J Neurophysiol
87: 1960–1973, 2002; 10.1152/jn.00780.2000.

Disparity-Selective Neurons in Area V4 of Macaque Monkeys

MASAYUKI WATANABE,[1] HIROKI TANAKA,[1,2] TAKANORI UKA,[2,3] AND ICHIRO FUJITA[1–3]
[1]*Division of Biophysical Engineering, Graduate School of Engineering Science, Osaka University;* [2]*Core Research for Evolutional Science and Technology, Japan Science and Technology Corporation, Osaka 560-8531; and*
[3]*Department of Cognitive Neuroscience, Osaka University Medical School, Osaka 565-0871, Japan*

Received 30 October 2000; accepted in final form 7 December 2001

Watanabe, Masayuki, Hiroki Tanaka, Takanori Uka, and Ichiro Fujita. Disparity-selective neurons in area V4 of macaque monkeys. *J Neurophysiol* 87: 1960–1973, 2002; 10.1152/jn.00780.2000. Area V4 is an intermediate stage of the ventral visual pathway providing major input to the final stages in the inferior temporal cortex (IT). This pathway is involved in the processing of shape, color, and texture. IT neurons are also sensitive to horizontal binocular disparity, suggesting that binocular disparity is processed along the ventral visual pathway. In the present study, we examined the processing of binocular disparity information by V4 neurons. We recorded responses of V4 neurons to binocularly disparate stimuli. A population of V4 neurons modified their responses according to changes of stimulus disparity; neither monocular responses nor eye movements could account for this modulation. Disparity-tuning curves were similar for different locations within a neuron's receptive field. Neighboring neurons recorded using a single electrode displayed similar disparity-tuning properties. These findings indicate that a population of V4 neurons is selective for binocular disparity, invariant for the position of the stimulus within the receptive field. The finding that V4 neurons with similar disparity selectivity are clustered suggests the existence of functional modules for disparity processing in V4.

INTRODUCTION

One of the most remarkable features of the human visual system is the ability to see the world in a three-dimensional depth. The visual system reconstructs depth from a pair of two-dimensional images projected on the retinas of the two eyes. The two retinal images, although similar, contain small differences in the position of corresponding visual features, resulting from the slightly different vantage points of the two eyes. This positional difference, termed binocular disparity, is sufficient to give rise to a vivid sensation of depth without the presence of any other depth cues (Julesz 1971; Wheatstone 1838).

Neurons that respond selectively to binocular disparity are involved in the neural substrate for stereopsis. In the monkey, these neurons are observed in visual areas of the dorsal pathway: V1, V2, V3, MT, MSTd, MSTl, and CIP (Burkhalter and Van Essen 1986; Eifuku and Wurtz 1999; Felleman and Van Essen 1987; Hubel and Livingstone 1987; Hubel and Wiesel 1970; Maunsell and Van Essen 1983; Poggio and Fischer 1977; Poggio et al. 1988; Roy et al. 1992; Taira et al. 2000). Disparity-selective neurons in area MT are organized into cortical columns based on their preferred disparity (DeAngelis and Newsome 1999); microstimulation applied to the disparity columns affects the behavioral decisions of monkeys performing a disparity-discrimination task (DeAngelis et al. 1998). Single-neuron analyses in monkeys are in accordance with clinical observations in that parieto-occipital lesions in humans impair local stereopsis and perception of motion in depth (Rothstein and Sacks 1972; Zihl et al. 1983). As the areas listed in the preceding text are critical for spatial and motion vision, this pathway may play an important role in stereopsis.

Neurons in the ventral visual pathway, crucial for object vision, respond to the surface characteristics and shapes of objects. Neurons in the final stage of the ventral visual pathway, the inferior temporal cortex (IT), are selective for color (Komatsu et al. 1992), texture (Sáry et al. 1995), and shape (Desimone et al. 1984; Gross et al. 1972; Tanaka et al. 1991). IT neurons, however, are also sensitive to horizontal binocular disparity (Uka et al. 2000), disparity gradients (Janssen et al. 2000a), and shape defined by disparity in random-dot stereograms (Tanaka et al. 2001). These new findings suggest that binocular disparity is processed by the ventral visual pathway in parallel with the dorsal visual pathway. It remains unknown, however, from where disparity-selective IT neurons receive their input.

Area V4, an intermediate stage of the ventral visual pathway, sends its major projection to IT (Desimone et al. 1980; DeYoe et al. 1994; Felleman and Van Essen 1991; Felleman et al. 1997). V4 is a candidate to provide information on disparity to IT neurons. In anesthetized monkeys, DeYoe and Van Essen (1985) demonstrated that some neurons in V4 exhibit binocular interactions. It has not been quantitatively determined whether V4 neurons have the ability to process information on disparity. We therefore investigated the responses of V4 neurons to binocularly disparate stimuli in awake, fixating monkeys. We demonstrate a population of V4 neurons are selective for binocular disparity; this disparity selectivity is invariant for position within the receptive field of a neuron. In addition, neurons with similar disparity selectivity are clustered within V4. Preliminary results have been reported elsewhere (Watanabe et al. 2000).

Address for reprint requests: I. Fujita, Lab. for Cognitive Neuroscience, Div. of Biophysical Engineering, Graduate School of Engineering Science, Osaka University, Machikaneyama 1-3, Toyonaka, Osaka 560-8531, Japan (E-mail: fujita@bpe.es.osaka-u.ac.jp).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

METHODS

Subjects

Experiments were performed using two male, Japanese monkeys (*Macaca fuscata*) weighing 6.5 and 7 kg. Each monkey was chronically fitted with a head holder to fix its head to a chair. Recording chambers were mounted on the skull, and search coils were implanted into both eyes to monitor eye positions (Judge et al. 1980) as previously described (Uka et al. 2000). All animal-care and experimental procedures were approved by the animal experiment committee of Osaka University Medical School and were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (1996).

Task and visual stimuli

Monkeys were made to sit on a primate chair facing a 15-in color monitor (screen size: 260 ×195 mm) at a distance of 57 cm. The monkeys were trained for a computer-controlled fixation task (PC486FS: Epson, Suwa, Japan). The positions of both eyes were sampled at a rate of 100 Hz using a search-coil technique; the acquired data were stored for off-line analysis while one eye position was constantly monitored on-line. Visual stimuli were presented on a PC/AT computer (Asus Computer International, San Jose, CA, display resolution: 1,024 × 768 pixels).

Monkeys were required to fixate within 500 ms on a 2.0 × 2.0° "electronic" window of a gray spot (0.2 × 0.2°) presented at the center of the monitor on a black background (luminance 1.0 cd/m^2). A 1-s visual stimulus followed 500 ms after the start of fixation. The monkeys were required to maintain their fixation within the fixation window throughout both the 500-ms prestimulus period and the 1-s stimulus presentation to receive the reward of a drop of water. The task was aborted when the monkeys broke fixation.

White solid bars (15.8 cd/m^2) were used as stimuli. When a neuron did not respond to white bars, red bars (5.7 cd/m^2) were substituted. These were stationary, not sweeping, bars. We used bar stimuli because we wanted to map the receptive field of our sampled neurons and examined the relationship between the receptive field size and eccentricity in the same way as did the previous studies on V4 neurons (Desimone and Schein 1987; Gattas et al. 1988). The preferred length, width, and orientation of the bar were first determined at zero disparity for each neuron tested. The preferred length and width of the bar were selected from 0.2, 0.4, 0.8, 1.6, 3.2, and 6.4°. The preferred orientation, from 0 to 150°, was selected in 30° increments. The minimum-response field was delineated by flashing the optimized bar at different locations. Disparity tuning was quantitatively measured with the bar at the center of the minimum-response field. Disparity stimuli were produced by shifting the location of the bar horizontally. For 111 of 121 neurons analyzed, we tested 0, 0.2, 0.4, 0.6, 0.8, and 1.0° of crossed and uncrossed disparities. For the remaining 10 neurons, only 10 disparities (0.1, 0.3, 0.5, 0.7, 0.9° crossed and uncrossed, not including 0 disparity) were tested. Stereoscopic stimuli were displayed using a liquid-crystal stereoscopic modulator (SGS610, Tektronix, Beaverton, OR; refresh rate, 70 Hz for each eye). Stimuli at each disparity value were presented 10 times in a random order.

Electrophysiological recording

A small hole (3 mm diam) was made in the skull within the recording chamber 1 day before testing. Using a micromanipulator (MO-95s, Narishige, Tokyo), a tungsten recording electrode (Frederick Haer, Bowdoinham, ME, 2–10 MΩ) was advanced from the lateral side of the skull into the dura matter to reach the lateral surface of V4. Action potentials from single neurons were recorded extracellularly using a conventional amplifier in conjunction with either a window discriminator or a waveform-based spike detector (Alpha Omega, Nazareth, Israel). The total number of action potentials observed during the task was recorded by a computer for off-line analysis. After 1–3 wk of recording, the hole was closed with dental cement, and a new hole was made for additional recording sessions.

To locate V4, we determined the positions of the superior temporal, inferior occipital, and lunate sulci for each hemisphere; these sulci differentiate V4 from neighboring areas. We mapped the receptive fields of the neurons recorded, measuring their positions and sizes. We determined the receptive field boundaries of 54 neurons reliably, then plotted the size of the receptive field against the eccentricity of the receptive field center (Fig. 1*A*). The slope and the *y* intercept of the regression line were 0.71 and 0.53, respectively. Many neurons possessing a large receptive field, although tested for binocular disparity, are not included because we could not reliably determine the edges of their receptive fields. The ranges of the eccentricity and size (the square root of areal extent) of the receptive field were 0.78–7.08° and 0.53–6.5°, respectively. Both the relationship between the eccentricity and the size and the relationship between the estimated positions of the sulci and the size and location of the receptive fields were in accordance with the previous examinations of V4 (Desimone and Schein 1987; Gattas et al. 1988). Neurons recorded within the superior temporal and lunate sulci were excluded from the analyses, as they may include neurons from adjacent cortical areas. These observations indicated that our recording sites were within the dorsal part of V4. After all the experiments were completed, four pins were implanted into the brain of one of the animals at the four corners of the recording chamber. The animal was anesthetized with an overdose of pentobarbital sodium (60 mg/kg ip). The animal was transcardially perfused

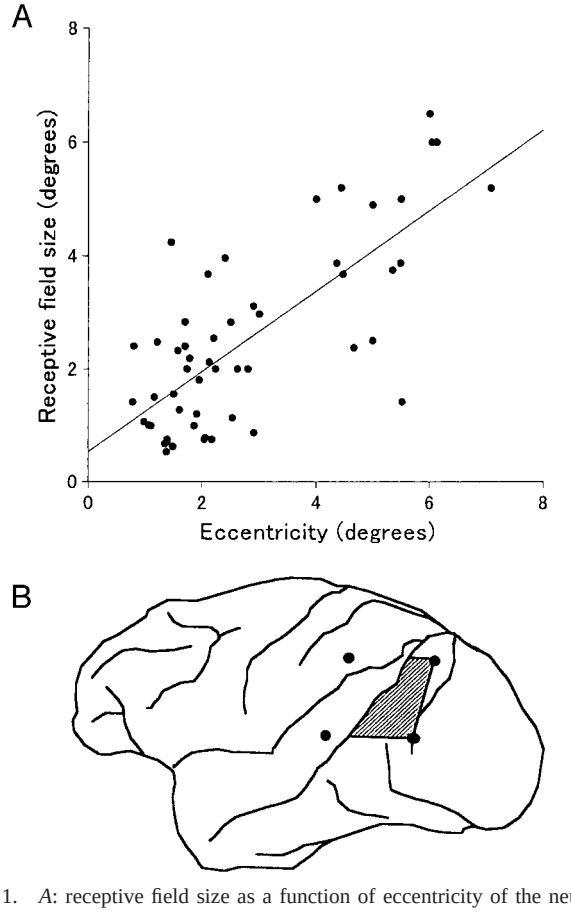

FIG. 1. *A*: receptive field size as a function of eccentricity of the neurons analyzed ($n = 54$). Receptive fields not reliably determined were excluded from this plot. The slope and the *y* intercept of the regression line were determined to be 0.71 and 0.53, respectively. *B*: lateral view of the left cerebral hemisphere of *monkey 2*. ▨, the recording region. ●, the location of the pins implanted at the edges of the recording chamber.

with phosphate-buffered saline and fixative solutions as in Uka et al. (2000), and the location of the implanted pins was verified for reconstruction of the recording area. Histological analysis revealed that our recording sites in this animal were indeed in V4 (Fig. 1*B*, ▨). The other animal is alive and is being used in related experiments.

Data analysis

The responses to each disparity value of neurons included in the following analyses were observed a minimum of five times. The spontaneous firing rate was determined during a 500-ms period immediately prior to stimulus presentation. Response magnitude was calculated for each trial from the firing rate observed during a 1-s period starting 80 ms after stimulus onset. The spontaneous firing rates were averaged over all trials for each neuron; the response magnitude for a given stimulus were averaged over the trials for that stimulus. The standard error of the mean was calculated for the magnitude of responses to each stimulus. All statistical analyses were performed using the magnitude of responses to the stimulus presentation without subtracting the spontaneous firing rates.

RESULTS

Responses of V4 neurons to binocularly disparate stimuli

We recorded the activity of 121 neurons ($n = 78$ in monkey 1, $n = 43$ in monkey 2) responding to at least one of the binocularly disparate bars (Welch's modified *t*-test, $P < 0.05$ divided by the number of stimuli). Ninety-two of these (76%; $n = 66$ in *monkey 1*, $n = 26$ in *monkey 2*) modulated their activity in response to changes in stimulus disparity (ANOVA, $P < 0.05$).

The receptive field of a representative neuron in V4 (Fig. 2) was 5 × 5° in size, centered at 5.5° contralaterally and 2.5° below the horizontal meridian (Fig. 2*C*). Based on electrophysiological mapping of the surrounding sulci, this neuron resides in a portion of the prelunate gyrus near the superior temporal sulcus, in agreement with the visuotopic organization of V4 (Gattass et al. 1988).

By an ANOVA test, this neuron modulated the response amplitude dependent on changes in the binocular disparity of the stimuli ($P < 0.00001$, Fig. 2*A*). The neuron demonstrated a greater response to stimuli with crossed disparity than to those with uncrossed disparity. We obtained a peak response at 0.4° crossed disparity with a minimal response at 0.4° uncrossed disparity (Fig. 2*B*). Using a ±1° range of manipulated disparity, the stimulus did not fall outside the neuron's receptive field even at the largest disparity, excluding the possibility that the modulation detected by the ANOVA test simply resulted from the stimuli falling outside the receptive field. Indeed, the neuron responded to all stimuli, irrespective of presentation to either both eyes or one eye alone (Fig. 2*B*).

Some neurons, however, possessed receptive fields smaller than the range of disparity manipulation (Fig. 1*A*), raising the possibility that modulation detected by the ANOVA test reflects an arrangement of the stimuli outside the receptive field. We therefore examined the responses to monocularly presented stimuli in 110 neurons ($n = 77$ in *monkey 1*, $n = 33$ in *monkey 2*) to determine if the binocularly disparate stimuli were contained within the neuron's receptive field. Positions of the stimulus that elicited a response when presented to either the left or right eye (*t*-test, $P < 0.05$) were considered to be inside the receptive field. This criterion underestimates the size of the receptive field for neurons that respond to binocular stimuli. The neuron in Fig. 4*B*, for example, demonstrates strong binocular facilitation when a binocular stimulus is presented at crossed disparities, although it hardly responds to monocular stimuli. Sixty-two ($n = 45$ in *monkey 1*, $n = 17$ in *monkey 2*) of the 110 neurons were classified as being stimulated within the receptive field. Forty-eight of these (76%, $n = 37$ in *monkey 1*, $n = 11$ in *monkey 2*) modulated their responses to changes in binocularly disparate stimuli (ANOVA, $P < 0.05$),

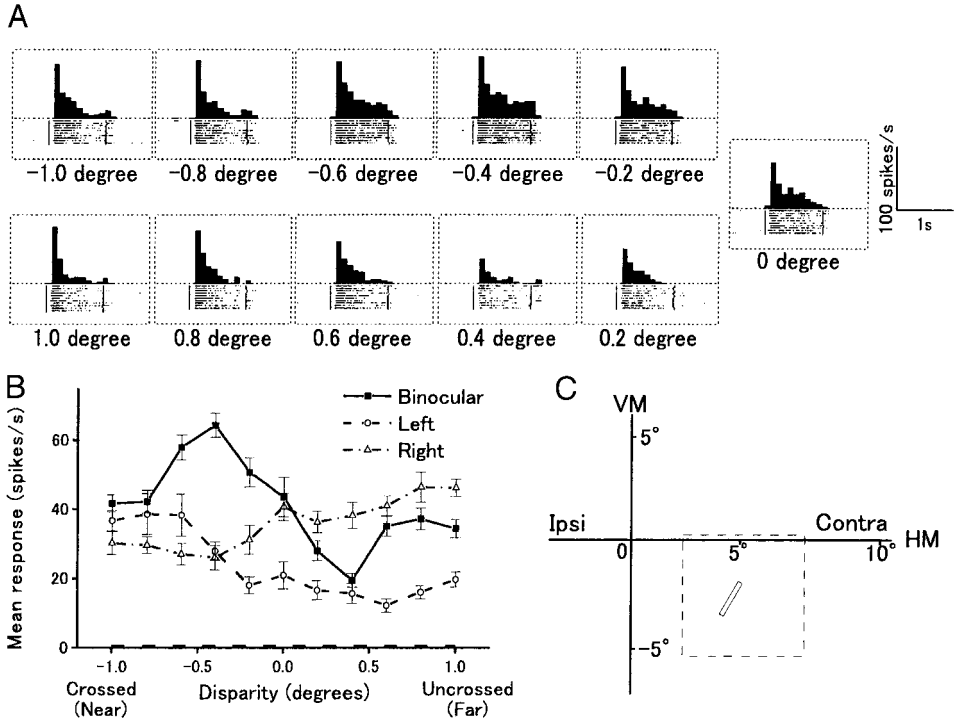

FIG. 2. A representative V4 neuron. *A*: peristimulus time histograms (PSTHs) and rastergrams demonstrating the responses to a white solid bar of various disparities. The vertical lines in the rastergrams indicate the onset and offset of visual stimuli. A dot in the rastergrams indicates the occurrence of a spike in 20 ms. Each bin corresponds to 100 ms in the PSTHs. *B*: tuning curves of binocular and monocular responses (mean ± SE). The broken line indicates the spontaneous firing rate. Disparity-discrimination index of this neuron is 0.68. *C*: the receptive field (broken line) and stimulus bar. The receptive field was 5 × 5° in size, centered at 5.5° contralaterally and 2.5° below the horizontal meridian. The stimulus bar was 1.6° × 0.2°, tilted by 30°. HM, VM: horizontal and vertical meridians. Contra and Ipsi: contralateral and ipsilateral visual fields relative to the recording hemisphere.

indicating that the modulation of neurons to stimulus disparity is not simply due to the arrangement of the stimuli outside the receptive field. There remained, however, the possibility that the modulation could be due to monocular responses within the receptive field, and does not reflect neuronal selectivity for binocular disparity (see following text).

The monocular responses of the neuron in Fig. 2 were indeed modulated by the shift of the stimulus in either eye (Fig. 2*B*; ANOVA, $P < 0.0001$). This modulation, however, was small and gradual across different disparities; therefore the monocular modulations cannot account for the binocular effect (see following text for analysis of a population of V4 neurons).

During the presentation of binocularly disparate stimuli to this neuron, the monkey did not respond with vergence eye movements (Fig. 3*A*). A small offset in the traces of the vergence angle, however, was observed. As the eye position monitor was adjusted manually and the vergence angle was constant before and after the onset of the stimuli, this offset was likely a calibration error not a vergence error of the monkey. We did not observe a difference in the average vergence angle for various disparity stimuli (ANOVA, $P > 0.5$, Fig. 3*B*). In most cases (for 97% of neurons tested), the average vergence angle was not modulated by changes in the stimulus disparity (ANOVA, $P > 0.05$). From these studies, we conclude that the binocular-response modulation of a population of V4 neurons did not result from either monocular responses or eye movements.

Tuning properties of V4 neurons

Poggio et al. (1988) defined six types of disparity tuning; we show responses from five of the six types of V4 neurons (Fig. 4). The responses of a "tuned-excitatory" neuron to binocular stimuli are close to zero (Fig. 4*A*). The tuning curve is sharp and symmetric around the peak. The response peak of a "tuned-near" neuron is shifted to a crossed disparity (Fig. 4*B*). A "near" neuron possesses strong responses to crossed disparities and weak responses to uncrossed disparities with an inflection point at zero disparity (Fig. 4*C*). A "far" neuron demonstrates strong responses to uncrossed disparities with weak responses to crossed disparities (Fig. 4*D*). A "tuned-inhibitory" neuron responded to nonzero disparities and not to zero disparity (Fig. 4*E*). These classifications, made by sight, are subjective. Although many neurons were fit into Poggio's classification scheme, a sizable number of neurons (30%, $n = 20$ in *monkey 1*, $n = 8$ in *monkey 2*) could not be grouped into a specific type. An unclassified neuron with two peaks at $\pm 0.6°$ is shown in Fig. 4*F*.

Although we observed multiple differing tuning curves, the majority of neurons preferred crossed disparities over uncrossed disparities (Fig. 5). A curve through the data points using a cubic spline fit was used to determine the response peak location. Neurons with a response peak location at the edge of the disparity range ($\pm 1°$ or $\pm 0.9°$) were excluded from this analysis, leaving 80 of the 92 binocularly modulated neurons ($n = 61$ in *monkey 1*, $n = 19$ in *monkey 2*) with response peaks solidly within the examined range. For *monkey 1*, the distribution of the response peak locations was clearly shifted toward crossed disparity (sign test, $P < 0.005$, median $= -0.20$). For *monkey 2*, the median of the distribution was -0.44, although this shift was not significant ($P = 0.06$). We did not observe a difference between the two monkeys in the distribution of the response peak locations (Mann-Whitney *U* test, $P > 0.1$). The distribution of the response peak locations for neurons with stimuli confined within the receptive field ($n = 44$, median =

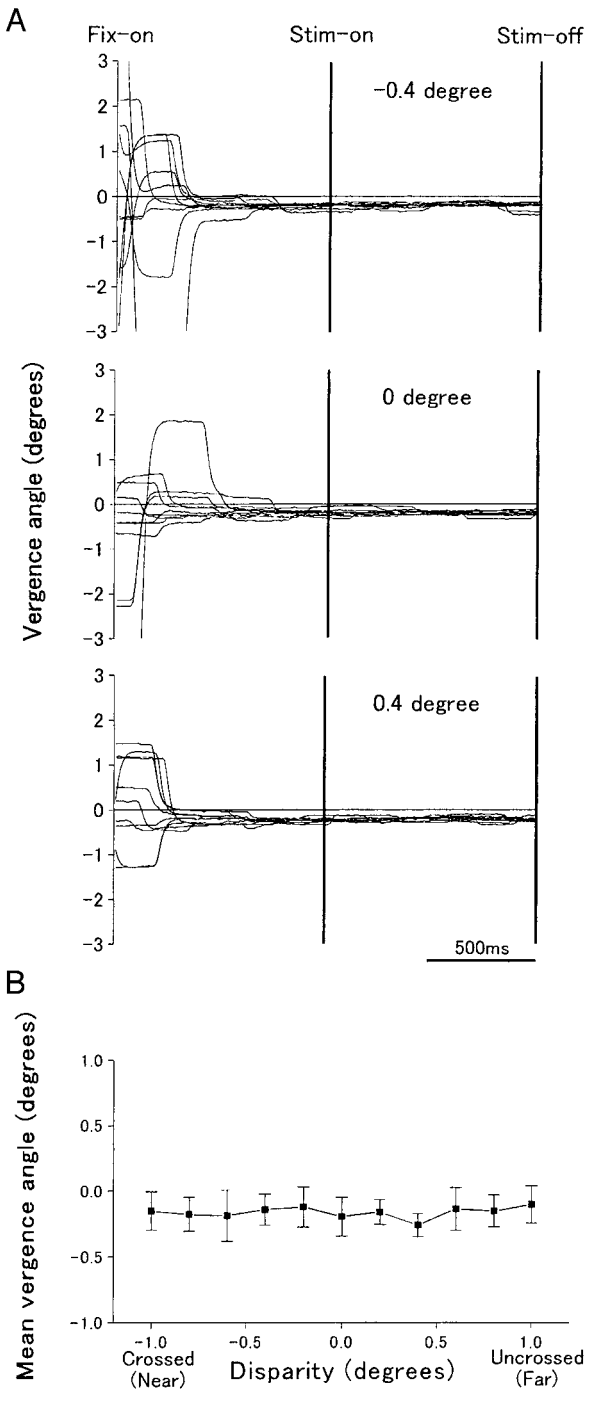

FIG. 3. Vergence eye movement during presentation of binocularly disparate stimulus. *A*: traces of the vergence angle are shown for 3 binocularly disparate stimuli during recording of the neuron in Fig. 2. Eye traces are shown from the onset of the fixation point (Fix-on) throughout the 1-s stimulus presentation (Stim-on to Stim-off). A stimulus of $\pm 0.4°$ was chosen for its strong neuronal modulation at these disparities. *B*: the vergence angle (mean $\pm$ SD) during the 1-s stimulus presentation is plotted for each disparity value. The monkey did not display systematic eye movements during the presentation of disparity stimuli. The average SDs of the vergence angle within and across the trials were 0.07 and 0.13°, respectively.

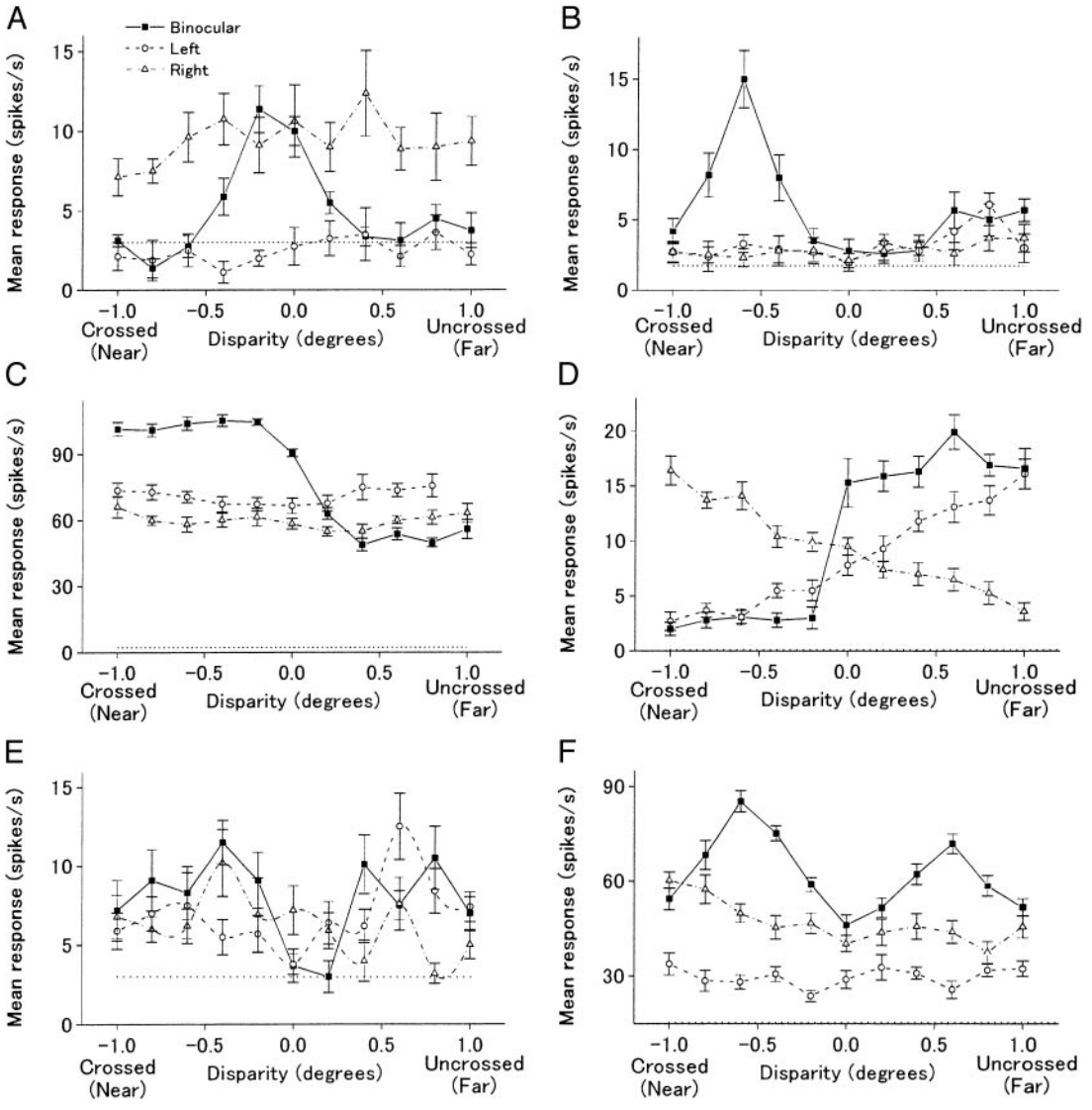

FIG. 4. Representative examples of different binocularly-modulated responses obtained in V4. *A*: a "tuned-excitatory" neuron. Disparity-discrimination index (DDI) = 0.6. *B*: a "tuned-near" neuron. DDI = 0.58. *C*: a "near" neuron. DDI = 0.76. *D*: a "far" neuron. DDI = 0.69. *E*: a "tuned-inhibitory" neuron. DDI = 0.49. *F*: an "unclassified" neuron. DDI = 0.65. Disparity tuning curves and their corresponding monocular tuning curves are shown (average ± SE). Horizontal dotted lines indicate spontaneous firing rates.

−0.20, using criterion described in the preceding text) did not differ from neurons excluded from the analysis ($n = 36$, median = −0.22, $P > 0.6$), with both shifted toward crossed disparity ($P < 0.03$). Therefore the shift toward crossed disparity cannot be attributed to an artifactual arrangement of the stimuli outside the receptive field.

We also compared responses to crossed disparities with those to uncrossed disparities in the 121 neurons examined. The response of each neuron to each disparity stimuli was normalized to the mean response of the neuron to all the disparity stimuli, and the normalized responses to both crossed and uncrossed disparities were pooled across the neurons. In accordance with the response peak locations, the normalized responses to crossed disparities were greater in magnitude than those to uncrossed disparities ($n = 78$, Mann-Whitney U test, $P < 0.0001$ in *monkey 1*, $n = 43$, $P < 0.005$ in *monkey 2*). We observed the same preference in both neurons with stimuli confined within the receptive field ($n = 62$, $P < 0.0001$) and neurons excluded from the analysis ($n = 48$, $P < 0.0005$). These results suggest that a bias exist in the preference of V4 neurons for stimuli with crossed disparities.

Monocular responses and binocular interaction

A large population of neurons in V4 modulated their responses dependent on the location of monocular stimuli (64%, 70/110; Figs. 2*B* and 4, *D–F;* ANOVA, $P < 0.05$; 45%, 49/110 for left eye, and 48%, 53/110 for right eye). Examination of this phenomenon in a single neuron demonstrated that the modulation by changes in location of stimuli presented to one eye could not explain the binocular-response modulation of the neuron (Fig. 2*B*). To examine this modulation in a group of neurons, we examined the monocular (left or right) and binocular responses in 87 binocularly modulated neurons (ANOVA, $P < 0.05$) using a two-way ANOVA. The main factors were the stimulus ocularity (binocular or left, or bin-

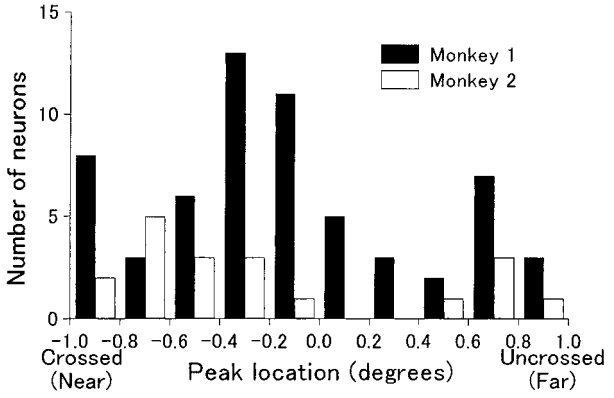

FIG. 5. Frequency histogram of the response peak location of disparity tuning curves. Response peak locations were determined from the spline-fit tuning curves. Neurons recorded from *monkeys 1* and *2* are indicated by ■ and □, respectively.

ocular or right) and the location of the stimuli. Responses to left and right eye stimuli were analyzed separately so that the ANOVA was conducted twice for each neuron. We defined a neuron as showing binocular-response modulation not explained by monocular modulation if it showed a significant result in the ANOVA for either stimulus ocularity or interaction between stimulus ocularity and translation ($P < 0.05$). Ninety percent (78/87) of the neurons demonstrated a significant effect for either the stimulus ocularity (73%, 80/110 for left eye, and 74%, 81/110 for right eye) or the interaction (71%, 78/110 for left eye, and 68%, 75/110 for right eye), indicating that the binocular responses in most neurons do not correspond to the responses to stimuli presented to either the right or left eye alone.

We examined whether a linear combination of the monocular responses could explain the binocular responses using a two-way ANOVA for the 87 binocularly modulated neurons, defining a neuron as having binocular selectivity not due to the linear combination of the monocular responses if it showed significance for interaction between stimulus ocularity and location ($P < 0.05$). We first conducted multiple regression analysis (left and right eye responses as independent variables and binocular responses as dependent variables) to determine weighting coefficients of responses to left and right eye stimuli. The responses to left and right eye stimuli were multiplied by its own coefficient and added in each trial within same recording block. Then the summed monocular responses were compared with the binocular responses by the ANOVA. Forty of the 87 neurons (46%) showed a significant interaction, indicating that binocular responses of these neurons could not be predicted from the linear combination of monocular responses. There remained a possibility that binocular responses of the remaining neurons could be explained by a linear combination of the monocular responses and that a nonlinear combination of monocular responses could predict the binocular responses of all recorded neurons.

Ability of V4 neurons to discriminate disparity stimuli

The ability of a V4 neuron to discriminate disparity stimuli was assessed by a disparity-discrimination index (DDI) (Cumming and DeAngelis 2001) defined by the following formula

$$\text{Disparity discrimination index} = \frac{R_{max} - R_{min}}{R_{max} - R_{min} + 2\text{RMS}_{error}}$$

where R_{max} and R_{min} denote the maximum and minimum of the mean responses, respectively, and RMS_{error} denotes the residual variance around the means across the whole tuning curve. All of these calculations were performed using square-root counts of the firings because the variability of neuronal firing across trials increases with mean firing rate (Dean 1981; Tolhurst et al. 1981) and the residual variance will be biased toward the larger values produced by firing rate. This index varies from zero when the variability of the neuron is far greater than the difference of R_{max} and R_{min} and approaches values near unity when the difference of R_{max} and R_{min} is greater than the variability of the neuron. We calculated the DDI for all the 121 neurons examined (Fig. 6*A*). The distribution median was 0.50, indicating that the difference between the maximum and minimum responses was close to 2RMS_{error}. The DDI distribution for binocularly modulated neurons ($n = 92$, median = 0.54, Fig. 6*A*, ■) shifted toward unity compared with that of nonbinocularly modulated neurons ($n = 29$, median = 0.39, Fig. 6*A*, □; Mann-Whitney *U* test, $P < 0.0001$). No significant difference was observed in the distribution of the DDI either between the two monkeys ($n = 78$, median = 0.51 for *monkey 1*, $n = 43$, median = 0.49 for *monkey 2*, Mann-Whitney *U* test, $P > 0.1$) or between neurons with stimuli confined within the receptive field ($n = 62$, median = 0.50, using criterion described in the preceding text) and neurons with stimuli classified as outside the receptive field ($n = 48$, median = 0.51, Mann-Whitney *U* test, $P > 0.7$). It might be possible that the DDIs were affected by the uneven structure

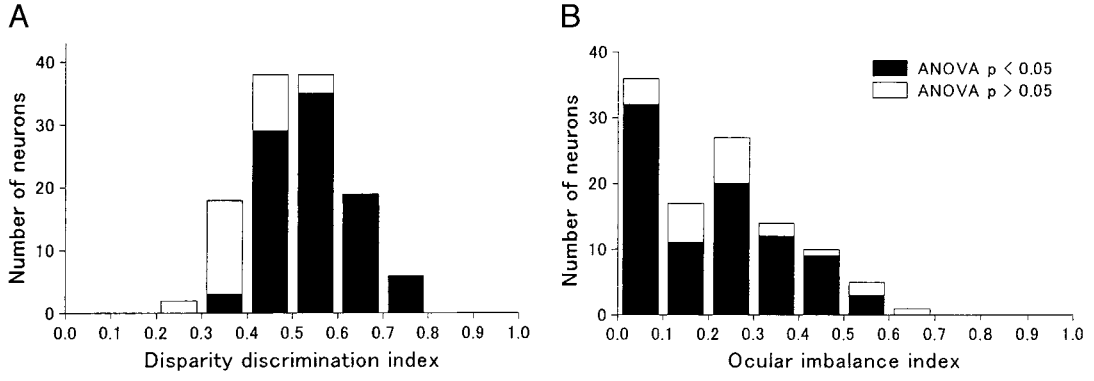

FIG. 6. Distribution of disparity-discrimination index (*A*) and ocular imbalance index (*B*). ■ and □, neurons that showed ANOVA $P < 0.05$ and $P > 0.05$, respectively.

of the receptive field. We show in the following text, however, that DDI is relatively position invariant within the receptive field of neurons (see *Position invariance of binocular responses*).

To evaluate whether V4 neurons receive balanced or unbalanced input from the left and right eyes, we calculated the ocular imbalance index, defined by the following equation

$$\text{Ocular imbalance index} = \frac{|R_R - R_L|}{|R_R - R_L| + \text{RMS}_{\text{errorR}} + \text{RMS}_{\text{errorL}}}$$

where R_R and R_L denote the mean responses to stimuli presented to the right and left eyes, respectively, and $\text{RMS}_{\text{errorR}}$ and $\text{RMS}_{\text{errorL}}$ denote the residual variance around the means across the whole tuning curve of the responses to stimuli presented to the right and left eyes, respectively. Again, all of these calculations were performed using square root counts of the firings. This index takes values near zero when the difference between R_R and R_L is far smaller than the sum of the variability of responses to stimuli presented to each eye and approaches values near unity when the difference between R_R and R_L is greater than the sum of the variability of responses to stimuli presented to each eye. The median of the index determined for the 110 neurons for which we recorded monocularly presented stimuli responses (Fig. 6*B*) was 0.21, indicating that the difference between the maximum and minimum responses was smaller than the sum of the variability of the responses. The distribution of the ocular imbalance index did not differ between either the two monkeys ($n = 77$, median = 0.20 for *monkey 1*, $n = 33$, median = 0.21 for *monkey 2*, Mann-Whitney *U* test, $P > 0.5$) or the binocularly modulated ($n = 87$, median = 0.20; Fig. 6*B*, ■) and the nonbinocularly modulated neurons ($n = 23$, median = 0.22, □; $P > 0.5$). We did not observe a correlation between the DDI and the ocular imbalance index (Pearson's correlation coefficient $r = 0.08$, $P > 0.4$, $n = 110$).

Position invariance of binocular responses

We next examined the variability of responses of the neurons resulting from changes in stimulus position within the neuron's receptive field. A neuron tested at the center and at four peripheral positions within the receptive field (Fig. 7*B*) demonstrated "near-cell"-type responses, regardless of the stimulus position (Fig. 7*A*). The magnitude of the response modulation, however, varied among the positions. This may be partly because we did not test the disparity tuning at different positions in the same block of trials. We calculated Pearson's correlation coefficient of the average response magnitude for disparity stimuli presented at the center and each off-center position, obtaining four correlation coefficients for this neuron. For example, the correlation coefficient between the responses at the "center" and "lower" was 0.97 ($P < 0.00001$, Fig. 7*C*). For all of pairs of responses, the correlation coefficients for the neuron were both high (mean $r = 0.93$) and statistically significant ($P < 0.005$).

We examined the responses of 34 neurons to stimuli presented in at least two different positions. Neurons were selected irrespective of their binocular-response modulation at the center of the receptive field. Sixteen neurons were examined for their responses to stimuli presented at five positions; the remaining 5, 8, and 5 neurons were examined either at two, three, or four positions, respectively. For each position, the neurons responded to at least one of the stimuli used (Welch's modified *t*-test, $P < 0.05$ divided by the number of stimuli). Stimulus positions were selected to cover the full receptive

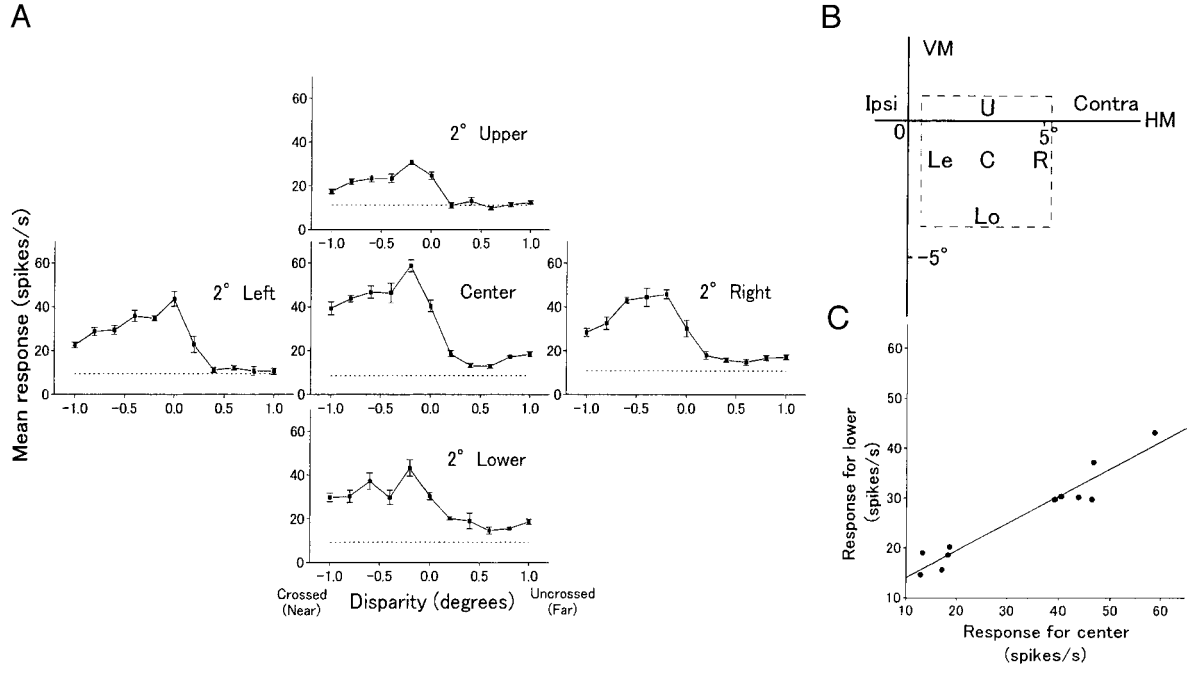

FIG. 7. Position-invariant binocular-response modulation of a V4 neuron. Binocular response was examined at 5 positions within the receptive field. Responses were first examined at the center, then at 4 positions off-center by 2° each to the left, right, upper, or lower. *A*: disparity-tuning curves at 5 positions. - - -, spontaneous firing rates. DDI: 0.77 (*middle*), 0.76 (*right*), 0.77 (*left*), 0.77 (*top*), 0.72 (*bottom*). *B*: the receptive field (- - -) and the 5 stimulus positions. *C*: mean responses to binocularly disparate stimuli at the lower position are plotted against those at the center. The correlation coefficient, *r*, was 0.97 ($P < 0.00001$).

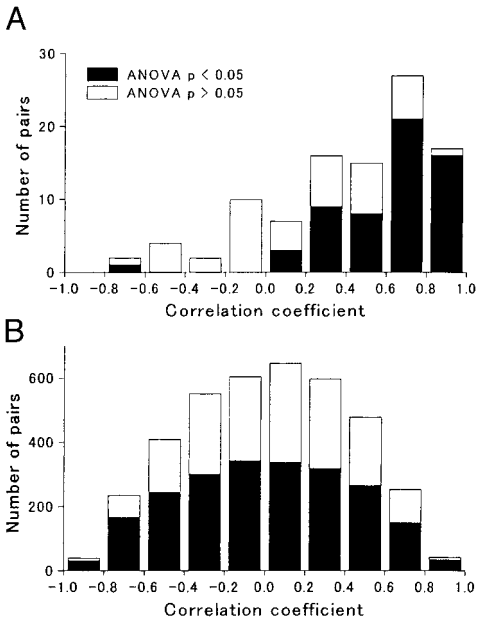

FIG. 8. Distribution of Pearson's correlation coefficients for responses to stimuli presented at center and off-center positions in the receptive field. *A*: distribution of correlation coefficients for responses from the same neurons. *B*: distribution of correlation coefficients for responses from different neurons. ■, pairs, both of which showed ANOVA $P < 0.05$; □, the remaining pairs.

field. For neurons with a receptive field larger than 5°, distances between the center and off-center positions were set at 2°. We calculated Pearson's correlation coefficient for the responses at the center and each off-center position. The overall distribution of the correlation coefficients was shifted toward positive values (Fig. 8*A*, $n = 100$, median = 0.49, sign test, $P < 0.0001$). As a control, we calculated the correlation coefficients for a response at the receptive field center of one neuron and the responses at all stimulus positions for another neuron (Fig. 8*B*). The distribution of correlation coefficients for responses from different neurons peaked near zero ($n = 3{,}861$, median = 0.03), showing no positive correlation of disparity selectivity between pairs of different neurons. Distributions shown in Fig. 8, *A* and *B*, are statistically different (Mann-Whitney *U* test, $P < 0.0001$).

The ability of discriminating disparity stimuli were similar at different positions within the receptive field. The DDI derived from responses for the center and off-center positions correlated significantly (Fig. 9*A*; Pearson's correlation coefficient, $r = 0.39$, $n = 100$, $P < 0.0001$). No significant difference was observed between the indices for the center and the off-center positions (Wilcoxon sign rank test, $P > 0.5$). We also examined response peak locations in the disparity-tuning curves for different positions within the receptive field. The response peak location was determined from a curve fitted to the data points using a cubic spline fit. Responses that were not modulated by disparity stimuli (ANOVA, $P > 0.05$) and that have a peak location at the edge of the disparities tested were excluded from this analysis. Eighteen of the 34 neurons met this criterion. The peak locations of the responses for the center agree well with those for off-center positions within the receptive field (Fig. 9*B*; Pearson's correlation coefficient, $r = 0.70$, $n = 37$, $P < 0.00001$). The results in Figs. 7–9 indicate that binocular-response modulation is invariant for position within a neuron's receptive field.

Position invariance of binocular responses and the monocular responses

We next compared the monocular responses with the binocular responses at positions separated horizontally. Figure 10, *A* and *B*, shows responses of a neuron examined at two locations horizontally separated by 2°. Note that the ordinates of these two graphs are different: the mean response magnitude for the right stimulus location (Fig. 10*B*) was larger than that of the left (Fig. 10*A*), indicating that the right stimulus location was nearer the center of the receptive field than the left stimulus location. In accordance to the results described in the preceding text, the shapes of the disparity-tuning curves were similar (Pearson's correlation coefficient, $r = 0.91$, $P < 0.0001$). The monocular responses were modulated by the shift of the stimulus at both stimulus locations (ANOVA, $P < 0.05$), although

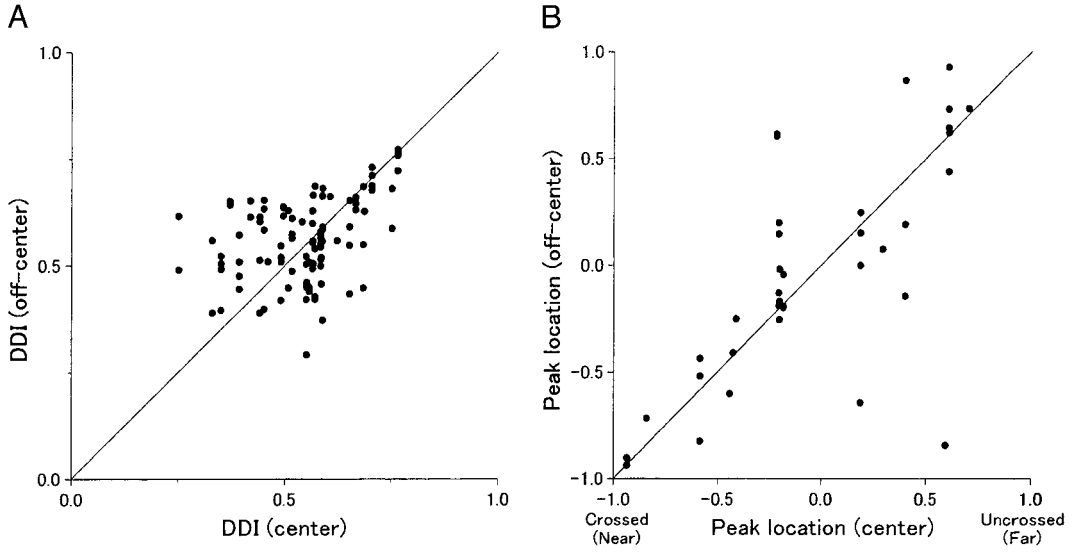

FIG. 9. Comparison of DDI (*A*) and the peak location (*B*) of disparity-tuning curves between center and off-center positions in the receptive field. Center data are plotted on the abscissa; data for off-center positions are plotted on the ordinate.

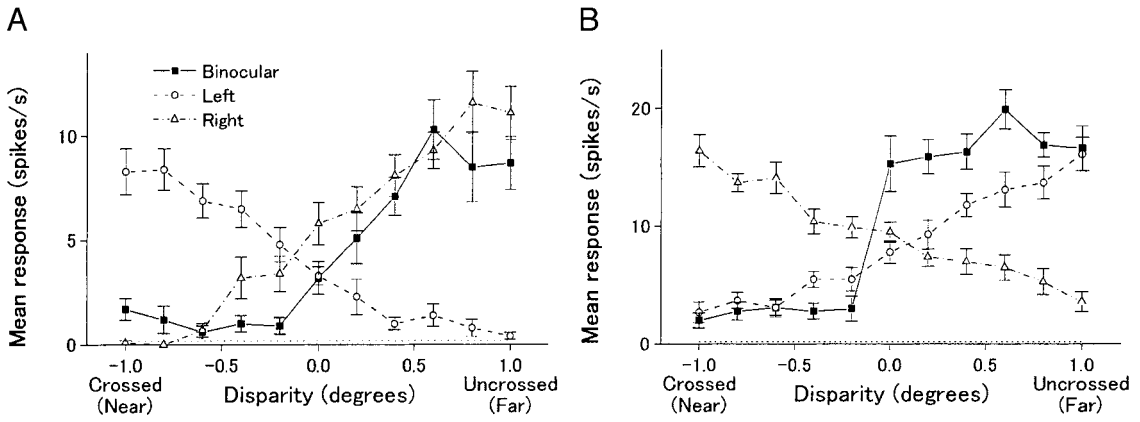

FIG. 10. Binocular and monocular responses of a neuron at 2 positions separated horizontally by 2° (*A* and *B*). Binocular modulation was preserved between the 2 positions; the pattern of right eye and left eye responses was reversed. The 2 positions had a positive correlation ($r = 0.91$) for the binocular responses and a negative correlation for the monocular responses ($r = -0.95$ for the left eye, $r = -0.96$ for the right eye). The scales of the 2 graphs are different as the magnitudes of the mean responses differed between the 2 positions.

the pattern of the modulation of the monocular responses was reversed when the position of the stimuli presentation was changed ($r = -0.95$, $P < 0.0001$ for the left eye, $r = -0.96$, $P < 0.0001$ for the right eye). At the left stimulus location (*A*), responses to the left-eye-presented stimuli became gradually weaker as the stimulus position progressed from crossed to uncrossed, as the responses at the right stimulus location (*B*) became stronger. The opposite was observed for right-eye-presented stimuli. Despite drastic differences in the modulation of the responses between the two locations, the shape of the binocular disparity-tuning curves was well preserved, consistently showing a "far-type" tuning.

We recorded the binocular and monocular responses at two or three horizontally separated positions in 33 and 28 neurons, respectively. For each position, the neurons responded to at least one of the stimuli used (Welch's modified *t*-test, $P < 0.05$ divided by the number of stimuli, as described in the preceding text). One of the stimulus positions was at or near the center of the neuron's receptive field, and another position was at an off-center position. For neurons with three different positions examined, two different off-center positions were left and right to the center. In Fig. 10, the right stimulus position (*B*) was nearer to the center than the left stimulus position (*A*) but not exactly on the center assuming a Gaussian-like receptive field profile of V4 neurons (Desimone and Schein 1987). If the stimulus location was set exactly on the center of the receptive field, the shapes of the tuning curves of the monocular responses would either peak at 0 or be flat.

We calculated the correlation coefficients between the binocular and monocular responses to stimuli presented at center and each off-center position in the 33 and 28 neurons, respectively. The correlation coefficients between the binocular responses to stimuli presented at the center and off-center positions were distributed toward positive values (Fig. 11*A*; $n = 55$, median = 0.45, sign test, $P < 0.005$), indicating that binocular responses between the two positions were similar. The distribution of correlation coefficients between the monocular responses to stimuli presented at the center and the off-center positions were centered at 0, indicating no systematic relationship between the monocular responses at different stimulus locations (Fig. 11*B*, $n = 72$, median = 0.10, $P > 0.5$). We calculated the correlation coefficients between the binocular responses to stimuli presented at the two different off-center positions of the receptive field in 22 neurons; the distribution shifted toward positive values although slightly short of statistical significance (Fig. 11*C*, median = 0.26, $n = 22$, sign test, $P = 0.052$). Correlation coefficients between the monocular responses to stimuli presented at two different off-center positions were also calculated in 20 neurons; the distribution was shifted toward negative values (Fig. 11*D*, median = -0.34, $n = 28$, sign test, $P < 0.001$). This distribution differed from the coefficients of the monocular responses for the center and the off-center position (Fig. 11*B*; Mann-Whitney *U* test, $P < 0.005$), the expected result assuming a Gaussian-like receptive field. Despite the dependence of the monocular responses on the stimulus positions within the neuron's receptive field, we did not observe a difference between the distribution of the correlation coefficients for binocular responses between the center and off-center positions and that of two off-center positions (Mann-Whitney *U* test, $P > 0.3$). No correlation existed between the correlation coefficients of the binocular responses and those of monocular responses (Fig. 12, Pearson's correlation coefficient, $r = 0.05$, $n = 91$, $P > 0.6$). These results indicate that the shape of the binocular disparity-tuning curve is preserved for position within the receptive field, whereas the monocular profile varied depending on the stimulus location.

Local clustering of neurons with similar binocular-response modulation

We simultaneously obtained recordings of both single-unit and background multi-unit activities using a single electrode at 73 recording sites, allowing the determination of clustering of V4 neurons according to disparity preference. To prevent contamination of spikes from one recording channel to another, we used two conventional window discriminators, with the upper level of one window set substantially below the lower level of the other window (Uka et al. 2000). We also monitored the spike form of single units to make sure that the second peak of triphasic spikes did not trigger counting in the multi-unit window.

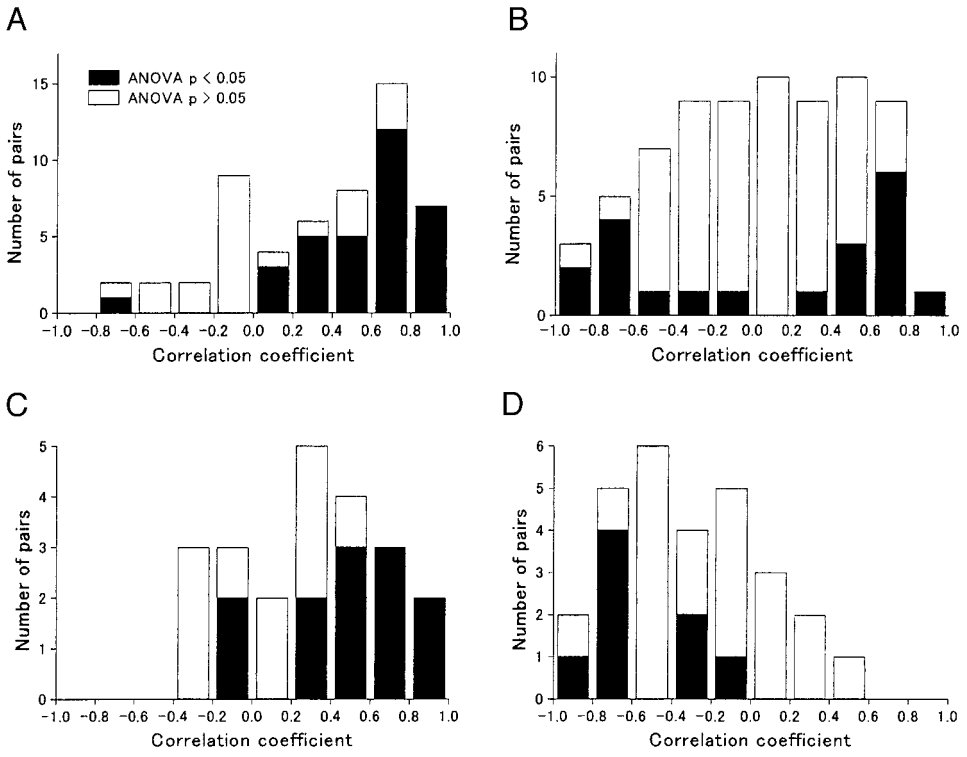

FIG. 11. Distributions of correlation coefficients between responses to stimuli presented at positions separated horizontally. *A*: distribution of correlation coefficients between binocular responses for the center and an off-center position in the receptive field. *B*: distribution of correlation coefficients between monocular responses for the center and an off-center position. *C*: distribution of correlation coefficients between binocular responses for 2 off-center positions. *D*: distribution of correlation coefficients between monocular responses for 2 off-center positions. ■, pairs, both of which showed ANOVA $P < 0.05$; □, the remaining pairs.

Figure 13, *A* and *B*, shows an example of a simultaneous recording of single- and multi-unit activities. The shapes of the disparity-tuning curves derived from the single and multi-units were similar, and both tuning curves had a clearly defined peak at 0.6° crossed disparity. Figure 13, *C* and *D*, shows another example. Both the single unit (*C*) and the multi-unit (*D*) responded more strongly to crossed disparities than to uncrossed disparities. The DDIs of the single and multi units were 0.58 and 0.48 (Fig. 13, *A* and *B*) and 0.63 and 0.77 (*C* and *D*), respectively.

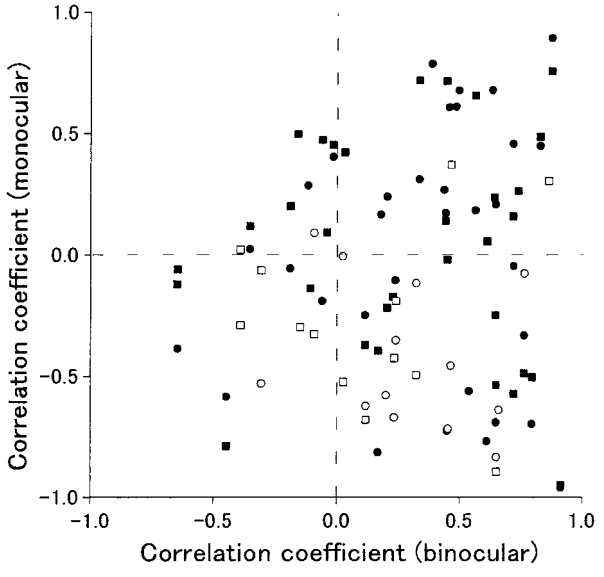

FIG. 12. Comparison between binocular and monocular correlation coefficients between responses to stimuli presented at positions separated horizontally. ■ and ● and □ and ○, the correlation coefficients between responses to stimuli presented at the center and off-center position in the receptive field and at 2 off-center positions in the receptive field, respectively. ■ and □ and ● and ○, correlation coefficients between responses to stimuli presented to both eyes and to either the left or right eyes, respectively.

Following calculation of the DDI for all the 73 simultaneously recorded pairs (Fig. 14*A*), the DDI of single units correlated well with that of multi-units (Pearson's correlation coefficient, $r = 0.41$, $P < 0.0005$). We also examined the relationship between response peak locations as determined from the tuning curves of simultaneously recorded single and multi-units (Fig. 14*B*). Data are plotted for a subset of recordings (33 of the 73 sites) where both single and multi-units exhibited significant binocular response modulation (ANOVA, $P < 0.05$) and the response peak location was within the examined range of disparity (±1 or ±0.9°). The peak locations of single- and multi-unit responses correlated significantly (Pearson's correlation coefficient, $r = 0.43$, $P < 0.05$). These results suggest that nearby neurons have similar binocular-response modulation.

DISCUSSION

Based on the results shown in the preceding text, we conclude that a population of V4 neurons is sensitive to changes in binocular disparity. Although monocular response profiles varied between positions, this disparity selectivity is invariant for the stimulus positions within the receptive field. In addition, neurons with similar disparity selectivity were locally clustered together, as previously shown for the IT (Uka et al. 2000). The present results suggest that disparity information is processed along the ventral visual pathway.

Are V4 neurons actually selective for binocular disparity?

V4 neurons modified their response magnitude following a change in the stimulus binocular disparity. Heterogeneity within the receptive field could not explain neuronal response

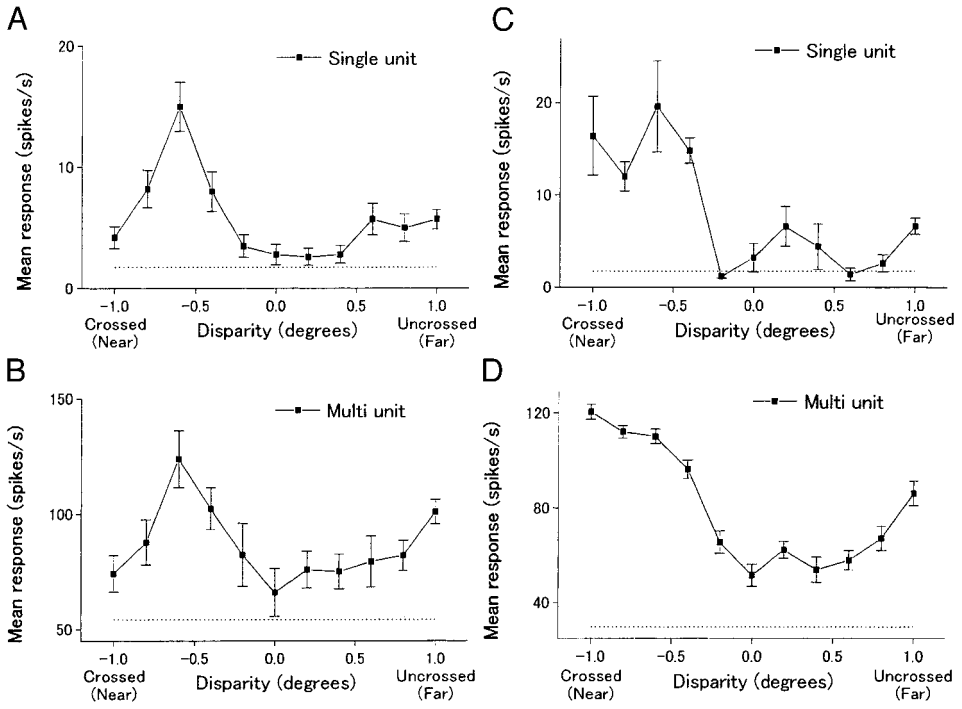

FIG. 13. Disparity tuning curves (mean ± SE) for 2 pairs of single and multiple neurons (*A* and *B* and *C* and *D*) simultaneously recorded from a single recording electrode. The single unit shown in *A* is the same as the neuron shown in Fig. 4*B*. · · · , the spontaneous firing rate.

modulation due to binocularly disparate stimuli. Shifts in the monocular image modulated the neuronal response (Figs. 2*B*, 4, *D–F*, and 10, *A* and *B*); the monocular responses, however, could not account for the binocular modulation as the profile of binocular responses remained unchanged for different positions within the receptive field while the monocular profile changed markedly (Figs. 10 and 11). It is uncertain to what degree the observed response modulation was contaminated by modulation due to monocular components (Cumming and DeAngelis 2001). To isolate purely binocular modulation, it will be necessary to test V4 neurons using stimuli, such as dynamic random-dot stereograms, which produce binocular disparity without a monocular contribution. Finally, we confirmed that the monkeys did not respond to the disparity stimuli through vergence eye movements (Fig. 3). These observations indicate that a population of V4 neurons possesses genuine selectivity for binocular disparity.

Possible inputs and outputs of disparity-selective V4 neurons

Half of the binocularly modulated V4 neurons show binocular responses not explained by a linear combination of the monocular responses. In addition, disparity selectivity is invariant for stimulus position within the receptive field, whereas the monocular profiles varied. These characteristics resemble complex cells more than the simple cells of V1 (Anzai et al. 1999a–c; DeAngelis et al. 1991; Ohzawa et al. 1990, 1997). Disparity-selective complex cells receive their input from dis-

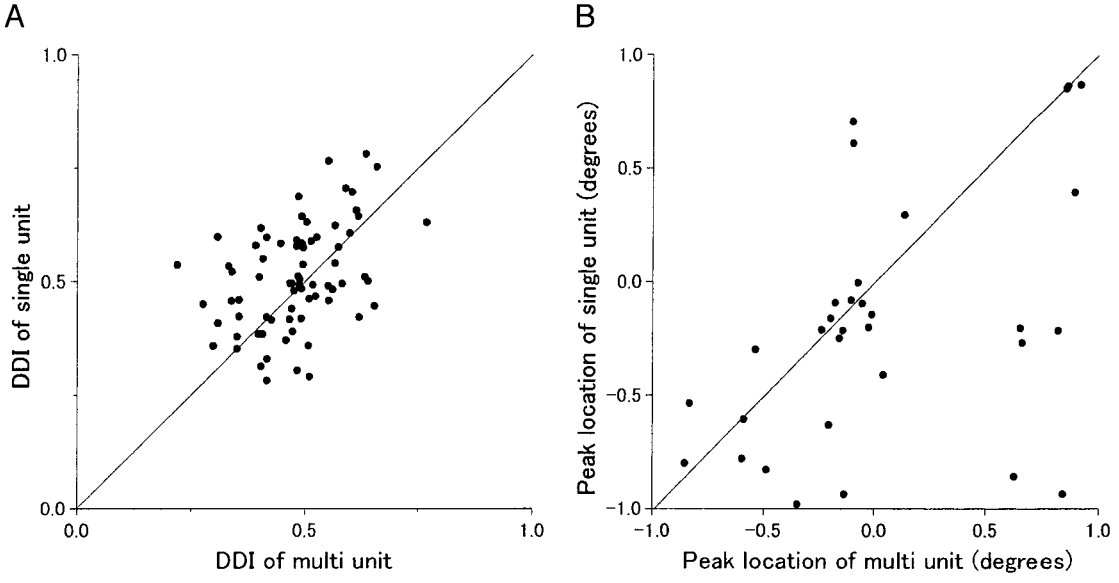

FIG. 14. Comparison of the DDI (*A*) and the response peak locations (*B*) for single- and multi-unit responses recorded simultaneously at the same sites.

parity-selective simple cells, creating a selectivity invariant for position and contrast (Anzai et al. 1999b,c; Ohzawa et al. 1990, 1997). We suggest that V4 neurons do not detect binocular disparity but receive information from disparity-encoding neurons at earlier stages of the visual pathway.

Based on anatomical connections, a major candidate area for the disparity information input into V4 is the thin and pale stripes in V2 (DeYoe et al. 1994; Felleman et al. 1997; Xiao et al. 1999). Disparity-selective neurons in V2, however, are mainly concentrated in the thick stripes projecting to the dorsal visual pathway; a fewer neurons in the thin and pale stripes are selective for disparity (Hubel and Livingstone 1987; Peterhans and von der Heydt 1993; Roe and Ts'o 1995). As V4 neurons also receive inputs from V3, V3A, and MT where the thick stripes in V2 send projections (Felleman and Van Essen 1991), another candidate route for disparity information would be from disparity-selective neurons in the thick stripes of V2 via V3, V3A, and MT.

These results and the anatomical connection between V4 and IT (Desimone et al. 1980; DeYoe et al. 1994; Felleman et al. 1997) suggest that V4 neurons transmit disparity information to IT neurons. It remains a possibility that V4 and IT neurons receive disparity information from either a common source in parallel or independent areas; studies examining the relationship between the anatomical modules and the clusters of disparity-selective neurons in V4 should shed light on this issue.

Comparison of disparity selectivity in V4 and other visual areas

More V4 neurons preferred crossed disparity than uncrossed disparity (Fig. 5), which is similar to a previous report in MT (Bradley and Andersen 1998). Many V4 neurons possess strong suppressive regions surrounding the classically defined receptive field (Desimone and Schein 1987; Desimone et al. 1993; Schein and Desimone 1990), suggesting that these suppressive regions contribute to figure-ground segregation. The biased preference for crossed disparity may reflect the function of figure-ground segregation. Uka et al. (2000), however, reported that although IT neurons recorded from one monkey showed a bias toward crossed disparity, neurons recorded from another monkey showed no such bias. As disparity-selective V4 neurons are clustered, and the size of the modules in V4 defined by functional and anatomical studies is large (DeYoe et al. 1994; Felleman et al. 1997; Ghose and Ts'o 1997; Xiao et al. 1999), our sampling of V4 neurons may possess a bias accounting for the present result. Additional studies are required to further examine the near-preference bias of V4.

The distribution of DDIs ranged from 0.28 to 0.78, and peaked at 0.50 (Fig. 6*A*). Compared with the results obtained from V1 and MT using dynamic random-dot stereograms (Cumming and DeAngelis 2001), the distribution of V4 neurons is narrower than those of V1 and MT neurons. We never observed V4 neurons showing DDI higher than 0.8, whereas such neurons exist in V1 and MT. Yet it is likely that we overestimated the DDI for each neuron because we used bar stimuli, and the modulation caused by the monocular responses could affect the binocular responses. These observations may indicate that V4 neurons are less sensitive to disparity than V1 and MT. There are, however, other differences between these studies that may affect DDI values: dynamics of stimuli and duration of stimulus presentation. Stimuli used in this study were presented at a location without movements; this might render neuronal responses phasic rather than tonic, as shown in Fig. 2*A*. The difference between the maximum and the minimum responses is likely to be smaller in phasic responses than in tonic responses, which may lead to low DDIs. The duration of stimulus presentation in this study (1 s) was shorter than the other studies (V1: 2 s, MT: 1.5 s), which may cause a difference in the magnitude of RMS_{error}. Long stimulus duration may decrease the variation of the mean firing rate of each trial, which yields small RMS_{error}. Further studies are necessary to establish the difference of strength of disparity tuning in different areas.

V4 neurons with similar disparity selectivity were clustered together, a phenomenon also observed in V1, V2, MT, and IT (Burkitt et al. 1998; Cumming and DeAngelis 2001; DeAngelis and Newsome 1999; Uka et al. 2000). MT neurons are organized into cortical columns based on preferred disparity, mapped systematically across the surface of MT (DeAngelis and Newsome 1999). Comparison of disparity selectivity clustering in V4 with other areas demonstrates that V4 has weaker clustering than MT, although comparable to V1 and IT. The stimuli used in this study, however, differed from those used to examine the neurons in V1 and MT; therefore a comparison of these areas should be interpreted with caution. Because we used bar stimuli with defined edges, the correlation of responses between single and multi-units may possibly contain correlations caused by monocular cues. The monocular response, however, could not account for the binocular response; the correlation for monocular responses is unlikely to fully explain the similarity of responses to binocularly disparate stimuli between simultaneously recorded units (Fig. 14). Although the degree of clustering of V4 disparity-selective neurons should be evaluated further using random-dot stereograms, the clustering of disparity-selective neurons in both V4 and IT suggests that a functional module for binocular disparity processing resides in the ventral visual pathway.

Role of disparity-selective neurons in V4

Disparity-selective neurons contribute to a range of visual or visuomotor functions. As V4, an intermediate stage of the visual pathway, is critical for object vision, disparity-selective V4 neurons may function in figure-ground segregation and 3-D surface reconstruction. Some IT neurons respond to the depth order of surfaces, irrespective of the type of disparity in the stimuli (Uka et al. 1997), whereas other IT neurons respond to disparity gradients rather than to local disparity cues (Janssen et al. 2000a). In addition, some IT neurons respond selectively to shapes defined by disparity (Tanaka et al. 2001). V4 neurons may provide the input to IT, creating the selectivity of these neurons for 3-D surfaces.

Neurons selectively responding to 3-D shapes defined by patterns of disparity gradients are more frequently found in the superior temporal sulcus (STS) lower bank than in the gyrus part of IT (area TE) (Janssen et al. 2000b). STS connects the parietal regions with the ventral visual pathway (Baizer et al. 1991); in the parietal lobe, area CIP contains neurons selective for surface orientation derived from disparity gradient (Taira et al. 2000). Although the recording sites in Janssen et al. (2000b) differs from those in other studies (Tanaka et al. 2001; Uka et

al. 1997), these results may suggest that this interconnection is sufficient for 3-D shape processing without the involvement of V4 and area TE.

Disparity-selective V4 neurons may play a role in the perception of depth. V4 neurons are more strongly selective for position in depth than for visual direction in monocularly presented stimulus (Figs. 2*B*, 4, and 10). Disparity selectivity of V4 neurons is invariant for position within the receptive field (Figs. 7–9). Position invariance of disparity selectivity has also been observed in IT (Uka et al. 2000), indicating that information on position in depth within the receptive field is preserved while that on visual direction is lost. These neurons may contribute to perception of depth, independent of the monocular visual direction. Lesions of IT in monkeys and lesions of the temporal lobe in humans impair depth discrimination in random-dot stereograms (Cowey and Porter 1979; Ptito and Zatorre 1988; Ptito et al. 1991). Lesions in V4 and MT, however, do not affect the behavioral scores of monkeys in tasks designed to detect a target defined by disparity (Schiller 1993).

V4 neurons may also be involved in guiding eye movements in response to binocular disparity. Neurons in V4 project directly to the parietal cortex (Blatt et al. 1990), the frontal eye field (Schall et al. 1995), and the superior colliculus (Fries 1984), areas which are involved in oculomotor behavior. Furthermore, V4 neurons show presaccadic activity (Fischer and Boch 1981), suggesting a role in the control of eye movement.

The findings that neurons in V4 and IT are selective for binocular disparity indicate that disparity processing is performed along both the ventral visual pathway and the dorsal visual pathway. These two pathways may play different roles in stereopsis. Distinguishing the different roles of the two visual pathways in stereopsis will be a major focus of future studies.

We thank Dr. Izumi Ohzawa for valuable comments on the manuscript and Dr. Hiroshi Tamura for advice on data analysis.

This work was supported by grants to I. Fujita from Core Research for Evolutional Science and Technology of the Japan Science and Technology Corporation, the Special Coordination Fund for Promoting Science and Technology of the Science and Technology Agency, the Ministry of Education, Science, Sports, and Culture (09268222), and Fujitsu Co.

REFERENCES

ANZAI A, OHZAWA I, AND FREEMAN RD. Neural mechanisms for encoding binocular disparity: receptive field position versus phase. *J Neurophysiol* 82: 874–890, 1999a.

ANZAI A, OHZAWA I, AND FREEMAN RD. Neural mechanisms for processing binocular information. I. Simple cells. *J Neurophysiol* 82: 891–908, 1999b.

ANZAI A, OHZAWA I, AND FREEMAN RD. Neural mechanisms for processing binocular information. II. Complex cells. *J Neurophysiol* 82: 909–924, 1999c.

BAIZER JS, UNGERLEIDER LG, AND DESIMONE R. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *J Neurosci* 11: 168–190, 1991.

BLATT GJ, ANDERSEN RA, AND STONER GR. Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. *J Comp Neurol* 299: 421–445, 1990.

BRADLEY DC AND ANDERSEN RA. Center-surround antagonism based on disparity in primate area MT. *J Neurosci* 18: 7552–7565, 1998.

BURKHALTER A AND VAN ESSEN DC. Processing of color, form, and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. *J Neurosci* 6: 2327–2351, 1986.

BURKITT GR, LEE J, AND TS'O DY. Functional organization of disparity in visual area V2 of the macaque monkey. *Soc Neurosci Abstr* 24: 1978, 1998.

COWEY A AND PORTER J. Brain damage and global stereopsis. *Proc R Soc Lond B Biol Sci* 204: 399–407, 1979.

CUMMING BG AND DEANGELIS GC. The physiology of stereopsis. *Annu Rev Neurosci* 24: 203–238, 2001.

DEAN AF. The variability of discharge of simple cells in the cat striate cortex. *Exp Brain Res* 44: 437–440, 1981.

DEANGELIS GC, CUMMING BG, AND NEWSOME WT. Cortical area MT and the perception of stereoscopic depth. *Nature* 394: 677–680, 1998.

DEANGELIS GC AND NEWSOME WT. Organization of disparity-selective neurons in macaque area MT. *J Neurosci* 19: 1398–1415, 1999.

DEANGELIS GC, OHZAWA I, AND FREEMAN RD. Depth is encoded in the visual cortex by a specialized receptive field structure. *Nature* 352: 156–159, 1991.

DESIMONE R, ALBRIGHT TD, GROSS CG, AND BRUCE C. Stimulus-selective properties of inferior temporal neurons in the macaque. *J Neurosci* 4: 2051–2062, 1984.

DESIMONE R, FLEMING J, AND GROSS CG. Prestriate afferents to inferior temporal cortex: an HRP study. *Brain Res* 184: 41–55, 1980.

DESIMONE R, MORAN J, SCEIN SJ, AND MISHKIN M. A role for the corpus callosum in visual area V4 of the macaque. *Eur J Neurosci* 10: 159–171, 1993.

DESIMONE R AND SCHEIN SJ. Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *J Neurophysiol* 57: 835–868, 1987.

DEYOE EA, FELLEMAN DJ, VAN ESSEN DC, AND MCCLENDON E. Multiple processing streams in occipitotemporal visual cortex. *Nature* 371: 151–154, 1994.

DEYOE EA AND VAN ESSEN DC. Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature* 317: 58–61, 1985.

EIFUKU S AND WURTZ RH. Response to motion in extrastriate area MSTl: disparity sensitivity. *J Neurophysiol* 82: 2462–2475, 1999.

FELLEMAN DJ AND VAN ESSEN DC. Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *J Neurophysiol* 57: 889–920, 1987.

FELLEMAN DJ AND VAN ESSEN DC. Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* 1: 1–47, 1991.

FELLEMAN DJ, XIAO Y, AND MCCLENDON E. Modular organization of occipitotemporal pathways: cortical connections between visual area 4 and visual area 2 and posterior inferotemporal ventral area in macaque monkeys. *J Neurosci* 17: 3185–3200, 1997.

FISCHER B AND BOCH R. Selection of visual targets activates prelunate cortical cells in trained rhesus monkey. *Exp Brain Res* 41: 431–433, 1981.

FRIES W. Cortical projections to the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. *J Comp Neurol* 230: 55–76, 1984.

GATTAS R, SOUSA APB, AND GROSS CG. Visuotopic organization and extent of V3 and V4 of the macaque. *J Neurosci* 8: 1831–1845, 1988.

GHOSE GM AND TS'O D. Form processing modules in primate area V4. *J Neurophysiol* 77: 2191–2196, 1997.

GROSS CG, ROCHA-MIRANDA CE, AND BENDER DB. Visual properties of neurons in inferotemporal cortex of the macaque. *J Neurophysiol* 35: 96–111, 1972.

HUBEL DH AND LIVINGSTONE MS. Segregation of form, color, and stereopsis in primate area 18. *J Neurosci* 7: 3378–3415, 1987.

HUBEL DH AND WIESEL TN. Stereoscopic vision in macaque monkey: cells sensitive to binocular depth in area 18 of the macaque monkey cortex. *Nature* 225: 41–42, 1970.

JANSSEN P, VOGELS R, AND ORBAN GA. Three-dimensional shape coding in inferior temporal cortex. *Neuron* 27: 385–397, 2000a.

JANSSEN P, VOGELS R, AND ORBAN GA. Selectivity for 3D shape that reveals distinct areas within macaque inferior temporal cortex. *Science* 288: 2054–2056, 2000b.

JUDGE SJ, RICHMOND BJ, AND CHU FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–538, 1980.

JULESZ B. *Foundation of Cyclopean Perception*. Chicago, IL: Univ. Chicago Press, 1971.

KOBATAKE E AND TANAKA K. Neuronal selectivities of complex object features in the ventral visual pathway of the macaque cerebral cortex. *J Neurophysiol* 71: 856–867, 1994.

KOMATSU H, IDEURA Y, KAJI S, AND YAMANE S. Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. *J Neurosci* 12: 408–424, 1992.

MAUNSELL JH AND VAN ESSEN DC. Functional properties of neurons in middle temporal visual area of the macaque monkey. II. Binocular interactions and sensitivity to binocular disparity. *J Neurophysiol* 49: 1148–1167, 1983.

OHZAWA I, DEANGELIS GC, AND FREEMAN RD. Encoding of binocular disparity by complex cells in the cat's visual cortex. *J Neurophysiol* 77: 2879–2909, 1997.

OHZAWA I, DEANGELIS GC, AND FREEMAN RD. Stereoscopic depth discrimination in the visual cortex: neurons ideally suited as disparity detectors. *Science* 249: 1037–1041, 1990.

PETERHANS E AND VON DER HEYDT R. Functional organization of area V2 in the alert macaque. *Eur J Neurosci* 5: 509–524, 1993.

POGGIO GF AND FISCHER B. Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *J Neurophysiol* 40: 1392–1405, 1977.

POGGIO GF, GONZALEZ F, AND KRAUSE F. Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity. *J Neurosci* 8: 4531–4550, 1988.

PTITO A AND ZATORRE RJ. Impaired stereoscopic detection thresholds after left or right temporal lobectomy. *Neuropsychologia* 26: 547–554, 1988.

PTITO A, ZATORRE RJ, LARSON WL, AND TOSINI C. Stereopsis after unilateral anterior temporal lobectomy. Dissociation between local and global measures. *Brain* 114: 1323–1333, 1991.

ROE AW AND TS'O DY. Visual topography in primate V2: multiple representation across functional stripes. *J Neurosci* 15: 3689–3715, 1995.

ROTHSTEIN TB AND SACKS JG. Defective stereopsis in lesions of the parietal lobe. *Am J Opthalmol* 73: 281–284, 1972.

ROY JP, KOMATSU H, AND WURTZ RH. Disparity sensitivity of neurons in monkey extrastriate area MST. *J Neurosci* 12: 2478–2492, 1992.

SCHALL JD, MOREL A, KING DJ, AND BULLIER J. Topography of visual cortex connections with frontal eye field in macaque: convergence and segregation of processing streams. *J Neurosci* 15: 4464–4487, 1995.

SCHEIN SJ AND DESIMONE R. Spectral properties of V4 neurons in the macaque. *J Neurosci* 10: 3369–3389, 1990.

SCHILLER PH. The effects of V4 and middle temporal (MT) area lesions on visual performance in the rhesus monkey. *Vis Neurosci* 10: 717–746, 1993.

SÁRY G, VOGELS R, KOVACS G, AND ORBAN GA. Responses of monkey inferior temporal neurons to luminance-, motion-, and texture-defined gratings. *J Neurophysiol* 73: 1341–1354, 1995.

TAIRA M, TSUTSUI KI, JIANG M, YARA K, AND SAKATA H. Parietal neurons represent surface orientation from the gradient of binocular disparity. *J Neurophysiol* 83: 3140–3146, 2000.

TANAKA H, UKA T, YOSHIYAMA K, KATO M, AND FUJITA I. Processing of shape defined by disparity in monkey inferior temporal cortex. *J Neurophysiol* 85: 735–744, 2001.

TANAKA K, SAITO H, FUKADA Y, AND MORIYA M. Coding visual images of objects in the inferotemporal cortex. *J Neurophysiol* 66: 170–189, 1991.

TOLHURST DJ, MOVSHON JA, AND THOMPSON ID. The dependence of response magnitude and variance of cat visual cortical neurones on stimulus contrast. *Exp Brain Res* 41: 414–419, 1981.

UKA T, TANAKA H, KATO M, AND FUJITA I. Disparity sensitivity and representation of 3-dimensional surface structure in monkey inferior temporal cortex. *Soc Neurosci Abstr* 23: 2063, 1997.

UKA T, TANAKA H, YOSHIYAMA K, KATO M, AND FUJITA I. Disparity selectivity of neurons in monkey inferior temporal cortex. *J Neurophysiol* 84: 120–132, 2000.

WATANABE M, TANAKA H, UKA T, AND FUJITA I. Disparity selective neurons in area V4 of macaque monkeys. *Soc Neurosci Abstr* 26: 954, 2000.

WHEATSTONE C. Contributions to the physiology of vision. I. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philos Trans R Soc Lond B Biol Sci* 2: 371–393, 1838.

XIAO Y, ZYCH A, AND FELLEMAN DJ. Segregation and convergence of functionally defined V2 thin stripe and interstripe compartment projections to area V4 of macaques. *Cereb Cortex* 9: 792–804, 1999.

ZIHL J, VON CRAMON D, AND MAI N. Selective disturbance of movement vision after bilateral brain damage. *Brain* 106: 313–340, 1983.