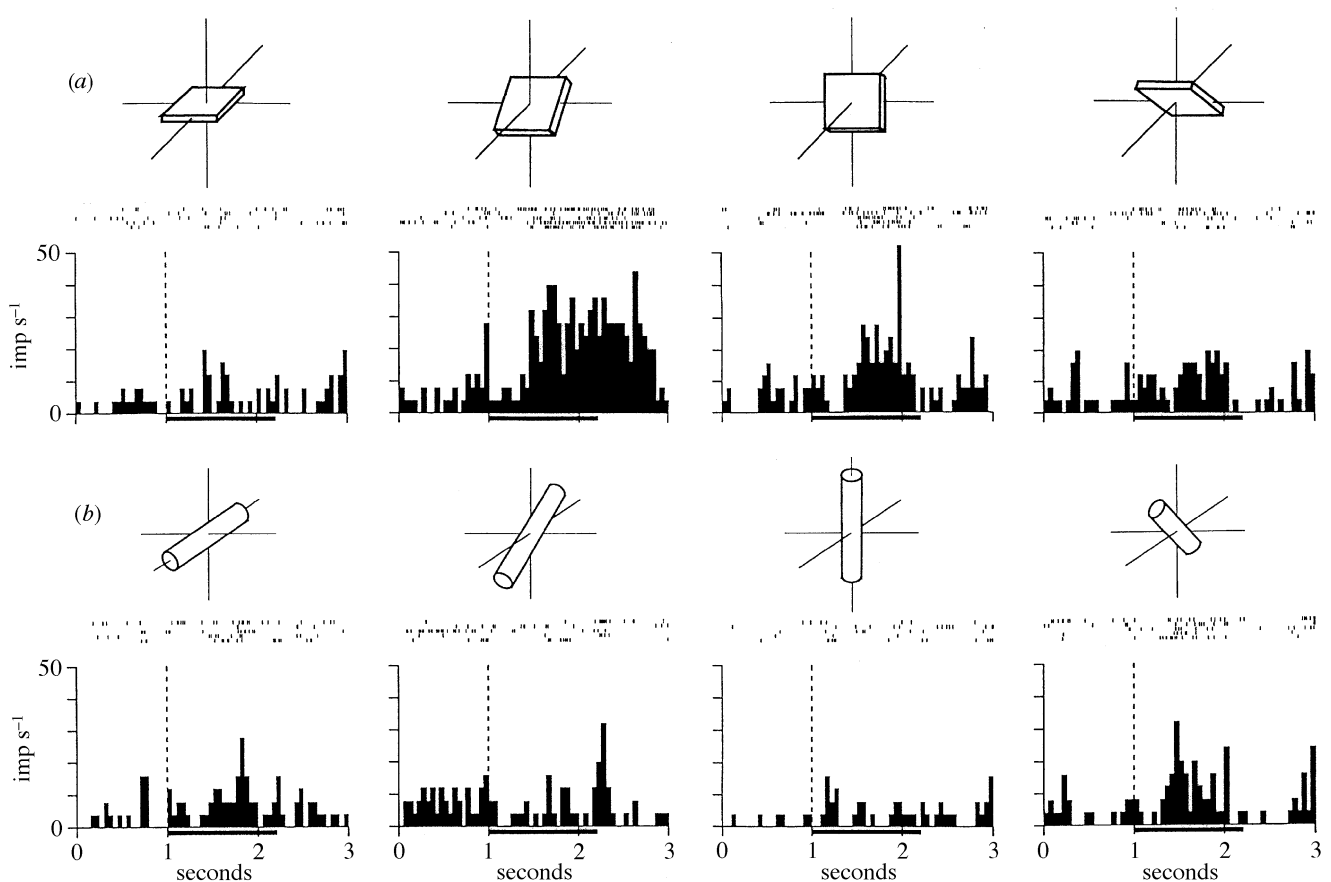


Figure 7. Responses of an SOS neuron that preferred a square plate ($15\text{ cm} \times 15\text{ cm} \times 2\text{ cm}$) tilted: (a) backward to a cylinder ($20\text{ cm} \times 4\text{ cm}$); (b) in the same orientation to the cylinder.

the task of placing of a rod, fixed on a support by a hinged joint, in the same orientation in space as a model. Therefore, the discrimination of axis orientation is one of the prominent functions of the parietal cortex in the domain of space perception.

4. SURFACE-ORIENTATION SELECTIVE NEURONS

According to Marr's theory of vision (Marr 1982), the main purpose of vision is object-centred representation of the 3D shape and spatial arrangement of an object. The main stepping stone toward this goal is representing the geometry of the visible surface. Therefore, if 3D shape is to be represented somewhere in the cerebral cortex, there should be an area in the visual cortical pathways that represents surface orientation and curvature.

Discrimination of viewer-centred surface orientation is also important on its own for manipulation of objects. We found that the hand manipulation-related neurons that responded to the view of a square plate showed selectivity to the orientation of the plane. This suggested that some of the parietal visual neurons can discriminate surface orientation. We found that some neurons in the c-IPS area, where we identified AOS neurons, responded preferentially to flat objects such as the square plate or circular disk. We used the 3D computer graphics display to present a solid plate or checkerboard at various orientations and distances and changed stimulus parameters

such as width and thickness. The following description is based on a study of 36 parietal visual neurons recorded in three hemispheres of two Japanese monkeys (*Macaca fuscata*; Shikata *et al.* 1996).

We first compared the responses of cells to a flat stimulus with responses to an elongated stimulus. A total of 17 cells that preferred the flat to the elongated stimulus (17 out of 32) showed selectivity to the surface orientation of the stimulus presented on the screen of the stereoscopic display. A total of 13 of these cells (13 out of 17) were defined as surface-orientation selective (SOS) neurons with a criterion of high orientation index (O.I. ≥ 2), with O.I. response to optimal surface–response to orthogonal surface. Figure 7 shows an example of an SOS neuron that responded preferentially to a square plate tilted 45° backward (figure 7a). No response was obtained when a cylinder was presented at the same orientation (figure 7b). Almost all SOS neurons responded more strongly to a binocular than to a monocular stimulus. The responses of all of the SOS neurons tested ($n=6$) changed with the depth on the stereoscopic display (we changed disparity while keeping the size of the stimulus on the screen constant). Half of these SOS neurons responded to near stimuli, and the other half responded to far stimuli. None of these neurons showed as sharp a tuning in depth as tuned excitatory cells, but their depth-tuning curves showed a plateau, similar to a near cell that responds over a range of crossed disparities or a far cell that responds over a range of uncrossed disparities as

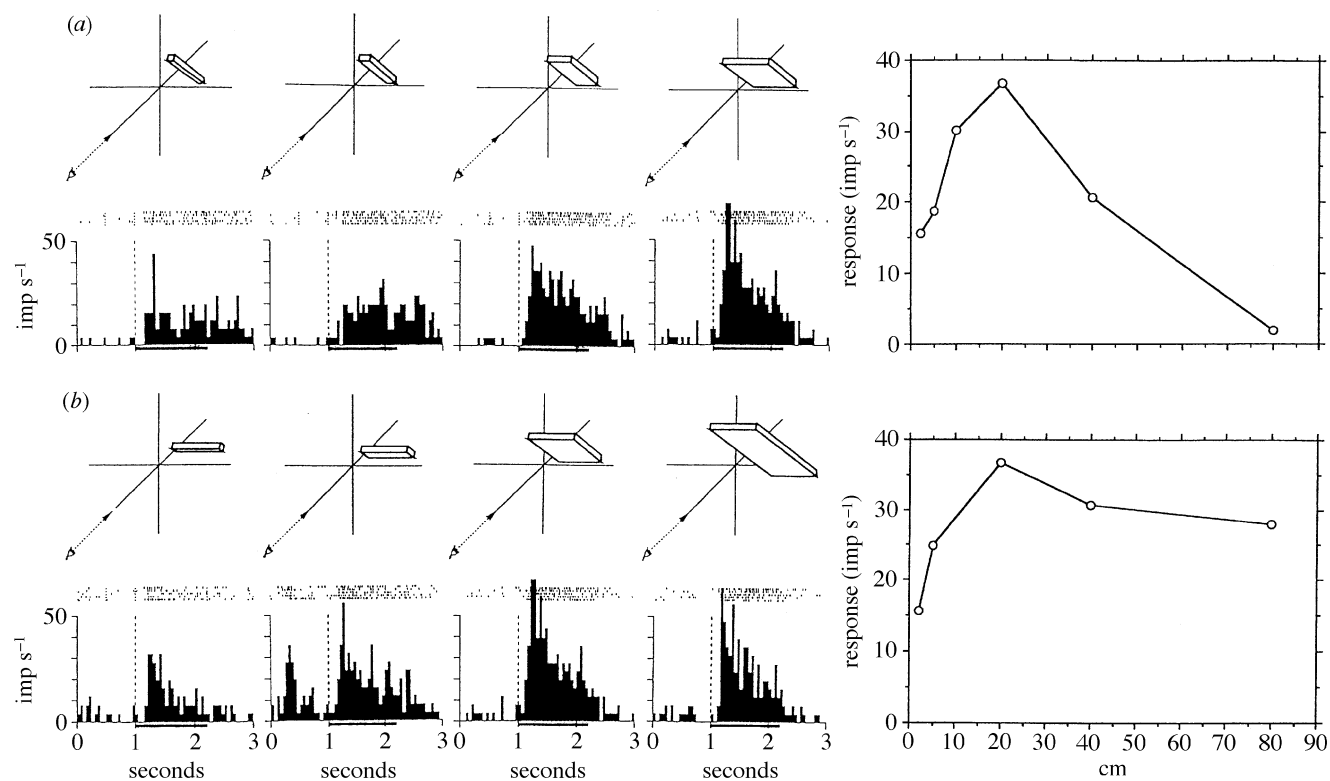


Figure 8. Responses of an SOS neuron to a plate of various widths and lengths. (a) Responses of the cell to a plate of various widths ranging from 2–20 cm and the width response curve up to 80 cm. (b) Responses of the cell to a plate of various lengths ranging from 2–40 cm and the length response curve up to 80 cm (from Shikata *et al.* 1996).

defined by Poggio & Fischer (1977), except that the range of disparity for the excitatory response was larger than that in the case of the disparity-selective neurons in VI and V3A (Poggio *et al.* 1988).

To verify that the SOS neurons responded to an extended surface rather than an edge or corner, we studied the effect of changing the width of the stimulus. In contrast to the AOS neurons, the magnitude of the response of SOS neurons to the stimulus decreased gradually as the width was reduced and the stimulus changed from a square to a narrow rectangular plate or bar as shown in figure 8, although the response reached a plateau or peak at some intermediate width. Most of the SOS neurons showed no change in response intensity with a change in stimulus shape (for example, disc compared with square plate) or even thickness, suggesting that they represented the orientation of the flat surface in space independently of shape. However, some of them preferred a thin to a thick plate, and a square plate to a disc, showing selectivity to both the shape and stimulus orientation.

More recently, we trained a monkey on a delayed match-to-sample (DMS) task discriminating surface orientation of the stereoscopic stimuli in a random dot stereogram (RDS) as well as in a solid figure stereogram (SFS) with binocular contour disparity, to discover whether SOS neurons respond to a square at various orientations embedded in the RDS (Tsutsui *et al.* 1997). We identified 27 SOS neurons in the c-IPS area and examined 18 of them for their response to RDS and SFS. All of these 18 cells showed tuning in surface orientation in the routine test of nine orientations; frontal, backward and

forward tilt (45°) leftward and rightward slant (45°), and four diagonal orientations of combined tilt and slant.

A total of 11 SOS neurons responded to RDS stimuli and showed orientation tuning. A total of five of these 11 cells showed orientation tuning even when the stimulus did not have any perspective cues at its edges, suggesting that the cells discriminated the surface orientation purely from disparity gradient as Marr (1982) predicted in his theory of vision. A total of nine out of 13 SOS neurons that responded to SFS with disparate contours showed orientation tuning even when the contours of the square did not have any perspective cues for orientation in depth, suggesting that the cells discriminated the surface orientation of the square using orientation disparity and/or width disparity.

There has not been much clinical evidence that the parietal cortex is involved in the perception of surface orientation, except for the confusion of planes in drawings by patients with right parieto-occipital lesions (Paterson & Zangwill 1944; McFie *et al.* 1950; Ettliger *et al.* 1957), for example, the frame of a bicycle was drawn in the frontal plane while the wheels were drawn in the sagittal plane. However, disturbances in the ability to draw 3D shapes such as houses (Piercy & de Ajuriaguerra 1960) or copy block designs (Critchley 1953) may be partly owing to a disturbance in the ability to perceive surface orientation. Recently, the performance of a visual agnosia patient with relatively intact parieto-frontal cortical function was studied in a task of matching the orientation of a plate held in the hand to that of a plate presented visually in front of the body (Dijkerman *et al.* 1996). The patient performed

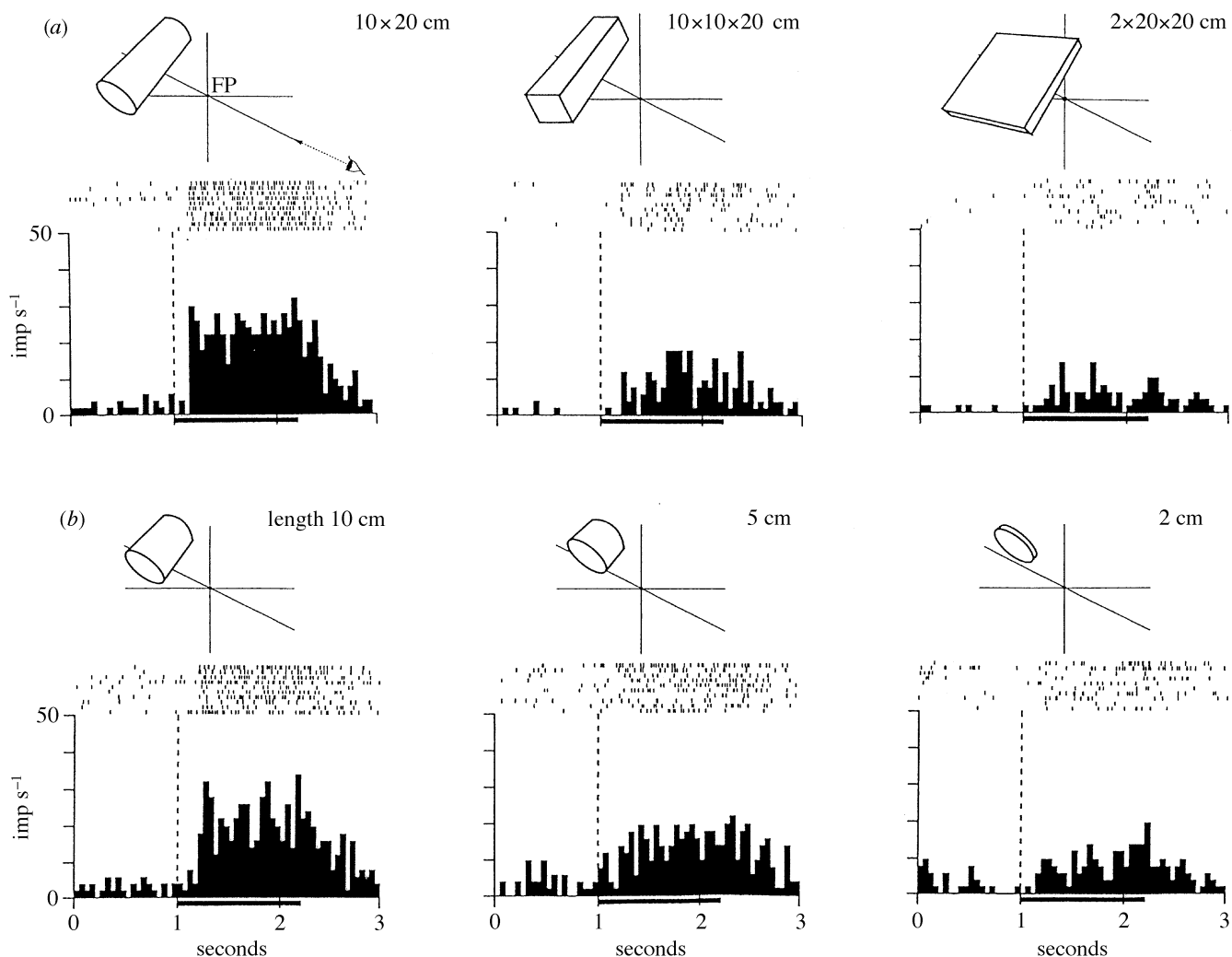


Figure 9. Responses of an AOS neuron that showed a stronger response to a cylinder of intermediate length and thickness. (a) Responses of the cell to a stimulus of different shapes in the same orientation, from the left, cylinder, square column and square plate. (b) Responses of the cell to a cylinder of various lengths ranging from 2–10 cm. (From Sakata *et al.* 1997b.)

very poorly in this task under monocular viewing conditions, suggesting that the parietal cortex depends on binocular input for the discrimination of surface orientation when information from the ventral visual pathways is unavailable.

5. SELECTIVITY IN 3D SHAPE

During the study of AOS neurons and SOS neurons, we found cells in the same area that preferred a solid stimulus to a flat or thin stimulus. Figure 9 shows the responses of one such cell that was classified as an AOS neuron. When we examined the effect of changes in thickness, we found that the cell responded most strongly to a cylinder of intermediate thickness (10 cm diameter). The length–response curve peaked at an intermediate length (20 cm), and a dramatic change was observed when we changed the shape of the stimulus (figure 9a). The cell responded most strongly to a cylinder (10 cm × 20 cm) tilted backward and to the right, but a square column of the same size and orientation elicited only a weak response, and a square plate (20 cm × 20 cm) in the same orientation was even

less effective than the square column. The cell was strongly binocular, showing almost no response to monocular stimulation, and was activated only by stimuli nearer than the fixation point. Thus, the cell was likely to discriminate a cylinder from a square column on the basis of surface curvature. This supports the hypothesis that there is a class of binocular stereoscopic neurons in the lateral bank of the caudal IPS that discriminates the 3D shape of objects using stereopsis.

There is no direct clinical neuropsychological evidence that the parietal cortex is involved in the perception of 3D shape. However, if one examines the drawings by a patient with a right parietal lobe lesion, disturbances in the ability to draw 3D objects such as a cube or a house may be seen clearly (for example, see Hécaen *et al.* 1956). The results of a number of studies on constructional apraxia owing to parieto-occipital lesion suggest that the right hemisphere supplies a perceptual component and the left hemisphere an executive component to visuoconstructional tasks (Warrington 1969). Therefore, the symptom of constructional apraxia owing to parietal lesion may be indirect

evidence that the parietal cortex is involved in the perception of 3D shape.

6. DISCUSSION

One of the most surprising findings from our study of hand manipulation task-related neurons in area AIP was that a number of task-related neurons showed selectivity for 3D shape, as visual form perception has previously been attributed to the ventral visual pathway and the inferotemporal cortex according to the concept of two cortical visual systems (Ungerleider & Mishkin 1982). However, our finding fits with the idea that the visual projection system to the parietal cortex provides action-relevant information about the structure and orientation of objects (Goodale & Milner 1992). Information about 3D shape is necessary to guide preshaping of the hand that is disturbed by posterior parietal lesions (Jeannerod *et al.* 1994). To manipulate objects, it is necessary to construct their 3D representations in viewer-centred coordinates (Sutherland 1979), and binocular stereopsis is essential for that purpose. The neurons of area c-IPS that were sensitive to binocular disparity and selective for the 3D orientation of the longitudinal axis or surface together with the neurons that were selective for 3D shape are likely to meet these requirements.

The most interesting finding from our studies of the functional properties of c-IPS neurons by using a 3D computer graphics display was that many of the SOS neurons responded to squares embedded in random dot stereograms, and showed orientation tuning in depth. This provided us with clear evidence that at least some of the SOS neurons discriminated surface orientation on the basis of the change of binocular disparity, as postulated by David Marr (1982) in his theory of vision. As shown in figure 1 a slanted surface produces a gradual increase of disparity from the fovea to the periphery along the horizontal meridian, and an inclined surface produces a similar gradient of binocular disparity along the vertical meridian. If one postulates that the SOS neurons integrate the signals of a set of disparity-sensitive neurons with different optimal disparities, neural computation of the surface orientation in depth is feasible. Equally important was the finding that some of the SOS neurons responded to squares with contours with orientation disparity and/or width disparity, without any monocular cues for depth such as linear perspective, texture gradient or shading. These disparities of contours are even more important for the discrimination of axis orientation in depth. As shown in figure 2, tilted and slanted lines in the sagittal and horizontal planes produce orientation disparity and width disparity, respectively. If one postulates that AOS neurons combine the signals from a pair of monocular neurons with slightly different preferred orientations or preferred lengths, the cell will be tuned to axis orientation in depth. The fact that AOS neurons and SOS neurons coexist in the c-IPS area suggests that the main processing site of these disparities is not at the level of the striate and prestriate cortex, but at the level of the association cortex. It also implies that integration of orientation and width disparity may not happen at an early stage of vision, as postulated by Julesz (1971), but may happen at a later stage after some

integration of line orientation. Thus, the present results have led us to a reappraisal of Wheatstone's original idea that the combination of slightly different perspective images from the two eyes results in the perception of the 3D features of objects.

The present results also provide some evidence that c-IPS neurons may be concerned with the discrimination of 3D shape on the basis of binocular disparity. However, further investigation is necessary to elucidate the mechanism of discrimination of surface curvature and surface boundary to get solid evidence that the representation of 3D shape is constructed in this area. It is also important to investigate how monocular cues of depth are integrated with binocular disparity cues in the parietal cortex, as there are reciprocal connections between the posterolateral bank of the IPS and inferotemporal cortex that may convey monocular cues for shape (Webster *et al.* 1994). It may be concluded from the present investigation that area c-IPS adjacent to area V3A is a higher centre of stereopsis that integrates various binocular disparity signals to represent neural codes of 3D features of objects and sends them to area AIP for the visual guidance of hand movement.

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