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Functional properties of rotation-sensitive neurons in the posterior parietal association cortex of the monkey

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Abstract We studied the functional properties of rotation-sensitive (RS) neurons of the posterior parietal association cortex in detail. We classified 58 neurons as RS neurons on the basis of statistical analysis, to indicate that their responses to rotary movement were significantly greater ($P < 0.01$) than those to linear movement of the same stimulus. We calculated rotation index, $1 - (L/R)$, in 82 cells, where L/R is the ratio of net response to linear movement to that to rotary movement. All the RS neurons had rotation index greater than or equal to 0.3. The recording site of these RS neurons was localized in the posterolateral part of area PG (area 7a of Vogt), on the anterior bank of the caudal superior temporal sulcus (STS), in the region partly overlapping the medial superior temporal (MST) area. We compared the response of RS neurons to rotation with that to shearing movement as well as to linear movement. In the majority of RS neurons the ratio of shearing response to rotation response (S/R) was smaller than the ratio of linear response to rotation response (L/R), indicating that the response to rotation was not due to a simple combination of linear movements in the opposite direction. Most of the RS neurons responded to the rotary movement of a single spot as well as that of a slit, although the response was smaller (average 70%) for the former. Most of the RS neurons had large receptive fields (60–180° in diameter) and their responses were independent of the position within the

receptive field. The responses of most RS neurons increased monotonically with the increase in angular velocity and were also dependent on the size of the stimulus, although the rate of increase was small when the length was more than 10°. The majority of RS neurons (37/58) responded better to rotation in depth than to that in the frontoparallel plane. Some of them (12/37) responded to diagonal rotation rather than to sagittal or horizontal rotation. We found that some depth RS neurons showed reversal in the preferred direction when we used a trapezoidal window-like plate as the rotating stimulus in the monocular viewing condition, just as occurs in the case of the Ames window illusion. The response of some RS neurons (5/7) was enhanced by tracking eye movement. The enhanced responses were observed during rotary tracking but not during linear tracking. Other RS neurons ($n=2$) showed maximum response to the rotation of the monkey chair in the light, as a result of convergence of visual and vestibular signals. We concluded that the continuous change of direction of movement was the most important cue for RS neurons to respond selectively to rotary movement in contrast to linear translational movement, and that these neurons were likely to discriminate the direction and orientation of the plane of rotation of the object in space.

Key words Parietal association cortex
Rotation-sensitive neurons · Depth rotation
Visual motion perception · Monkey

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Introduction

Rotation is movement of an object around an axis without changing its overall position and is different from linear translative movement. Physical motion can be described fully by six components, three of translation and three of rotation, with respect to the axes of a coordinate system (Gibson 1966). These components can be described by velocity vectors, and the visual sensitivities to

looming and rotary motion were suggested to be mediated by the detectors of divergence and curl of optical flow field, respectively (Koendrink 1986; Regan 1986). Recent psychophysical studies provided more evidence to support the idea that the human visual system contains "rotation detectors" by demonstrating rotational motion aftereffects (Cavanagh and Favreau 1980; Peterik et al. 1984; Hershenson 1987) and the selective elevation of threshold (Regan and Beverley 1985; Freeman and Harris 1992) after prolonged adaptation to rotary movements.

The neurophysiological evidence of rotation detectors was obtained beyond the level of the middle temporal (MT) area (area V5 of Zeki; Zeki and Shipp 1988), where the retinotopic organization breaks down (Maunsell and Van Essen 1983c; Gattass and Gross 1981). First we found rotation-sensitive neurons in the posterior parietal association cortex (area PG) of the alert monkey (Sakata et al. 1985, 1986). Subsequently Saito et al. (1986) found that some neurons in the medial superior temporal (MST) area of the anesthetized monkey were sensitive to rotary movement. Tanaka and Saito (1989) analyzed the functional properties of "rotation cells" together with direction and expansion/contraction cells of dorsal MST (MSTd) in more detail and proposed that a circular arrangement of movement directions in the wide-field stimuli was essential for the activation of rotation cells (Tanaka et al. 1989). Duffy and Wurtz (1991a, b) also found that some of the MSTd neurons were sensitive to circular motion of optic flow stimuli. However, the properties of these cells did not necessarily fit the direction mosaic hypothesis as suggested by Tanaka et al. (1989), whereas at least part of them were more consistent with the vector field hypothesis that required a curl detector (Duffy and Wurtz 1991b). Both of these two groups used large field stimuli of dot patterns and found that most of the MSTd neurons preferred such stimuli to small field stimuli or a simple stimulus such as a slit (Saito et al. 1986). These studies as well as the recent study of Roy et al. (1992) suggested that MSTd neurons were mainly related to the perception of self-motion.

In contrast, the rotation-sensitive (RS) neurons which we recorded (Sakata et al. 1985, 1986) responded well to the rotation of a slit (bar) or a spot and were likely to be concerned with the rotation of the external objects rather than that of the background. Moreover, the majority of RS neurons responded to depth rotation better than rotation in the frontoparallel plane (Sakata et al. 1986; Sakata 1991), whereas most of the rotation cells in MSTd responded only to frontoparallel rotation (Saito et al. 1986; Tanaka and Saito 1989; Duffy and Wurtz 1991a). Recording sites of RS neurons were mostly localized in the middle part of the anterior bank of caudal superior temporal sulcus (STS), outside MSTd. Thus the RS neurons of area PG were likely to belong to a different group of neurons than the rotation cells of MSTd. Since our previous papers (Sakata et al. 1985, 1986; Sakata 1991) were preliminary reports, we carried

out a more detailed analysis of the functional properties of RS neurons in the present investigation. The results support the hypothesis that the activity of RS neurons is the neural correlate of the perception of rotation of objects in space.

Materials and methods

Six rhesus monkeys (*Macaca mulatta*) under general anesthesia (pentobarbital sodium) were prepared for single-cell recording by surgically implanting stainless steel bolts for attachment to a halo-like head holder, two pairs of Ag-AgCl pellet electrodes for recording vertical and horizontal electrooculograms, and a recording cylinder on the skull. Monkeys were trained to fixate on the small spot of a light-emitting diode (LED) or a small spot projected on a tangent screen for 2–3 s. The animal pressed a key at lap level when the fixation spot was turned on and released the key when it dimmed, to be rewarded with a drop of juice upon doing so. Visual stimuli were given during this period of fixation. For single-cell recording, a hydraulic microdrive (Narishige MO-9) was mounted on a recording cylinder over a trephine hole in the skull, over the inferior parietal lobule. A glass-coated platinum-iridium microelectrode was used to penetrate the intact dura mater. The chamber was filled with mineral oil and sealed with silicon rubber packing during recording.

In this series of experiments we selected visual neurons that responded to the manual rotation of a bar or a plate during the survey of the parietal neurons. Then we recorded the response of such neurons to several kinds of moving stimuli during the fixation period as follows. For rotation in three-dimensional (3-D) space we used a luminous acrylic bar (regular size, 30 cm in length, 1 cm in diameter) fixed on a small turntable, which was mounted on a stand with a ball joint in such a way as to change its orientation in the sagittal, horizontal, or diagonal plane as well as in the frontoparallel plane. The clockwise or anticlockwise rotation in the frontal, horizontal, and sagittal plane was defined in reference to the forward, downward, and leftward directions, respectively, from the monkey's point of view. The back of the acrylic bar was painted white to reflect the light of a pair of LEDs implanted on each end to illuminate the bar from the inside. This regular bar was rotated around its center, whereas we also used a bar of half the size (15 cm in length), which was rotated around its end. Usually an LED spot for fixation was mounted in the center of rotation, but it was placed separately in front of the animal when the center of receptive field was in the contralateral hemifield. We also used a short bar (12 cm) for the measurement of receptive fields.

In order to present a shearing movement we used a special device to move two acrylic bars of half-size (15 cm) in opposite directions along a pair of parallel rails at an interval of 15 cm (in the range of 30 cm). The bars started to move from the opposite ends and crossed in the center. The same device was used to present linear movement of a half-bar. We also used an LED mounted on the end of an acrylic bar to achieve rotary movement of a small spot in the dark. We occasionally used a tangent screen to achieve rotary or linear movement of a slit in the frontoparallel plane (regular size $34 \times 7^\circ$; half-size $17 \times 7^\circ$). The stimulus was rotated 180° (half a turn) each time at the angular velocity of $90\text{--}100^\circ/\text{s}$ routinely. In order to examine the relationship of the response of RS neurons to velocity, we varied the angular velocity in a range from 2.5 to $180^\circ/\text{sec}$. To examine the effect of size of the stimulus, we used tablets of cardboard of different sizes (2.8–68 cm in diagonal length) mounted on the shaft of the turntable. The monkey was seated on a rotating chair, which could be rotated manually in the horizontal, sagittal, or frontal plane, to test the effect of vestibular stimulation.

After recording in both hemispheres, we made several guide penetrations in each hemisphere. Two or three electrolytic lesions were made in each penetration, passing negative current of $5 \mu\text{A}$ for 5 s. Each monkey was deeply anesthetized with pentobarbital

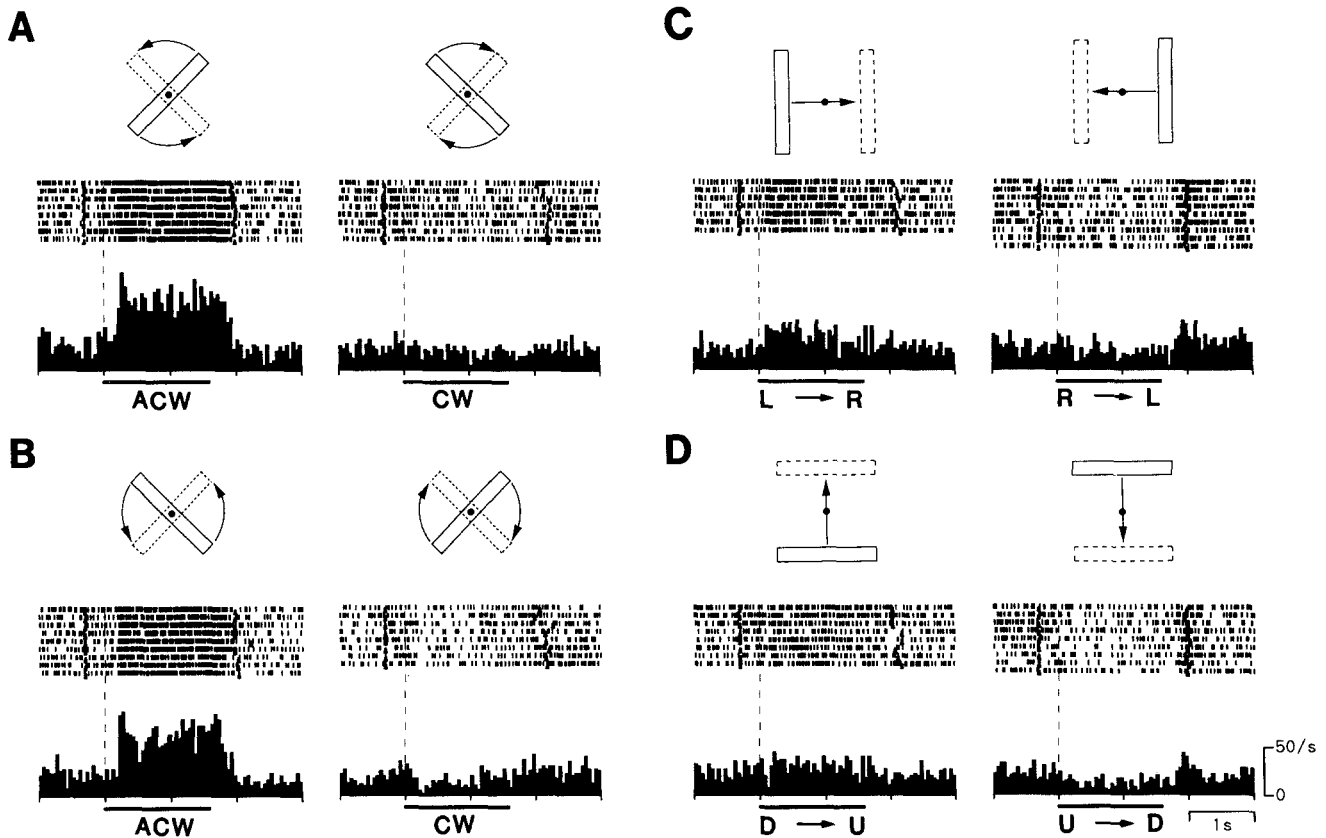


Fig. 1A–D A typical example of rotation-sensitive (RS) neuron in the posterior parietal association cortex (area PG). **A, B** Response of the cell to rotation of a slit on a tangential screen, either anti-clockwise (ACW) or clockwise (CW), in vertical (**A**) and horizontal (**B**) sectors. **C, D** Response of the same neuron to linear movement of the slit in either the rightward (L-R) or leftward (R-L) direction (**C**), and either the upward (D-U) or the downward (U-D) direction (**D**). Impulse rasters of 7–10 trials (*top*) and peristimulus histograms of them (*bottom*) are aligned with the start of movement (vertical dashed lines) in this and following figures. Filled triangles in the rasters indicate the timing of key press and key release, which correspond to the beginning and the end of the fixation period, respectively. The duration of stimulus was 2 s, as indicated by thick lines below the histograms

before perfusion with saline followed by 10% formalin. Recording sites were plotted in reference to the electrolytic lesions on a series of projected drawings of Nissl-stain preparations.

Results

In the present investigation we studied selectively those neurons which responded to rotary movement of a visual stimulus during the initial survey with manual stimulation. Quantitative measurements were made in 101 visual neurons recorded in 46 penetrations in the posterior part of area PG (or area 7a of Vogts: Vogt and Vogt 1919) on the anterior bank of the caudal part of the STS (caudal STS) of ten hemispheres. Figure 1 illustrates the responses of a typical RS neuron of the posterior parietal cortex. The cell responded vigorously to anti-clockwise rotation of a slit on the screen with a sus-

tained discharge while the monkey was fixating on the center (Fig. 1A, B, left). Spontaneous discharge of the cell was slightly suppressed when the slit was rotated clockwise (Fig. 1B, right). The response was the same whether the stimulus was moved in the vertical sector (Fig. 1A) or in the horizontal sector (Fig. 1B). On the other hand, the response of the same cell to linear movement was much smaller, even in a preferred direction from left to right (Fig. 1C, left). There was a slight suppression of the discharge when the stimulus was moved leftward or downward.

Criteria and site of recording of RS neurons

First we performed statistical analysis to compare the net response of the cell (response to the stimulus: average discharge rate during stimulus movement, minus spontaneous discharge: average discharge rate for 1 s before fixation) to rotary movement with that to linear movement. In earlier experiments, we used only a regular bar or slit, as shown in Fig. 1, and classified those neurons which gave a more significant response to the rotary movement ($P < 0.01$) than to linear movement in the preferred direction as rotation-sensitive (RS) neurons ($n = 12$). Later, we used a half-bar routinely, as shown in Figs. 4–6, and classified the RS neurons on the basis of significant difference between the response to the rotary movement and that to the linear movement on both sides of the center of rotation ($n = 46$). We routinely measured the ratio of the net response of the cell to linear movement to that to rotary movement (L/R),

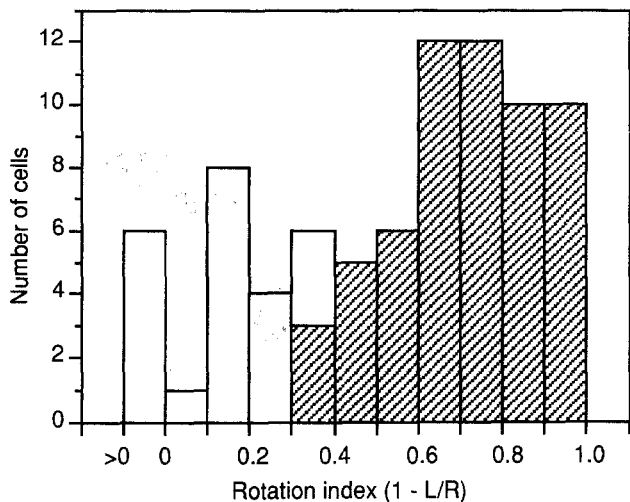
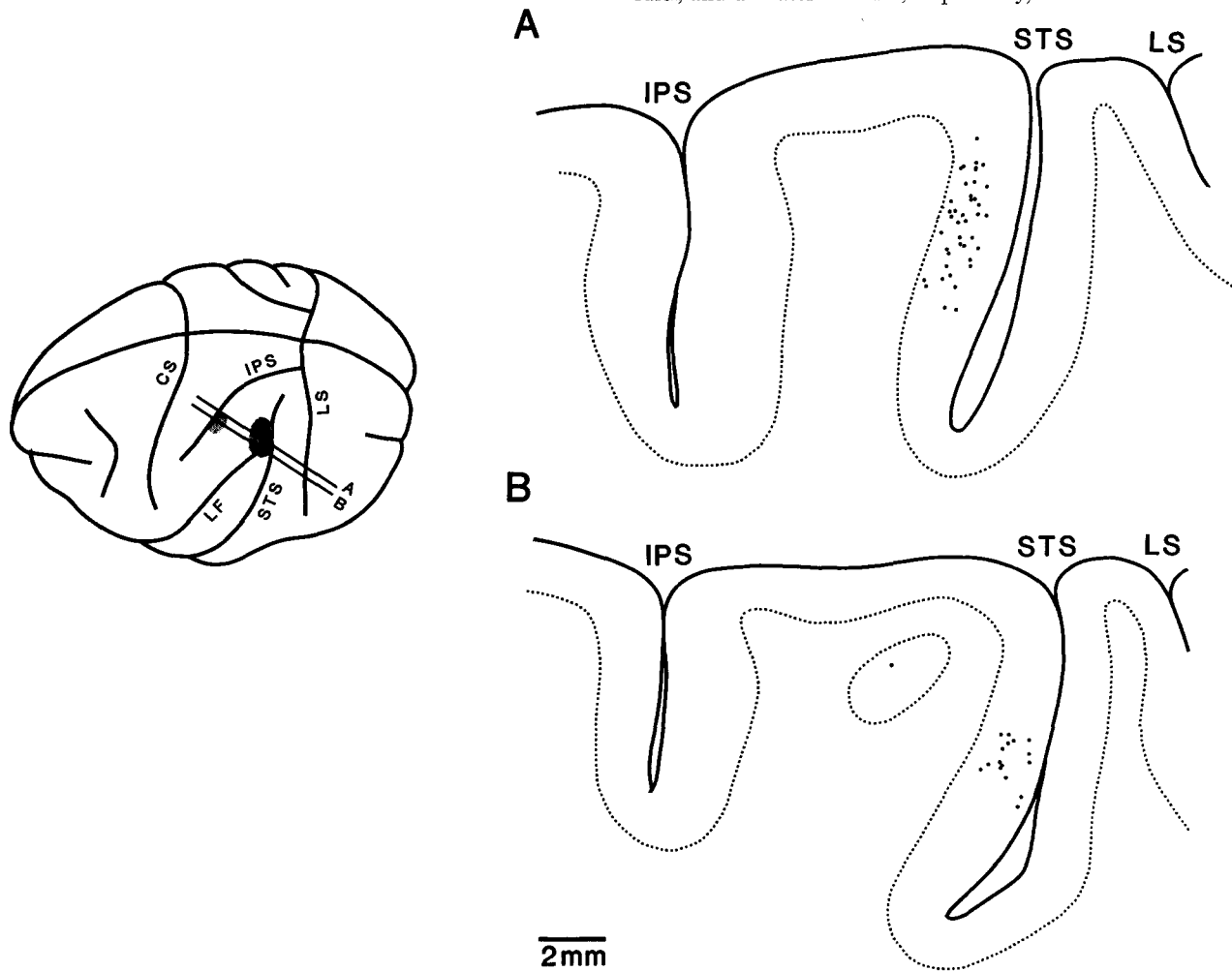


Fig. 2 Distribution of the rotation index, $1 - (L/R)$, where L/R is the ratio of net response of the cell to linear movement to that to rotary movement, for a sample of 80 parietal neurons. *Shaded columns* represent statistically defined RS neurons; the rotation indices of all 58 RS neurons were greater than or equal to 0.3

and calculated the rotation index defined as $1 - (L/R)$. Whenever the cell showed preferred direction of the linear movement we calculated the rotation index for the side on which the direction of rotation of a half-bar was parallel to the preferred direction of linear movement, since the response to both the rotation and the linear movement was better on that side. The histogram in Fig. 2 shows the distribution of this rotation index for 80 neurons in which we recorded the response to both linear and rotary movements of comparable speed and extent. All of the RS neurons ($n = 58$) had a rotation index of 0.3 or more. Almost all neurons which did not match the criteria of RS neurons (19/22) had a rotation index of less than 0.3.

The sites of recording of 58 RS neurons are shown in Fig. 3. We plotted the sites of ten hemispheres in two

Fig. 3 Sites of recording of 58 RS neurons in the inferior parietal lobule. All the sites were plotted on the diagrams of two sections made 2 mm apart, as indicated by *two lines (A, B)* in the drawing of the lateral view of the left hemisphere. The section at the end of the lateral fissure was used as the reference to assemble the sites of ten hemispheres. The *shaded area* in the lateral view indicates the approximate distribution area of the recording sites. Sites within 2 mm from the end of the lateral fissure were plotted for section *A* and those between 2 and 5 mm were plotted for *B*. (*CS, IPS, STS, LS, LF* the central, intraparietal, superior temporal and lunate sulci, and the lateral fissure, respectively)



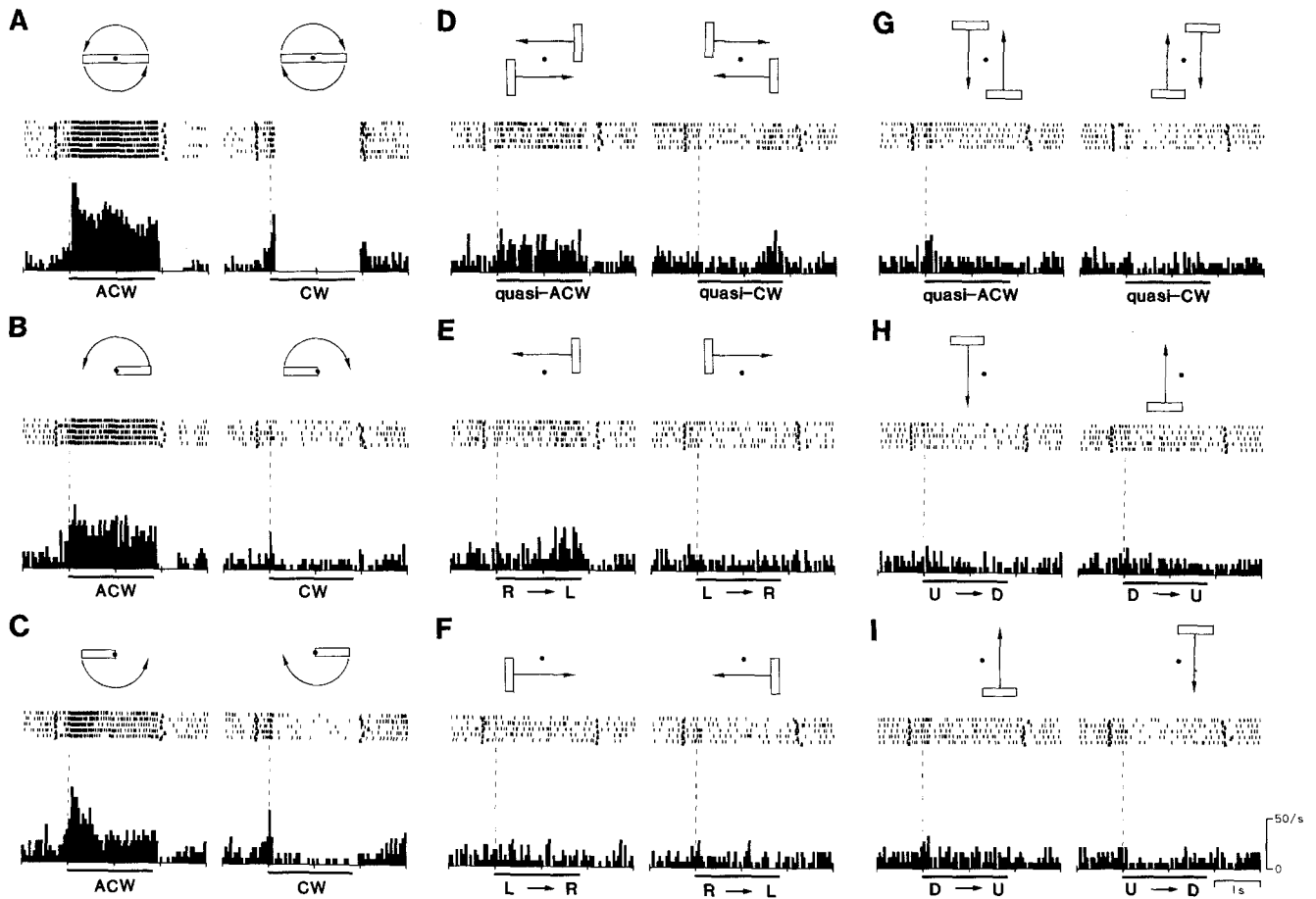


Fig. 4A–I Comparison of responses of an RS neuron to rotary, shearing, and linear movement in the frontal plane. Type of movement is illustrated above each raster diagram. **A** Response to rotation of a regular bar around its center. **B, C** Response to rotation of a half-bar around one end in the upper and lower visual field, respectively. **D** Response to the horizontal shearing movement of a pair of half-bars (moving in opposite directions). **E, F** Response to the horizontal linear movement of a half-bar in upper and lower visual fields, respectively. **G** Response to the vertical shearing movement of a pair of half-bars. **H, I** Response to the vertical linear movement of a half-bar in left and right visual fields, respectively. (ACW anticlockwise, CW clockwise)

(diagrams of) representative sections, one near the end of the lateral fissure and the other 2 mm medial to the former, according to the distance of the section of a particular site from the end of the lateral fissure, and the distance of the site from the top of the anterior bank. They were localized in the posterolateral part of area PG, on the anterior bank of caudal STS. Almost all cells were localized in the sections within 5 mm medial to the end of the lateral fissure. This region partly overlapped with the MST area (V5a of Zeki; Zeki and Shipp 1988) but extended to the upper part of the anterior bank of STS. It appeared to be different from MSTd or MSTl, since we recorded only a few RS neurons in the region where we recorded a cluster of visual tracking neurons (Sakata et al. 1983) which were recorded in MSTd and MSTl by Komatsu and Wurtz (1988).

Comparison between rotary and linear movement

Figure 4 illustrates the response of an RS neuron to a set of rotary, linear, and shearing movements. This cell preferred anticlockwise rotation in the frontoparallel plane (Fig. 4A). Clockwise rotation of a regular bar suppressed the discharge of this cell except for a transient discharge at the beginning of rotary movement (Fig. 4A). Anticlockwise rotation of a half-bar elicited a good response in both the upper field and the lower field (Fig. 4B, C), although the direction of the linear component was opposite on each side of the field covered by the stimulus rotation of 180°. This is in sharp contrast to the ordinary directionally selective movement-sensitive cells, which prefer one particular direction anywhere in the receptive field.

In contrast, there was almost no response to linear movement in the transverse direction, either in the upper field or in the lower field (Fig. 4E, F). Response to the shearing movement was also very small, i.e., only a small response to the shearing movement in the direction corresponding to anticlockwise rotation (Fig. 4D). In order to roughly assess the preferred direction, linear or shearing movement in the vertical direction was given, but no response was obtained (Fig. 4G–I).

A similar type of analysis made for a depth RS neuron is shown in Fig. 5. This cell responded vigorously to clockwise rotation of a regular bar in the horizontal

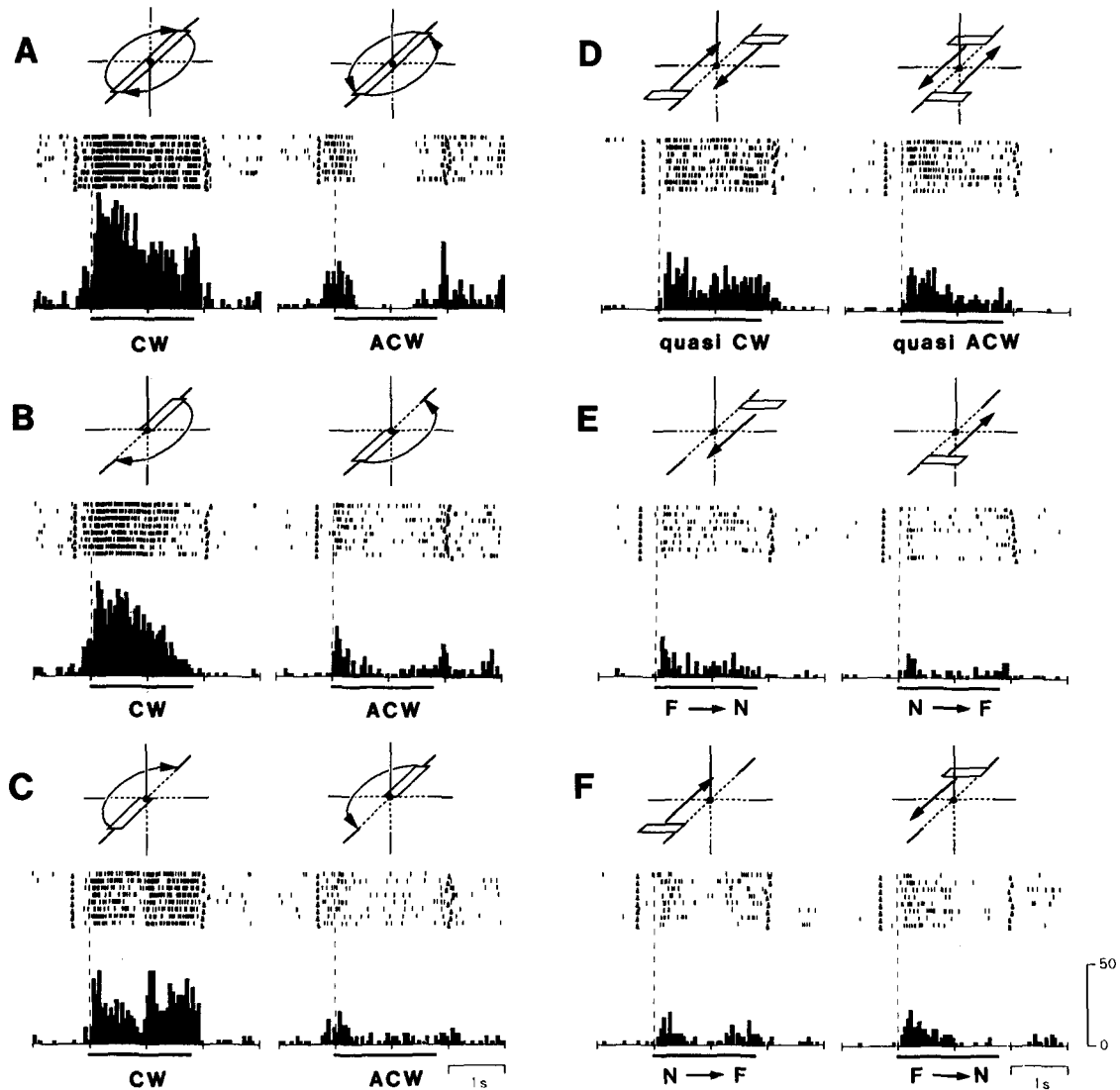


Fig. 5A–F Comparison of responses of an RS neuron to rotary, shearing, and linear movement in the horizontal plane. **A–C** Response to rotation of a regular bar (**A**) or a half-bar (**B**, **C**). **D–F** Response to shearing movement of a pair of half-bars (**D**) or linear movement of a half-bar (**E**, **F**) in the horizontal plane (*F* far, *N* near)

plane (Fig. 5A). The response to rotation of a half-bar was smaller but consistent with that of a regular bar; i.e., preferred direction was clockwise both on the right and on the left side of the center of rotation (Fig. 5B, C). There was a small response to the shearing movement in the horizontal plane, but no obvious difference in response was observed between the directions corresponding to clockwise and anticlockwise rotations (Fig. 5D). Depth movement of the half-bar was not effective either on the right or on the left side of the fixation point (Fig. 5E, F). Linear and shearing movements in the transverse direction in the horizontal plane were also much less effective in activating the cell than horizontal rotation (not shown).

In some RS neurons (when the rotation index was less than 0.5), the response to the linear movements was

considerably large in the preferred direction, even though the difference in the amount of response was highly significant between rotary and linear movements. In such cases, we could compare the characteristics of the responses to rotary movement with those to linear movement, as shown in Fig. 6. The cell responded vigorously to clockwise rotation of a regular bar in the frontal plane (Fig. 6A). Responses to rotation of a half-bar (Fig. 6B, C) were smaller but consistent in directional selectivity with that to rotation of a regular bar (Fig. 6A). Since rotation of a regular bar is the combination of rotations of two half-bars connected at the center, the response to the former may be the summation of those to the latter. In contrast, the response to shearing movement was not greater than that to linear movement of the half-bar and was not a simple summation of the latter (Fig. 6D). On the other hand the preferred direction to linear movement was the same both in the upper and the lower visual fields (Fig. 6E, F).

A paradoxical relationship was observed between the responses to linear and rotary movements of a half-bar. There was a good response to the clockwise rota-

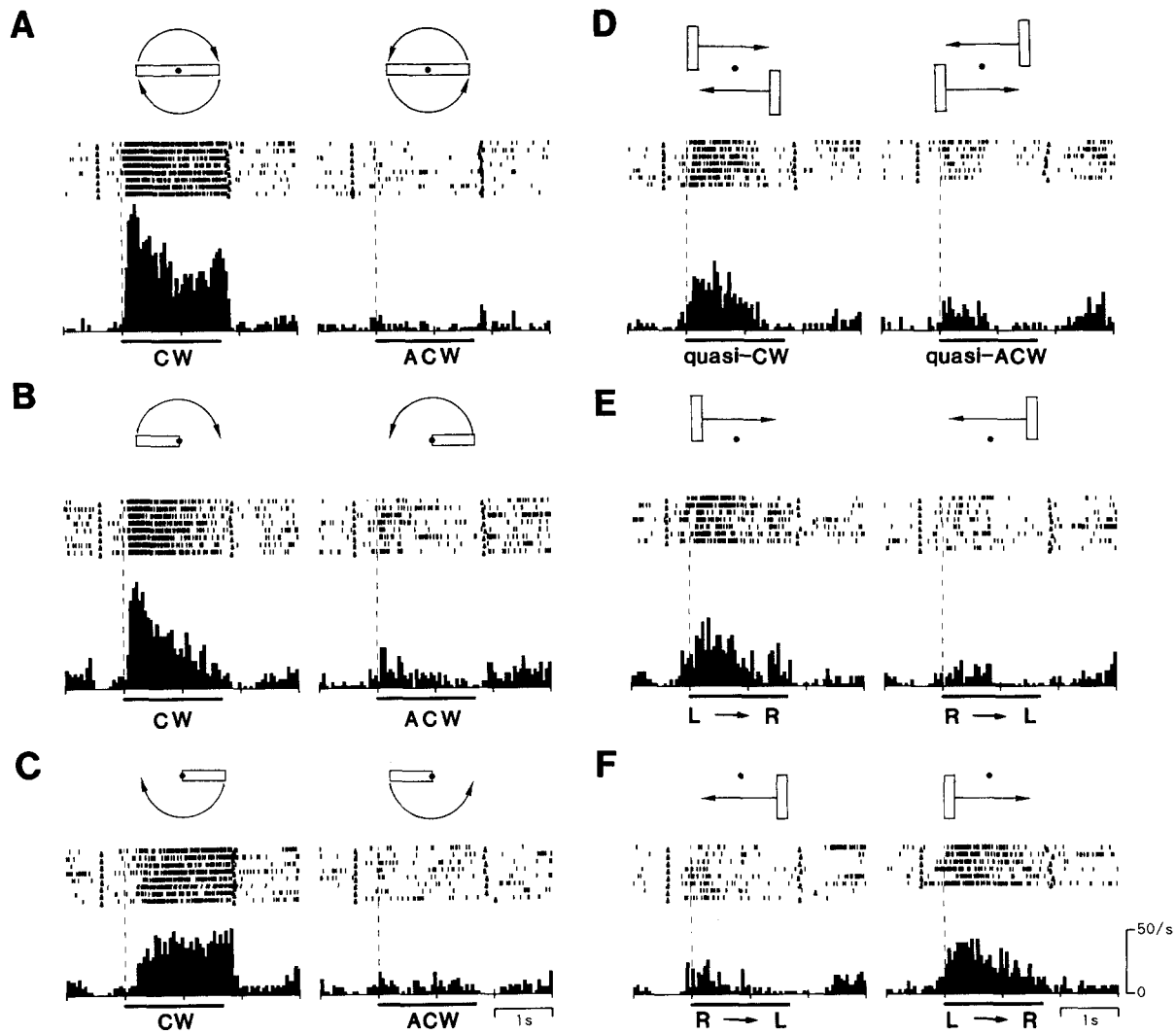


Fig. 6A–F Comparison of responses of an RS neuron to rotary, shearing, and linear movement in the frontal plane. **A–C** Response to rotation of a regular bar (**A**) or a half-bar (**B**, **C**). **D–F** Response to shearing (**D**) or linear movement (**E**, **F**) in the frontal plane. Note the preferred direction of rotation of a half-bar in the lower field (**C**, *left*) is nearly opposite the preferred direction of linear movement of a half-bar in the same area (**F**, *right*)

tion in the lower field (Fig. 6C, *left*), although its linear component corresponded to the null direction of the linear movement (Fig. 6F, *left*). On the other hand there was no response to the anticlockwise rotation in the lower field (Fig. 6F, *right*), although its linear component corresponded to the preferred direction of the linear movement (Fig. 6F, *right*). In general, the preferred direction of RS neurons in linear movement was the same throughout the receptive field, so that the preferred direction in rotary movement was consistent with that in linear movement on one side of the center of rotation, but opposite on the other side. In other words, the stimulus that moved in the null direction of linear movement could activate the cell when the stimulus rotated in an appropriate direction. This paradoxical relationship in the directionality to rotary and linear move-

ments was observed in almost all RS neurons (17/19) in which the preferred direction of linear movement was clearly defined.

In order to compare the effect of shearing with that of linear movement of a half-bar, we measured the ratio of the net response to shearing movement to that to rotation of a regular bar or slit (S/R) in 34 RS neuron and plotted them against the L/R ratio (Fig. 7). In the majority of these RS neurons (23/34), the S/R ratio was less than the L/R ratio. This implies that the combination of a pair of opposite linear movements was relatively less effective than a simple linear movement in activating RS neurons. Of nine cells whose S/R ratios were larger than L/R ratios, only one had an S/R ratio of more than 1.0 (1.07). All the other cells (8/9) had S/R ratios of less than 1.0, so that the response to rotary movement was larger than that to the combination of a pair of linear movements.

Comparison between a slit and spot

Since we routinely used a slit or a bar as the rotated stimulus, many factors may be effective as the cues of

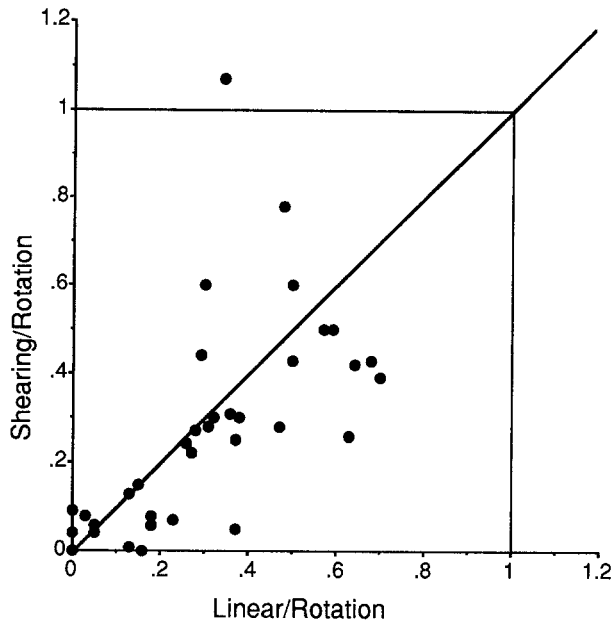
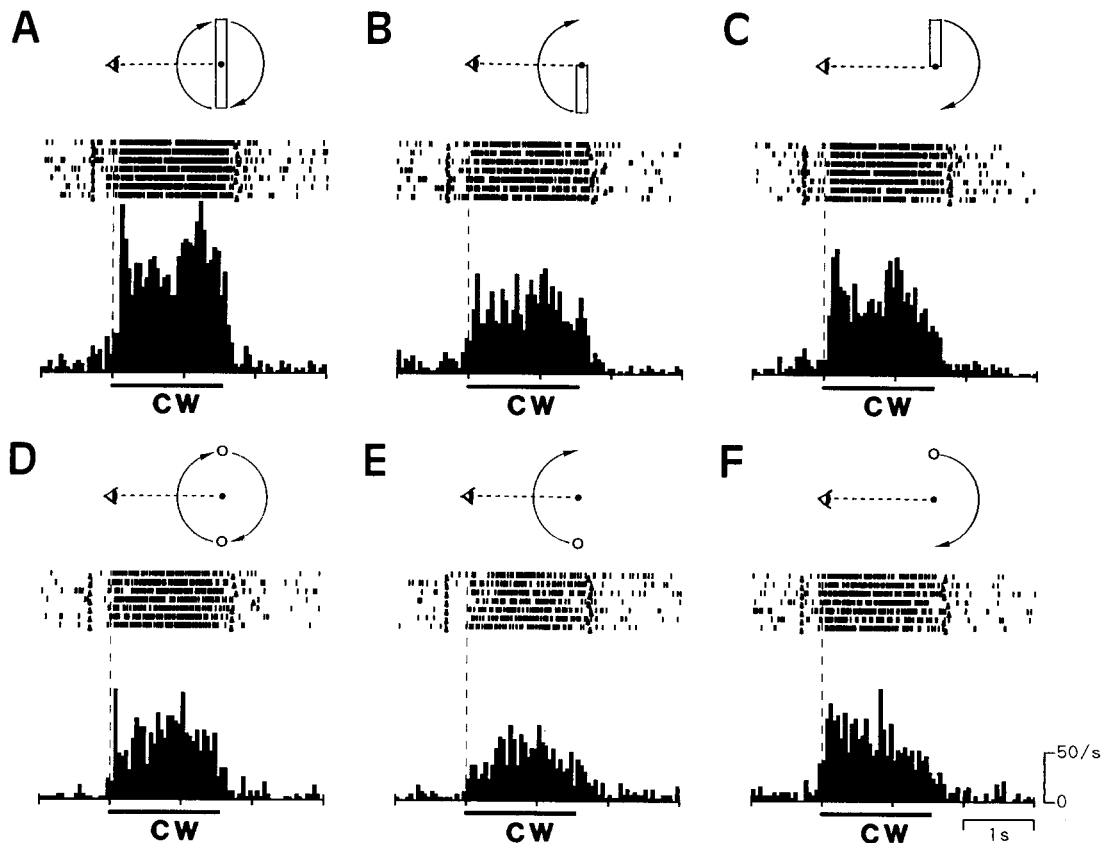


Fig. 7 Scatter diagram of the shearing/rotation (S/R) and linear/rotation (L/R) ratios of the responses of 34 RS neurons. The *diagonal line* indicates $S/R = L/R$. In the majority of the RS neurons (23/34), S/R was less than L/R, indicating that shearing was less effective in activating RS neurons than linear movement

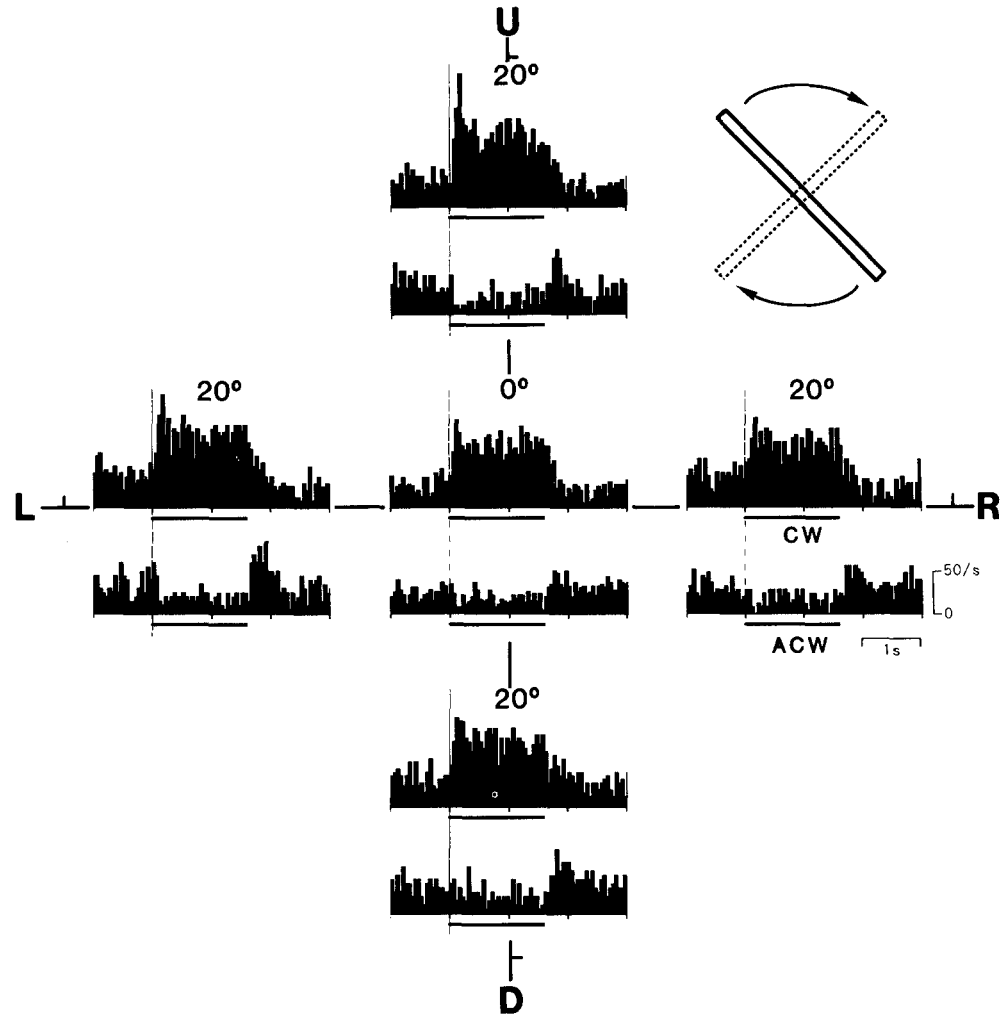
Fig. 8 Comparison of the response of an RS neuron to rotation of a regular bar (A) or a half-bar (B, C) with that to the rotation of a pair of spots (D) or a single spot (E, F) of light in the sagittal plane in the dark. Distance of the light spot from the center of rotation was the same as the length of a half-bar



rotary movement, including continuous change of orientation and the gradient of velocity from the center to the periphery. In order to simplify the factors of the stimulus, we used a pair of spots or a single spot of light moving around the fixation point in which the change of direction of movement was the only factor to serve as the cue of rotary movement. Figure 8 shows an example of the comparison of the responses of an RS neuron to rotation of a bar with those to rotation of a spot. The response to sagittal rotation of a regular bar (Fig. 8A) was much larger than that to rotation of a pair of spots separated by a distance equal to the length of a bar (Fig. 8D). Responses to rotation of a half-bar (Fig. 8B, C) were also larger than those to rotation of a single spot whose distance from the center was the same as the length of a half-bar (Fig. 8E, F).

We compared the responses to rotation of a bar with those to rotation of a pair of spots in 23 RS neurons. In the majority of them (15/23), rotation of a regular bar was more effective in eliciting responses than that of a pair of spots. Mean ratio of the response to spot rotation to that to slit rotation was 0.7. Thus a rotating spot was a sufficient stimulus to activate RS neurons, although a bar was usually more effective than a spot. This suggested that the change in the direction of movement was likely to be the most effective stimulus for RS neurons, although a change in orientation or the gradient of velocity might also be effective in activating RS neurons.

Fig. 9 Responses of an RS neuron to rotation of a regular bar at different positions in the visual field. Responses to clockwise (*above*) and anticlockwise (*below*) rotations at the center and at 20° above, below, left, and right of the fixation point are shown at corresponding locations. No significant differences in responses were observed among the different positions within this range



Position invariance and receptive fields

The receptive fields of the RS neurons were, in general, quite large, and a shift of the center of rotation within the receptive field did not cause a large difference in response, as illustrated in Fig. 9. This neuron responded preferentially to the anticlockwise rotation in the frontal plane. We used a regular bar of 30 cm and shifted the center of rotation upward, downward, left and right with the step of 20°, while the fixation spot was kept in the center of the field. There was almost no difference in response at each point compared with the one in the center. The area covered with the neighboring rotating slit overlapped about 5°, in which the directions of the linear components of the neighboring rotation were opposite each other. This again contradicted the hypothesis that the simple summation of the responses of linear movements in small subdivisions of the receptive field represents the response to rotary movement. Position invariance of the response to rotation was observed in a similar way in two other RS neurons in early experiments. Moreover, the response to rotation was constant in the central area of the receptive field in the following seven neurons.

Since the receptive fields of RS neurons were very large and difficult to plot, we made precise measurements in only a small number of cells ($n=7$). We measured the responses of RS neurons at 15° steps along the horizontal and vertical meridians, using an acrylic bar 12 cm in length as the stimulus. The contours of the receptive fields were extrapolated from these data, as shown in Fig. 10. All the receptive fields of RS neurons we examined included fovea, but the majority of them were skewed toward the contralateral side. We also found a considerable number (3/7) of bilateral and symmetrical receptive fields. The minimum size among the seven examples was $40 \times 80^\circ$ and the maximum field covered the entire visual field.

Effect of angular velocity and size of the stimulus

The response of RS neurons depended on the angular velocity of rotary movement. We measured the responses of 9 RS neurons to rotations at various speeds and plotted velocity-response curves, as shown in Fig. 11. In the majority of them ($n=6$), the velocity-response curve was a monotonically increasing function and the re-

Fig. 10 Receptive fields of seven RS neurons. Response to rotation of a short bar (12 cm) was recorded at intervals of 15–30° along the horizontal and vertical meridians. The most eccentric position of the center of rotation was defined as the border of the receptive field. Asymmetric receptive fields (skewed to the contralateral side) are enclosed by continuous lines. Symmetric receptive fields are enclosed by broken lines

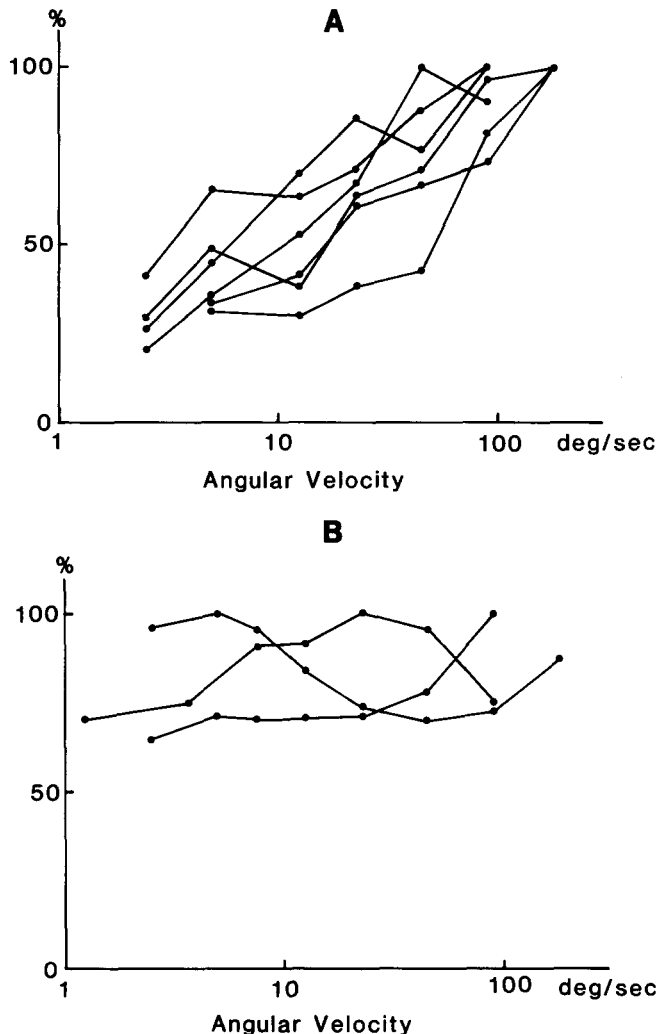
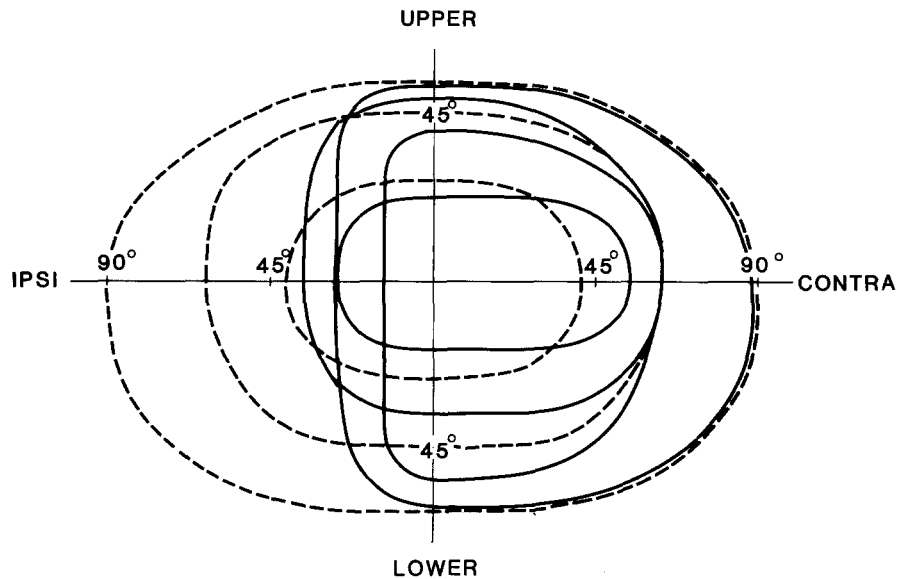


Fig. 11A, B Velocity response curve of nine RS neurons. **A** Six RS neurons showed monotonically increasing functions within a wide range of angular velocity (2.5–100°/s or more). **B** Three RS neurons showed relatively constant response in a wide range of velocity. *Ordinate*, relative response expressed as a percentage of the maximum response; *abscissa*, angular velocity expressed on a logarithmic scale

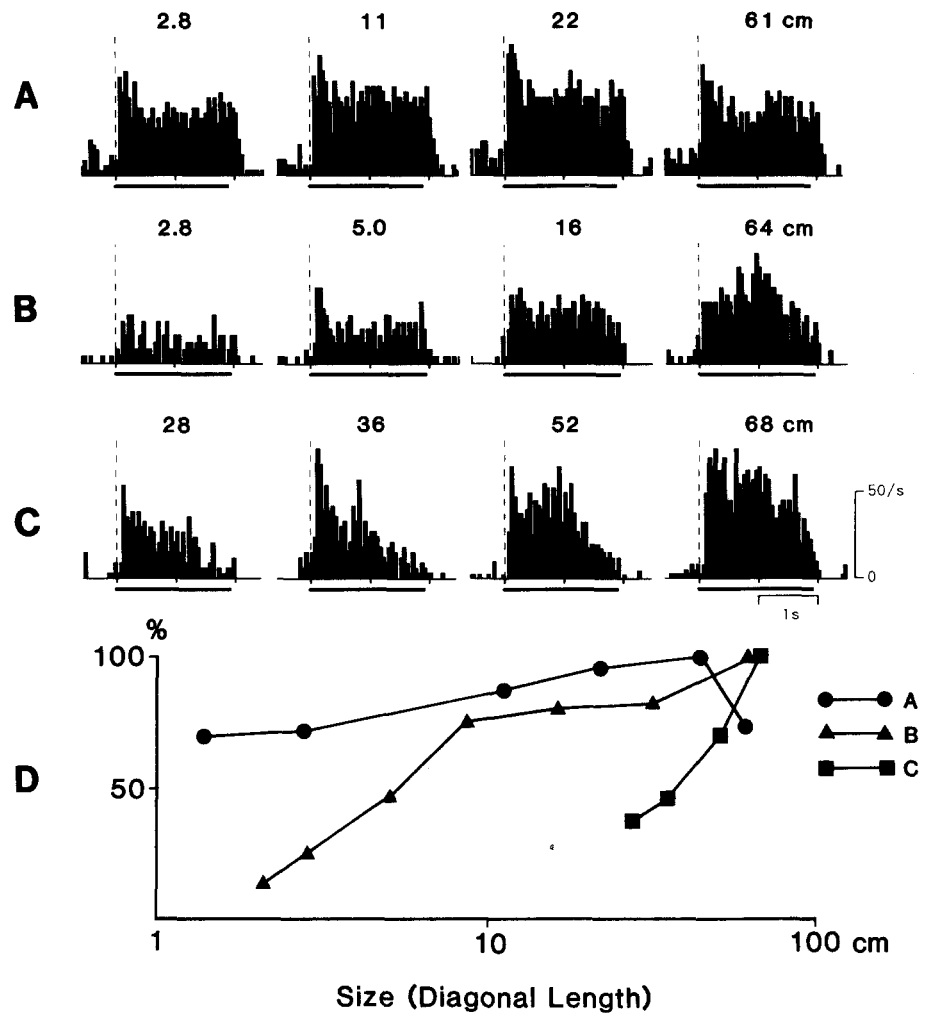
sponse was less than half of the maximum velocity at the speed of 2.5°/s (Fig. 11A). However, in a third of the cells examined (3/9), response remained more or less constant up to the velocity of 2.5°/s (Fig. 11B).

The response of RS neurons was also a function of the size of the stimulus. We measured the responses of six RS neurons to rotation of stimuli of various lengths, and three examples are shown in Fig. 12. Since we found length is more important than area by comparing the effect of the two in a couple of RS neurons, we plotted the size in terms of the diagonal length. Cell A was an exceptional RS neuron that responded vigorously to the rotation of a small square (2 × 2 cm). Cell C was another extreme case of an RS neuron that required a large stimulus to be activated adequately (50 cm for more than 50% of maximum response). Cell B was an example of a common RS neuron (4/6) with a monotonically increasing function of size-response curve, reaching nearly maximum at 10 or 15 cm.

Response to depth rotation

The majority of RS neurons (37/58) responded better to rotation in depth than to that in the frontoparallel plane, and we call them depth RS neurons. We routinely examined the response of RS neurons to rotation in three orthogonal surfaces, frontal, horizontal, and sagittal planes. Quantitative measurement in three planes was made in 36 RS neurons, although preferred plane of rotation was determined by manual stimulation in 22 RS neurons in which the cell was predominantly sensitive to the rotation in one of these orthogonal planes. The majority of depth RS neurons (25/37) preferred either sagittal ($n=15$) or horizontal rotation ($n=10$). However, a considerable number of depth RS neurons ($n=12$) did not show a sharp tuning to any one of the three orthogonal rotations and preferred rotation in the diagonal plane in between. Figure 13 illustrates an ex-

Fig. 12A–D Examples of size-response curves of three RS neurons. **A** An RS neuron that responded well to a small stimulus and showed only a small increase in response as the size of the stimulus increased. **B** An RS neuron that increased its response gradually as the stimulus increased in size. **C** An RS neuron that preferred a large stimulus. Size-response curves of the three RS neurons (*A*, *B*, *C*) in *A–C* are shown in *D*. *Ordinate*, relative response expressed as a percentage of the maximum response; *abscissa*, diagonal length of the stimulus expressed on a logarithmic scale



ample of an RS neuron that preferred diagonal rotation in the frontosagittal plane. It responded moderately to clockwise rotation in the sagittal plane (Fig. 13A) and in the frontal plane (Fig. 13B). However, no response was obtained with the horizontal rotation of either direction (Fig. 13C). The most appropriate stimulus for this neuron was clockwise rotation in the diagonal plane between frontal and sagittal planes and slanted to the left (Fig. 13D). Seven neurons preferred diagonal rotation in the frontosagittal plane, two cells preferred the sagitto-horizontal planes and three cells preferred a diagonal plane tilted to all three planes, fronto-sagitto-horizontal plane.

One of the most probable cues for depth rotation is the dynamic change of binocular disparity. Therefore, we compared the response of depth RS neurons in the monocular viewing condition with that in the binocular viewing, as illustrated in Fig. 14. The responses of an RS neuron that preferred anticlockwise rotation in the sagittal plane measured at different distances of the stimulus either in the binocular or in the monocular viewing conditions are shown in the series of impulse histograms (upper two rows) and plotted in a graph shown below. The response in monocular viewing was consistently smaller than that in binocular viewing up

to the distance of 200 cm. The ratio of the monocular response to binocular response was about 0.7 on average. Monocular/binocular ratio was measured at the distance of 57 cm in five depth RS neurons, ranging from 0.3 to 0.8.

Response to Ames window

There is a peculiar illusion for depth rotation called "Ames window" (Ames 1951). It is caused by the rotation of a trapezoidal window-like plate, which appears to be a rectangular window viewed from an oblique angle. When this is rotated around an axis parallel to the bottom of the trapezoid and viewed with one eye from some distance (several meters in human subjects), it appears to reverse its direction every half a turn (180°), even though it actually rotates continuously in one direction (Ames 1951).

Figure 15 illustrates an example of a depth RS neuron which displayed a reversal of preferred direction in response to rotation of trapezoid window in the monocular viewing condition. The cell responded preferentially to the *clockwise* rotation of a regular bar in the sagitto-horizontal plane in the binocular viewing condition

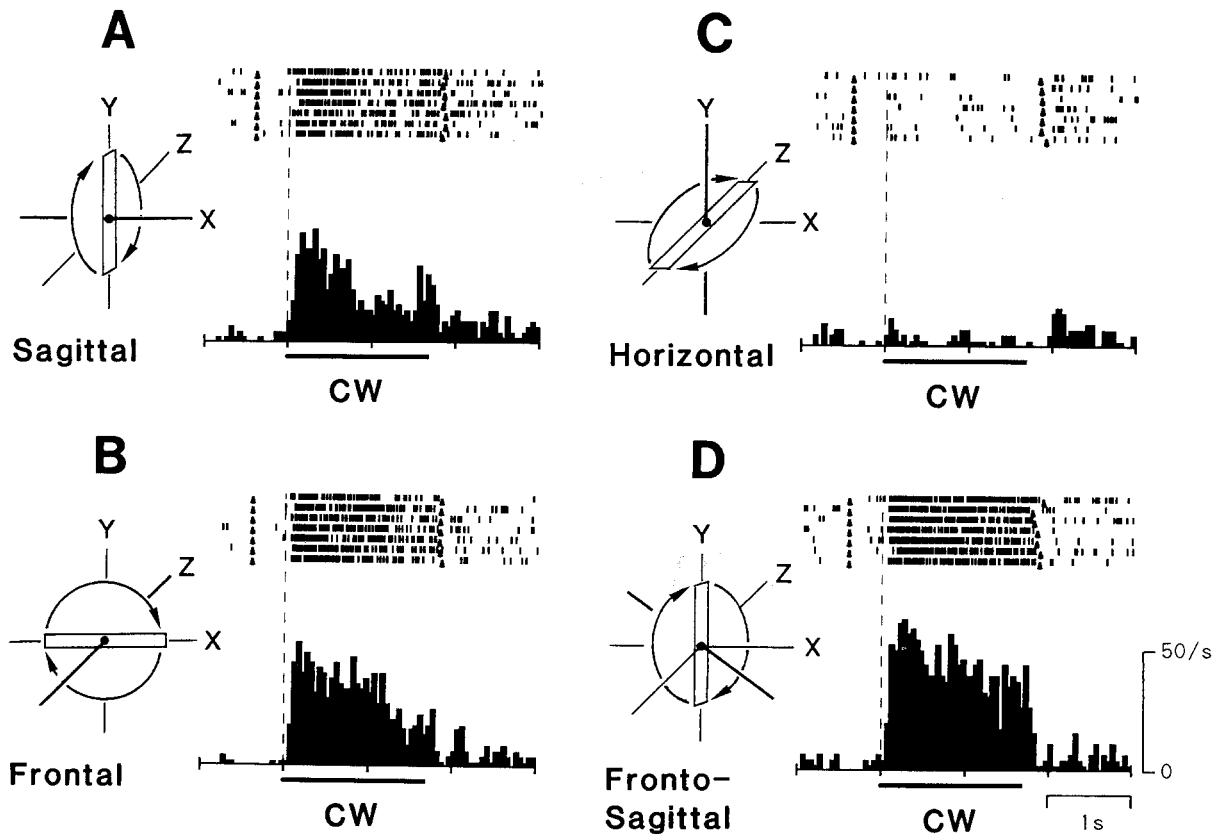


Fig. 13A–D Responses of a depth RS neuron preferring rotation in the diagonal plane. This cell responded to sagittal (**A**) and frontal (**B**) rotation, but not to horizontal rotation (**C**) of a bar. It responded maximally to rotation in the diagonal plane between frontal and sagittal planes (**D**)

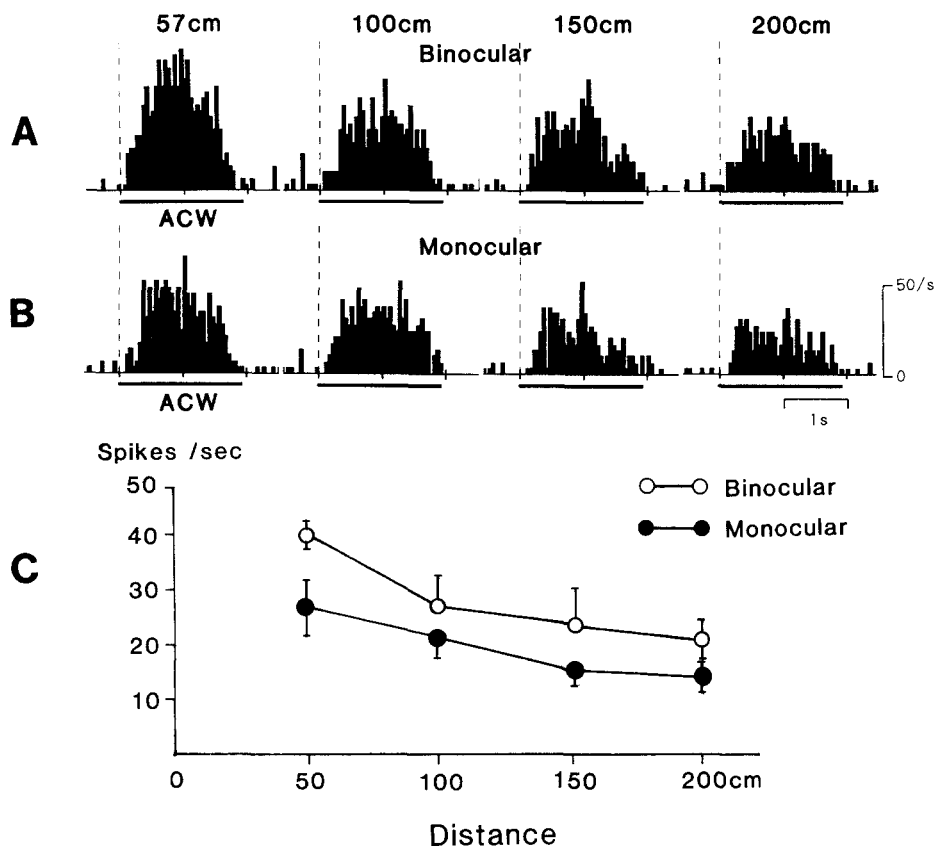
(Fig. 15A). Its response to the same stimulation was much smaller in the monocular than in the binocular viewing condition (Fig. 15B). The response to rotation of half a turn of trapezoidal window (around the axis parallel to the base) was the same in the preferred direction, but better than that to rotation of a bar, when the longer edge (the base) moved in front of the axis of rotation (Fig. 15C). However, the same cell showed a strong response to the *anticlockwise* rotation when the longer edge moved behind the axis (Fig. 15D). This corresponded very well to the reversal of perceived direction of rotation in the illusion of Ames window. The longer edge always appears to move in front of the axis (perhaps because it appears nearer than the shorter edge) when binocular disparity is absent, so that the perceived direction of rotation is opposite to the actual rotation when the longer edge moves behind the axis. Reversal of the preferred direction of depth rotation occurred only in the monocular viewing condition, but not in the binocular viewing condition, as illustrated in Fig. 16. The cell preferred anticlockwise rotation in the sagittal plane when the longer edge moved in front of the axis either in the binocular or in the monocular viewing condition (Fig. 16A). It responded to the same direction of rotation in the binocular viewing condition

even when the longer edge moved behind the axis (Fig. 16B, top). However, in the monocular viewing condition, the preferred direction reversed to clockwise when the longer edge moved behind the axis (Fig. 16B, bottom).

The response to rotation of the trapezoidal window also depended on the distance of the stimulus. Figure 17 illustrates the change of the response to Ames window due to the change of distance. This is the same cell as the one shown in Fig. 16. The cell responded to clockwise rotation alone in the monocular viewing condition at the distance of 100–200 cm (Fig. 17B). However, it responded also to anticlockwise rotation at 50 cm (ambiguous response), and at 20 cm it responded only to anticlockwise rotation (Fig. 17A), even in the monocular viewing condition. Return to the normal directional preference at a short distance may suggest the contribution of motion parallax to the discrimination of depth rotation.

We examined the response to rotation of a trapezoidal window in seven depth RS neurons. Five of them showed reversal of preferred direction in the monocular viewing condition at 150 or 200 cm, as shown in Figs. 15 and 16. Two others, however, showed ambiguous responses with little difference between clockwise and anticlockwise rotation in monocular viewing at 150 or 200 cm.

Fig. 14A–C Comparison of response of a depth RS neuron between binocular (A) and monocular (B) viewing conditions. Responses to rotation of a bar in the sagittal plane at four viewing distances are illustrated. Response was consistently low for monocular viewing at any distance, as shown in the distance-response curve (C). Vertical lines are standard deviations of discharge rate during the stimulation



Enhancement by tracking eye movement

We occasionally observed that some parietal visual neurons responded better when the monkey tracked the rotating object with its eyes. Figure 18 shows a typical example of an RS neuron whose response to rotation was enhanced by the tracking eye movement. It responded fairly well to clockwise rotation of the bar in the frontal plane when the animal fixated on the spot in the center of the bar (Fig. 18A). However, it responded even more vigorously when the animal followed the movement of the spot at the end of a rotating bar (Fig. 18B). Furthermore, the cell was activated when the monkey tracked the rotary movement of an LED spot without any additional stimulus object (Fig. 18C). However, there was no response when the animal pursued linear movement of a spot (Fig. 18D). All these experiments were performed in the dark with a luminous bar or spot without any visible background. Thus the strong response during the tracking of a spot on the end of the rotating bar seemed to be the summation of the response of the cell to rotation of the retinal image of a bar around the fovea and that to rotary tracking. We examined the effect of tracking eye movement on the response of those RS neurons which appeared to be influenced by eye movement. Responses of five cells out of seven RS neurons we examined were found to be enhanced by tracking eye movement, although overt response to rotary tracking alone was found in only two of them.

Vestibular and visual interaction in RS neurons

In the posterior parietal cortex there are neurons which respond to vestibular stimulation (Kawano et al. 1984; Akbarian et al. 1988; Grusser et al. 1990). In the present investigation, we occasionally examined the effect of rotation of the monkey chair upon the activity of RS neurons, both in the light and in the dark. Two RS neurons were found to respond more vigorously to rotation of a monkey chair in the light than to rotation of a bar in the same plane. They also responded to rotation of the monkey chair in the dark, indicating reception of a vestibular input. Figure 19 illustrates an example of such a neuron. The cell was initially found to respond to anticlockwise rotation of a slit in the frontoparallel plane (Fig. 19A). The same cell was found to discharge much more vigorously when a monkey chair was rolled clockwise (from right to left) in the frontal plane (Fig. 19B). It responded to rolling of the chair also in the dark (Fig. 19C), although the response was not as vigorous as in the light. It appeared as if the response to rotation of the chair in the light was the summation of the visual and vestibular response to rotation of the chair. It should be noted that the visual image of the edge of the chair or body rotates in the same direction as the chair because the eye rotates in the opposite direction due to the ocular counter-rolling (Collewijn et al. 1985).

Unfortunately we tested the effect of rotation of the monkey chair in an early stage of this investigation, so

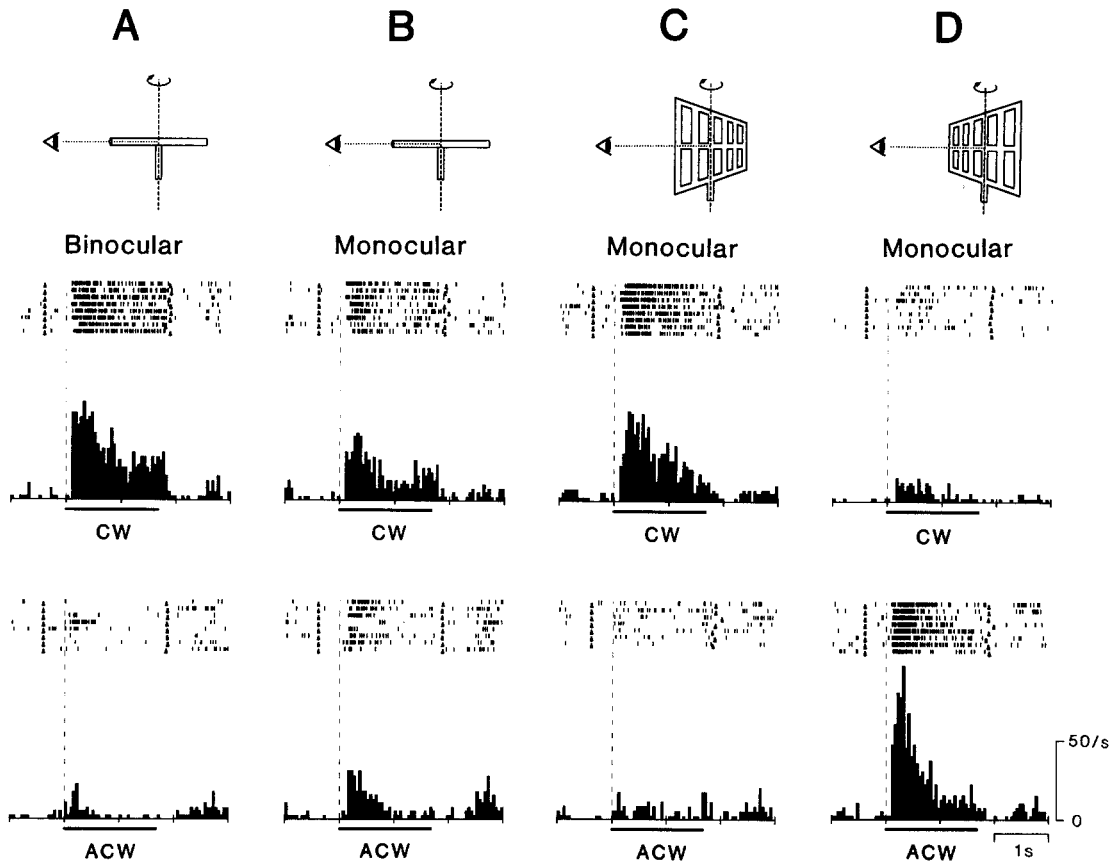


Fig. 15A–D Responses of a depth RS neuron to rotation of Ames window (trapezoid 21 cm in height, with long edge of 25 cm and short edge of 14 cm), compared with those to a regular bar. **A** Response to rotation of a bar in binocular viewing condition. **B** Response to rotation of a bar in monocular viewing condition. **C, D** Response to rotation of a trapezoidal (window-shaped) plate (around the axis parallel to the base) in monocular viewing condition, with the longer edge moving in front of (**C**) or behind (**D**) the axis. The range of rotation was half a turn (180°) and the viewing distance was 150 cm for all recordings. Note a reversal of preferred direction of rotation in **D**. Stimuli were rotated in the sagittohorizontal plane, although diagrams are drawn in the horizontal plane for simplicity

that many of the neurons which showed strong influence of vestibular input ($N = 4$) were examined only with rotary movement but not with linear movement of the visual stimulus. However, all of these neurons preferred the same direction and orientation of the rotation both for visual stimulus and for a monkey chair.

Discussion

In the present investigation we analyzed several different aspects of the response characteristics of rotation-sensitive (RS) neurons in area PG which preferred rotation to linear translational movement. The results were relevant to addressing the issues of what the most essential cues to discriminate rotation from translation are and how the rotation of objects in 3-D space is represented in the parietal RS neurons.

Change of direction is essential for activating RS neurons

Several lines of evidence suggested that the continuous change of the direction of movement was essential for activating RS neurons. First we compared the response of RS neurons to linear shearing movement as well as that to linear translational movement with the response to rotation of the same stimulus. In the majority of RS neurons, the ratio of the response to shearing to that to rotation (S/R) was smaller than the ratio of the response to linear movement to that to rotation (L/R), indicating that the response to rotation was not due to a simple summation of the responses to linear movements (in opposing directions on the side opposite the center of rotation). This was not without exception, since shearing movement was more effective than linear movement in some RS neurons (9/34). Second, we often observed a paradoxical relationship in preferred direction between rotary and linear movements when a half-bar was used as a stimulus and rotated around its end. Either clockwise or anticlockwise rotation of a half-bar activated RS neurons even when it was moving in the null direction of linear movement. Therefore, the selectivity of RS neurons to the moving stimulus did not depend on the local directional selectivity tested with linear movement.

Third, we observed good response of RS neurons to rotary movement of a single spot or a pair of spots, which excluded the change of orientation of the contour or velocity gradient along the radial direction as a possi-

Fig. 16A, B Response of a depth RS neuron to rotation of Ames window either during binocular (*upper records*) or monocular viewing (*lower records*) conditions at 200 cm. **A** The response while the longer edge moved in front of the axis. **B** The response while the longer edge moved behind the axis. Note the reversal of preferred direction in monocular viewing condition (*bottom*)

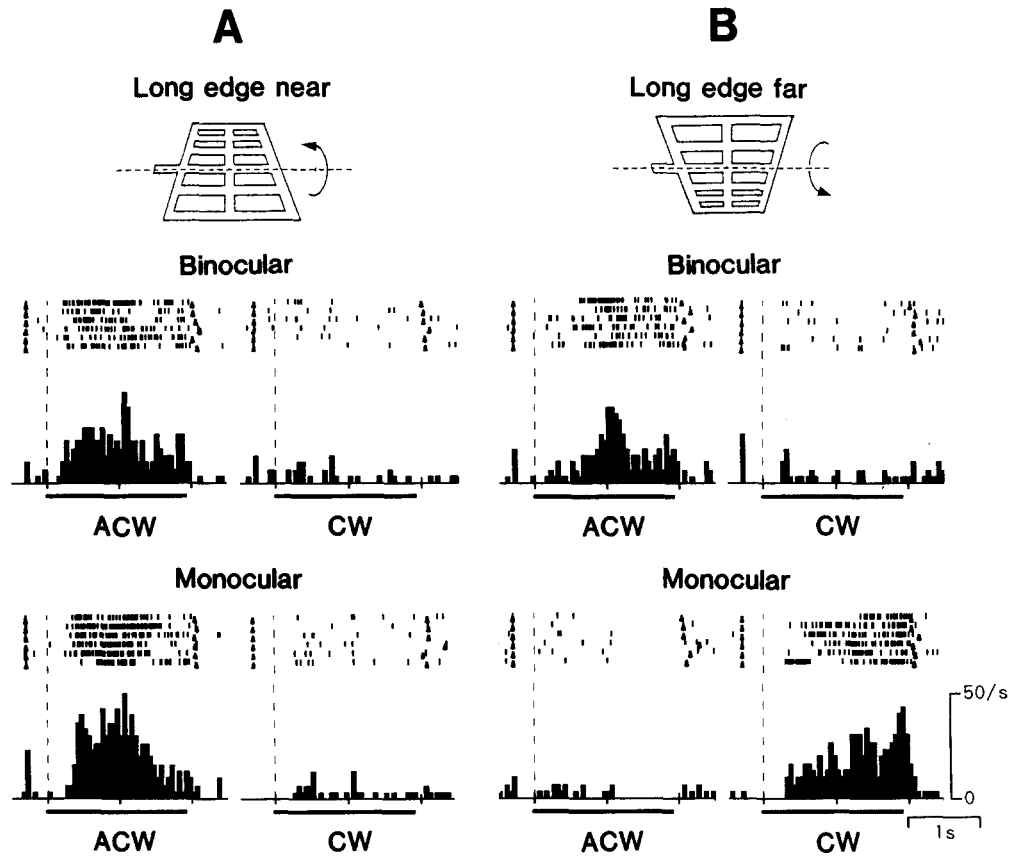
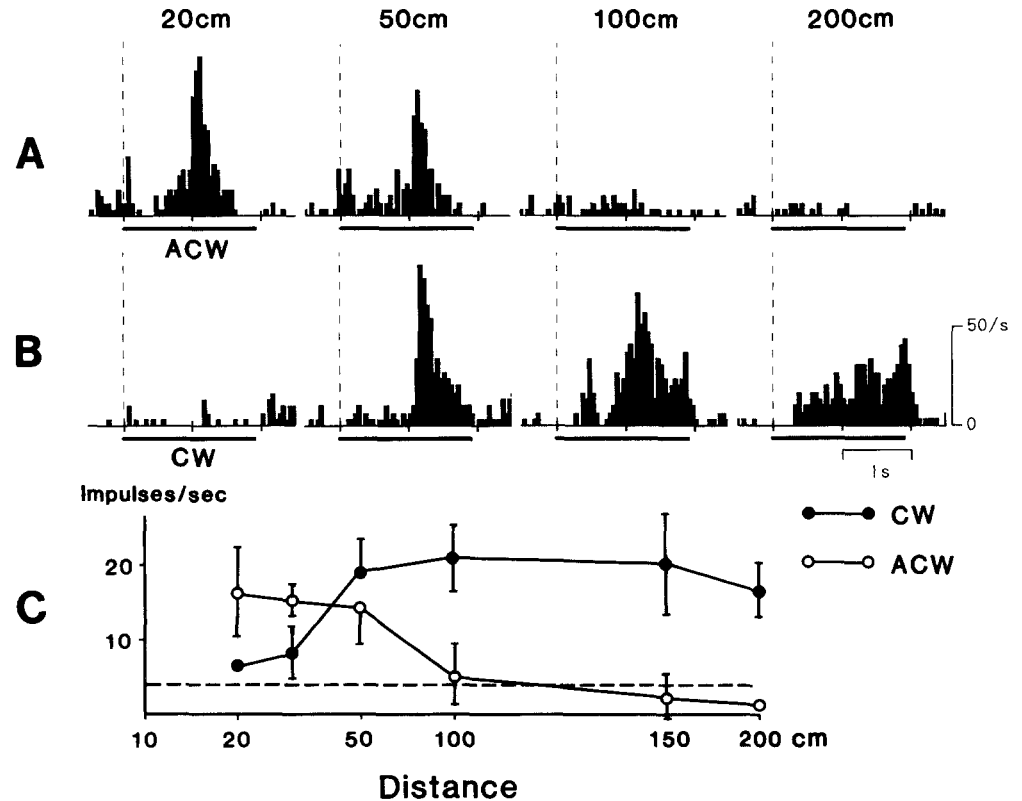


Fig. 17A-C Change of directional selectivity to rotation of Ames window due to the change of distance. This cell is the same one as shown in Fig. 16 and preferred anticlockwise rotation in the sagittal plane. The responses to anticlockwise (**A**) and clockwise (**B**) rotations of a trapezoidal plate while the longer edge moved behind the axis in the monocular viewing condition are illustrated with impulse histograms. **C** Distance-response relationship. *Vertical lines* are SD of discharge rate. Note that the preferred direction of the cell returned to normal (anticlockwise) as the viewing distance decreased. *Broken line* indicates the rate of spontaneous discharge



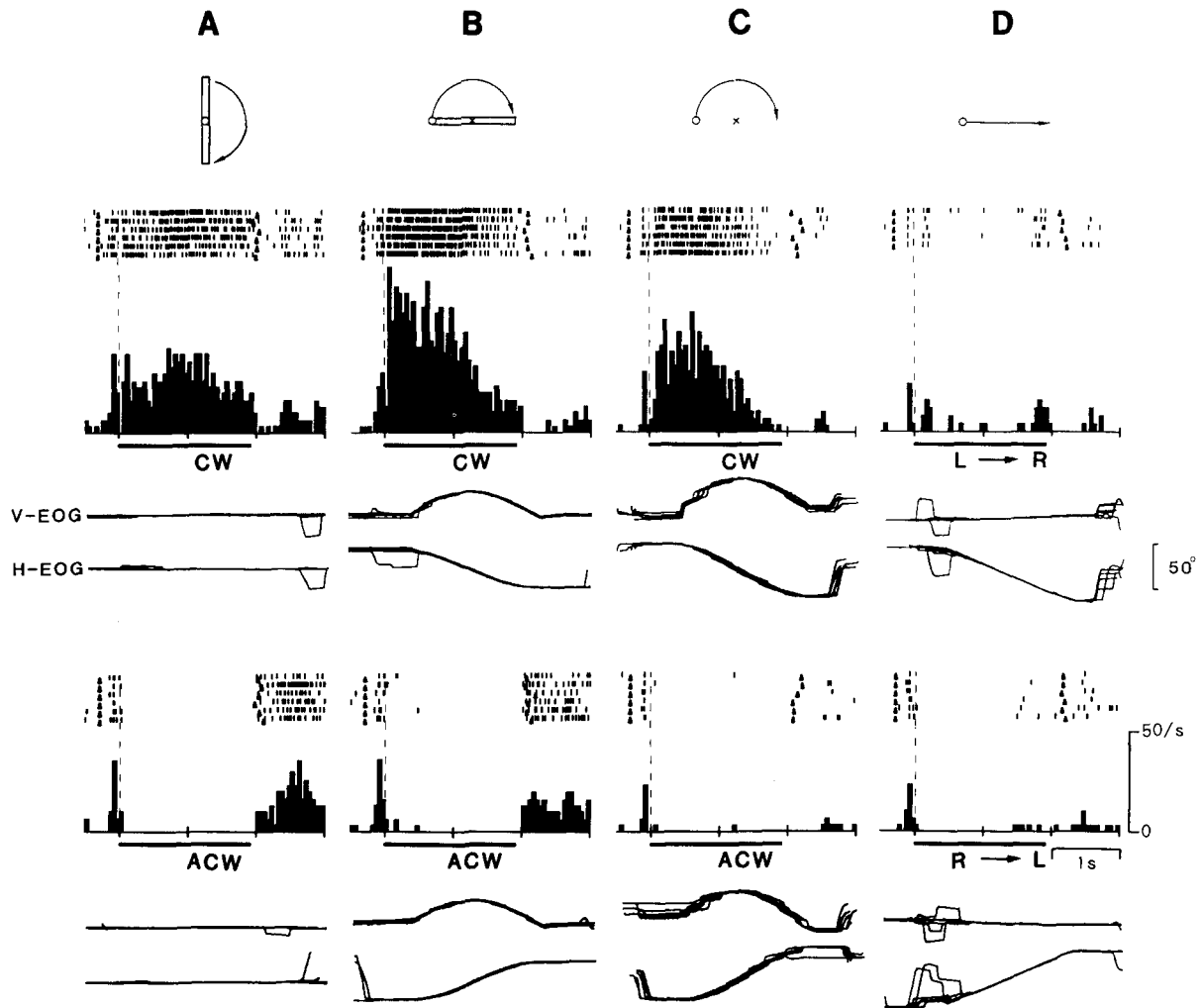


Fig. 18A–D Enhancement of the response of RS neurons by tracking eye movement. This cell responded well to rotation in the frontal plane (A). Its response was strongly enhanced when the monkey visually tracked rotary movement of a spot at the end of the bar (B). The cell was also activated during tracking of a rotating spot (C), but was not activated during tracking of a spot moving linearly (D). Vertical and horizontal electrooculograms (EOG) are shown below each histogram

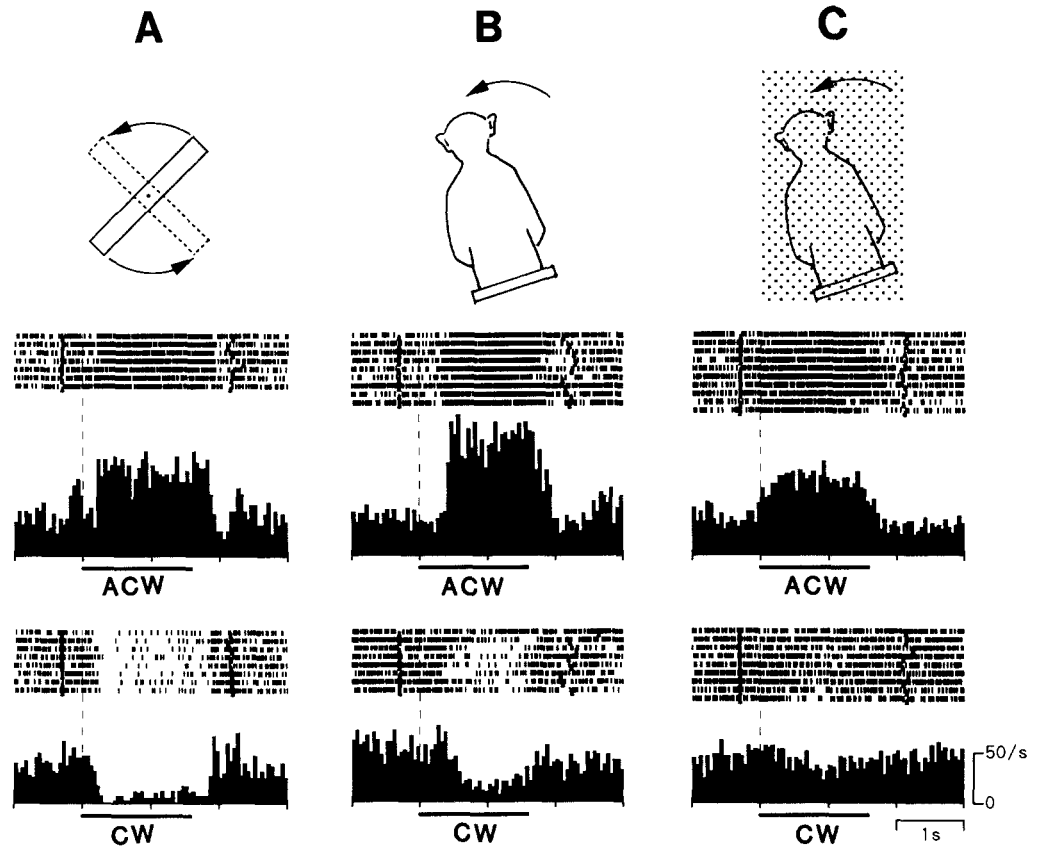
ble factor to activate the cell. Especially in the case of a single spot, there was no possibility of spatial summation of linear movement of different directions as in the case of a multiple dot pattern (Tanaka and Saito 1989; Duffy and Wurtz 1991a), and the continuous change of direction was the only difference that distinguished rotary from linear movement. Fourth, the receptive fields of RS neurons were large and their responses to rotation did not change with a wide range of change in position of the center, showing position invariance. Position invariance is contradictory to the direction mosaic hypothesis with circular arrangement of directions suggested by Tanaka et al. (1989) and compatible with the vector field hypothesis which relies on the uniform responsiveness for circular motion throughout the receptive field (Duffy and Wurtz 1991b).

All these properties may be explained if one postulates a mechanism to detect a sequential change of direction of movement by integrating the signals across a set of directionally selective neurons with different preferred directions with a common large receptive field (Sakata et al. 1986). A similar type of neural network model for the detection of rotational motion was proposed by Liaw et al. (1993). However, other factors such as the sequential change of orientation of the stimulus must also be taken into account, since the response to rotation of a slit or a bar was, on average, considerably larger than that to rotation of a single spot or a pair of spots.

Discrimination of rotation in depth

One of the salient characteristics of RS neurons of the posterior area PG was that the majority of them preferred rotation in depth to rotation in the frontoparallel plane. It is possible that the preferred plane of rotation of depth RS neurons was not only the horizontal or sagittal plane but also the diagonal plane in between. This implies that a set of depth RS neurons with differ-

Fig. 19A–C An RS neuron that responded both to visual and to vestibular rotations. **A** Response of the cell to frontal rotation of a slit on a tangent screen. **B** Response of the same cell to rotation of the monkey chair in the lighted room. **C** Response of the cell to rotation of the chair in the dark. Note preferred direction was the same in all three conditions, anticlockwise from the monkey's point of view



ent preferred planes of rotation is present to allow discrimination of any kind of rotation in space.

One of the essential factors to activate depth RS neurons was the change of binocular disparity, since the response to depth rotation was smaller in the monocular viewing condition than in the binocular viewing condition. However, the difference between the two conditions was not very distinct, and most of the depth RS neurons we examined showed considerable responses in the monocular viewing condition. One of the monocular cues of depth rotation is the sinusoidal change of length of the bar as suggested by Johansson and Jansson (1968), although it is ambiguous with respect to the direction.

Since we observed a reversal of preferred direction of depth RS neurons in response to rotation of a trapezoidal window in the monocular viewing condition, monocular factors for activation of depth RS neurons may be more complicated, as suggested by the psychophysical studies of the illusion of Ames window. A number of explanations have been offered for the apparent reversal of the direction of rotation of a trapezoid. Ames (1951) postulated that subjects unconsciously assumed a trapezoid to be a slanted rectangle so that the shorter side always appeared tilted away. Likewise, the changes in perspective or the apparent orientation of an object in depth were considered to be the basis of the apparent reversal of rotation (Graham and Gillam 1970; Murch 1970; Power and Day 1973), whereas Braunstein (1971; Braunstein and Stern 1980) emphasized that direction judgements were based primarily on the dynamic

change in angle between horizontal and vertical contours. Such factors might have activated the depth RS neurons in response to the rotating trapezoid. Change of moving parallax might also have been a factor to activate them, as suggested by the change of preferred direction back to normal when the rotating trapezoidal plate was placed close to the animal (at the distance of 20 cm) in the monocular viewing condition.

Effect of extraretinal signals

The finding of the enhancement of the response of some RS neurons by visual tracking suggests that an extraretinal signal of eye movement may be incorporated in the excitatory input of these neurons, as in the case of visual tracking neurons (Sakata et al. 1983) or smooth pursuit cells (Komatsu and Wurtz 1988). These neurons probably distinguished rotary movement of the target object from the optical flow of the background because the retinal image of the surroundings moved in the direction opposite the image of the object during tracking (Sakata et al. 1983; Komatsu and Wurtz 1988). It was also suggested that there may be a mechanism in the posterior parietal cortex to distinguish the oculomotor signal of rotary eye movement from that of linear eye movement, since we found some RS neurons were specifically activated during rotary tracking.

Another extraretinal signal that enhanced the response of some RS neurons was the vestibular signal of the head rotation. Recently, Akbarian et al. (1988) and

Grusser et al. (1990) recorded vestibular neurons in the parietoinsular vestibular cortex (PIVC). Almost all PIVC neurons tested responded to visual stimulation. Since the most effective stimulus for PIVC neurons was a large structured visual pattern (rotation of striped cylinder surrounding the animal), visual vestibular interaction of RS neurons may be different from that of PIVC neurons. The preferred direction of RS neurons for rotation of the visual stimulus was the same as the preferred direction for vestibular stimulation, whereas the preferred direction of the majority of PIVC neurons for visual stimulation was opposite that for vestibular stimulation. This suggests that RS neurons responded to movement of the image of the monkey's own body or the chair rather than movement of the visual background as in the case of PIVC neurons. It should be noted that rotation of the retinal image of the body or chair was produced by vestibulo-ocular reflex (VOR) in the horizontal plane (Kawano et al. 1984) or ocular counterroll (OCR) in the frontal plane (Collewijn et al. 1985) because the eyes rotate in the direction opposite the rotation of the monkey's head. As the gain of VOR is 1.0 in the horizontal plane, the visual image of the body and chair rotate in the same direction and velocity as those of the rotating chair, while the background image is stationary. The image of the body and chair rotate in the same direction as that of the rotating chair also in the frontal planes. However, the velocity is slower in the frontal rotation, since the gain of OCR is less than 0.7.

Role of RS neurons in the perception of rotary movement

All the arguments mentioned above lead to the conclusion that the parietal RS neurons are likely to play a major role in the perception of rotary movement of objects in space. Recent psychophysical studies demonstrated that the human visual system contains "rotation detectors". Cavanagh and Favreau (1980) produced a rotational motion aftereffect (MAE) by prolonged adaptation to a rotating spiral. Rotational MAE was demonstrated also with depth rotation of a square (Petersik et al. 1984), as well as with rotation of a short spiral, whereas rotation of a long spiral caused radial MAE (Hershenson 1987). Freeman and Harris (1992) showed by means of complementary masking that the detection of rotation is unaffected by the presence of expansion (size change) and vice versa. The present results, showing that the RS neurons were selectively sensitive to rotary movement in contrast to linear translational movement, suggested that they were the neural substrate of rotation detectors. Moreover, the fact that some depth RS neurons showed a reversal of preferred direction in their response to the rotation of Ames window, in the same way that we perceive apparent reversal, strongly suggests that the activity of RS neurons is closely related to the subjective experience of percep-

tion of rotary movements. Psychophysical study of the perception of the stimulation of three-dimensional rotation on a two-dimensional display suggested that the rotation judgement may be based on a higher-level representation of a 3-D object (Petersik 1991). This is consistent with our finding that depth RS neurons may incorporate a number of monocular cues for depth perception (size difference, linear perspective, motion parallax, etc.). Perceived magnitude of rotation of 3-D objects projected on the screen was a monotonically increasing function of actual rotation, although perceived rotation associated with larger spheres was somewhat greater than that associated with smaller spheres (Kaiser and Calderone 1991; Petersik 1991). This was in good agreement with our finding that the responses of most RS neurons we examined were monotonically increasing functions of the angular velocity of the stimuli, although they were also dependent on the size of the stimuli, to some extent. Therefore, the discharge rate of the RS neurons was likely to be related to the perceived magnitude of rotation.

It may be emphasized that the RS neurons we recorded were likely to be concerned with the perception of movement of the external objects rather than that of self-motion through the environment, as in the case of rotation neurons of Tanaka and Saito (1989) and Tanaka et al. (1989), MSTd neurons sensitive to optic flow as studied by Duffy and Wurtz (1991a, b), or disparity-sensitive MSTd neurons of Roy et al. (1992). These neurons in the MSTd area responded preferentially to large field stimuli of dot patterns, whereas the RS neurons responded to rotation of a simple stimulus such as a slit, a pair of spots, or even a single spot, and their responses were independent of the shape of the stimulus, in contrast to the neurons in the anterior STS that responded selectively to rotation of the head and other 3-D objects (Perrett et al. 1985).

Flow of information processing for the RS neurons

The recording sites of RS neurons were concentrated in the middle and upper parts of the anterior bank of caudal STS. This region overlapped partly with the MST area which occupies the lower half of the anterior bank and a part of the fundus of caudal STS (Desimone and Ungerleider 1986), whereas most of the recording sites were outside the MST area and localized in the posterior parietal (PP) area between the lip of STS and the dorsal boundary of MST as defined by Desimone and Ungerleider (1986). The MST area receives direct projection from MT by definition (Maunsell and Van Essen 1983c; Ungerleider and Desimone 1986), but the PP area does not. Recently, Boussaoud et al. (1990) studied the cortical connection of the MST area and showed that area PP receives forward connection from both the central and the peripheral representation areas of MST (MSTc and MSTp), suggesting that area PP is higher in the hierarchy of cortical pathways for visual motion analysis.

In general, the functional properties of MST neurons were more complicated than those of MT neurons (Maunsell and Van Essen 1983a, b). Receptive fields of MST neurons were much larger than that of the MT neuron (Gattass and Gross 1981; Desimone and Ungerleider 1986). Many MST neurons as well as area 7a neurons were sensitive to size change or radial movement (Motter and Mountcastle 1981; Saito et al. 1986; Steinmetz et al. 1987; Tanaka and Saito 1989; Duffy and Wurtz 1991a, b). We recently found depth-movement-sensitive neurons in MST, which integrated both size change and disparity change signals (Sakata et al. 1993). However, the information processing for RS neurons, especially depth RS neurons, could be even more complicated, since it required the integration of signals of movement-sensitive cells of different preferred directions in 3-D space. Therefore, many RS neurons may well be higher in the hierarchy of information processing than MST neurons. Some RS neurons incorporated extraretinal signals of eye movement, similarly to many visual cells in area 7a or the lateral intraparietal area (Andersen and Mountcastle 1983; Andersen et al. 1990; Sakata et al. 1983). Other RS neurons integrated visual and vestibular signals. Thus most of the RS neurons we recorded were likely to be localized in the domain of the true association cortex, and represent one of the final stages of processing of visual motion signals in the cortical visual pathway for space vision (Mishkin et al. 1983; De Yoe and Van Essen 1988).

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