Exp Brain Res (1999) 128:160–169

REVIEW ARTICLE

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Neural representation of three-dimensional features of manipulation objects with stereopsis

Received: 21 September 1998 / Accepted: 23 March 1999

Abstract In the first part of this article, we review our neurophysiological studies of the hand-manipulation-related neurons in the anterior part of the lateral bank of the intraparietal sulcus (area AIP) . We describe the properties of visually responsive neurons in area AIP. Object-type visual-dominant neurons responded to the sight of objects and showed selectivity not only for simple geometrical shapes, but also for complex objects such as a knob-in-groove and a plate-in-groove. Some of the object-type visual-dominant neurons showed selectivity for the orientation of the longitudinal axis or the plane (surface) of a plate or a ring. In the second part of this article, we review our study of binocular visual neurons in the caudal part of the lateral bank of the intraparietal sulcus (c-IPS area), in particular, of axis-orientation-selective (AOS) neurons and surface-orientation-selective (SOS) neurons. AOS neurons preferred long and thin stimuli, were sensitive to binocular disparity, and tuned to the axis orientation in three-dimensional (3D) space. SOS neurons preferred broad and flat stimuli and were tuned to the surface orientation in depth. Some SOS neurons responded to a square in a random dot stereogram (RDS) with orientation tuning, suggesting that they encode surface orientation from a disparity gradient. Others responded to solid figure stereograms with orientation disparity and/or width disparity. It was concluded that the c-IPS area is a higher center for stereopsis, which integrates various binocular disparity signals received from the V3 complex and other prestriate areas to represent the neural code for 3D features. It may send projections to the AIP area and contribute to visual adjustment of the shape of the handgrip and/or hand orientation for manipulation and grasping. Neurons of the AIP area may also receive monocular cues of depth from the ventral visual pathway to discriminate the 3D shape of the object of manipulation.

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Key words Hand-manipulation-related neurons · Anterior intraparietal (AIP) area · Caudal intraparietal (c-IPS) area · Axis-orientation-selective (AOS) neurons · Surface-orientation-selective (SOS) neurons · Binocular disparity

Introduction

The three-dimensional (3D) representations of objects in the brain are considered to serve two functions: to enable recognition and guide manipulation. In order to manipulate objects and avoid bumping into them, organisms must be able to perceive and represent the disposition of the object surfaces in space (Sutherland 1979). Although Marr (1982) emphasized the importance of building 3D representations in an object-centered coordinate system for recognition, it is necessary to build a description of objects in terms of viewer-centered coordinates to allow reaching for and grasping an object, and real depth can be perceived only with binocular stereopsis.

Our previous studies on hand-manipulation-related neurons in the anterior part of the lateral bank of the intraparietal sulcus, namely the anterior intraparietal (AIP) area, in alert monkeys demonstrated that many of them were visually sensitive to the shape, orientation, and size of the object of manipulation. However, the source of information for the visual responses of these neurons was largely unknown. Recently, we identified binocular visual neurons in the lateral bank of the caudal intraparietal sulcus (c–IPS area) that preferentially responded to a bar, plate, or solid object in a particular orientation in space. This suggested the possibility that the neurons in the c-IPS area may be sensitive to binocular disparity and represent the 3D features of objects in a way that is useful for the control of hand action.

We studied the visual properties of c-IPS neurons, first using a luminous bar and plate (Kusunoki et al. 1993; Sakata and Taira 1994) as stimuli and, then, using 3D computer graphics with a stereoscopic display (Kusunoki et al. 1996; Shikata et al. 1996; Sakata et al.

1997). Two classes of neurons were identified: (1) axis-orientation-selective (AOS) neurons, and (2) surface-orientation-selective (SOS) neurons. Most AOS neurons preferentially responded to long and thin stimuli, such as a cylinder or square column, and showed tuning to the 3D orientation of the longitudinal axis (Kusunoki et al. 1996). In contrast, most SOS neurons preferred flat and broad objects and showed tuning to the surface orientation in depth (Shikata et al. 1996).

In this article, we first describe some of the characteristics of the visual responses of hand-manipulation-related neurons in AIP area. We then describe the functional properties of AOS and SOS neurons in the c-IPS area and discuss the most crucial cues required by these neurons for discriminating the orientation of the visual stimulus in depth. Finally, we will discuss how these two areas are interrelated in providing visual guidance for hand movement.

Visual responses of hand-manipulation-related neurons in the AIP area

In our previous studies of hand-manipulation-related neurons (Sakata et al. 1995), we found that these neurons were localized in the AIP area that is closely connected with the inferior premotor cortex (Matelli et al. 1986). They were classified into three groups according to the differences in their level of activity during the manipulation of objects in the light and in the dark, as “motor-dominant” neurons, “visual-motor” neurons, and “visual-dominant” neurons (Taira et al. 1990). Motor-dominant neurons likely receive signals from area F5 of the ventral premotor areas, in which Rizzolatti et al. (1988) recorded neurons related to the grasping movements of the hand. Neurons belonging to the other two types of visually responsive neurons were either activated by the sight of objects during fixation before grasping (object-type), or not activated during object fixation (non-object-type) (Sakata et al. 1995). In these studies, we used four different types of objects, which required different patterns of hand movements, namely, push button, pull-lever, pull-knob, and pull-knob-in-groove. In a more recent study, we used six simple geometrical solids (sphere, cube, cylinder, cone, ring, and square plate) of three different sizes together with a small plate-in-groove (Murata et al. 1996). Approximately 40% of the object-type visually responsive neurons in the AIP area were highly selective, preferring one of the six geometrical solids (Murata et al., unpublished observation). In our most recent experiments, we used both of the aforementioned sets of objects as targets for grasping, together with a cylinder and square column in various orientations (Miyashita et al. 1998). In this review, we take examples of visually responsive hand-manipulation-related neurons (n=56) from this most recent study.

Selectivity for complex objects

About one-third of the object-type hand-manipulation-related neurons were classified as being highly selective for the shape of objects, since the activity of neurons during fixation for one object was significantly higher than for other objects. We found that highly selective object-type visual-dominant neurons may exhibit preference not only for a simple geometrical solid, but even for a complex object.

Figure 1A is an example of neurons that highly selectively responded to the knob-in-groove. The cell was fully activated during manipulation of the knob-in-groove in the light with a hook grip of the index finger (Fig. 1Aa). The same cell was also strongly activated during the fixation on the knob-in-groove in the light (Fig. 1Ab). None of the six geometrical solids, nor the square column in the same orientation as the groove (Fig. 1Ad), induced activation of the cell. It should be noted that the cell was not activated during manipulation of the small plate-in-groove (Fig. 1Ac), although it is similar to the knob-in-groove, due to a small graspable part being buried in the vertical groove.

Figure 1B shows the response of another object-type visual-dominant neuron that preferentially responded to the plate-in-groove. The cell was fully activated during grasping of the plate-in-groove in the light with tip opposition between the index finger and the thumb (Fig. 1Ba). It was also activated during fixation on the same object (Fig. 1Bb). In contrast to the cell shown in Fig. 1A, it was neither activated during fixation nor during manipulation of the knob-in-groove (Fig. 1Bc). None of the other objects, including the six geometrical solids, the vertical cylinder, and the square column (Fig. 1Bd), elicited significant activation of the cell. These two examples illustrate that the object-type visual-dominant neurons in area AIP discriminate not only between simple geometrical shapes, but also between complex shapes composed of two or more components. They may even be sensitive to differences in fine detail when these are critical for the selection of a different pattern of grip.

Selectivity for the orientation of objects

In earlier studies, we examined the effect of change in the orientation of a pull-lever (thin metal cylinder), plate, and ring as well as that of a knob-in-groove. Many of the visually responsive cells that preferred the pull-lever showed orientation tuning to the longitudinal axis in the frontoparallel plane (Taira et al. 1990). Most of the cells that preferentially responded to the square plate or ring also showed orientation tuning when the orientation of the plane was changed around the sagittal axis. We examined the orientation tuning of two cells for the plate and ring and showed similar tuning for both objects. In our most recent study, we changed the orientation of the cylinder and the square column not only in the frontal plane, but also in the sagittal and horizontal planes.

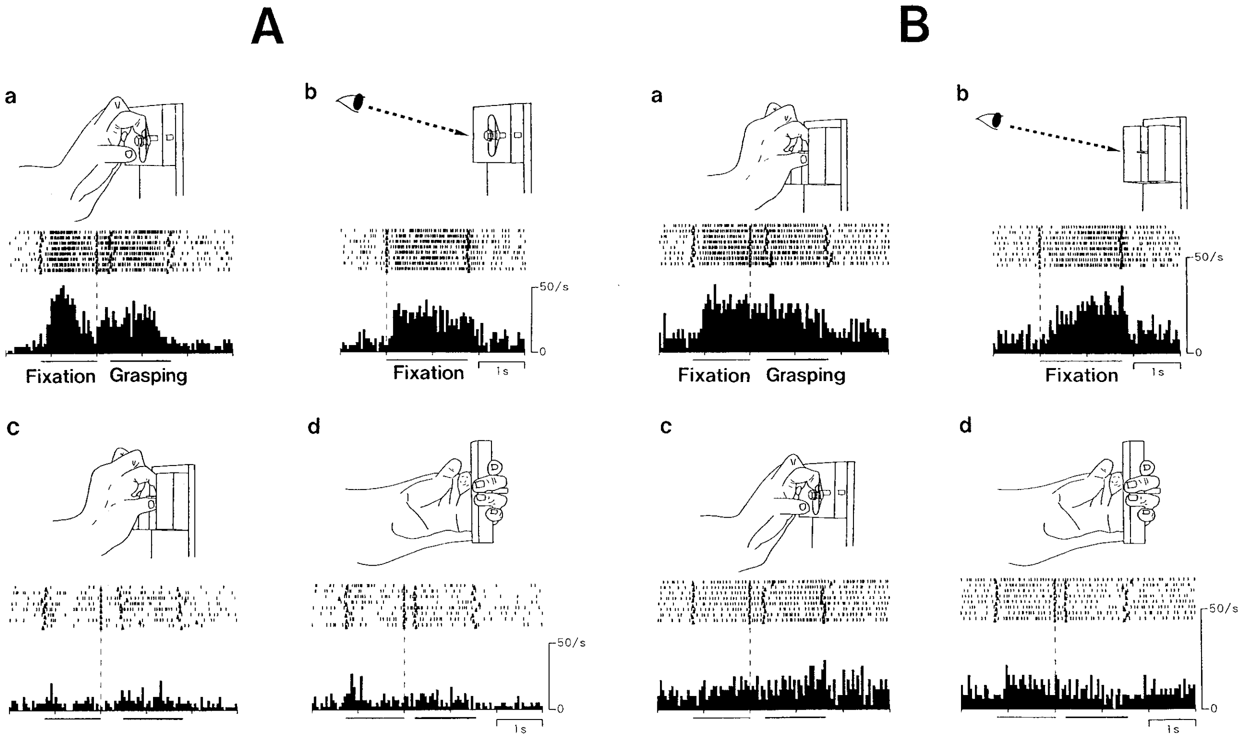

Fig. 1A, B Two examples of object-type visual-dominant neurons in the anterior part of the lateral bank of the intraparietal sulcus (area AIP). **A** A cell that preferred knob-in-groove during the manipulation and fixation tasks. **Aa** The cell was activated during manipulation of a knob-in-groove in the light. **Ab** The cell was fully activated during fixation on a knob-in-groove in the light **Ac, Ad** The cell was neither activated by the plate-in-groove, nor by the vertical square column. **B** An object-type visual-dominant neuron that preferred the small plate-in-groove. **Ba** The cell was maximally activated during manipulation of the plate-in-groove. **Bb** The cell was maximally activated during fixation on the plate-in-groove. No significant response was observed either to a knob-in-groove (**Bc**) or to a vertical square column (**Bd**). Activity of the neuron is shown by the impulse rasters and peristimulus histograms synchronized at the time of key release in the manipulation task and at the time of key-down in the fixation task. (Modified from Miyashita et al. 1998)

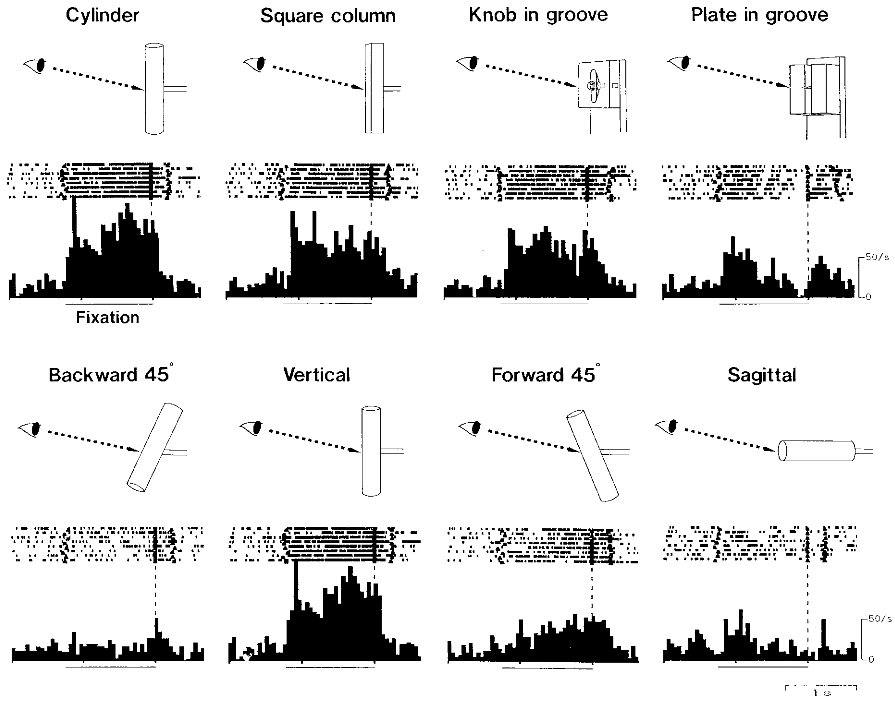

Fig. 2 An example of an object-type visual-dominant neuron that showed tuning for the axis orientation independent of the shape. *Top row* Strong response to a vertical cylinder, square column, and vertical knob-in-groove during fixation in light. Note the much smaller response to the vertical plate-in-groove in which the orientation of the small plate was orthogonal to that of the groove. *Bottom row* Tuning of the cell's response for the axis orientation in the sagittal plane. (Taken with permission from Miyashita et al. 1998)

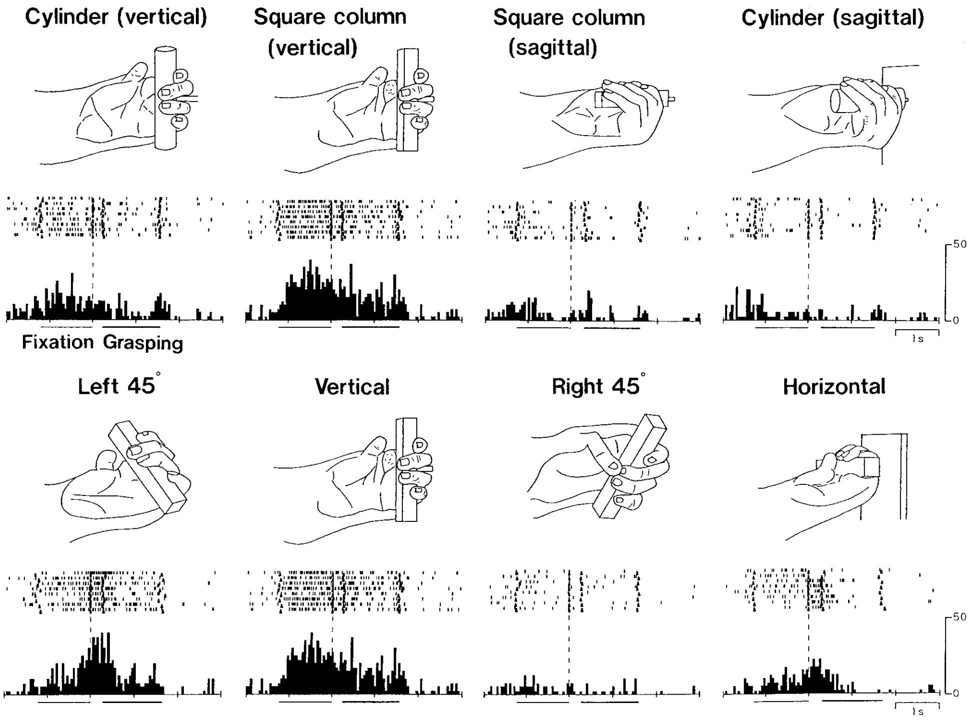

Fig. 3 An example of object-type visual-dominant neurons with combined selectivity for the shape and axis-orientation. *Top row* The cell was activated by a vertical square column, but not by a vertical cylinder. It was not activated by either a sagittal square column or a sagittal cylinder. *Bottom row* Tuning for the axis-orientation of the square column in the frontal plane. (Taken with permission from Miyashita et al. 1998)

Figure 2 shows an example of an object-type visual-dominant neuron that showed the same orientation tuning for several different shapes of objects. It responded vigorously during fixation on the vertical cylinder and square column as well as on the vertical knob-in-groove, whereas the response was much weaker during fixation on a small plate-in-groove (top row, right). In the latter object, the horizontal small plate appeared to have had some inhibitory effect because its orientation was orthogonal to the preferred axis-orientation of the cell. The orientation tuning of the cell for the sagittal plane was quite sharp, since almost no response was obtained in orientations other than the vertical, except for a small response to the cylinder tilted 45° forward (Fig. 2, bottom row).

Several neurons were selective not only for axis orientation, but also for the shape of the object. Figure 3 is an example of an object-type visual-dominant neuron that preferred a vertical square column. The cell was activated when the animal fixated on the vertical square column and continued to discharge (although the discharge rate decreased) during the manipulation period. However, no significant activation was obtained during fixation on or manipulation of a cylinder of the same size and orientation (upper left). Furthermore, activation of the cell was not elicited by fixation on or manipulation of either a sagittal square column or a sagittal cylinder (Fig. 3 upper right). The axis-orientation-tuning of the cell in the frontal plane is shown in the bottom row of Fig. 3. We found three neurons that preferred a square column to a cylinder and were selective for the orientation. These examples suggest that the axis orientation and shape are often represented as a combined 3D feature in the AIP area.

Stereoscopic neurons in the caudal IPS area

Axis-orientation-selective neurons

During further investigation, we found a group of visual neurons in the lateral bank of the caudal part of the intraparietal sulcus (c-IPS area) that showed selectivity for the orientation of a luminous bar (Kusunoki et al. 1993; Sakata and Taira 1994). We recorded the activity of axis-orientation-selective (AOS) neurons during the task of fixation on a spot from a light-emitting diode (LED) placed at a distance of 57 cm, using an acrylic bar illuminated with an LED at each end from inside as a stimulus. We changed the orientation of the bar in the frontal, sagittal, and horizontal planes and examined the orientation tuning of the neurons in 3D space. Figure 4 shows an example of AOS neurons that preferentially responded to a bar tilted 45° backward (Ohtsuka et al. 1995); no response was obtained when the bar was tilted 45° forward (Fig. 4A). When the right eye or left eye was closed and monocular viewing condition was created, no response was obtained (Fig. 4B, C). We recorded 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 between the two planes. It was clear that these neurons exhibited orientation selectivity in 3D space in a viewer-centered 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, which responded much less strongly or

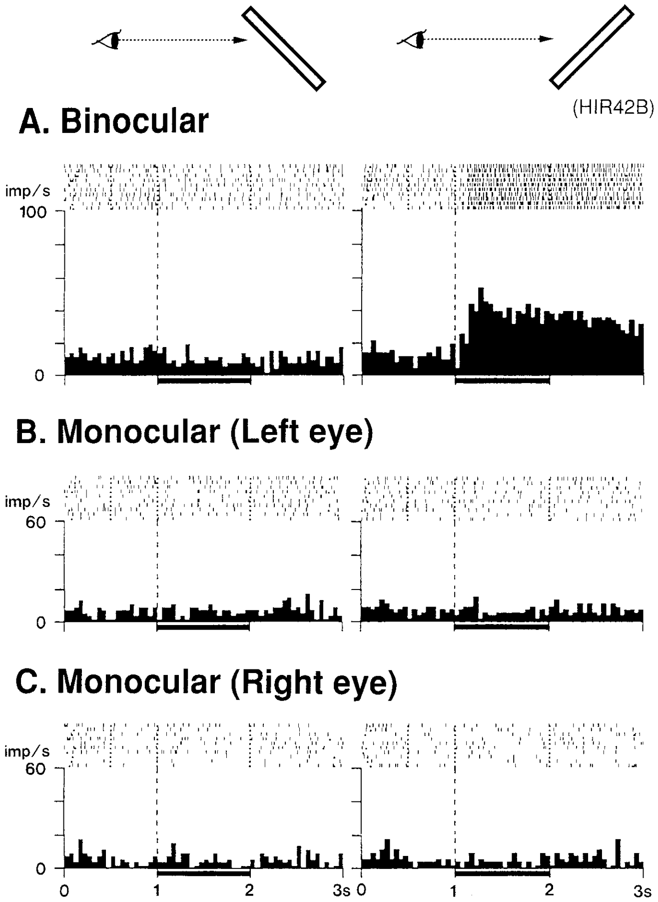

Fig. 4A–C Response of an axis-orientation-selective (AOS) neuron in the caudal part of the lateral bank of the intraparietal sulcus (c-IPS area) to a luminous bar tilted 45° forward (*left*) or 45° backward (*right*) in the sagittal plane. **A** Response of the cell under binocular viewing conditions. No response to a bar tilted forward (*left*), and a sustained response to a bar tilted backward. **B, C** Activity of the cell during stimulation under a monocular viewing condition, no response with either the left or the right eye. (Modified from Ohtsuka et al. 1995)

not at all under monocular viewing conditions, as shown in Fig. 4.

Therefore, in our more recent experiments (Kusunoki et al. 1996; Sakata et al. 1998), we used a 3D computer graphics display to present stimuli with binocular disparity in various orientations, sizes and, positions. A back-projection stereoscopic display with a screen size of 105×150 cm was used. Polarizing filters were set in front of the projector and a pair of images with binocular disparity were alternately presented (refresh rate: 60 Hz each). A monkey, wearing polarized glasses, fixated on a small spot at the center of the screen placed at a distance of 100 cm. Figure 5 shows an example of an AOS neuron that strongly responded to a diagonal cylinder in the steroscopic display. An initial survey of the orientation tuning of this neuron showed that the preferred orientation was between vertical and 45° backward in the sagittal plane (Fig. 5A), and between vertical and 45° leftward in the frontal plane (Fig. 5B). Thus, the most preferred orientation was a 22° backward and 22° leftward tilt, and a far stimulus (50 cm from the screen) was better than a near stimulus (Fig. 5C). When the polarized glasses were removed and double images were seen, the strength of response to the most preferred stimulus was reduced and the difference observed due to the distance (far vs. near) was lost (Fig. 5D). The response under monocular viewing conditions with either the right or left eye closed was smaller than that under binocular viewing conditions.

We examined the effect of change of thickness of the displayed elongated object upon the response of the same AOS neuron (Sakata et al. 1998). The response to the square column decreased as the thickness of the column increased, and the width response curve showed a monotonic decrease. This is a general feature of AOS neurons, although the response reached a plateau at an intermediate thickness in a few AOS neurons. We also examined the effect of change in the length of the stimulus on the screen upon the responses of AOS neurons (Sakata et al. 1998). The discharge rate of the AOS neurons increased monotonically with increasing length of the stimulus.

These results suggest that AOS neurons represent the orientation of the longitudinal axes of elongated objects in 3D space. The most likely cue for the orientation of a line in the sagittal plane is orientation disparity, as initially demonstrated by Wheatstone (1838). Blakemore et al. (1972) reported that some neurons in the cat striate cortex showed a slight difference in the preferred orientation between the two eyes. Hänny et al. (1980) also reported a few neurons in the monkey striate cortex that showed tuning for orientation disparity. In the present study, the response of AOS neurons that showed orientation tuning in the sagittal plane reduced dramatically when the polarized glasses were removed or when the stimulus was presented binocularly with zero disparity, suggesting their sensitivity to binocular disparity. However, further studies are necessary to verify that orientation disparity is a critical cue for AOS neurons.

In human patients with parietal lobe lesions, a considerable shift of the vertical and horizontal axes toward the side contralateral to the side of the lesion was reported by Bender and Jung (1948). McFie et al. (1950) described a similar symptom in several patients with a right occipitoparietal lesion. Similar deficits in the perception of line orientation due to a parietal lobe lesion were reported recently by von Cramon and Kerkhoff (1993). De Renzi et al. (1971) reported that patients with parietal lobe lesions exhibited deficits in their judgment of the axis orientation in depth. Therefore, the discrimination of axis orientation is one of the prominent functions of the parietal cortex in the domain of space perception.

Surface-orientation-selective neurons

According to Marr’s theory of vision (Marr 1982), the main purpose of vision is object-centered representation

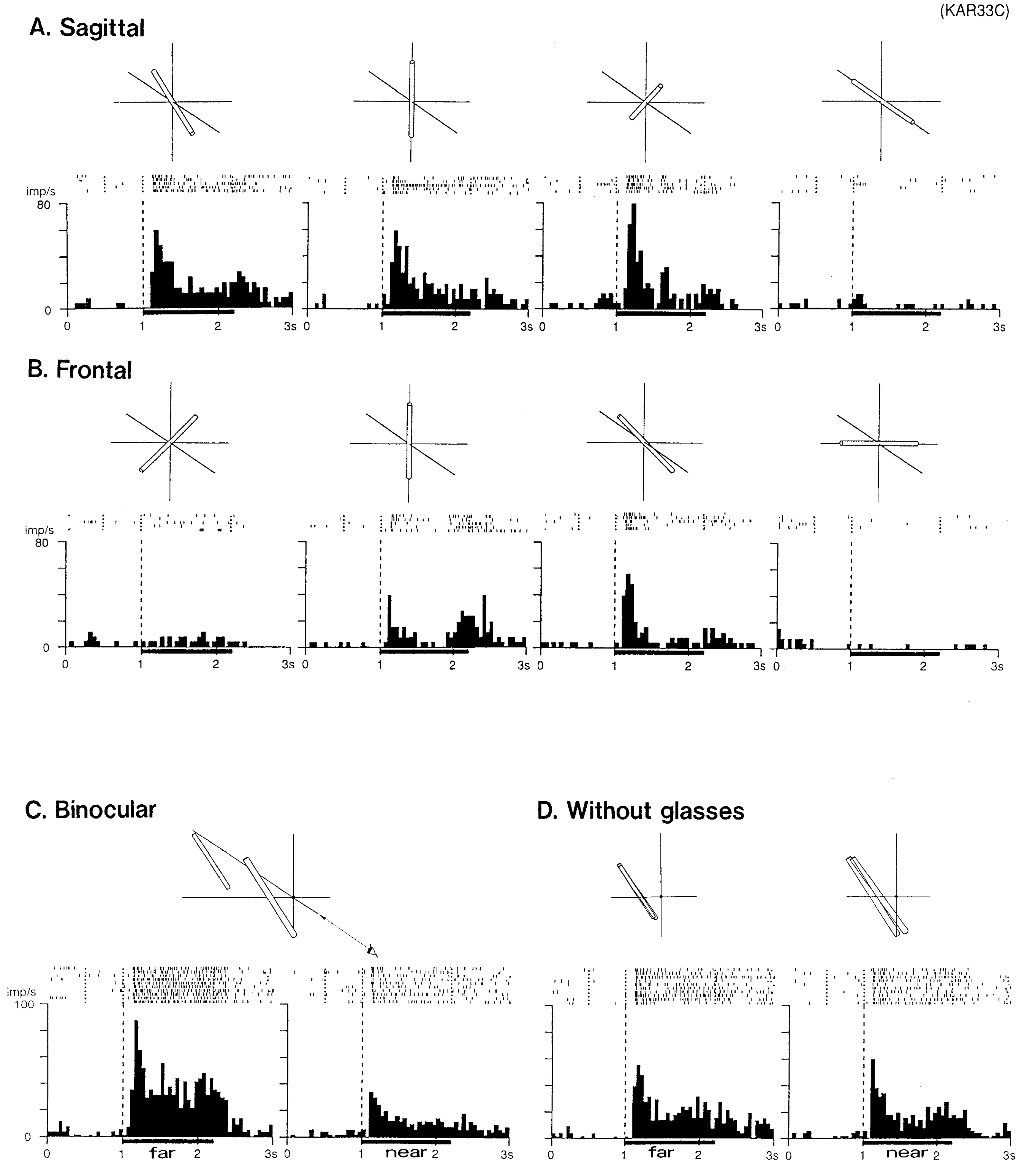

Fig. 5A–D Response of an axis-orientation-selective (AOS) neuron to a cylinder on a stereoscopic display of 3D computer graphics. **A** Response of the cell to a cylinder at the distance of 100 cm presented in various orientations in the sagittal plane at intervals of 45°. Note the broad tuning. **B** Response to the stimulus presented at various orientations in the frontal plane. **C–D** Response of the cell to the stimulus presented in the best orientation (22° to the left, 22° backward) at the far (150 cm) and near (50 cm) positions. Comparison of response under binocular viewing conditions with (**C**) and without (**D**) polarized glasses. (Modified from Sakata et al. 1998)

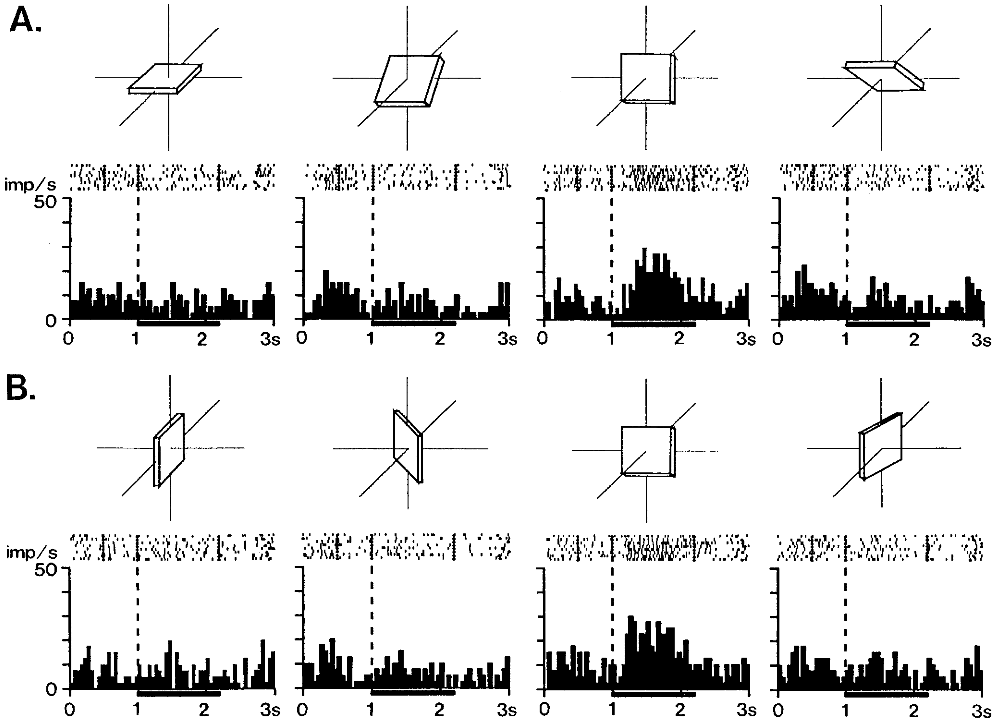

Fig. 6A, B Response of a surface-orientation-selective (SOS) neuron to a square plate presented in various orientations at the distance of 200 cm. **A** Responses to the stimuli presented in various orientations around the horizontal axis at 45° intervals. **B** Responses to the stimulus presented in different orientations, varied around the vertical axis

of a 3D shape and spatial arrangement of an object. The main stepping stone toward this goal is representation of the geometry of the visible surface. Therefore, if a 3D shape is to be represented somewhere in the cerebral cortex, there must be an area in the visual cortical pathways that represents surface orientation and curvature.

Discrimination of viewer-centered surface orientation is also important on its own for the manipulation of objects. We found that the hand-manipulation-related neurons that responded to the view of the square plate showed selectivity for the orientation of the plate. 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, preferentially responded to flat objects, such as a square plate or circular disk. We used a 3D computer graphics display to present a solid plate or checkerboard at various orientations and distances, also varying other stimulus parameters,such as width and thickness. The following description is based on a study of 36 parietal visual neurons recorded from three hemispheres of two Japanese monkeys (*Macaca fuscata*; Shikata et al. 1996).

We first compared the responses of the cells to a flat stimulus and an elongated stimulus. Seventeen cells (17/32) preferentially responded to the flat stimulus and showed selectivity for the surface orientation of the stimulus presented on the screen of the stereoscopic display. Thirteen of these cells (13/17) were defined as surface-orientation-selective (SOS) neurons based on the criterion of a high orientation index (O.I. ≥ 2.0), where O.I. is the ratio of the response to the optimal surface orientation to the response to the orthogonal surface orientation. Figure 6 shows an example of an SOS neuron that preferentially responded to a square plate in the frontal plane presented beyond the fixation point (200 cm) (Fig. 6A, B). No response was obtained when the plate was inclined backward or forward around the horizontal axis (Fig. 6A) or slanted leftward or rightward around the vertical axis (Fig. 6B). Neither the horizontal nor the sagittal plane elicited activation of the cell.

Almost all SOS neurons responded more strongly under binocular than under monocular viewing conditions. The difference in the response of SOS neurons between the binocular and monocular viewing conditions is shown in Fig. 7A, in which a circular disk was used as the stimulus. No response was obtained with the monocular stimulus applied for the left eye, and the response was much smaller than that to a binocular stereoscopic stimulus when the monocular stimulus was applied for the right eye or a diplopic stimulus was applied after removing the polarizing glasses. Figure 7B shows the change of the response of this SOS neuron to the frontal disk with a change of distance. The cell responded to the stimulus placed beyond the fixation point (2 or 4 m), but no response was obtained with the stimulus placed nearer than or at the fixation point (0.5 or 1 m). The responses of all the SOS neurons tested (n=6) changed with the depth on the stereoscopic display (we changed the disparity while keeping the size of the stimulus on the screen constant). Half of these SOS neurons responded to far stimuli, as shown in Fig. 7B, and the other half responded to near stimuli. None of these neurons showed as sharp a tuning for depth as the tuned excitatory cells defined by Poggio and Fischer (1977). Most of the SOS neurons showed no change in response intensity with changes in the shape of the stimulus (for example, disc

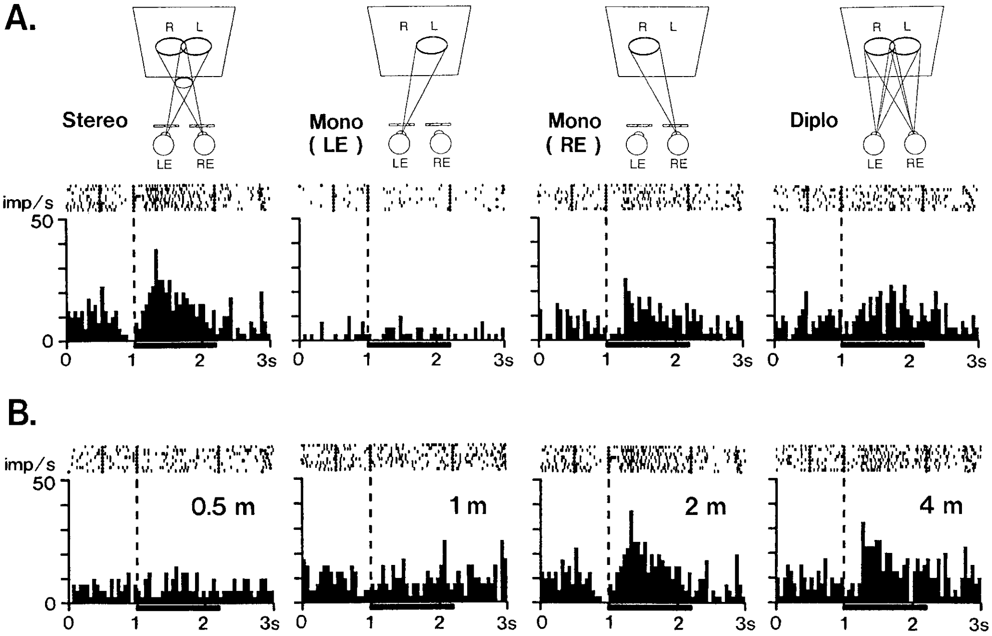

Fig. 7 **A** Comparison of the responses of the same cell shown in Fig. 6 under binocular and monocular viewing conditions and the effect of removal of polarized glasses. The stimulus was a circular disk presented in the frontal plane at a distance of 200 cm. **B** The change of response of the cell to the disk in its best orientation with changes in distance; *from left to right* 50, 100, 200, and 400 cm

vs. square plate) or even its thickness, suggesting that they usually represented the orientation of the flat surface in space, independent of the shape. However, some of them preferred a thin to a thick plate, and a square plate to a disc, showing selectivity both for the shape and stimulus orientation.

More recently, we trained monkeys on a delayed match-to-sample (DMS) task by varying the surface orientation of the stereoscopic stimuli in a random dot stereogram (RDS) generated by computer (Julesz 1971) as well as in a solid figure stereogram (SFS) with binocular contour disparity, in order to specify the disparity cues for surface orientation in depth (Tsutsui et al. 1997). The results of this study suggested that at least a proportion of SOS neurons in the c-IPS area discriminated the surface orientation purely from the disparity gradient, as Marr (1982) predicted in his theory of vision (Sakata et al. 1998). We also tested the effect of texture gradient on the activity of SOS neurons and found that some SOS neurons were sensitive to the texture gradient as well as the disparity gradient (Tsutsui et at. 1998).

There is not much clinical evidence to show that the parietal cortex is involved in the perception of surface orientation. However, disturbances in the ability to draw 3D shapes, such as houses (Piercy et al. 1960), or copy block designs (Critchley 1953) may be in part due to a disturbance in the ability to perceive surface orientation in depth. Recently, a visual agnosia patient with relatively intact parieto-frontal cortical function (Milner et al. 1991) showed deficits in performance in a task of matching the orientation of a rectangular plate 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 (Dijkerman et al. 1996).

Discussion

A surprising finding in our study of hand-manipulation-task related neurons in AIP area was that a number of task-related neurons responded to a view of the objects and showed selectivity for 3D shape, since visual form perception is attributed to the ventral visual pathway and the inferotemporal cortex, according to the concept of two cortical visual systems (Ungerleider and Mishkin 1982). However, it 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 and Milner 1992), although we do not exclude the possibility that the dorsal pathway is involved in the perception of 3D features of objects.

Recent clinical neuropsychological studies on optic ataxia demonstrated that the disturbance of visual control of the distal movements of fingers, grasping, and manipulation may be dissociated from that of the proximal movement of reaching. Jeannerod et al. (1994) reported a case with bilateral parietooccipital infarction showing a deficit in grasping without any deficit in reaching. The impairment was characterized by the lack of preshaping of the hand according to the size of object. More recently, Binkofski et al. (1998) reported cases of cortical lesions in the human homologue of the AIP area, in which selective deficits in the coordination of finger movements required for object grasping were noted, whereas reaching was disturbed to a much lesser extent. A functional MRI study in normal subjects demonstrated that the grasping of a rectangular object, at various orientations in space, strongly activated the contralateral AIP area. It is most likely that the posterior lesions of Jeannerod et al. (1994) involved a visual area to represent the 3D features of objects (the human homologue of the c-IPS area).

In order to manipulate objects, it is necessary to construct their 3D representations in viewer-centered coordinates (Sutherland 1979), and binocular stereopsis is essential for that purpose. The neurons of area c-IPS that are sensitive to binocular disparity and selective for the 3D orientation of the longitudinal axis or surface, together with some neurons that are selective for 3D shape, are likely to meet these requirements, although further investigation is necessary to find a visual area for 3D shape discrimination. AOS neurons and SOS neurons in the c–IPS area may provide adequate information for the control of hand orientation in space. It is highly likely that the orientation-selective visually responsive neurons in the AIP area may receive input from these neurons in the c-IPS area. A recent anatomical study by Luppino et al. (personal communication) revealed projections from the c-IPS to AIP area. Visual information for the control of preshaping of handgrip appears to be more complicated than that for hand orientation, as illustrated by the AIP neurons that were selective for complex objects.

Another interesting finding of our studies of the functional properties of c-IPS neurons 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 (Sakata et al. 1998). This provided evidence suggesting that at least some SOS neurons discriminated the surface orientation on the basis of a change in binocular disparity, as postulated by Marr (1982) in his theory of vision. On the other hand, tilted and slanted lines in the sagittal and horizontal planes produce orientation disparity and width disparity, respectively (see Howard and Rogers 1995 for a review). AOS neurons may integrate the disparity signals of different preferred orientations or preferred lengths. The coexistence of AOS and SOS neurons in the c-IPS area suggests that the major 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 may be concluded from the present investigation that area c-IPS, adjacent to area V3A, is a higher center of stereopsis, which integrates various binocular disparity signals received from the V1, V2, and V3 complex (Poggio and Fischer 1977; Zeki 1978; Hubel and Livingstone 1987; Poggio et al. 1988) to represent the neural codes of 3D features of objects and sends them to area AIP for visual guidance of hand movements. However, further investigation is necessary to elucidate the mechanism of discrimination of surface curvature and surface boundary in order to obtain concrete evidence that the representation of 3D shape involves the parietal cortex. It is also important to investigate how monocular cues of depth are integrated with binocular disparity cues in the parietal cortex, since Castiello et al. (1996) demonstrated that the difference in the perceived dimensions of objects based on the monocular cue of shading influences the shaping of the handgrip. There are reciprocal connections between the anterior lateral bank of the IPS and inferotemporal cortex (Webster et al. 1994), which may convey monocular cues for shape to the lateral bank of the IPS. Therefore, the visually responsive neurons of area AIP may integrate binocular and monocular visual cues to represent the 3D shapes of the objects of manipulation.

Acknowledgements We gratefully acknowledge the support from the Ministry of Education, Science and, Culture of Japan (nos. 05267105, 07244103, and 04NP0101) and the research grant from the Human Frontier Science Program (1990–1992 and 1993–1995).

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