Visual Response Properties of Neurons in the Parahippocampal Cortex of Monkeys

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INTRODUCTION

The parahippocampal (PH) and perirhinal (PR) cortices are subdivisions of the medial temporal lobe. These two cortices are regarded as an interface between unimodal and multimodal association cortices and hippocampal formation (Squire and Zola-Morgan 1991; Van Hoesen 1982). However, there are differences in anatomical connections between the PH and PR cortices. The PR cortex receives cortical inputs principally from area TE, the higher-order visual area related to object vision (Martin-Elkins and Horel 1992; Suzuki and Amaral 1994). Neurons in area TE are known to have large, nontopographically organized visual receptive fields (RFs), which almost always include the center of gaze (Desimone and Gross 1979; Gross et al. 1972; Tanaka et al. 1991). On the other hand, the PH cortex receives inputs from various cortical areas such as the inferior temporal, posterior parietal, frontopolar, and cingulate cortices (Barnes and Pandya 1992; Cavada and Goldman-Rakic 1989; Distler et al. 1993; Goldman-Rakic et al. 1984; Jones and Powell 1970; Martin-Elkins and Horel 1992; Seltzer and Pandya 1976, 1984, 1991; Suzuki and Amaral 1994). The PH cortex receives inputs only from the peripheral visual field representation of areas V2 and TEO (Distler et al. 1993; Gattass et al. 1997). These anatomical characteristics suggest that the PH cortex receives information from the peripheral as well as central visual fields, whereas the PR cortex principally receives information from the central visual field related to object vision.

So far the effect of the lesion of the PH cortex is not clear, but neuropsychological studies suggest some functional differences between the PH and PR cortices. A lesion in the PR cortex induces deficits in various visual recognition memory tasks, such as delayed nonmatching-to-sample tasks (e.g., Buckley et al. 1997; Meunier et al. 1993), whereas that in the PH cortex does not (Ramus et al. 1994). A few studies suggest that combined lesions of the PH and the other area induce some impairment. Lesions in both the PH and PR cortices produce deficits in a tactual memory task (Suzuki et al. 1993) and those in both the PH cortex and hippocampus produce deficits in spatial memory tasks (Angeli et al. 1993; Parkinson et al. 1988).

Neuronal responsiveness in the PR cortex has been relatively well investigated in the context of visual memory tasks (e.g., Miller et al. 1993; Nakamura et al. 1994; Riches et al. 1991). Those studies found that neurons in the PR cortex responded selectively to complex visual stimuli such as images. In contrast, response properties of PH neurons are poorly understood. Riches et al. (1991) examined visual response properties of various areas in the medial temporal lobe using simple geometrical shapes and reported that the stimulus selectivity in the PR cortex and area TE was higher than that in the PH cortex and hippocampus. Boussaoud et al. (1991) examined an RF property of neurons in the posterior portion of the inferior temporal cortex and reported that neurons in the posterior portion of the PH cortex (area VTF) had a relatively small, contralateral RF and tended to have a visuotopographic organization. Nakamura et al. (1994) examined neuronal responses...
to images of various natural objects in the anterior medial temporal areas and reported that neurons in the PH and PR cortices selectively responded to complex visual stimuli. However, these studies did not focus on the function of PH neurons. Creutzfeldt and colleagues attempted to elucidate the functions of the hippocampus and PH cortex and reported that PH neurons responded to some obscure events (e.g., opening or closing of a door of a shielded room; Salzmann et al. 1993; Vidyaasagar et al. 1991). Thus response properties of PH neurons are still unclear.

In the present study we examined visual response properties of PH neurons, such as an RF property, a direction selectivity, and selectivities for images, shapes, and colors to elucidate the role of the PH cortex in visual processing. For some aspects we further compared visual response properties of PH neurons with those of PR neurons. Based on the previous studies described above, it is expected that neurons in the PH cortex convey more information concerning spatial processing, whereas those in the PR cortex do more information concerning object processing (Nakamura and Kubota 1996).

**METHODS**

**Subjects**

Three male rhesus monkeys (Macaca mulatta, 4.5–6.2 kg, 3- to 5-yr-old) were used as subjects. Each monkey was housed in an individual cage. Water was withheld before each daily session and juice was given as reward in an experimental room. Supplemental water and fruit were given after the session, when needed. Food (monkey chow) was available ad libitum. All experiments were performed in accordance with the guidelines outlined in the “Guide for the Care and Use of Laboratory Animals” of the National Research Council (1996) and the “Guide for Care and Use of Laboratory Primates” published by Primate Research Institute, Kyoto University (1986, 2002).

**Behavioral procedure**

All experiments were performed in a dark soundproof room. Each monkey was seated in a primate chair with its head fixed by a head-restraining device during the experimental session. All of the monkeys had been habituated to the experimental room and the primate chair with the head restraint. A 20-in. CRT monitor was placed 28 cm from the monkeys’ eyes. During the experiment, the monkeys’ behavior was monitored by an infrared camera, and was observed through a TV monitor. The monkeys were trained to perform visual reaction time and delayed nonmatching-to-sample tasks by pressing and releasing a lever attached to the primate chair (Fig. 1).

**VISUAL REACTION TIME TASK.** Each trial started by the monkey pressing the lever. After the monkey pressed the lever and kept it pressed for 1.5 s, a circular fixation spot (0.6 deg in diameter) was presented at the center of the monitor display. The monkey was required to fixate the spot within 3 deg for 3.5–5.0 s and to release the lever when the spot was replaced by a cross. If the monkey correctly released the lever within 0.8 s of the presentation of the cross, a drop of juice (approximately 0.4 ml) was administered as a reward. If the monkey broke fixation or released the lever during the trial, the trial was aborted without any rewards. After the monkey started to fixate the spot for 1.0 s, a visual stimulus was presented for 0.5 s.

**DELAYED NONMATCHING-TO-SAMPLE TASK.** The monkey had to press the lever and keep it pressed throughout a trial in the delayed nonmatching-to-sample task. After a waiting period of 1.5 s, a fixation spot (0.6 deg in diameter) was presented at the center of the monitor. After the monkey fixated the spot within 5 deg for 0.5 or 1.0 s (usually 1.0 s), a sample stimulus was presented for 0.5 s. After the sample stimulus was presented repeatedly one to three times (at random) with a delay period of 1.5 s, a different (nonmatching) stimulus was presented. The monkey was required to remember the sample stimulus during the delay period, to maintain its fixation on the spot throughout a trial, and to release the lever within 0.8 s of the presentation of the nonmatching stimulus. If the monkey correctly released the lever, a drop of juice was given as a reward. If the monkey released the lever before the nonmatching stimulus presentation or broke fixation at any time during the trial, the trial was aborted without providing any rewards.

First the monkey was trained to perform both tasks without eye control. After a surgery to implant a head-restraining device, the monkey was retrained in the tasks with eye control.

**Visual stimuli**

We prepared 3 types of visual stimuli: bars, geographical shapes, and images. The bar and shape stimuli were generated by a personal computer to present equiluminantly in 5 colors (blue, green, yellow, red, and white). The bar was a rectangle subtending the visual angle of 0.6 × 8 deg. A set of the shape stimuli consisted of 8 simple geometrical patterns (see Figs. 7B and 8B). The images were full-colored images of a human face, a monkey face, a fruit, and a tool. These image stimuli were presented on the monitor by a personal computer via a video board (Canopus, Kobe, Japan). Each image was presented with a gray square (14 × 14 deg) as the background. The images of a human or monkey face were whole-faced calm facial images. A set of the image stimuli consisted of 2 images of each category (8 images in total). Two sets of image stimuli were prepared (see Figs. 7A and 8A).

**Surgery**

After the monkey had learned visual reaction time and delayed nonmatching-to-sample tasks, a head-holding device was implanted. After the monkey performed both tasks with eye control at a level of >90% correct responses, a recording cylinder was implanted. The surgery was carried out under pentobarbital sodium anesthesia (20–25 mg/kg, intravenous). Antibiotics were administered postoperatively for >1 wk to protect against infection. After a recovery period of >10 days, retraining was started.

**Recording procedure**

During recording, the monkey’s head was tightly fixed to a chair frame. The activity of single neurons was recorded extracellularly...
with a polyurethane-coated tungsten or cobalt-nickel alloy including iron (Elgiloy) microelectrode (1.5–3.0 MΩ, 0.3 mm in diameter). We inserted a stainless steel guide tube (50 mm in length, 1.1 mm in diameter) to 10–20 mm below the surface of the dura to penetrate an electrode without distortion and to allow accurate placement of the electrode into the deepest brain site. For parallel penetration of the guide tube and electrodes, we used a grid system (Crist et al. 1988). The electrode was advanced using a hydraulic microdrive (Narishige, Tokyo, Japan).

Neuronal activity was amplified and converted into pulses using a window discriminator (BAK Electronics, Germantown, MD). The timings of each pulse and task events were stored on disks with a resolution of 0.5 ms using a personal computer. The neuronal activity was transmitted to another computer to generate on-line peristimulus time histograms.

When a single neuron was isolated, we tested response properties of this neuron according to the following procedure (Fig. 2). First, we manually determined the optimal stimulus position using basic stimuli of 4 shapes (Fig. 2) with 4 colors (red, green, blue, and white) using a computer mouse. If we could not determine the optimal stimulus position manually, we presented visual stimuli at the center of gaze to perform the following tests. We examined the orientation selectivity of the neuron using 4 oriented bar stimuli presented at the manually determined optimal position (Fig. 2). Using the optimally oriented bar stimulus, we next examined the color selectivity of the neuron using 5 colors [blue, 0.143 (X), 0.119 (Y); green, 0.289, 0.670; yellow, 0.432, 0.535; red, 0.584, 0.372; white, 0.273, 0.303]. Using the optimally oriented and colored stimulus presented at 3 × 3 grid positions (including the optimal stimulus position but excluding the center), we next examined systematically each neuron’s RF property and determined the position where the stimulus induced the maximal response of the neuron. We also investigated the direction selectivity of the neuron using a bar stimulus moving in 8 directions in steps of 45 deg (Fig. 2). The moving distance and speed were 14 deg and 28 deg/s, respectively.

After the orientation, color, position, and direction tests or if the bar stimuli did not induce responses in the neuron, we examined whether the neuron responded to the shape and image stimuli presented at the center of gaze. If the bar stimuli could not induce the responses but the shape or image stimuli induced the responses, we examined the RF property using the shape or image stimuli (7/25 neurons in the PR cortex). All of the tests using the bar stimuli were carried out during the visual reaction time task. Parts of the data in the shape and image tests were obtained using stimuli presented during the delayed nonmatching-to-sample task (29/40 neurons in the PH cortex and 11/88 neurons in the PR cortex).

**Eye position measurement**

To determine the monkey’s eye position, a measurement system equipped with a charge-coupled device (CCD) camera and an infrared ray irradiation device was used. From an eye image, the center of an approximated oval fitted to the pupil was obtained. The monkey’s eye position was computed by transforming the coordinates of the center in the eye image into the vector of the eye direction (Matsuda 1996; Sato and Nakamura 2001). The eye position data were obtained with a resolution of 0.7 deg at a sampling rate of 30 Hz. At the beginning of each daily session, the eye measuring system was calibrated during the visual reaction time task using 9 locations of a fixation spot arranged in a 3 × 3 grid, 20 deg apart from each other.

**Data analysis**

Neuronal data stored in disks were analyzed off-line. A period of 0.5 s before the stimulus presentation was used as the control period. We regarded a neuron as responsive to a visual stimulus if the number of spikes during visual stimulation was significantly different from that during the control period (Wilcoxon ranked sum test, P < 0.05). With regard to the data obtained in the delayed nonmatching-to-sample task, the number of spikes during the first sample stimulus presentation was compared with that during the control period. For the data in the direction test, the number of spikes from 250 to 750 ms after the stimulus onset was analyzed.

We calculated the response latency of each visually responsive
neuron from the maximal response of the neuron. We measured the time of the first of consecutive bins differing from the discharge rate during the control period by >2SDs.

If a neuron showed differential responses to different stimuli in a stimulus set (Kruskal–Wallis test, \( P < 0.05 \)), the neuronal response was considered to be stimulus selective. To evaluate the strength of stimulus selectivity, we used Kruskal–Wallis’s H value as the index for the selectivity. This index approaches zero if the responses to different stimuli are not different and increases as the difference becomes prominent. Because the H value has an approximate chi-square distribution, it can be regarded as an index for dispersion. To compare the present results with those of previous studies, we also calculated the selectivity index (SI) used by Rainer and Miller (2000).

To evaluate the RF property of each neuron, we classified the types of RF into 5 categories. If a neuron has an RF extending more than 10 deg from the vertical meridian to the contralateral, ipsilateral, or bilateral visual field, we regarded the neuron as having a central RF. If a neuron has an RF extending no more than 10 deg from the vertical meridian and extending more than 10 deg from the horizontal meridian, we regarded the neuron as having a vertical RF. If a neuron has an RF extending no more than 10 deg from both the horizontal and vertical meridians, we regarded the neuron as having a central RF.

**Histology**

Microlesions were made at 2 or 3 sites of representative recording tracks by passing an anodal current (3–4 μA, 600 μC) through Eligiloy microelectrodes. After all of the recording sessions, the monkeys were deeply anesthetized with pentobarbital sodium (30–35 mg/kg, intravenous), and perfused with saline and 10% buffered formalin. Ferricyanide (2%) was mixed with the formalin solution and the mixture was used to stain iron deposits from the Eligiloy electrodes by the Prussian blue reaction. The brains were frozen and sectioned coronally at 50- or 100-μm intervals, and stained with cresyl violet. The locations of neurons were determined using the sites of the microlesions as reference points. Area boundaries were determined based on the previous studies (Bonin and Bailey 1947; Goldman-Rakic et al. 1984; Insausti et al. 1987; Suzuki and Amaral 1994; Tranel et al. 1988; Yukie 2000).

**RESULTS**

We recorded the activity of 359 neurons in the PH cortex. Of these neurons, 104 neurons (29%) were regarded as visually responsive. Of these visually responsive neurons, 87% (90/104) showed excitatory responses and the remaining neurons showed inhibitory responses (13%, 14/104). The discharge frequencies of these neurons during the control period, that is, 500 ms before the stimulus presentation, ranged from 0.0 to 34.3 spikes/s (4.9 ± 5.5 spikes/s, mean ± SD). The discharge frequencies of the maximal excitatory responses ranged from 0.6 to 37.4 spikes/s (10.9 ± 8.0 spikes/s). The discharge frequencies of the inhibitory response ranged from 0.3 to 12.6 spikes/s (4.3 ± 3.5 spikes/s). The mean onset latencies were 165 ± 110 ms.

We also examined the activity of 189 neurons in the PR cortex. Of these neurons, 81 neurons (43%) were regarded as visually responsive. The proportion of visually responsive neurons was significantly higher in the PR cortex than that in the PH cortex (\( \chi^2 = 10.68, df = 1, n = 548, P < 0.005 \)). Of these visually responsive neurons, 93% (75/81) showed excitatory responses. The control rate of these neurons ranged from 0.0 to 17.4 spikes/s (2.2 ± 4.0 spikes/s) and were significantly lower than those of PH neurons (\( t(176) = 3.70, P < 0.001 \)). The discharge frequencies of the maximal excitatory responses ranged from 1.0 to 87.2 spikes/s (16.4 ± 13.6 spikes/s) and were significantly higher than those of PH neurons (\( t(153) = 3.14, P < 0.005 \)). The mean onset latencies were 170 ± 83 ms and were not significantly different from those of PH neurons.

During recording sessions, the monkeys made few errors in behavioral tasks, except for error in fixation, averting its gaze outside of the electronic window. The proportions of correct responses for the 3 monkeys were more than 98%. Including the fixation errors, the proportions of correct responses were 83.1 ± 14.7, 76.4 ± 12.1, and 77.2 ± 10.2% (means ± SD). The reaction times for the 3 monkeys were 264 ± 47, 362 ± 57, and 414 ± 51 ms, respectively.

**Spatial information**

**RECEPTIVE FIELD PROPERTY.** We systematically examined the RF property of 36 PH neurons (Fig. 3A). Of these neurons, 22 (61%) had bilateral, 3 (8%) had contralateral, 0 (0%) had ipsilateral, 2 (6%) had vertical, and 9 (25%) had central RFs. For 8 of the 36 PH neurons (22%), the RF did not include the center of gaze (e.g., Fig. 3Ab). We examined the optimal stimulus position where a stimulus induced the maximal response of the neurons (Fig. 4). About one-half of the PH neurons (47%, 17/36) had the optimal stimulus position within 10 deg of the center of gaze, whereas the remaining neurons (53%) had that with an eccentricity of more than 10 deg (Fig. 4A). We also examined 25 visually responsive neurons in the PR cortex. The RF of the PR neurons always included the center of gaze and most neurons (80%, 20/25) had the optimal stimulus position around the center of gaze (Fig. 4B). The proportion of neurons having the “central” optimal stimulus position was significantly higher in the PR cortex than in the PH cortex (\( \chi^2 = 6.64, df = 1, n = 61, P < 0.01 \)). These data indicate that PH neurons receive more information from the peripheral visual field than PR neurons.

Differences in neuronal responses as to the stimulus positions may be attributed to differences in the monkey’s eye position and eye movement. For example, a PH neuron in Fig. 3Ba showed stronger responses to the stimulus presented in the lower ipsilateral quadrant of the visual field (b) than that presented in the more distant, contralateral visual field (c–e). During the stimulus presentation, there were no apparent differences in eye position. As shown, horizontal eye position (x in Fig. 3, Bb, Bc, Bd, and Be) was within 1 deg. Vertical eye position (y) was more variable than the horizontal one, but was within 2 deg. In addition, there were no large saccadic eye movements defined by more than 1-deg shift of visual angle within 20 ms (Fig. 3, Bb, Bc, Bd, and Be). Similarly, no large saccadic eye movements were observed during recordings of the other 8 neurons. For the remaining neurons investigated, only a few saccadic eye movements were recorded. On average, 0.07 times saccadic eye movements per trial were observed in the investigated 11 neurons. There was no correlation between the number of the saccadic eye movements and that of spikes. Therefore it is unlikely that the differential responses to stimuli presented at different positions were a consequence of the monkey’s eye position and movement.

**DIRECTION SELECTIVITY.** Eighty-five PH neurons were tested for direction selectivity systematically using a bar stimulus. About half of the neurons (46%, 39/85) were responsive and 11...
those to a static bar. Consequently, we classified neurons (13%) showed direction-selective responses. However, because we used a bar stimulus in the direction test, the direction-selective responses may be explained by their selective responses to the orientation of the bar. To examine this possibility, we compared the responses to a moving bar with those to a static bar. Consequently, we classified neurons into 3 types as follows (Fig. 5A). Neurons that responded more strongly to the moving bar than to the static bar of the same orientation as the moving bar were classified as M-type neurons (Fig. 5Aa). Neurons that responded less strongly to the moving bar than to the static bar were classified as S-type neurons (Fig. 5Ab). The remaining neurons were classified as MS-type neurons (Fig. 5Ac). Forty-four PH neurons were examined using both orientation and direction stimuli. Of these, 10 (23%) were M-type, 2 (5%) were S-type, and 32 (73%) were MS-type neurons. Of the 10 M-type neurons, 5 showed direction- but not orientation-selective responses (Fig. 5B; DSON neurons). The direction selectivity of these neurons was probably a consequence of the direction of movement, not of the orientation of the bar. In addition, some PH neurons showed unidirectional response patterns (4 of 11 direction-selective neurons; Fig. 5C) in which the maximal response was significantly stronger than that in the other directions except for the two neighboring directions. These neuronal responses also could not be explained by the orientation selectivity of those neurons.

**EYE-POSITION-SENSITIVE NEURONS.** We investigated the effect of the monkey’s eye position on activity of 67 PH neurons by changing the position of the fixation spot in the visual reaction time task. During the test, no visual stimulus except for the fixation spot was presented. Of the 67 neurons, 27 (40%) showed changes in their activity depending on the monkey’s eye position (Fig. 6).

**Object information**

**SELECTIVITY TO COMPLEX STIMULI.** Using 16 full-colored images, we tested selectivity for image stimuli in 175 PH and 151 PR neurons. Of these neurons, 15 PH neurons (9%) and 59 PR neurons (39%) were responsive. Six PH neurons (3%) showed image-selective responses, whereas 49 PR neurons (32%) did (Figs. 7A and 8A). The proportions of the visually responsive (χ² = 42.98, df = 1, n = 326, P < 0.0001) and image-selective neurons (χ² = 48.68, df = 1, n = 326, P < 0.0001) were significantly higher in the PR cortex than in the PH cortex.

To evaluate the image selectivity, we used Kruskal–Wallis’s H value as the index of selectivity. This index approaches zero if the responses to all stimuli are similar in magnitude and increases as the difference in response magnitude becomes prominent. The mean H values of the responsive neurons in the PH and PR cortices were 7.6 ± 4.1 (mean ± SD) and 30.0 ± 15.1, respectively (Fig. 9Aa). The mean H value of these neurons was significantly larger in the PR cortex than in the PH cortex [t(66) = 5.02, P < 0.0001]. The selectivity index (SI) used by Rainer and Miller (2000) was also calculated. The mean SI values in the PH and PR cortices were 0.38 ± 0.24 and 0.55 ± 0.21, respectively (Fig. 9Ba). The SI values of PR neurons were almost double those of PH neurons. This result indicates that the PR cortex is more selective for image stimuli than the PH cortex.
neurons was significantly larger than those of PH cortex \[ t(58) = 2.09, P < 0.05 \]. These data suggest that PR neurons can convey more information about complex images than PH neurons.

SELECTIVITY TO SIMPLE STIMULI. Responsiveness to 8 geometrical shapes was studied in 173 PH and 44 PR neurons. Of these neurons, 13 PH (8%) and 17 PR (39%) neurons were responsive to simple shapes, and 7 PH (4%) and 8 PR (18%) neurons showed shape-selective responses (Figs. 7B and 8B). The proportions of the responsive \( \chi^2 = 28.52, df = 1, n = 217, P < 0.001 \) and selective neurons \( \chi^2 = 11.96, df = 1, n = 227, P < 0.001 \) for the shape stimuli were significantly higher in the PR cortex than in the PH cortex. We also tested selectivity for the orientation of a bar stimulus in 131 PH and 58 PR neurons. Of these neurons, 46 PH (35%) and 20 PR (34%) neurons were responsive, and 10 PH (8%) and 6 PR (10%) neurons showed orientation-selective responses (Fig. 7C). Both of the proportions of the responsive \( \chi^2 = 0.01, df = 1, n = 189, P > 0.1 \) and orientation-selective neurons \( \chi^2 = 0.38, df = 1, n = 189, P > 0.1 \) for the orientation of the bar stimuli were not significantly different between the two areas.

The H values for the responses to the simple stimuli were compared between the PH and PR cortices. The H values of the neurons responsive to the shape stimuli were 11.4 ± 7.6 (mean ± SD) in the PH cortex and 14.3 ± 11.6 in the PR cortex (Fig. 9Ab), and those of the neurons responsive to the bar stimuli were 5.2 ± 4.3 in the PH cortex and 7.5 ± 5.7 in the PR cortex (Fig. 9Ac). There were no significant differences in the H values of both types of neurons between the two areas [shape, \( t(30) = 0.79, P > 0.1 \); orientation, \( t(64) = 1.76, P >

FIG. 5. Responses of neurons to moving bars. A: examples of 3 types of neuronal responses. a: neuron responded more strongly to moving stimuli than to static ones (M-type). Optimal direction: 0 deg. b: neuron responded more strongly to static stimuli than to moving ones (S-type). Optimal direction: 270 deg. c: neuron responded to moving stimuli as strongly as to static ones (MS-type). Optimal direction: 90 deg. Right column: histograms indicate responses of each neuron to static bar with same orientation as optimal direction stimulus. (See legend for Fig. 2.) B: classification of the M-type neurons in PH cortex (n = 10) based on direction and orientation selectivity. DNON, direction- and orientation-nonselective; DNOS, direction-nonselective and orientation-selective; DSON, direction-selective and orientation-nonselective; DSOS, direction- and orientation-selective. C: examples of response profiles of direction-selective neurons in PH cortex presented as radar charts. Circles indicate activity during control period.

FIG. 6. Example of activity of eye-position-sensitive PH neuron. Each location of histogram corresponds to fixation position in visual reaction time task, i.e., eye position of monkey. Numbers indicate x and y coordinates of eye position in degrees regarding position being straight ahead as the origin. Monkey fixated the spot for duration of data acquisition. Note that discharge rate of this neuron was higher at left positions than at right positions and at upper positions than at lower positions.
0.05]. The SI values for shape were $0.46 \pm 0.21$ in the PH cortex and $0.33 \pm 0.12$ in the PR cortex (Fig. 9Bb) and those for orientation were $0.26 \pm 0.16$ in the PH cortex and $0.25 \pm 0.13$ in the PR cortex (Fig. 9Bc). Again, there were no significant differences [shape, $t(23) = 0.76$, $P > 0.05$; orientation, $t(57) = 0.24$, $P > 0.1$]. These data suggest that the ability of PH neurons to discriminate simple stimuli is similar to that of PR neurons.

COLOR SELECTIVITY. Of 72 PH neurons systematically tested for color selectivity, 42 (58%) neurons were responsive and 17 (24%) neurons showed color-selective responses (Fig. 7D). The mean $H$ values were $13.9 \pm 9.3$ (mean $\pm$ SD).

Locations of responsive neurons

Viewed on the basis of the RF property, we examined the distribution of the visually responsive neurons. The neurons that had the optimal stimulus position in the central (filled circles) and peripheral visual fields (open circles) were intermingled both in the PH and PR cortices (Fig. 10). We could not find any relationship between the eccentricity of the optimal stimulus position and the location of the neurons.

Viewed on the basis of stimulus selective property, the distribution of the visually responsive neurons was examined. In the PH cortex, the neurons that responded only to images and not to simple shapes and bars (filled squares) seemed to be observed more frequently at its anterior portion. This was confirmed in one of two monkeys by a statistical test (Mann–Whitney’s $U = 68.00$, $P < 0.01$; the statistical test was not carried out in the other monkey because most neurons were sampled within a few millimeters of the anterior–posterior axis. See Fig. 11B).

We also examined the distribution of the eye-position–sensitive neurons. The eye-position–sensitive neurons (filled triangles) did not seem to be clustered at some specific locations but were scattered over the PH cortex, although they tended to be observed at specific recording tracks (Fig. 10).

DISCUSSION

Spatial processing

First of all, PR neurons rarely responded to the bar stimuli that were used in our RF search and direction test. This is a prominent characteristic of PR neurons. Therefore our comparison between responses of PH and PR neurons with respect

FIG. 7. Selective responses of PH neurons in image (A), shape (B), orientation (C), and color (D) tests. A: responses of image-selective neuron. This neuron showed maximal response to image of strawberry. $H$ value of neuron was 4.8. B: responses of shape-selective neuron. This neuron responded maximally to star shape. $H$ value of neuron was 9.4. C: responses of two orientation-selective neurons. These neurons showed maximal responses to horizontal bar (a) and 45-deg bar (b) and $H$ values were 22.0 (a) and 7.9 (b), respectively. D: responses of two color-selective neurons. These neurons showed maximal responses to yellow (a) and white (b) bars and $H$ values were 43.8 and 29.5, respectively. (See legend for Fig. 2.)

FIG. 8. Selective responses of PR neurons in image (A) and shape tests (B). A: responses of image-selective neuron. This neuron showed maximal response to image of cutter. $H$ value was 66.8. B: responses of shape-selective neuron. This neuron responded maximally to circle on triangle. $H$ value was 11.6.
to spatial processing is not enough at present. Even though the number of PR neurons examined was limited, our present results demonstrate that the PH cortex is more involved than the PR cortex in processing visual information in the periphery. Some PH neurons did not include the center of gaze in their RFs, whereas the RFs of the PR neurons always included the center of gaze. About half of PH neurons had the peripheral optimal stimulus position, whereas most of PR neurons had the central one. The representation of the peripheral visual field in the PH cortex is suggested by previous anatomical studies, which showed that afferents from area TEO and V2 to area TF were only from the peripheral representation region of the areas (Distler et al. 1993; Gattass et al. 1997).

Boussaoud et al. (1991) investigated visual responsiveness of PH neurons. They found visually responsive neurons at the most posterior portion of the PH cortex, area VTF according to their terminology, and failed to find responsive neurons at its anterior portion. They reported that neurons in area VTF had relatively small, contralateral RFs, and tended to have a visuo-topographic organization. In contrast, we found many visually responsive neurons in the anterior portion of the PH cortex. About half of them had relatively large, bilateral RFs. These discrepancies may be attributed to the difference in the condition of the subjects. They recorded and investigated the activity of PH neurons of anesthetized monkeys, whereas we examined that of behaving monkeys. Some PH neurons, particularly those in the anterior PH cortex, may respond to visual stimuli only under the awake condition, or change their responsiveness depending on the conditions of the subjects. Previous studies also reported visual responsive neurons in the anterior PH cortex of behaving monkeys (Nakamura et al. 1994; Riches et al. 1991; Salzmann et al. 1993; Vidyasagar et al. 1991). There may be subareas in the PH cortex. Neurons in the posterior portion have small and topographically RFs, whereas those in the anterior portion have relatively large, bilateral RFs and are difficult to be activated under anesthesia.

The present results of direction selectivity suggest that some PH neurons convey information about the direction of a moving object. The PH cortex receives inputs from visual areas in the dorsal pathway (Cavada and Goldman-Rakic 1989; Jones and Powell 1970; Martin-Elkins and Horel 1992; Seltzer and Pandya 1976, 1984, 1991; Suzuki and Amaral 1994) and has connections with area MST, area FST, and the superior temporal polysensory area (Barnes and Pandya 1992; Boussaoud et
al. 1990; Seltzer and Pandya 1976, 1991; Suzuki and Amaral 1994). These areas are considered to be involved in higher-order motion processing (Desimone and Ungerleider 1986; Oram and Perrett 1996; Perrett et al. 1985; Sakata et al. 1985; Tanaka et al. 1986). These data support our present results that some PH neurons process motion information.

There were neurons in the PH cortex that were sensitive to the monkey’s eye positions. These neurons have been observed in areas in the dorsal pathway, such as V6a, area 7a, and area LIP (Andersen et al. 1990; Galletti et al. 1995; Nakamura et al. 1999; Sakata et al. 1980). The PH cortex receives afferents from these areas (Andersen et al. 1990; Barnes and Pandya 1992; Cavada and Goldman-Rakic 1989; Jones and Powell 1970; Martin-Ellins and Horel 1992; Seltzer and Pandya 1976, 1984, 1991; Suzuki and Amaral 1994). In addition, PH neurons showed responses related to saccadic eye movement (Ringo et al. 1994; Sobotka et al. 1997).

In summary, our present results together with those of the previous studies indicate that the PH cortex is involved in spatial processing.

Object processing

Consistent with our previous results (Nakamura et al. 1994), we found neurons in the PH cortex as well as in the PR cortex showing selective responses to complex visual images. The PH cortex receives inputs from higher-order visual areas, such as areas TE and TEO (Distler et al. 1993; Seltzer and Pandya 1976; Suzuki and Amaral 1994). Fellemann and Van Essen (1991) regarded the PH cortex as a visual area higher than area TE in the hierarchy of visual processing. Together with these anatomical data, the selective responses of the PH neurons to complex visual stimuli suggest that visual information related to object processing reaches the PH cortex as well as the PR cortex. However, it is unlikely that the PH cortex plays a central role in visual object recognition or identification. Lesions of the PH cortex did not affect the performance of delayed nonmatching-to-sample task (Ramus et al. 1998) and object discrimination task (Murray et al. 1998), whereas lesions in the PR cortex induce deficits in various visual recognition memory tasks (Buckley et al. 1997; Meunier et al. 1993). Consistent with these data, our present data suggest that the PR cortex is more involved than the PH cortex in processing of complex images. The function of the PH neurons selectively responding to complex stimuli is as yet unclear. Previous studies have suggested that neurons in the PH cortex are correlated with the tone signaling the start of a trial (Ringo and O’Neill 1993) and with a complex behavioral context (Salzmann et al. 1993; Vidyasagar et al. 1991). It is possible that the selective responses of PH neurons could be explained by other factors such as behavioral significance, as observed in the amygdala (Nakamura et al. 1992; Nishijo et al. 1988).

Function of PH cortex

The human PH cortex has been implicated in visual processing related to recognition of local environments. Damage to the PH cortex causes a syndrome known as “topographical disorientation” (Aguirre and D’Esposito 1999; Habib and Sirigu 1987; Landis et al. 1986). Patients with this syndrome are unable to navigate from one place to another in familiar and/or novel environments. The involvement of the PH cortex in navigation has also been shown by functional neuroimaging studies (Maguire et al. 1997, 1998a,b; Owen et al. 1996). Recognition of a current location from a scene is required for navigation (Aguirre and D’Esposito 1999) and actually functional neuroimaging studies have revealed that the PH cortex is involved in perception and/or recognition of a scene of a local environment (Aguirre and D’Esposito 1997; Epstein and Kanwisher 1998; Epstein et al. 1999; Nakamura et al. 2000; Sato et al. 1999). Van Diepen and colleagues (van Diepen and Wampers 1998; van Diepen et al. 1994) investigated effects of deprivation of central or peripheral information on scene processing and demonstrated that it was possible to recognize a scene even if the central part of the stimulus was missing, suggesting the importance of peripheral information for scene recognition. PH neurons reported in the present study, which have relatively large and peripherally emphasized RFs and often show responsiveness to complex images, seem to be convenient for such scene processing. Our PH neurons responsive to complex images may respond to objects associated with certain locations in their daily life. Further studies are needed to clarify this issue.

The PH cortex is regarded as a polymodal area, receiving information from higher-order unimodal visual, auditory, and somatosensory cortical regions as well as from other polymodal areas (Jones and Powell 1970; Suzuki and Amaral 1994; Van Hoesen 1982). Lesion of the PH and PR cortices impaired tactual as well as visual recognition memories (Suzuki et al. 1993). In the present study, visually responsive neurons are fewer in the PH cortex than in the PR cortex. These results might reflect the involvement of the PH cortex in modalities other than visual.

The authors thank Prof. S. Kojima for kind encouragement and support and S. Nagumo for technical assistance.

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DISCLOSURES

This work was supported by the Cooperation Research Program of the Primate Research Institute, Kyoto University (1997–1999) and Grants-in-Aid for Scientific Research on Priority Areas from the Ministry of Education, Culture, Sport, Science and Technology (12210092 and 13210080), and Strategic Information and Communications R&D Promotion Scheme.

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