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Authors: Yamawaki, Yoshifumi, and Toh, Yoshihiro

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Response Properties of Visual Interneurons to Motion Stimuli in the Praying Mantis, *Tenodera aridifolia*

Yoshifumi Yamawaki* and Yoshihiro Toh

Department of Biology, Faculty of Science, Kyushu University,
Fukuoka 812-8581, Japan

ABSTRACT—Intracellular responses of motion-sensitive visual interneurons were recorded from the lobula complex of the mantis, *Tenodera aridifolia*. The interneurons were divided into four classes according to the response polarity, spatial tuning, and directional selectivity. Neurons of the first class had small, medium, or large receptive fields and showed a strong excitation in response to a small-field motion such as a small square moving in any direction (SF neurons). The second class neurons showed non-directionally selective responses: an excitation to a large-field motion of gratings in any direction (ND neurons). Most ND neurons had small or medium-size receptive fields. Neurons of the third class had large receptive fields and exhibited directionally selective responses: an excitation to a large-field motion of gratings in preferred direction and an inhibition to a motion in opposite, null direction (DS neurons). The last class neurons had small receptive fields and showed inhibitory responses to a moving square and gratings (I neurons). The functional roles of these neurons in prey recognition and optomotor response were discussed.

Key words: motion-sensitive neurons, spatial tuning, lobula complex, praying mantis, insect vision

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INTRODUCTION

Predatory animals receive sensory input and extract crucial information such as the location and distance of prey. Praying mantises are predatory insects that detect potential prey primarily by means of vision. After detection of a potential prey, they sometimes fixate or track it with movements of their head and/or body (Levin and Maldonado, 1970; Lea and Mueller, 1977; Rossel, 1980; Liske and Mohren, 1984; Yamawaki, 2000b). During visual fixation and tracking, mantises try to keep the target image on a foveal region, which is a limited retinal zone particularly designed for high spatial resolution (Horridge and Duelli, 1979; Rossel, 1979). They also try to keep the target image on a binocular visual field and use binocular disparity to estimate prey distance (Rossel, 1983, 1986). If the prey is sufficiently close, they strike it with rapid grasping movements of forelegs. The strike is occasionally accompanied with a displacement of the body, called lunge (Copeland and Carlson, 1979; Corrette, 1990; Prete and Cleal, 1996; Cleal and Prete, 1996). During these events, the mantis' central nervous system (CNS) extracts spatial characteristics about the prey (e.g. location in the visual field, distance and size) from visual information and

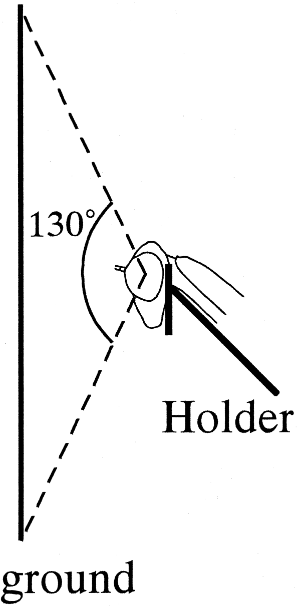

Fig. 1. Arrangement of the mantis head and computer display. Visual stimuli were generated on the computer display. A black square or black gratings on a white background was presented as motion stimuli. The white background subtended 130° in both height and width as seen by the mantis. The mantis was waxed to a holder dorsally.

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* Corresponding author: Tel. +81-92-642-2315;
FAX. +81-92-642-2315.
E-mail: yyamascb@mbox.nc.kyushu-u.ac.jp

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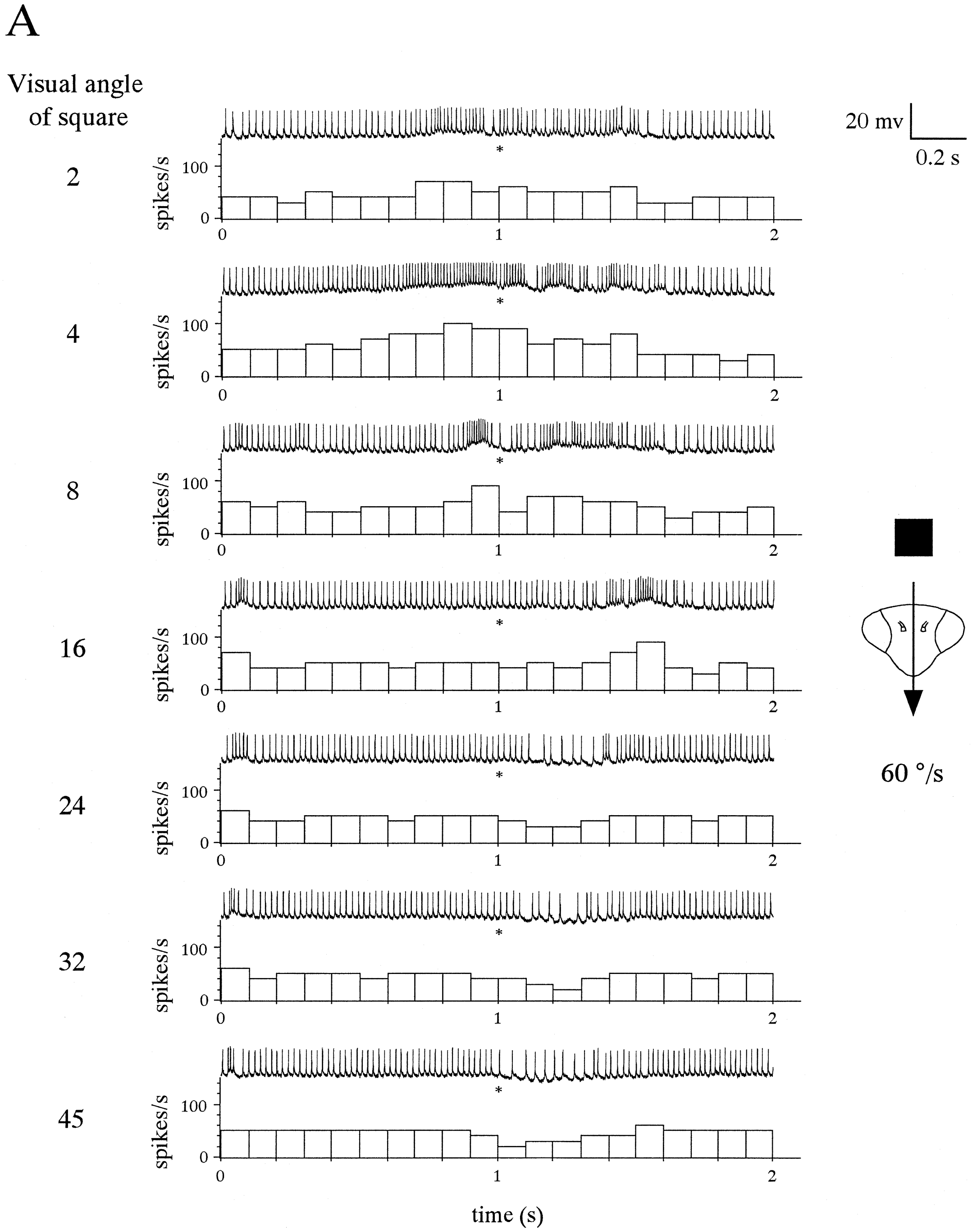
computes the motor command for the motoneurons controlling head and body turn and strike. However, little is actually known about how information about the prey is encoded in the CNS.

Prey recognition in the mantis has been examined in many behavioral experiments (e.g. Rilling *et al.*, 1959;

Table 1. Response properties of motion-sensitive neurons

Class	Response to motion	Spatial tuning	Directional selectivity	No. of recordings
DS	Excited	LF	yes	5
ND	Excited	–	no	50
SF	Excited	SF	no	10
I	Inhibited	–	no	6

LF, large-field motion-sensitive; SF, small-field motion-sensitive.



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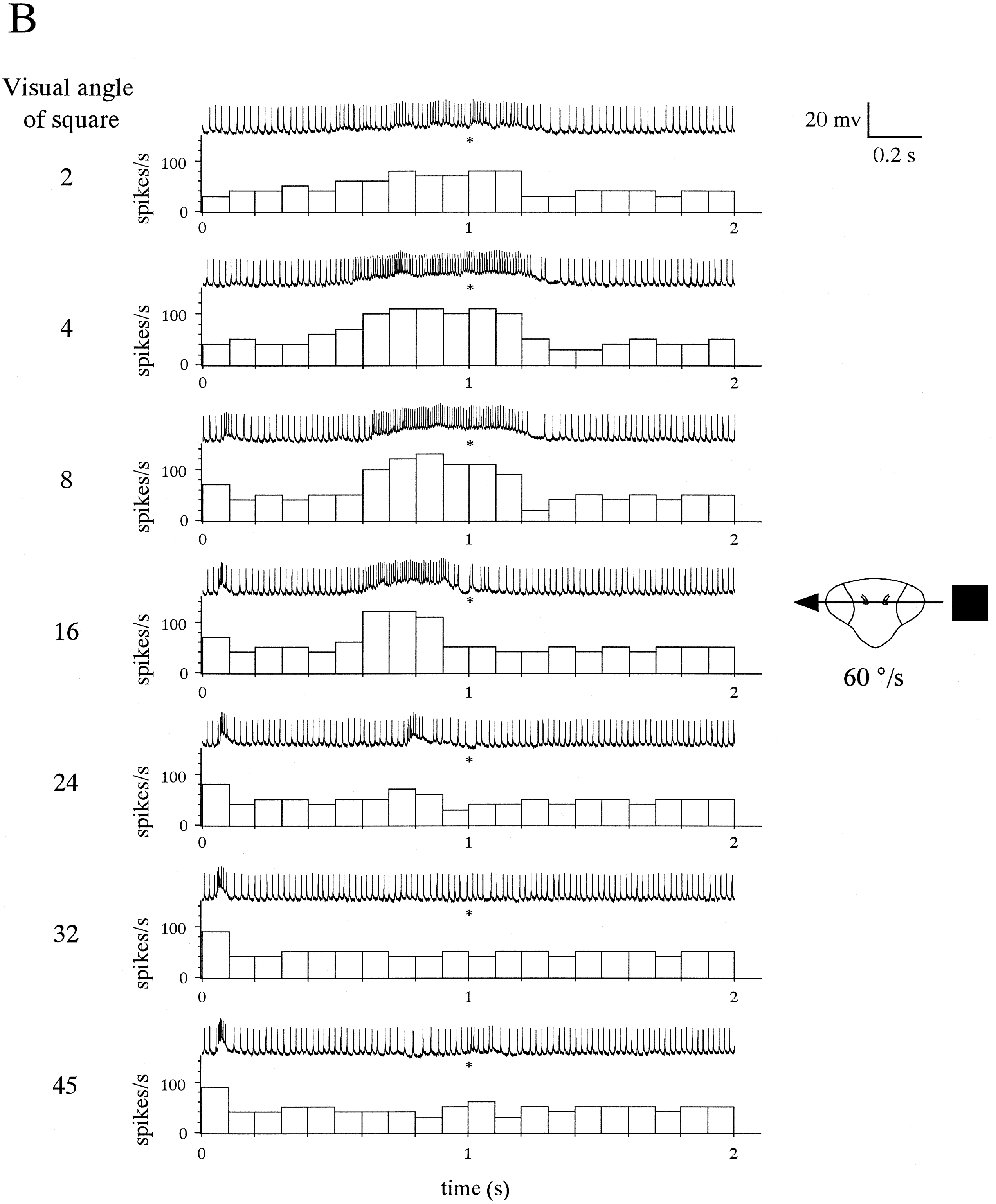

Fig. 2. Responses to moving squares of a class SF neuron. **A** Intracellular responses to squares moving from top (θ = 60°) to bottom (θ = –60°) through the midline of the mantis head (ψ = 0°) at an angular velocity of 60°/s. The visual angle of the squares ranged from 2 to 45°. Asterisks indicate the moment when the center of the square passed in front of the mantis head (θ = 0° and ψ = 0°). Peristimulus time histograms (PSTH) with 100 ms bins are also shown beneath the records. **B** Intracellular responses to squares moving from left (ψ = –60°) to right (ψ = 60°)

Holling, 1964; Iwasaki, 1990; Yamawaki, 2000a). Over the last decade, Prete and his colleagues have been studying the prey recognition algorithm used by the mantis. Their studies indicate that mantises recognize a moving object as prey if it falls within an envelope defined by stimulus parameters such as (1) overall size, (2) geometry in relationship to

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direction of movement, (3) length of the leading edge, (4) relative contrast, and (5) apparent speed (see Prete, 1999, for review). Contrary to these behavioral analyses, few electrophysiological experiments have been carried out to investigate the neural mechanism underlying prey recognition in the mantis. Gonka *et al.* (1999) have extracellularly recorded the responses of motion-sensitive descending neurons from the cervical nerve cord and found units preferentially responding to prey-like stimuli. Although such units may encode the presence of prey, the study provides little information about neural encoding of prey location in the visual field. In an early stage of that process, prey information may be represented by the spatio-temporal pattern of neural activity in the visual interneurons of the optic lobe.

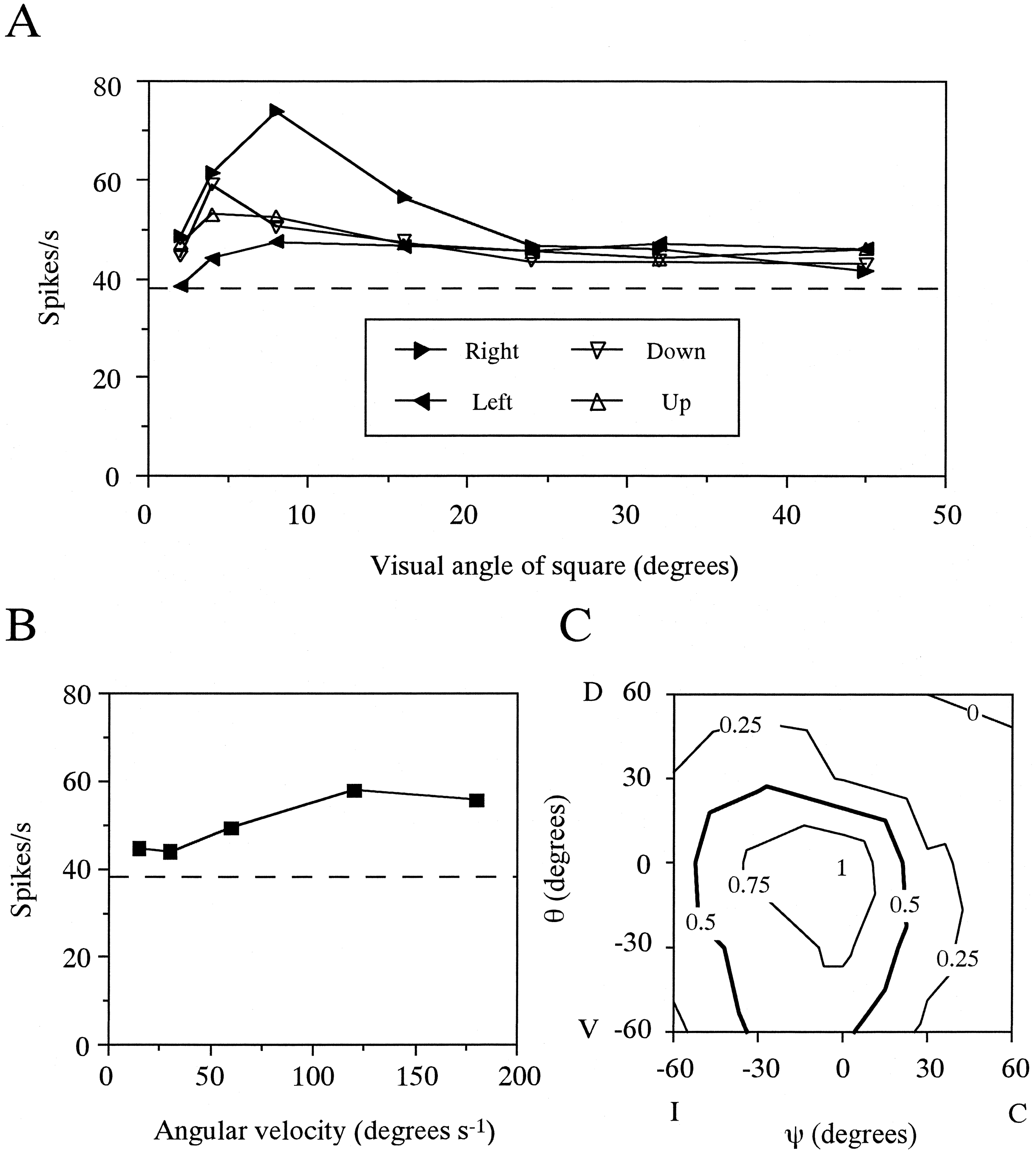

Fig. 3. Spatial and velocity tuning of a class SF neuron, and its receptive field. **A** Spike frequency of the neuron shown in Fig. 2 as a function of the visual angle of the square moving horizontally or vertically at an angular velocity of 60°/s. Broken line indicates the spontaneous activity. **B** Spike frequency of the neuron shown in Fig. 2 as a function of the angular velocity of the moving square (16°). **C** Receptive field of the neuron shown in Fig. 2. Contour map represents normalized response of the neuron, in which "0" and "1" indicate the spontaneous activity and maximum spike frequency, respectively. Positions in space are defined by the angles of azimuth (ψ) and elevation (θ). D, V, I, and C indicate the dorsal, ventral, ipsilateral, and contralateral directions in the visual field, respectively.

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In the present study, responses of visual interneurons in the lobula complex of the mantis have been recorded intracellularly. Recorded neurons have then been classified by their response properties to motion stimuli.

MATERIALS AND METHODS

Animals and preparation

Adults of the mantis *Tenodera aridifolia* were used. The egg

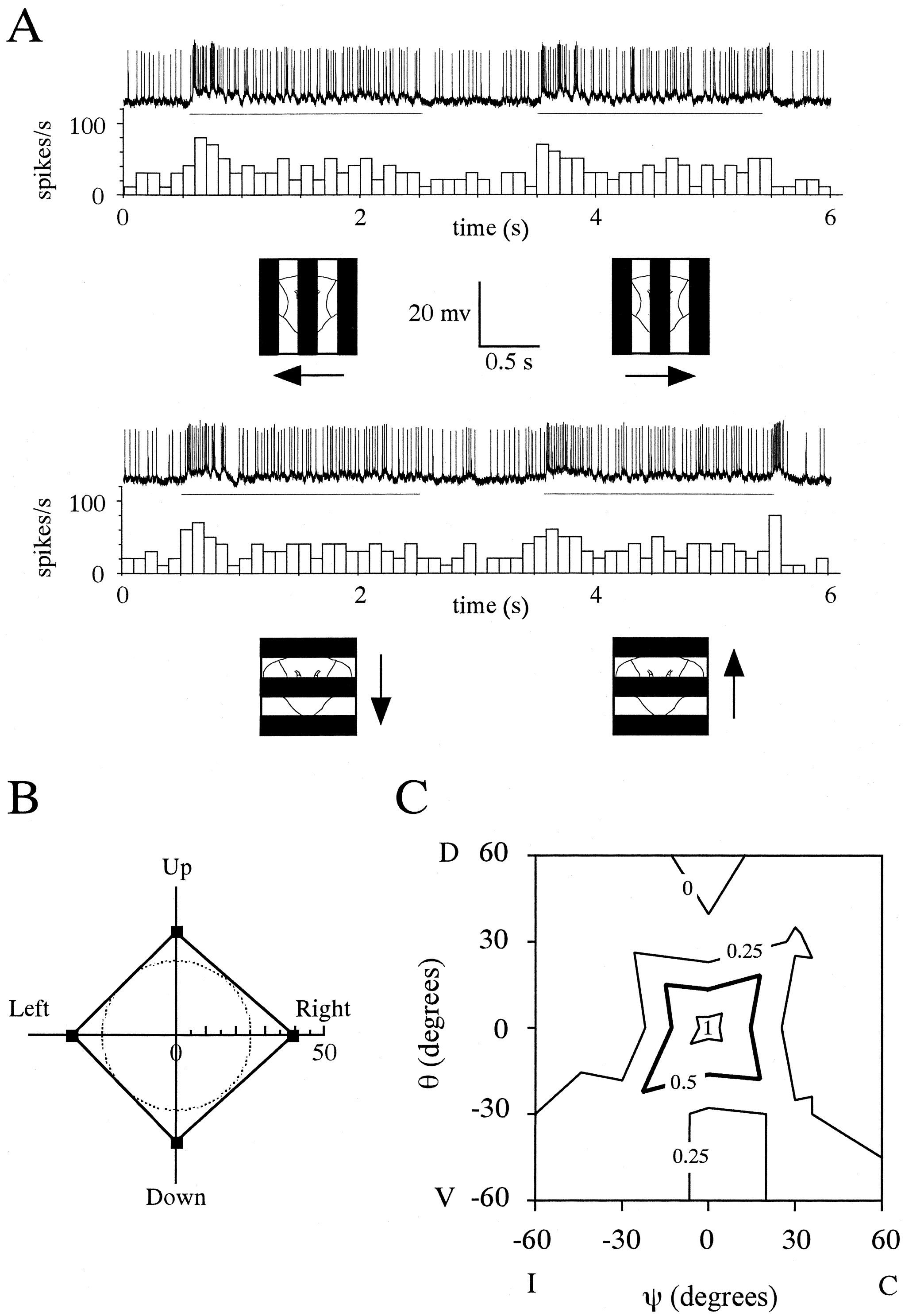

Fig. 4. Responses of a class ND neuron to moving gratings, its directional tuning , and its receptive field. **A** Intracellular responses to the gratings with a 32° spatial period moving to the right, the left, downward, or upward, at an angular velocity of 30°/s. Thin bars indicate stimulus presentation. **B** Directional tuning in response to moving gratings shown in A. Spike frequency as a function of four directions are plotted on polar coordinates. Broken circle indicates the spontaneous activity. **C** Receptive field of the neuron shown in A.

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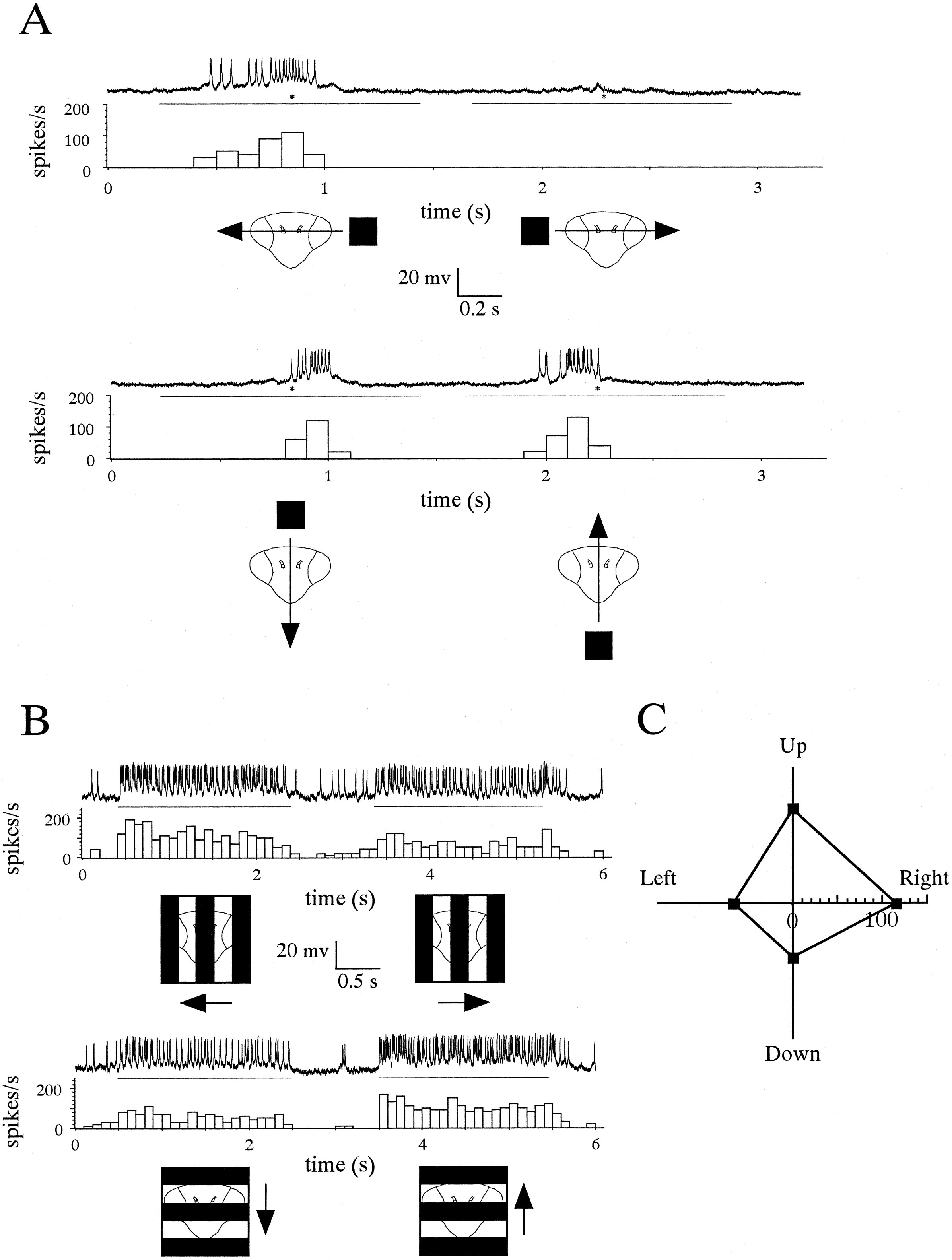

Fig. 5. Responses of a class ND neuron to moving squares and gratings, and its directional tuning. **A** Intracellular responses to the 16° squares moving horizontally or vertically through the center of the visual field at an angular velocity of 120°/s. Thin bars indicate stimulus presentation. Asterisks indicate the moment when the center of the square passed in front of the mantis head ($\theta = 0°$ or $\psi = 0°$). **B** Intracellular responses to the gratings with a 32° spatial period moving to the right, the left, downward, or upward, at an angular velocity of 30°/s. **C** Directional tuning in response to moving gratings shown in B. This neuron showed little spontaneous discharge.

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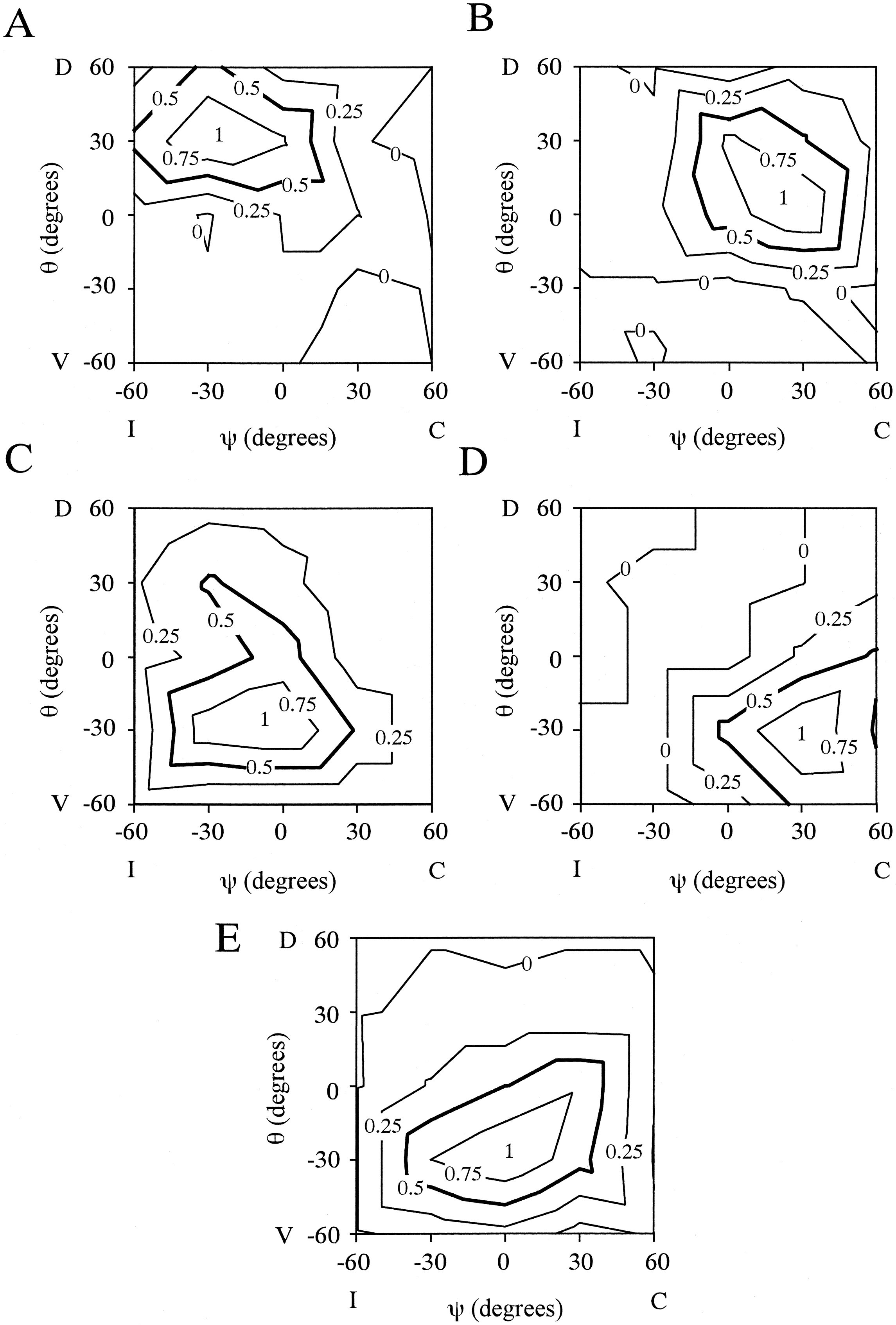

Fig. 6. Typical receptive fields of class ND neurons, responses of which were dependent on the direction of motion. One (C) is the same neuron as that shown in Fig. 5.

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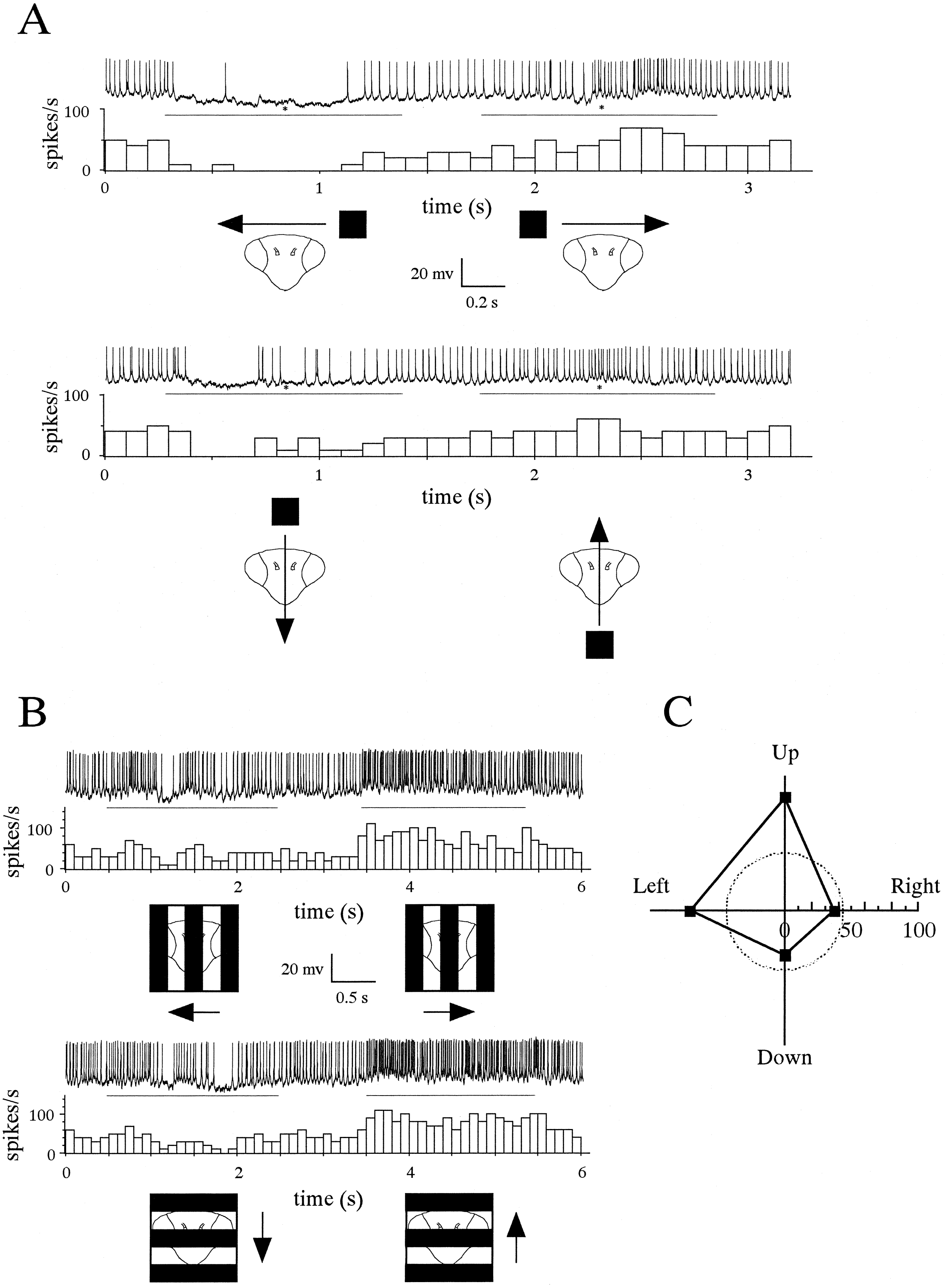

Fig. 7. Responses of a class DS neuron to moving squares (A) and gratings (B), and its directional tuning (C). The stimuli are the same as those in Fig. 5 except that squares were moved horizontally through the sweep 30° above the center of the visual field.

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cases were collected in the suburbs of Fukuoka. First- to third-instar nymphs of the mantis were fed on live fruit flies, and nymphs older than the third-instar were fed on live cockroaches.

After cold anesthesia, mantises were waxed to a holder to stabilize the thorax and abdomen dorsally. Their antennae, legs and wings were removed. The head was waxed in place, leaving the eyes uncovered. The dorsal part of the head capsule and muscles were removed to expose the left optic lobe. The preparation was perfused with a cockroach saline solution (Yamasaki and Narahashi, 1959) to prevent desiccation.

Intracellular recording

Intracellular recordings were made from neurons in the lobula complex of the left optic lobe using glass microelectrodes. The electrode was filled with 3 M KCl, and had a tip resistance of between 70 and 100 MΩ when measured in a saline solution. A silver wire was placed in the saline solution in the head capsule as an indifferent electrode. Electrical signals were amplified with a D.C. amplifier. Some data were stored on magnetic tapes for off-line analysis by a computer equipped with an analog-digital converter (Mac Lab, AD Instruments), and the others were stored directly in a computer equipped with another analog-digital converter (1401, Cambridge Electronic Design).

Stimuli

Visual stimuli were generated on the TFT liquid crystal display (LCM-T133A, Logitec) by a computer. The display was placed parallel to the frontal plane of the mantis' head at a distance of 4 cm (Fig. 1). The motion stimulus was a black square or black gratings on a white background. The luminances of white and black on the display were 66.59 and 0.63 cd/m^2, respectively. The contrast between black and white is: (66.59–0.63)/(66.59+0.63)=0.98. The angular subtense of the white background was 130° in both height and width. The black square was moved in front of the mantis head in four directions (up, down, right, or left) from one of the edges of the white background to the other. The angular subtense of the black square at the center of the white background was varied from 2 to 45°. The average angular velocity of the square was varied from 15 to 180°/s. In each case, the average spike frequency between the appearance and disappearance of the square was calculated. The angular subtense of gratings was 100° in both height and width. The vertical gratings were moved to the right or left, whereas horizontal gratings were moved up or down. The spatial period of the gratings was varied from 16 to 45°, and its average angular velocity was varied from 5 to 45°/s. The average spike frequency during the first second of gratings presentation was calculated. Light-on and light-off stimuli were presented by changing the square part (130°×130°) of the display from black to white or vice versa. The spontaneous activity was measured during the period 1-4 seconds before each stimulus presentation.

To determine the receptive field of each motion-sensitive neuron, we repeatedly moved the black square (16°) five times with different paths in the neuron's preferred direction at an average angular velocity of 120°/s. The center position of the square on the path in the visual field is specified by the angles of azimuth ψ or elevation θ. For example, when the square was moved horizontally from ψ = –65° to 65°, the square was moved with five different elevation paths (θ = –60, –30, 0, 30, and 60°). Each recording of the neuron's responses to these was divided into five regions according to the angle of azimuth ψ (–60, –30, 0, 30, and 60°): these five regions were [–65°, –45°], [–45°, –15°], [–15°, 15°], [15°, 45°], and [45°, 65°], respectively. Then, the average spike frequencies in all 25 regions were calculated. To make the angular sensitivity contour map, we normalized the spike frequencies so that spontaneous activity and maximum spike frequency became 0 and 1.0 respectively. In the case of neurons that were mainly inhibited by motion stimuli, spike frequencies were normalized so that spontaneous activity and minimum spike frequency became 0 and –1.0 respectively. The diameter of the receptive field was roughly expressed by the angular subtense of the contour at a normalized spike frequency of 0.5 (or –0.5), and the receptive field was classified into small (0–30°), medium (30–60°), and large (60–90°).

RESULTS

Seventy-six neurons were recorded from 47 mantises: 71 neurons showed a marked response to motion stimuli, and the remaining 5 neurons usually responded to light-on and/or off stimuli. The motion-sensitive neurons could be divided into four classes according to the response polarity, spatial tuning, and directional selectivity (Table 1). Ten neu-

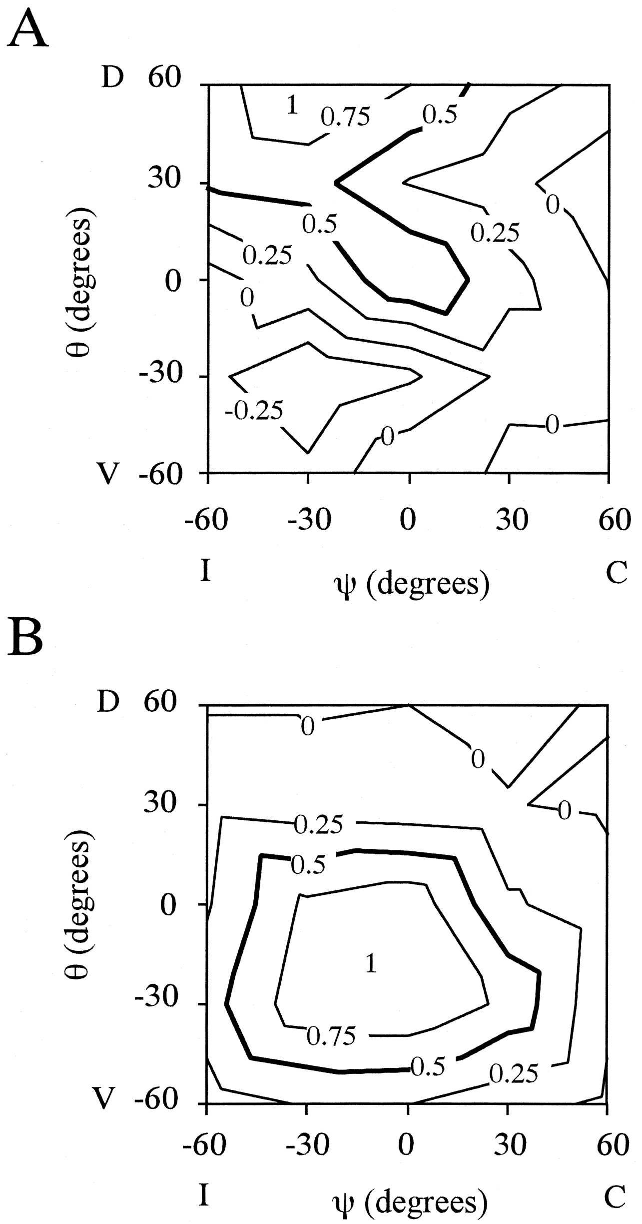

Fig. 8. Receptive fields of two class DS neurons. One (A) is the same neuron as that shown in Fig. 7.

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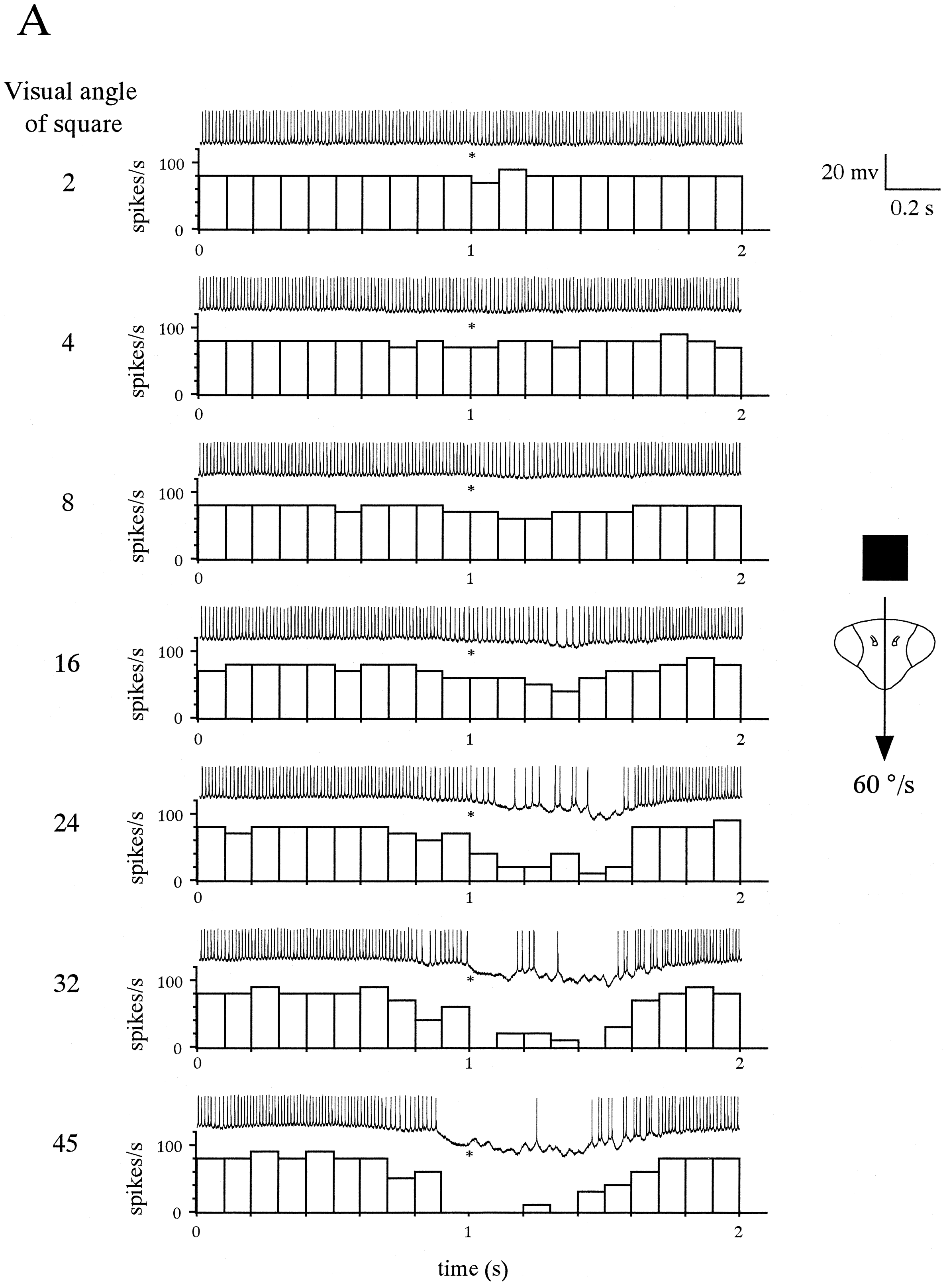
rons showed a strong excitation in response to a small-field motion such as small square moving in any direction. They were termed SF neurons. Fifty neurons showed a non-directionally selective response: an excitation to a large-field motion of gratings in any direction. They were termed ND neurons. Five neurons exhibited directionally-selective responses: an excitation to a large-field motion of gratings in the preferred direction and an inhibition to motion in the



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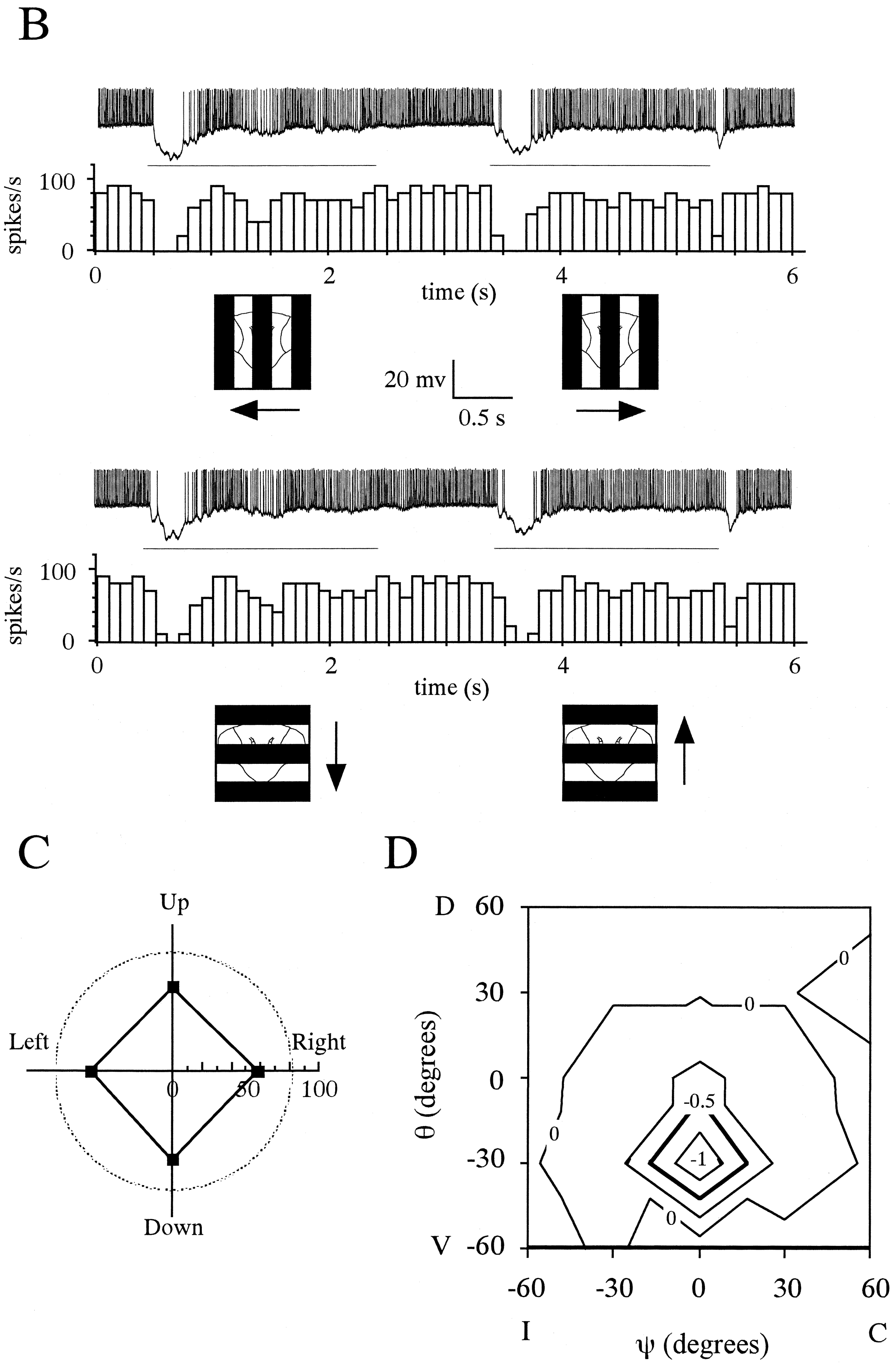

Fig. 9. Responses of a class I neuron to moving squares (A) and gratings (B), its directional tuning (C), and its receptive field (D).

opposite, null direction. They were termed DS neurons. The remaining 6 neurons showed inhibitory responses to a moving square and gratings. They were termed I neurons.

SF neurons showed a stronger excitation to a small moving square than to a large moving square (Figs. 2 and 3A). Some of them were inhibited by a large moving square

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(Fig. 2A), while the others responded slightly to a large moving square and to moving gratings. The spike frequency of the former appeared to vary, depending on the direction of motion (Fig. 3A), but did not show clear directional selectivity. The spike frequency of them increased as the square was moved more rapidly (Fig. 3B). They had small (0–30°), medium (30–60°), or large (60–90°) receptive fields in the central or ventral area of the visual field. The SF neuron shown in Fig. 3C had a large receptive field in the central area.

ND neurons responded with similar spike frequency to motion in any direction (Fig. 4). They had small, medium, or large receptive fields. Small receptive fields were located only in the central or ventral area of the visual field. Medium-size receptive fields were located in one of the quadrants (ventro-ipsilateral, dorso-ipsilateral, ventro-contralateral, or dorso-contralateral), or in the ventral or central area of the visual field. One had a large receptive field in the central area of the visual field.

Some ND neurons showed larger responses to a stimulus moving in one direction than in the opposite direction (Fig. 5). They had receptive fields of medium size in one of the quadrants of visual field, or in its ventral area (Fig. 6).

Of the neurons recorded in the present study, only DS neurons showed clear directional selectivity. These neurons were excited by motion in one particular direction and inhibited by motion in the opposite direction (Fig. 7). These neurons had large receptive fields in the visual field (Fig. 8). Thus, it is suggested that they respond to a large-field motion such as optic flow generated by rotation of the mantis head.

The I neurons responded to moving squares with a decrease in spike frequency. In some I neurons, the spike frequency decreased as the square's size increased (Fig. 9A). These cells responded to moving gratings with phasic depression of their spike discharge (Fig. 9B). These cells did

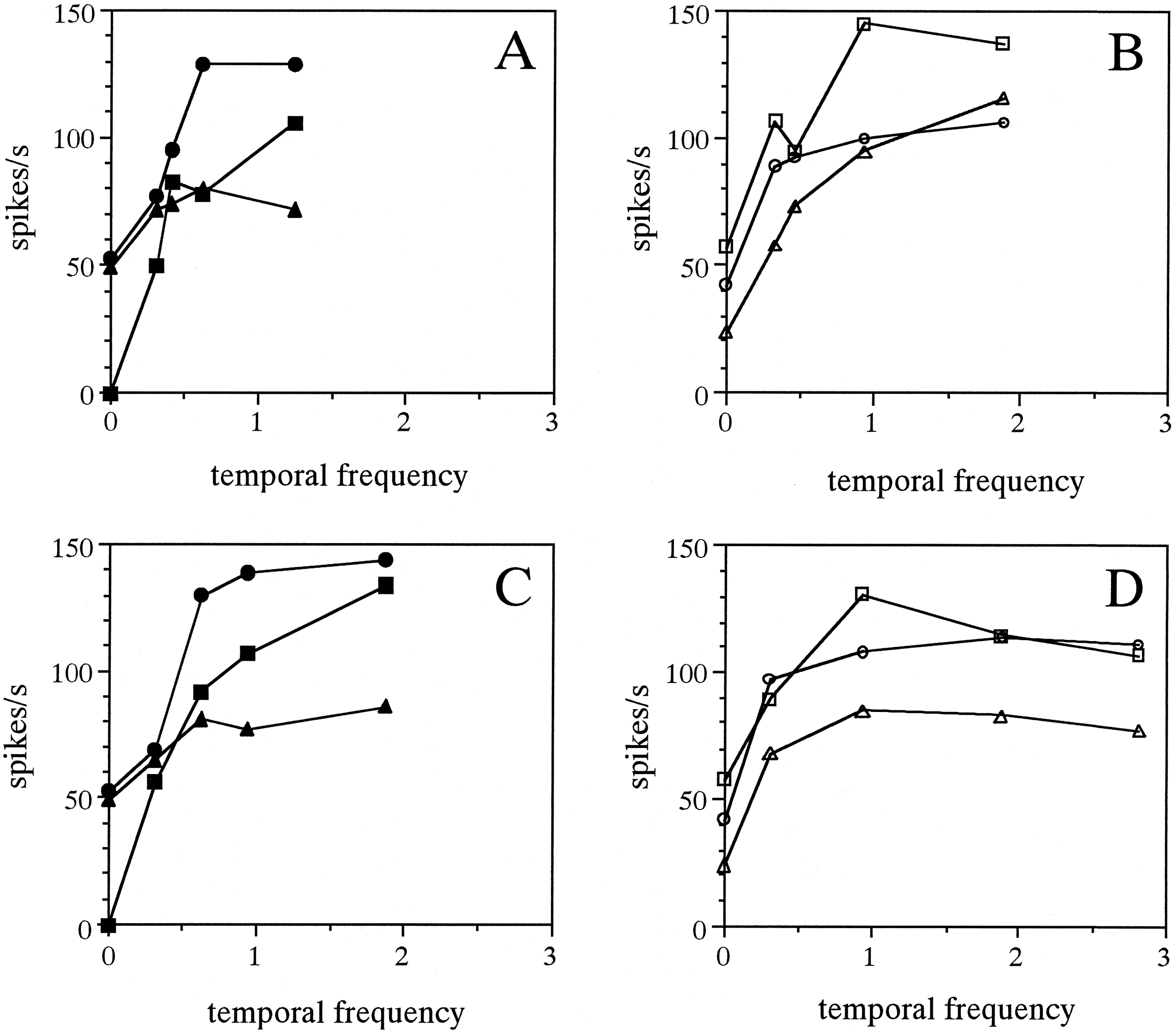

Fig. 10. Spike frequencies of DS and ND neurons as a function of temporal frequency of gratings moving in the preferred direction. Temporal frequency is the number of cycles of the periodic pattern to move across a point on the retina per second. It was varied by changing the spatial periods of the gratings (A and B) or the angular velocities (C and D). The spike frequency when the temporal frequency is 0 indicates spontaneous activity. Each neuron has the same symbol in all plots: filled triangle, a DS neuron; other symbols, ND neurons.

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not show clear directional selectivity (Fig. 9C). They had small receptive fields in the ventral part of the visual field (Fig. 9D).

Effects of the spatial period and velocity of the grating

In some neurons, except those of SF, the effects of the spatial period and velocity of the gratings on the responses were examined. The firing rate of DS and ND neurons tended to increase as the spatial period of the gratings was decreased or as the velocity of the gratings was increased. The response properties of these neurons appeared to depend on the temporal frequency of the gratings, because all the response curves to temporal frequency were almost the same irrespective of whether either the spatial period (Fig. 10A, B) or the velocity (Fig. 10C, D) was varied. In most of these neurons, the firing rates increased until the temporal frequency reached 1.0, and then the rates appeared to plateau. The firing rate of I cells tended to decrease as the temporal frequency of the gratings increased.

DISCUSSION

In the present work, we recorded responses of four groups of motion-sensitive neurons. Even though anatomical information on these neurons is lacking, the results of the present work give us some clues to understand the neural representation of prey information in the mantis CNS.

Encoding the size of motion stimuli

The spatial tuning of class SF neurons suggests that these neurons respond best to small moving objects such as a prey. In behavioral experiments, the mantis frequently strikes a small moving block (Iwasaki, 1990; Prete, 1990) or a small moving square generated on a computer display (Prete and Mahaffey, 1993; Prete and McLean, 1996). This behavioral size-preference coincides with the spatial tuning of the SF neurons. These neurons may therefore encode the size of a moving object and whether the image of a prey falls within their receptive fields or not. However, the velocity tuning of these neurons was slightly different from the behavioral velocity-preference. The spike frequency of these neurons increased as the square moves faster, but it appeared to plateau when the velocity reached around 120°/s. On the other hand, the strike rate of the mantis increases until the velocity of the square reaches around 90°/s and then decreases (see Prete, 1999, for review).

Small-field motion-sensitive cells have been reported in various insects (Collett, 1971; Olberg, 1981, 1986; Egelhaaf, 1985a, b, c; Okamura and Toh, 2001). Most of them, for example the FD cells in the fly (Egelhaaf, 1985b) and most of the TSDNs in the dragonfly (Olberg, 1986), are directionally selective, but SF neurons found in the present study did not show clear directional selectivity. Not only in the mantis, but also in the tiger beetle larvae, the neurons responding to small moving objects are non-directionally selective (Okamura and Toh, 2001). The difference in directional selectivity may be due to whether the insects fly in the sky or walk on the ground during tracking an object. During flight, both the insects themselves and the prey move rapidly. When the insects try to track a moving object, the object moves a long distance during the insect's response time (the latency period). Hence, detection of the direction of object motion is crucial for continuous tracking because it can assist the insect to track the object predictively. Actually, predictive tracking has been reported in the hoverfly (Collett and Land, 1978). By contrast, tiger beetle larvae ambush prey, and mantises ambush prey or walk slower than flying insects during pursuit of prey. Hence, the direction of object motion may not be of such importance for them.

Encoding the location of motion stimuli

ND neurons with small or medium size receptive fields may encode the location of moving stimuli in the visual field. Although each ND neuron responded strongly to a large-field motion such as provided by moving gratings, the population of ND neurons acting in concert can give information on the spatial property of motion stimuli. For example, most of the medium-size receptive fields of ND neurons were located in one of the quadrants of visual field. These neurons can comprise the coordinate system for locating objects in the visual field.

In some ND neurons, the firing rates varied depending on the direction of motion. Hence, they may encode not only the position of the object but also the direction of its motion. For example, the cell in Figs. 5 and 6C had a receptive field in the ventro-ipsilateral part and it responded best to the motion of dorso-contralateral direction. This implies that its response is largest when the object is moving towards the center of the visual field.

The ND neurons which had receptive fields in the contralateral visual field may have their dendrites and cell body in the contralateral optic lobe, and project their axons from there. Connection cells projecting between the optic lobes have previously been identified in the fly (Hausen, 1993).

Most small receptive fields of the ND neurons are located at the center or in the ventral area of the visual field. Neurons having a receptive field in the center of the visual field are considered to form part of the coordinate system for locating objects described above. The ventral area of visual field is considered important because this area may correspond to the foveal region. According to Rossel (1979), the foveal region seems to view a downward direction, roughly $\theta = -45°$ in the visual field.

Detection of self-motion

DS neurons were directionally selective, and they responded best to a large-field motion. This suggests that they detect the retinal image flow generated by the insect's self-motion. In the fly's lobula plate, many motion-sensitive neurons so-called tangential cells have been identified, most of which are tuned to a large-field motion (see Hausen, 1993, for review). Among these, for example, HSN and HSE

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cells generally respond to horizontal backward (from head to tail) motion in the ipsilateral visual field and are inhibited by forward motion. These two cells receive additional input from the contralateral visual field and show sensitivity to rotatory motion. This suggests that these cells are designed to monitor preferentially rotation of the fly around its vertical body axis and involved in sensory control of the course-stabilizing optomotor response during flight. Likewise, DS neurons in the present study may be involved in the optomotor response.

Tuning to temporal frequency

It has been reported that the responses of tangential cells in the fly depend on the temporal frequency of the stimulus, and show a response optimum at 1–10 Hz (see Hausen, 1993, for review). A similar dependency on temporal frequency was found in the responses of mantis neurons in the present study, except with class SF neurons. However, because the responses were tested only in a narrow range of temporal frequency (0.3–2.8 Hz), their response optimum is uncertain. Further experiments are needed to clarify the tuning property of motion-sensitive neurons in the mantis to temporal frequency.

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REFERENCES

Cleal KS, Prete FR (1996) The predatory strike of free ranging praying mantises, *Sphodromantis lineola* (Burmeister). II: strikes in the horizontal plane. Brain Behav Evolut 48: 191–204

Collett T (1971) Visual neurones for tracking moving targets. Nature 232: 127–130

Collett TS, Land MF (1978) How hoverflies compute interception courses. J Comp Physiol 125: 191–204

Copeland J, Carlson AD (1979) Prey capture in mantids: A non-stereotyped component of lunge. J Insect Physiol 25: 263–269

Corrette BJ (1990) Prey capture in the praying mantis *Tenodera aridifolia sinensis*: coordination of the capture sequence and strike movements. J Exp Biol 148: 147–180

Egelhaaf M (1985a) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly I. Behavioral constraints imposed on the neuronal network and the role of the optomotor system. Biol Cybern 52: 123–140

Egelhaaf M (1985b) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly II. Figure-detection cells, a new class of visual interneurones. Biol Cybern 52: 195–209

Egelhaaf M (1985c) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly III. Possible input circuitries and behavioral significance of the FD-cells. Biol Cybern 52: 267–280

Gonka MD, Laurie TJ, Prete FR (1999) Responses of movement-sensitive visual interneurons to prey-like stimuli in the praying mantis *Sphodromantis lineola* (Burmeister). Brain Behav Evolut 54: 243–262

Hausen K (1993) Decoding of retinal image flow in insects. In "Visual motion and its role in the stabilization of gaze" Ed by FA Miles, J Wallman, Elsevier, Amsterdam, pp 203–235

Holling CS (1964) The analysis of complex population processes. Can Entomol 96: 335–347

Horridge GA, Duelli P (1979) Anatomy of the regional differences in the eye of the mantis *Ciulfina*. J Exp Biol 80: 165–190

Iwasaki T (1990) Predatory behavior of the praying mantis, *Tenodera aridifolia* I. Effect of prey size on prey recognition. J Ethol 8: 75–79

Lea JY, Mueller CG (1977) Saccadic head movement in mantids. J Comp Physiol A 114: 115–128

Levin L, Maldonado H (1970) A fovea in the praying mantis eye III. The centring of the prey. Z vergl Physiol 67: 93–101

Liske E, Mohren W (1984) Saccadic head movements of the praying mantis, with particular reference to visual and proprioceptive information. Physiol Entomol 9: 29–38

Okamura J-Y, Toh Y (2001) Responses of medulla neurons to illumination and movement stimuli in the tiger beetle larvae. J Comp Physiol A 187: 713–725

Olberg RM (1981) Object- and self-movement detectors in the ventral nerve cord of the dragonfly. J Comp Physiol 141: 327–334

Olberg RM (1986) Identified target-selective visual interneurons descending from the dragonfly brain. J Comp Physiol A 159: 827–840

Prete FR (1990) Configural prey recognition by the praying mantis, *Sphodromantis lineola* (Burr.); Effects of size and direction of movement. Brain Behav Evolut 36: 300–306

Prete FR (1999) Prey recognition. In "The praying mantids" Ed by FR Prete, H Wells, PH Wells, LE Hurd, Johns Hopkins University Press, Baltimore, pp 141–179

Prete FR, Cleal KS (1996) The predatory strike of free ranging praying mantises, *Sphodromantis lineola* (Burmeister). I: strikes in the mid-sagittal plane. Brain Behav Evolut 48: 173–190

Prete FR, Mahaffey RJ (1993) Appetitive responses to computer-generated visual stimuli by the praying mantis *Sphodromantis lineola* (Burr.). Visual Neuroscience 10: 669–679

Prete FR, McLean T (1996) Responses to moving small-field stimuli by the praying mantis, *Sphodromantis lineola* (Burmeister). Brain Behav Evolut 47: 42–54

Rilling S, Mittelstaedt H, Roeder KD (1959) Prey recognition in the praying mantis. Behaviour 14: 164–184

Rossel S (1979) Regional differences in photoreceptor performance in the eye of the praying mantis. J Comp Physiol 131: 95–112

Rossel S (1980) Foveal fixation and tracking in the praying mantis. J Comp Physiol 139: 307–331

Rossel S (1983) Binocular stereopsis in an insect. Nature 302: 821–822

Rossel S (1986) Binocular spatial localization in the praying mantis. J Exp Biol 120: 265–281

Yamasaki T, Narahashi T (1959) The effects of potassium and sodium ions on the resting and action potentials of the cockroach giant axon. J Insect Physiol 3: 146–158

Yamawaki Y (2000a) Effects of luminance, size, and angular velocity on the recognition of nonlocomotive prey models by the praying mantis. J Ethol 18: 85–90

Yamawaki Y (2000b) Saccadic tracking of a light grey target in the mantis, *Tenodera aridifolia*. J Insect Physiol 46: 203–210

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