

# Response to Motion in Extrastriate Area MSTl: Disparity Sensitivity

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**Eifuku, Satoshi and Robert H. Wurtz.** Response to motion in extrastriate area MSTl: disparity sensitivity. *J. Neurophysiol.* 82: 2462–2475, 1999. Many neurons in the lateral-ventral region of the medial superior temporal area (MSTl) have a clear center surround separation in their receptive fields. Either moving or stationary stimuli in the surround modulates the response to moving stimuli in the center, and this modulation could facilitate the perceptual segmentation of a moving object from its background. Another mechanism that could facilitate such segmentation would be sensitivity to binocular disparity in the center and surround regions of the receptive fields of these neurons. We therefore investigated the sensitivity of these MSTl neurons to disparity ranging from three degrees crossed disparity (near) to three degrees uncrossed disparity (far) applied to both the center and the surround regions. Many neurons showed clear disparity sensitivity to stimulus motion in the center of the receptive field. About 1/3 of 104 neurons had a clear peak in their response, whereas another 1/3 had broader tuning. Monocular stimulation abolished the tuning. The prevalence of cells broadly tuned to near and far disparity and the reversal of preferred directions at different disparities observed in MSTd were not found in MSTl. A stationary surround at zero disparity simply modulated up or down the response to moving stimuli at different disparities in the receptive field (RF) center but did not alter the disparity tuning curve. When the RF center motion was held at zero disparity and the disparity of the stationary surround was varied, some surround disparities produced greater modulation of MSTl neuron response than did others. Some neurons with different disparity preferences in center and surround responded best to the relative disparity differences between center and surround, whereas others were related to the absolute difference between center and surround. The combination of modulatory surrounds and the sensitivity to relative difference between center and surround disparity make these MSTl neurons particularly well suited for the segmentation of a moving object from the background.

## INTRODUCTION

In a previous study on the lateral region of the medial superior temporal area (MSTl) of monkey extrastriate cortex (Eifuku and Wurtz 1998), stimulation of the surround regions of the receptive fields of these neurons was shown to modulate their response to stimuli falling in the center of the receptive field. This modulation occurred whether the surround stimulus was stationary or moving. We suggested that one role for this surround modulation was the segmentation of a moving object from the background.

Another mechanism for such segmentation of object from background is the difference in the depth in the visual field between the object and the background, which can be detected by the relative difference in disparity of their images falling on the retina. Neurons in the middle temporal area (MT) have

been shown to be disparity sensitive (Maunsell and Van Essen 1983b), and this disparity, like direction of motion, has a spatial organization (DeAngelis and Newsome 1999). The disparity sensitivity in MT has recently been shown to be important for the separation of overlapping planes in transparent motion and image segmentation (Bradley and Andersen 1998; Bradley et al. 1995). Neurons in the dorsal region of MST (MSTd) also have been shown to be sensitive to the disparity of moving stimuli, and some MSTd neurons even show a reversal of preferred directions for stimuli moving at different disparities (Roy et al. 1992; Roy and Wurtz 1990).

In contrast to MT and MSTd, the disparity sensitivity of MSTl neurons has remained largely unknown. In the present experiments we have investigated the disparity sensitivity of these MSTl neurons, and the relation of this sensitivity to the segmentation already provided by the interaction of the center and surround regions of the visual receptive field (RF). We find that many neurons are sensitive to changes in disparity not only in the center but also in the surround of the visual field and that some neurons convey information about the relative differences between center and surround disparity rather than about the absolute disparity of either.

An abstract of these findings has been published previously (Eifuku and Wurtz 1997).

## METHODS

### *Physiological and behavioral procedures*

We studied areas MSTl in the same two adult male rhesus monkeys (*Macaca mulatta*) used in the previous report (Eifuku and Wurtz 1998), and the monkeys were trained, cared for, and prepared for single neuron and eye movement recording as described in that paper. All experimental protocols were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals including the Principles of Laboratory Animal Care.

During the experiment, the monkey sat in a primate chair with its eyes 58 cm away from the center of a  $120 \times 100^\circ$  translucent tangent screen. Each trial began with the appearance of a spot of light ( $0.3^\circ$  in diameter) at the center of the screen. The monkey's task was to fixate the spot within 500 ms of the onset and maintain fixation. The position of each eye was monitored separately so that any change in vergence was easily detected; such recording indicated that the monkey usually maintained binocular fixation within  $\pm 0.25^\circ$  so that the trial was rarely terminated when either eye left the  $2^\circ$  square fixation window.

We used the same computer-generated random dot patterns projected onto the screen in front of the monkey as those in the previous report, but in these experiments the stimuli were presented to each eye separately. To avoid the dim stimuli necessary to achieve color separation in the overlapping red/green disparity stimuli used previously in this laboratory (Roy et al. 1992), we projected separate images to each eye. A prism was positioned in front of each eye so

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that the line of sight was deflected to the right for the right eye and to the left for the left eye. The image projected onto the screen by the TV projector was also divided into separate right and left halves with a fixation point included in each half. The prisms were checked for alignment by determining that the fixation spots in the two half images were superimposed when the correct interocular distance was set for the subject. Center and surround stimuli were presented in each half stimulus. The random dots used for stimulation were generated for each session, and the pattern had 90% dark and 10% light areas. Each random dot subtended  $0.4^\circ$ . The disparity stimulus could be extended only  $30^\circ$  horizontally from the midline of the projected image to each eye (due to the horizontal limit of the prisms and the overlap of the 2 prism images) but  $50^\circ$  down and  $50^\circ$  up from the fixation point. This larger vertical region allowed for study of a few neurons with larger RF center eccentricities than was possible on the horizontal meridian. On each side of the central  $30^\circ$  area was a band of nondisparity random dot pattern (monocular), but this extension generally did not fall on the most effective region of the surround of the neurons studied. We extended the dot pattern in this way to have as large a stationary field as possible to increase the stability of the monkey's fixation in the presence of moving stimuli even though this exposed each eye to a nondisparity stimulus (Liu et al. 1994; Nakayama et al. 1995). The fixation point was always at zero disparity. The display to each eye had a maximum of 1,660 dots. Otherwise the display was identical to that in our previous report (Eifuku and Wurtz 1998).

Disparity was produced by shifting the location of the dots in either the center or the surround to produce 1, 2, or  $3^\circ$  of crossed or uncrossed disparity. The disparity calculation was the same as that described previously (Roy et al. 1992). We used a wide range of disparity ( $+3^\circ$  to  $-3^\circ$ ) to see the range of disparity in this first survey of MSTl disparity, and to allow comparison to MSTd. Even the  $1^\circ$  disparity stimulus could not be fused while fixating on the screen and appeared to the investigators as a dot pattern lying just in front of or just behind the screen. We used a  $+3^\circ$  disparity stimulus even though it produced a disparity that was beyond the normal physiological range.

Recordings were made in one hemisphere in each of the two monkeys. MSTl was identified using the same physiological criteria as in the previous paper: neurons responded preferentially to moving stimuli, were directionally selective, had RF centers with a medial edge close to the fovea, had relatively large receptive fields, and responded to single spots of light as well or better than to the motion of random dot patterns. Again, we first mapped the RF center of each neuron using either a small spot or a random dot pattern at zero disparity; this procedure meant that we only studied neurons that responded at least somewhat to zero disparity stimuli. This procedure was identical to that used in the previous study on MSTd in this laboratory (Roy et al. 1992; Roy and Wurtz 1990). We then determined the optimal speed and direction of motion across the RF center at zero disparity using computer-controlled stimuli with eight directions (0, 45, 90, 135, 180, 225, 270, and  $315^\circ$ ;  $0^\circ$  was horizontal to the right) and five speeds (6, 10, 20, 40, and  $80^\circ/\text{s}$ ). In the subsequent experiments on disparity sensitivity, we used a random dot field that matched the size of the RF center and that moved at the optimal speed and in the preferred or opposite direction. The surround stimulus was also a random dot pattern of the same density as the center stimulus, was usually  $90 \times 100^\circ$ , and was stationary. We presented stimuli in the center and the surround with different disparities, with the presentation of these stimuli randomly interleaved. The time of stimulus onset was separated from the time of stimulus motion: after looking at the fixation point for 400–800 ms, the visual stimulus appeared as a stationary random dot field, which on some trials had disparity, and then after 800 ms the dots moved for 400 or 600 ms.

### Data analysis

We quantified the activity of each neuron by measuring spike frequency in the 400-ms period beginning 70 ms after stimulus motion onset to allow for the latency we observed in the MSTl neurons under our stimulus conditions (Eifuku and Wurtz 1998). Because the only motion used in these experiments was in the center of the RF, and a large surround of stationary dots was frequently present, we did not see evidence of the ocular following responses, which we had seen in the previous report with the motion of the large surround stimulus, and we therefore did not truncate the response measuring period at 170 ms as we had in the previous report. As in that previous study, the onset of the image projected by the Sharp 850 (LCD) projector had a fixed phase lag of 4 ms in the onset of the projected image and a variable one of between 0 and 16 ms, which produced a mean stimulus delay of 12 ms. We shifted the responses studied by 12 ms to allow for this delay (82–482 ms). We did not measure or report visual latencies.

For comparison of the responses of a neuron at different disparities, we used a one-way ANOVA (factor: disparity) with a significance level of  $P < 0.05$ . We also plotted the magnitude of the response at each disparity and fitted a curve through these data points using a cubic spline fit. We determined the peak location from this curve. Those curves that had two crossing points at which the value was equal to the peak value on the curve divided by the  $\sqrt{2}$  (Poggio and Talbot 1981; Schiller et al. 1976) we classified as having a peak in their disparity tuning curve. For those cells with such a peak, we took the width of the response as equal to those two  $\sqrt{2}$  reference points, which includes  $\sim 60\%$  of the area under the curve. For the strength of the disparity tuning we used a contrast comparison as an index of tuning strength:  $(\max - S) - (\min - S) / (\max - S) + (\min - S)$ , where  $\max$  and  $\min$  are the maximum and minimum value of the disparity tuning curve and  $S$  is the spontaneous activity during 200 ms before the stimulus motion onset. The maximum and minimum responses were taken from the disparity tuning after cubic spline fitting. The index was similar to that used recently in area MT (Bradley and Andersen 1998).

Displays used for off-line data analysis were spike density histograms created by replacing the millisecond-wide square pulses representing spikes with Gaussian pulses with a width corresponding to a standard deviation of 10 ms using the method of McPherson and Aldridge (1979).

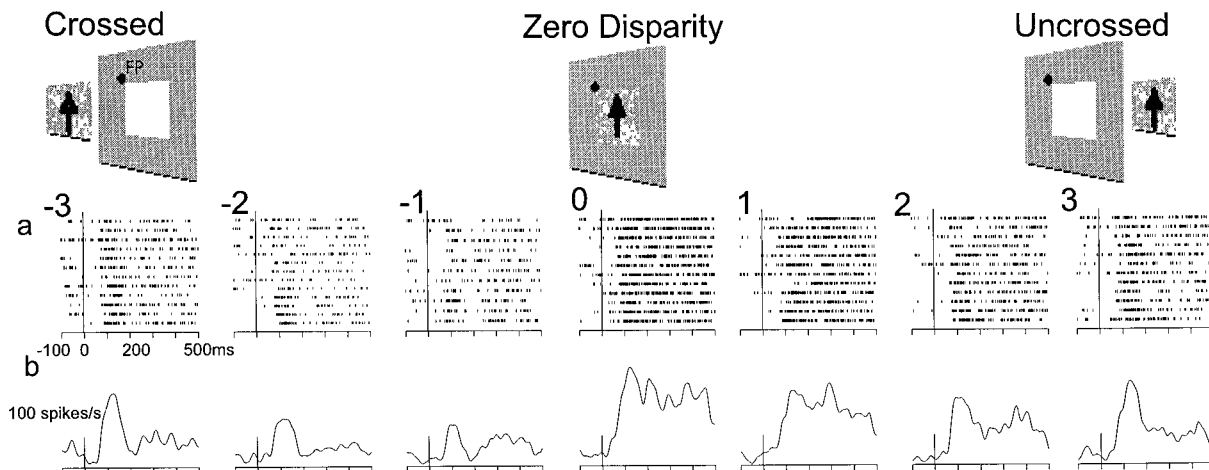
## RESULTS

### Types of response to disparity shifts in the RF center

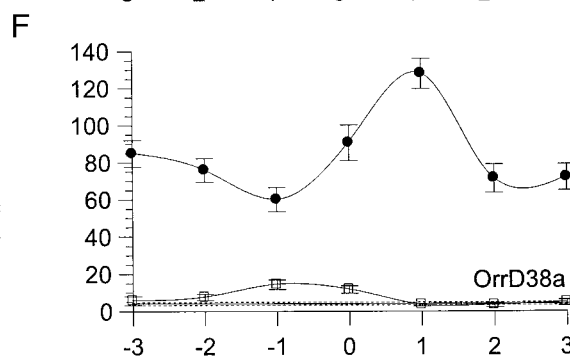
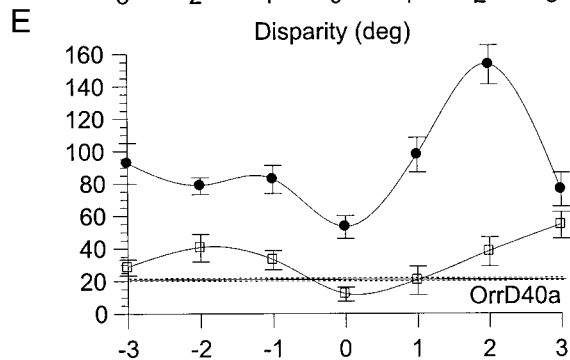
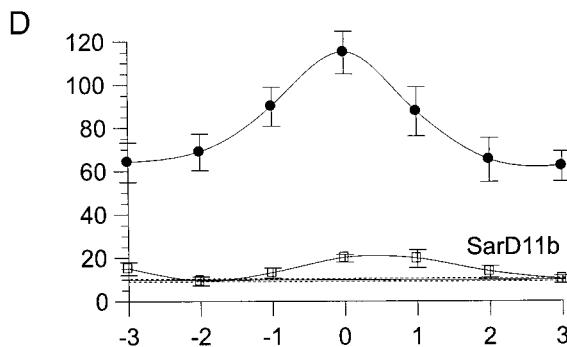
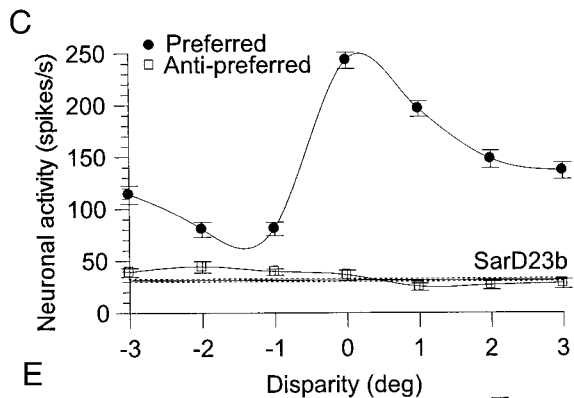
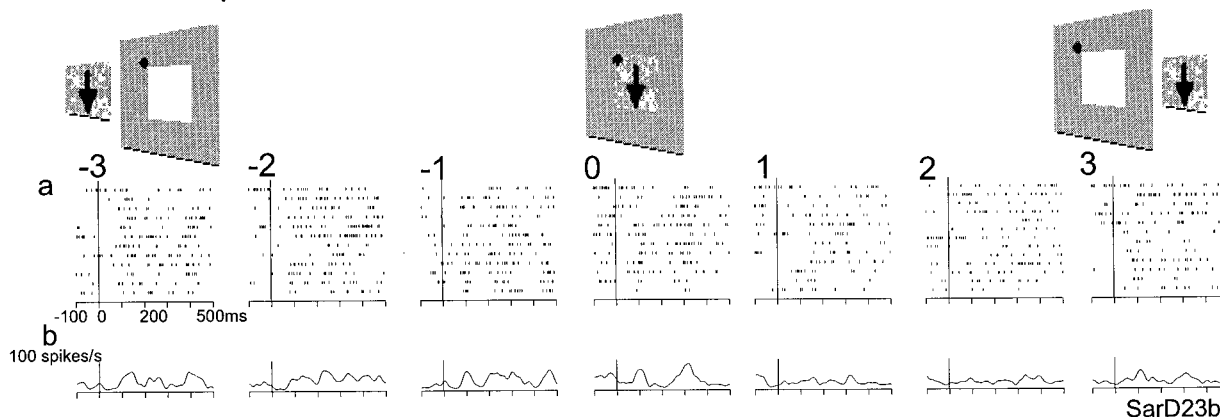
We recorded from 104 MSTl neurons (67 from the right hemisphere of one monkey and 37 from the right hemisphere of the other monkey) and tested the disparity sensitivity of the RF center of each. We first determined the size and location of the RF center and the direction and speed of preferred motion. The range of RF center sizes and eccentricities in the present study were  $10\text{--}15^\circ$  and  $3.3\text{--}21.9^\circ$ , respectively. We then randomly varied the disparity of the stimulus matched to the RF center size and moved the stimulus at the preferred speed in both the preferred and anti-preferred directions. Many neurons responded more strongly to moving stimuli at some disparities than at others, and we classified neurons as being sensitive to disparity by using a one-way ANOVA (factor: disparity) with a significance level of  $P < 0.05$ . Of the 104 neurons, 74 (71.1%) showed significantly different responses as disparity was varied.

Figure 1A shows an example of such a disparity-sensitive neuron. This neuron responded better to a few uncrossed disparities (far stimuli) than to crossed disparities (near stimuli)

**A Center Preferred Direction**



**B Center Anti-preferred Direction**



with the strongest response at zero disparity. The disparity of the stimuli minimally affected the response to motion in the anti-preferred direction (Fig. 1*B*). We fit the means of the responses to each of the seven different disparities with a cubic spline function, and Fig. 1*C* shows the curve for the range of disparities shown in Fig. 1, *A* and *B*. The shapes of the curves and the location of the peaks varied considerably across neurons (Fig. 1, *C–F*). Figure 1*D* shows another example of a cell with a peak at zero disparity, whereas Fig. 1, *E* and *F*, shows two neurons with peaks away from zero.

In spite of the substantial variation in the shape of the curves that is evident in Fig. 1, *C–F*, they all had a clear peak in their response to the disparity range tested. While we observed a great variation in the disparity tuning curves among the neurons, we frequently found neurons with such peaks in the tuning. To objectively classify neurons as having a peak in the response profile, we required the curve to have two crossing points at which the value was equal to the peak value on the curve divided by the  $\sqrt{2}$  (Poggio and Talbot 1981; Schiller et al. 1976). We found 36 neurons that met this criterion, and Fig. 2*A* shows the distribution of the disparities at which the peak occurred. Although the peak is most frequently at zero disparity, both crossed and uncrossed disparities are also represented. Figure 2*B* shows the substantial variation in the width of the disparity tuning of these neurons with a peaked tuning curve, and the lack of any obvious relationship between the location of the disparity peak and the tuning width.

Other neurons were sensitive to stimulus disparity (as indicated by the ANOVA) but did not meet the above criteria for a peaked response. Of the 38 neurons that did not meet the criteria for a peaked response, 33 had broadly tuned curves, and the remaining 5 neurons had multiple peaks. Figure 3, *A* and *B*, shows an example of a more broadly tuned neuron, which responded to many disparities, and Fig. 3*C* shows the graph of these responses. Again there was considerable variation in such broader tuning curves as indicated in the examples shown in Fig. 3, *C–F*. The peaks of these neurons were also distributed over both crossed and uncrossed disparities. There is no indication of a preponderance of neurons responding preferentially to near or far disparities as was the case in MSTd (Roy et al. 1992).

We also found no indication in any of the MSTl neurons of a change in direction preference of the neurons as the disparity changed, as has been described previously for neurons in MSTd (Roy et al. 1992; Roy and Wurtz 1990). The neurons in MSTd that show this effect have a striking characteristic: they respond to one direction of motion at one disparity and to another direction at another disparity. Therefore for the MSTd neurons there is a clear response at some disparities for what

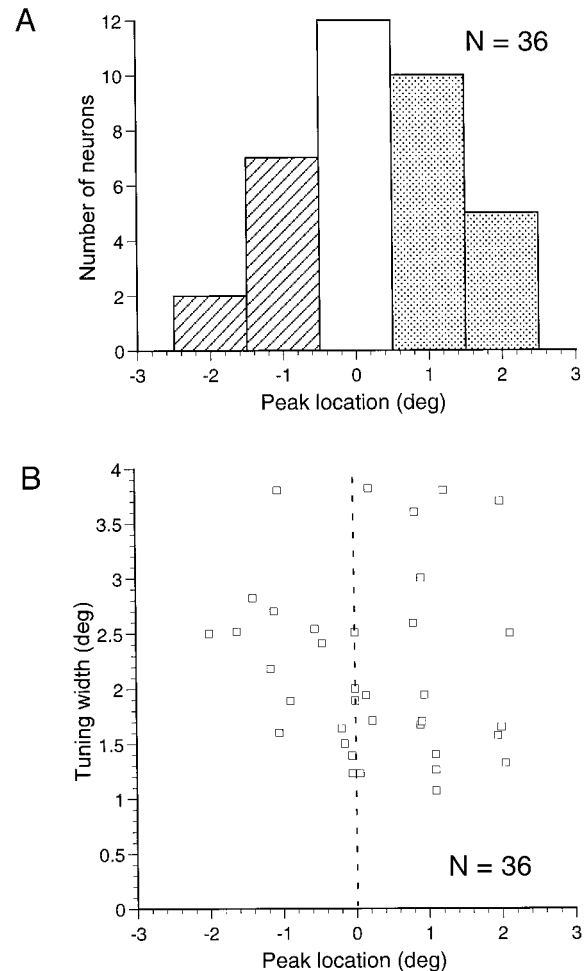
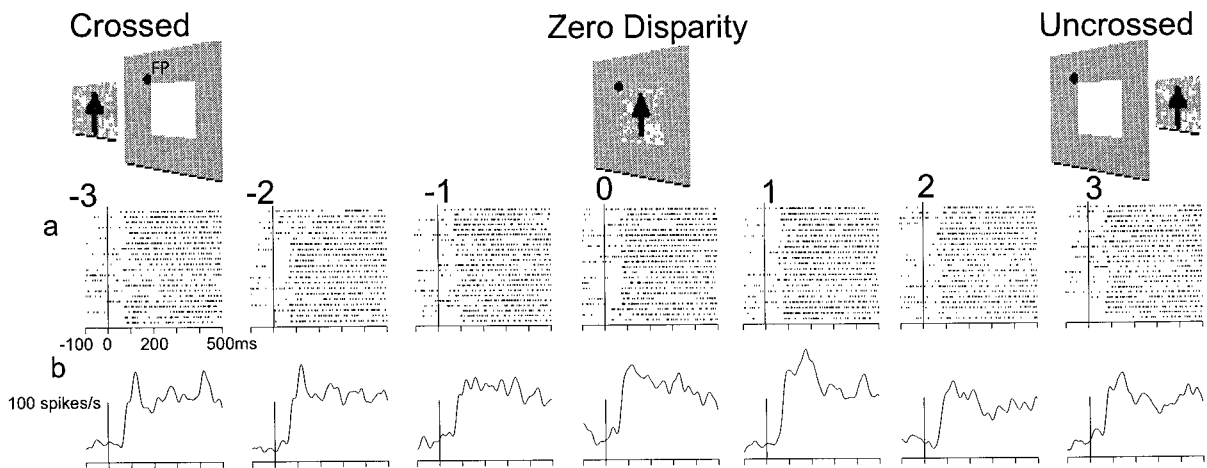


FIG. 2. Distribution of responses of neurons with a peak in disparity tuning. *A*: frequency histogram of the disparity at which the peak response occurred. Peak location was taken from the spline fit curve. *B*: scatter plot of disparity of the peak response against the width of disparity tuning. The width of the response was taken between the 2 points at which the value was equal to the peak value on the curve divided by the  $\sqrt{2}$ , which includes  $\sim 60\%$  of the area under the curve. That the points are largely aligned around 0, +1, and +2° is probably related to the large steps used in disparity testing.

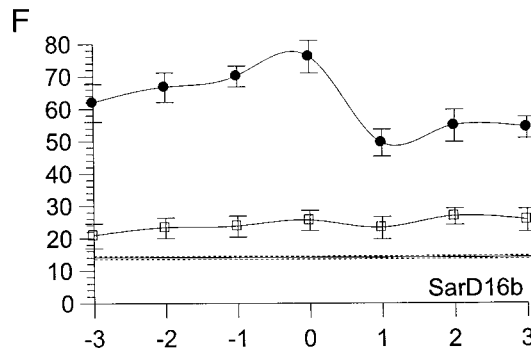
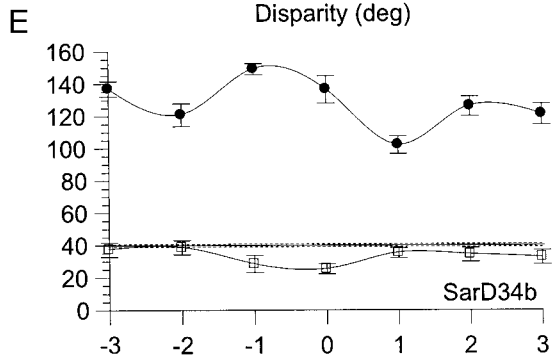
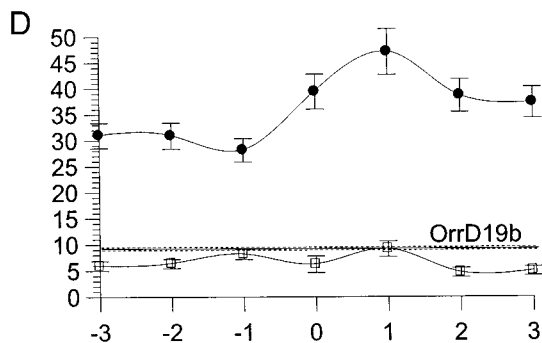
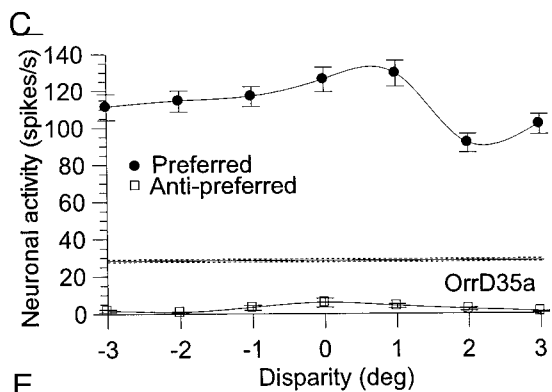
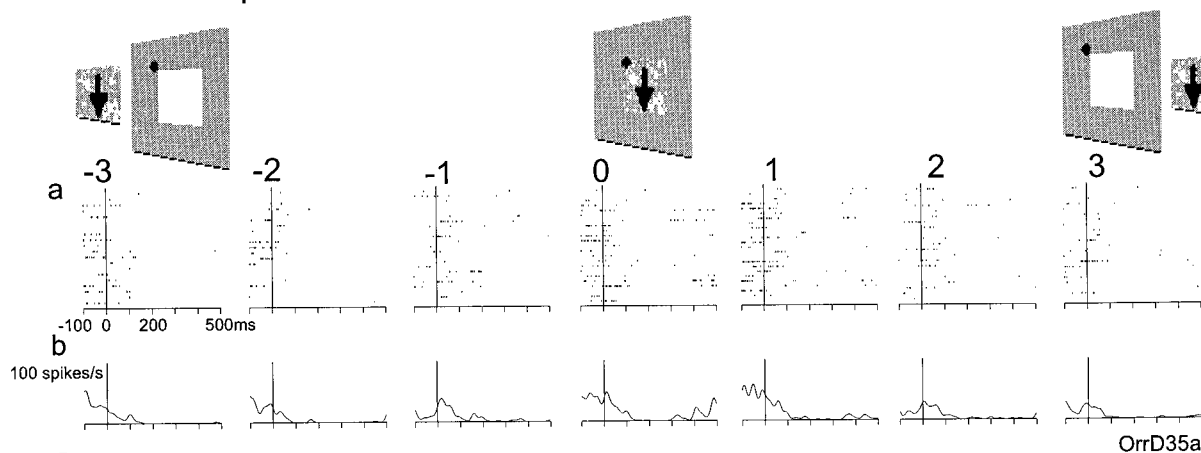
we have referred to as the anti-preferred direction and at other disparities in the preferred direction. Figures 1 and 3 show that there is no such response in the eight example neurons shown, and we never observed such a response comparable to that seen in MSTd in any of our sample of 74 disparity-sensitive neurons. One of the strongest variations in response in the anti-preferred direction is that shown in Fig. 1*E*, and this is not comparable to that seen in MSTd. Based on our current sample

FIG. 1. Examples of neurons that had a peak in their response to stimuli of different disparities. *A–C*: typical example of a neuron with the peak at zero disparity. *A*: responses of the neuron in the preferred direction of motion for zero disparity, crossed disparities (negative 1–3°), and uncrossed disparities (positive 1–3°). The crossed stimuli appear as if in front of the screen (near stimuli), and the uncrossed stimuli appear as if behind the screen (far stimuli). The schematic drawing at *top* shows the fixation point (FP) that was at zero disparity while the stimulus was at different disparities. The RF center of the neuron was 7.5° to right and 7.5° down and was 15° on each side. Preferred direction of motion was 0° and optimal speed was 20°/s. Rasters and spike density functions (SD = 10 ms) are aligned on stimulus motion onset (0). *B*: responses in the anti-preferred direction. *C*: responses of the same neuron showing responses in the preferred (●) and in the anti-preferred (□). Curves were fit by a cubic spline function. Error bars show standard errors of the mean. The mean  $\pm$  SE of the spontaneous activity level during 200 ms before the stimulus motion onset is indicated by the solid and dashed horizontal lines, respectively. A 1-way ANOVA (factor: disparity) showed a significant difference:  $F(6, 77) = 58.622$  ( $P < 0.0001$ ). *D–F*: 3 other examples of similar neurons with a peaked tuning curve. One-way ANOVAs (factor: disparity) showed significant differences: for *D*,  $F(6, 96) = 4.621$  ( $P = 0.0004$ ), for *E*,  $F(6, 84) = 10.565$  ( $P < 0.0001$ ), and for *F*,  $F(6, 106) = 8.608$  ( $P < 0.0001$ ), respectively. Note that *E* and *F* have their peaks at uncrossed disparities, not at zero.

A Center Preferred Direction



B Center Anti-preferred Direction





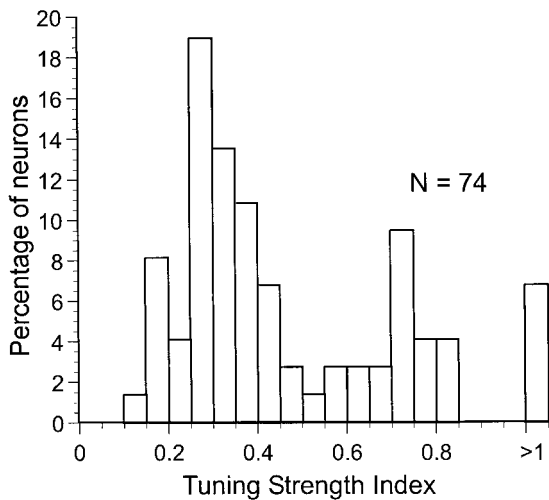


FIG. 4. Strength of tuning to stimulus disparity. Tuning strength is a contrast measure:  $(\max - S) - (\min - S) / (\max - S) + (\min - S)$ , where  $\max$  and  $\min$  are the maximum and minimum value of the disparity tuning curve and  $S$  is the spontaneous activity during 200 ms before the stimulus motion onset. The response to the 36 neurons with a peak in the disparity tuning curve as well as the remaining disparity-sensitive neurons are included. Tuning strength index for cells shown in Fig. 1, *D–F*, are 0.75, 0.35, 0.62, and 0.39, respectively. Those for cells shown in Fig. 3, *D–F*, are 0.25, 0.33, 0.28, and 0.30, respectively.

of neurons, the disparity-dependent direction selectivity is not present in MSTL.

For the strength of the disparity response, we used a contrast measure, and Fig. 4 shows the range of variations that we observed across the 74 neurons that had significant disparity sensitivity. The strength of the response using this measure ranged from 0.27 to 2.94 (median: 0.62) for the 36 neurons with a peak response and from 0.19 to 1.77 (median: 0.29) for the 33 more broadly tuned neurons.

There was also considerable variation in the time course of the response to the disparity stimuli. For example, the neuron shown in Fig. 1A showed a change in both the initial response and the continuing discharge to motion for stimuli at uncrossed and zero disparities, but the initial response was present for crossed disparities as well. To see the extent of differences in the initial and continuing responses in our sample of neurons, we divided the response into two periods: the first 200 ms and the last 200 ms of the 400-ms period we have used for quantification of the response magnitudes. We observed all combinations of initial and continuing responses to disparity stimuli: those in which the response in the first 200 ms was consistently greater than that in the second 200 ms, those in which they were the same, and those in which the second 200-ms period showed much larger responses. Activity in both periods contributed to the activity of both the peaked and broadly tuned group of neurons.

For 15 neurons with disparity tuning, we checked to see whether monocular stimulation of one eye or the other was the source of the apparent disparity sensitivity. For these experi-

ments we covered the prism in front of one eye or the other so that the binocular and the two monocular presentations were run in blocks of trials. The response curve to binocular stimuli always differed from that for monocular stimulation, and Fig. 5, *A* and *B*, shows sample graphs for neurons with a peaked tuning curve and a more broadly tuned curve, respectively. We did two one-way ANOVA based on disparity. The first was neuronal response versus disparity for binocular viewing; the second was neuronal response versus disparity for monocular viewing (separate eye conditions were pooled). All 15 neurons tested showed a significant disparity effect for binocular viewing ( $P < 0.05$ ) but no significant effect for monocular viewing. Figure 5C shows a scatter plot of the strength of the response of each of the 15 neurons to stimulation through each eye and reveals no systematic bias toward either the contralateral or the ipsilateral eye.

In summary, we found that about two-thirds of the neurons sampled in MSTL were sensitive to the disparity of the stimulus moving in the RF center. Although there was substantial variation in the shape of the tuning of the neurons, about half of the disparity-sensitive neurons tested had a clear peak in their disparity tuning curves. None of the MSTL neurons showed the disparity-dependent direction sensitivity reported previously for MSTd neurons.

#### *Effect of stationary surround stimuli*

In previous experiments (Eifuku and Wurtz 1998), we found that a surround stimulus in MSTL modulated the response to motion in the RF center and that the modulation was frequently as great with a stationary stimulus as with a moving one. We therefore studied the effect of a stationary surround on the response to motion in the center of the RF by first varying the disparity of the RF center stimulus during motion in the preferred direction of the neuron with the addition of a stationary surround at zero disparity (Fig. 6A). We then varied the disparity of the stationary surround while holding the disparity of the center stimulus at zero disparity with motion in the preferred direction (Fig. 6B). Before studying each neuron, we first verified that we could elicit no response from stimulating the surround areas alone.

Figure 7A shows the response of a neuron to stimuli at seven different disparities in the RF center. When the surround was added, the neuron responded better, but the peak remained at zero disparity. Such modulations also occurred in broadly tuned neurons (Fig. 7, *B* and *C*) and included both increases and decreases in activity. These results extend our previous finding that the stationary surrounds simply modulate the directional response to motion in the RF center by showing that it modulates the response to stimuli with disparity as well.

A factor that could account for the effect of the surround in Fig. 7 would be a systematic change in the monkey's vergence during fixation, and this vergence was measured on all trials. Figure 7, *D–F*, shows the mean  $\pm$  SE of the difference in the horizontal eye positions recorded during each condition shown

FIG. 3. Examples of neurons with broad disparity tuning. Figure organization is the same as that of Fig. 1. *A–C*: a typical example of a neuron with the response in the crossed disparities. The receptive field (RF) center was  $10.0^\circ$  to the right and  $10.0^\circ$  up from the fixation point and was  $15^\circ$  on each side, and the preferred direction of motion was  $270^\circ$  with an optimal speed of  $20^\circ/\text{s}$ . A 1-way ANOVA (factor: disparity) showed significant difference:  $F(6, 147) = 4.699$  ( $P = 0.0002$ ). *D–F*: 3 other examples of responses of broadly tuned cells. One-way ANOVAs (factor: disparity) showed significant differences: for *D*,  $F(6, 124) = 4.285$  ( $P = 0.0006$ ), for *E*,  $F(6, 79) = 6.145$  ( $P < 0.0001$ ), and for *F*,  $F(6, 65) = 4.376$  ( $P = 0.0009$ ), respectively.

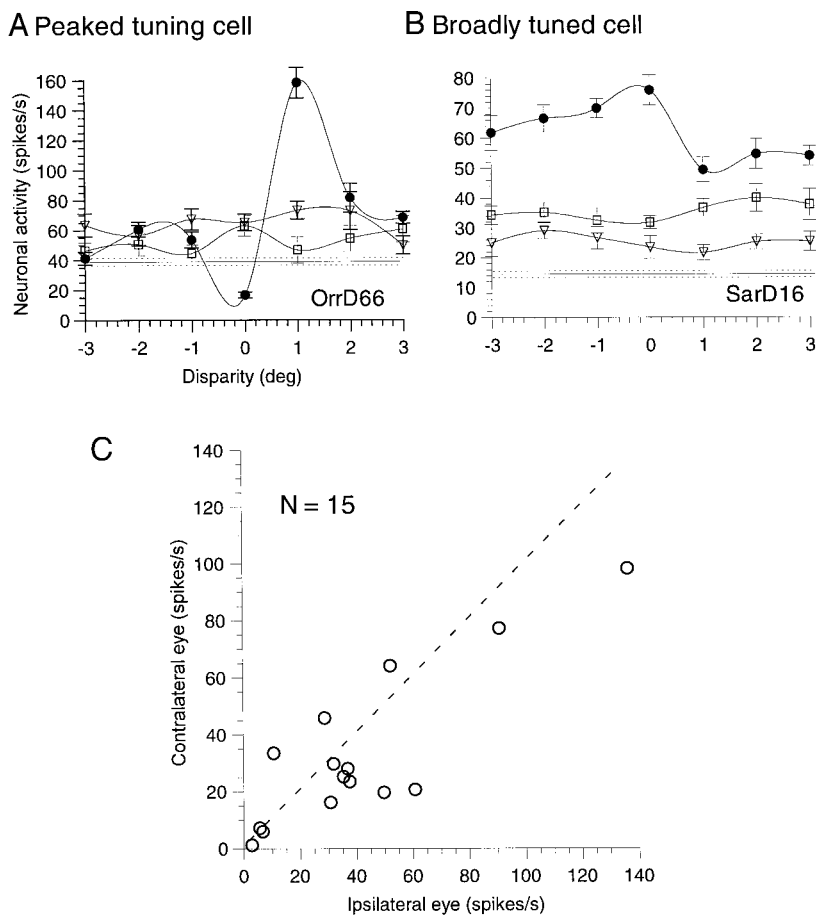


FIG. 5. Comparison of the response to binocular and monocular stimulation. *A*: example of a neuron with a peaked tuning curve. *B*: example of a more broadly tuned neuron. Binocular (●) and monocular (ipsilateral: □; contralateral: ▽) stimulations are compared. Monocular stimulation reduced the response. Two 1-way ANOVA (see text) revealed that both cells showed significant disparity effect for binocular viewing [for *A*,  $F(6, 104) = 49.898$  ( $P < 0.0001$ ), and for *B*,  $F(6, 65) = 4.376$  ( $P = 0.0009$ ), respectively] but not for monocular viewing [for *A*,  $F(6, 161) = 0.663$  ( $P = 0.6796$ ), and for *B*,  $F(6, 145) = 0.868$  ( $P = 0.5199$ ), respectively]. *C*: scatter plot of the strength of the response to stimulation through the ipsilateral and contralateral eye. Responses to the 7 disparity stimuli viewed monocularly were pooled.

in Fig. 7, *A–C*. The changes in disparity sensitivity of the neurons cannot be ascribed to the small changes in vergence that were measured simultaneously.

To quantify the effect of the surround on disparity tuning in the RF center across our sample of neurons, we plotted the location of the peak of the disparity tuning for the 36 neurons with a peaked tuning curve with and without a surround (Fig. 8*A*). We found that the disparities producing the peak response with and without a surround were well correlated. To compare the amplitude of the response, we computed a modulation ratio for the response of neurons to center motion with a stationary surround divided by the response to center motion alone; ratios differing from one indicate effects of the surround. Figure 8*B* shows that the modulations cover a range of increases and decreases, but the effect of the surround was usually an increase in the response, and this effect was similar to that found previously when there was no change in RF center disparity

(Fig. 10, Eifuku and Wurtz 1998). Thus a stationary stimulus falling on the surround of these MSTl neurons modulates the response to motion in the RF center but does not change the disparity tuning in the RF center.

We next determined the effect of changing the disparity of the surround (as in Fig. 6*B*). We kept the center stimulus motion in the preferred direction and at zero disparity and varied the surround disparity, and we compared these responses to those to the surround at zero disparity and the center at different disparities. The graph in Fig. 9*A* shows the responses of the same neuron as that in Fig. 7*A*. For changes in center disparities (□) the maximum response was close to zero disparity as was the maximum for changes in the surround disparity. For this neuron the optimal disparity in both the center and surround was about the same, but this was not the case for many other neurons. Figure 9*B* shows a case in which the maximum response to disparity in the center was at +1 and

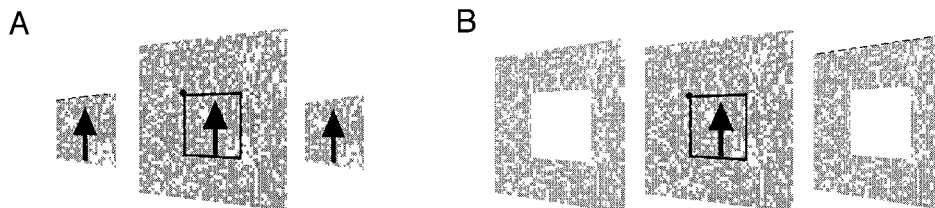


FIG. 6. Two experiments on the effect of disparity on the interaction between center and surround. *A*: effect of addition of a surround at zero disparity on the response to motion in the RF center at zero and near and far disparities. *B*: effect of addition of a surround at zero and near and far disparities on the response to motion in the RF center at zero disparity. In all cases the motion in the center was in the optimum direction and at the optimum speed, and the stimulus in the surround was stationary.

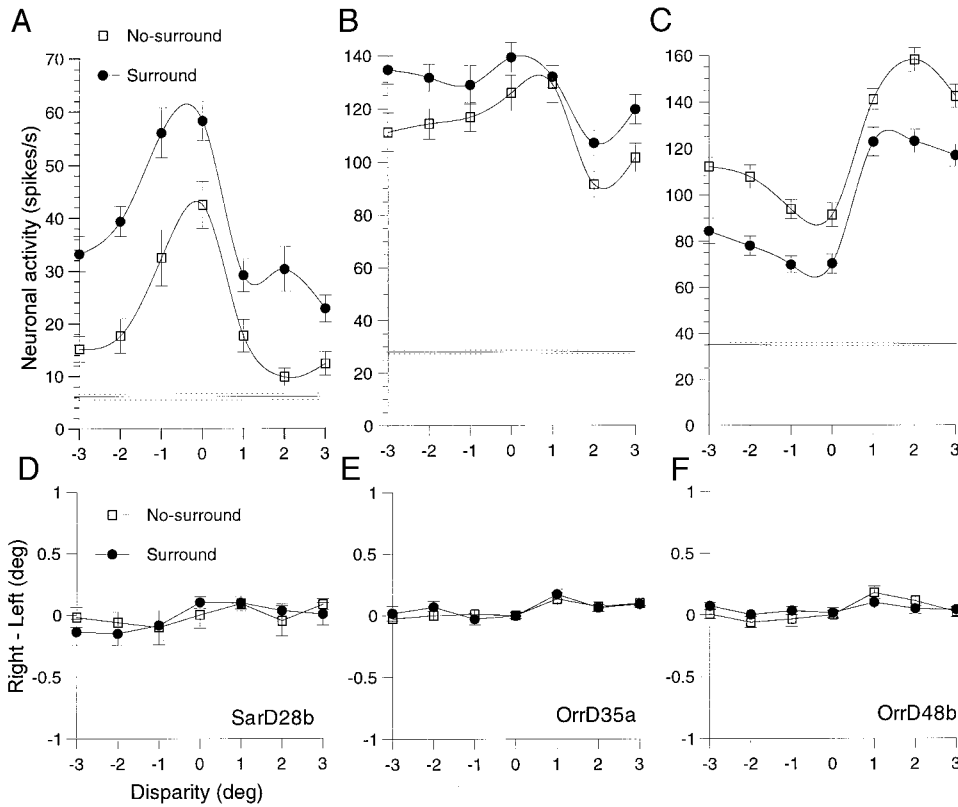


FIG. 7. Effect of a stationary surround stimulus at zero disparity on the response to motion in the RF center at different disparities. *A*: plot of the responses (mean  $\pm$  SE) of a neuron with a peak in its tuning curve showing that the added surround produced an increased response but did not change the preferred disparity. Solid and dashed horizontal lines indicate mean  $\pm$  SE of the spontaneous activity level during 200 ms before the stimulus motion onset. *B* and *C*: plots of 2 broadly tuned neurons that produced an increased or decreased response but no change in the preferred disparity. *D–F*: difference in eye position during the recording in each condition for the cells in *A–C*. The difference is that between the average of horizontal eye position of the right eye minus that of the left eye during the analysis period used for neuronal activity (70–470 ms after stimulus motion onset). The relatively flat curves indicate that changes in vergence are unlikely to account for differences in the neuronal response to disparity differences.

the minimum was at  $-1$  to  $-2$ , but for the surround these values were reversed with a minimum at  $+2$  and a maximum at  $-2$ . Figure 9C shows a similar striking reversal of maximum and minimum.

Again, variations in vergence during fixation in the presence of these changing disparity stimuli did not account for the changes in disparity response of the neurons because the graph of the difference in the position of the two eyes during recording in each condition for each neuron (Fig. 9, *D–F*) was largely flat across disparities ( $-3$  to  $3^\circ$ ). To verify that there were no systematic changes across our sample of neurons, we plotted the mean difference in eye positions across all fixation trials for each of the disparity conditions in our series of experiments: center disparity stimuli with no surround (Fig. 10A), center disparity with a surround (Fig. 10B), and center stimulus with no disparity but with surround disparity (Fig. 10C). The mean  $\pm$  SE of the difference in right and left eye were flat across disparities ( $-3$  to  $3^\circ$ ) in each condition.

To compare the disparity giving the maximum response to motion in the RF center to the disparity giving the maximum modulation in the surround, we used a scatter plot. In Fig. 11A for the neurons with peaked tuning, if the center and surround maximums were similar, all the points should lie in the upper right quadrant for far disparities (uncrossed, positive) or the lower left quadrant for near disparities (crossed, negative). That is clearly not the case, and although a complete reversal of maximums between center and surround was not frequent (the examples in Fig. 9, *B* and *C*, are indicated by filled squares), a shift in the maximum was common. The same can be said for the minimums of these tuning curves (Fig. 11B). Thus these MSTL neurons frequently had different disparity

sensitivities for stimuli in the RF center as compared with the modulatory surrounds.

The difference in the most effective disparity in the RF center and surround for some neurons raised the possibility that these MSTL neurons might be sensitive to the *difference* between the center and surround rather than to the absolute disparity of either. Although we had not set out to systematically study this issue, we did have a number of comparisons between center and surround disparities that would allow us to make such difference comparisons. Figure 12, *A* and *B*, show this comparison to relative disparity for one of the neurons that had a near reversal in the peak disparity preferred by the center and the surround (Fig. 9C). To determine the relative disparity we compared the response to the same disparity difference in center and surround. For example, center zero to surround  $-1$  is compared with surround  $+1$  to center zero, zero to  $-2$  is compared with  $+2$  to zero, etc. This is equivalent to reversing the sign of all of the surround disparities, and Fig. 12A plots this reversal of the response curve for the surround disparities. Figure 12B plots these relative differences with the horizontal axis showing the response with disparity in the RF center with the surround at zero disparity, and the vertical axis shows responses with surround disparity and zero center disparity. The regression line through the six disparity differences has a positive slope indicating that the neuronal response generally varies with the disparity difference between center and surround.

Figure 12, *C* and *D*, compares the response of this same neuron to the absolute disparity difference between center and surround. We take the response to each disparity difference for the center disparity and the surround disparity stimuli (Fig.



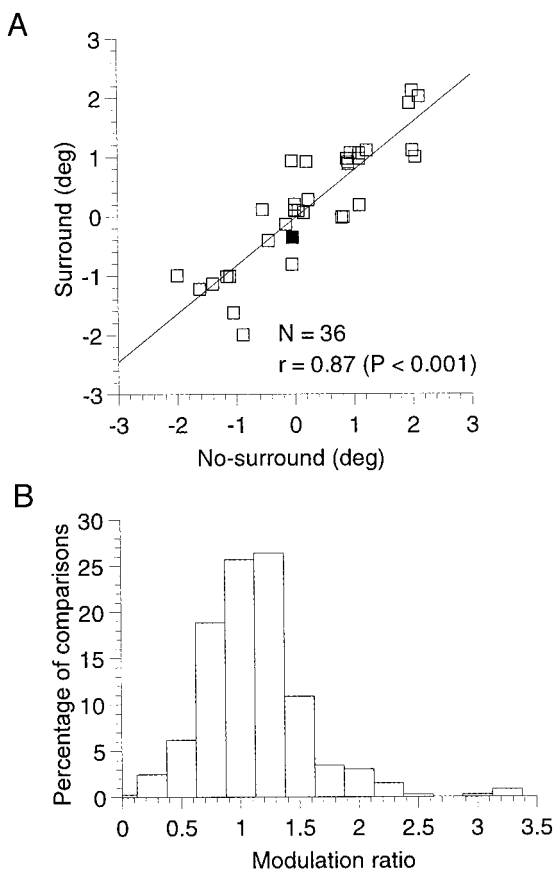


FIG. 8. Modulation of the response to motion in the RF center in the optimum direction and speed by the addition of a stationary surround. *A*: scatter plot comparing the disparity giving the peak response with and without a stationary surround stimulus. Each point corresponds to the locations of the peak in the disparity tuning curves for one of the neurons with a peaked tuning curve. The horizontal axis is peak location of the responses to the center stimulus at 7 disparities ( $-3, -2, -1, 0, 1, 2, 3$ ) with no surround, and the vertical axis is the same with the surround at zero disparity. Locations of peaks are well correlated (linear regression, slope = 0.81, intersect =  $-0.03$ ,  $r = 0.87$ ,  $P < 0.001$ ). Solid line is the regression line, and the filled square is the value for the neuron in Fig. 7*A*. *B*: histogram of the magnitude of the modulation showing both increases and decreases in response with the addition of a stationary surround. The modulation ratio is the response to the center stimulus with the surround at zero disparity/response with no surround. All neurons with either peaked or broadly tuned curves are plotted together ( $n = 728$ : 104 neurons for 7 disparities) because both groups showed the modulation by the surround.

12*C*). Because the peaks of the center and surround disparity curves are at nearly opposite disparities, the graph that compares the six pairs of absolute differences (Fig. 12*D*) shows a regression line with a negative slope so that the same absolute value of disparity in center and surround can produce large differences in neuronal activity. We conclude that the discharge rate of this neuron indicates the relative disparity between center and surround rather than the absolute disparity of either.

Figure 13 illustrates the types of neuronal responses to relative and absolute disparities we observed in the 31 neurons with adequate data on the effect of both center and surround disparity. Six neurons showed a significant positive slope to relative disparity differences as in the example of Fig. 13*A* and either a significant negative slope or one not significantly different from zero for absolute disparity. Four neurons

showed a significant positive slope to absolute disparity differences as in the example of Fig. 13*B* and either a significant negative slope or one not significantly different from zero for relative disparity. The remaining neurons that belong to neither group included neurons that did not have marked differences between center and surround disparity as shown by the example in Fig. 13*C* (same neuron as in 9*A*). There was therefore no indication that these neurons were preferentially related to absolute or relative disparity.

In summary, we found that a stationary surround at zero disparity simply modulated up or down the tuning curve for disparity of the moving stimulus in the RF center. When the disparity of the stationary surround was varied, the strongest modulation by surround disparity was frequently at a disparity different from the disparity most effective in the center. Some of these neurons with different disparity preferences in center and surround responded best to the relative disparity differences between center and surround, whereas others were related to the absolute difference between center and surround.

## DISCUSSION

Our goal was to determine the effects of disparity on both the receptive field center and the receptive field surrounds of MSTl neurons, neither of which had been investigated previously. We have found that MSTl neurons have clear disparity sensitivity to stimuli presented in either the center or the surround, and we will compare this disparity sensitivity in the RF center to that in other extrastriate areas, particularly MSTd, then compare the RF surround sensitivity to other areas, particularly MT, and then consider how these phenomena might contribute to the perceptual segmentation of objects from background. Finally we suggest that this new information strengthens the possibility that MSTl makes functional contributions that differ from those of MSTd.

### *Disparity sensitivity in RF center*

We found that about two-thirds of the neurons sampled in the ventral-lateral region of MST (MSTl) were sensitive to the disparity of the stimulus moving in the RF center. Although there was substantial variation in the shape of the tuning of the neurons, those with disparity sensitivity were about equally divided between those with a clear peak in their disparity tuning curves (Fig. 1), and those tuned to a broader range of disparities (Fig. 3).

Disparity sensitivities of neuronal responses have been identified in a series of cortical areas in the monkey including V1, V2, V3A, V4 (Cumming and Parker 1997; Hubel and Wiesel 1970; Poggio and Fischer 1977; Poggio et al. 1985, 1988; Poggio and Talbot 1981; Smith et al. 1997), MT (Bradley and Andersen 1998; Bradley et al. 1995; DeAngelis and Newsome 1999; Maunsell and Van Essen 1983b), and MSTd (Roy et al. 1992; Roy and Wurtz 1990), but the disparity sensitivity of MSTl neurons has not been previously studied. In many of these studies it was convenient to classify the disparity tuning curves into the categories adopted by Poggio et al. (1985, 1988): near, far, tuned excitatory (near, zero, far), and tuned inhibitory. In the motion pathway, these categories were originally used in MT, where neurons were described as being near, far, and tuned excitatory or inhibitory (Maunsell and Van

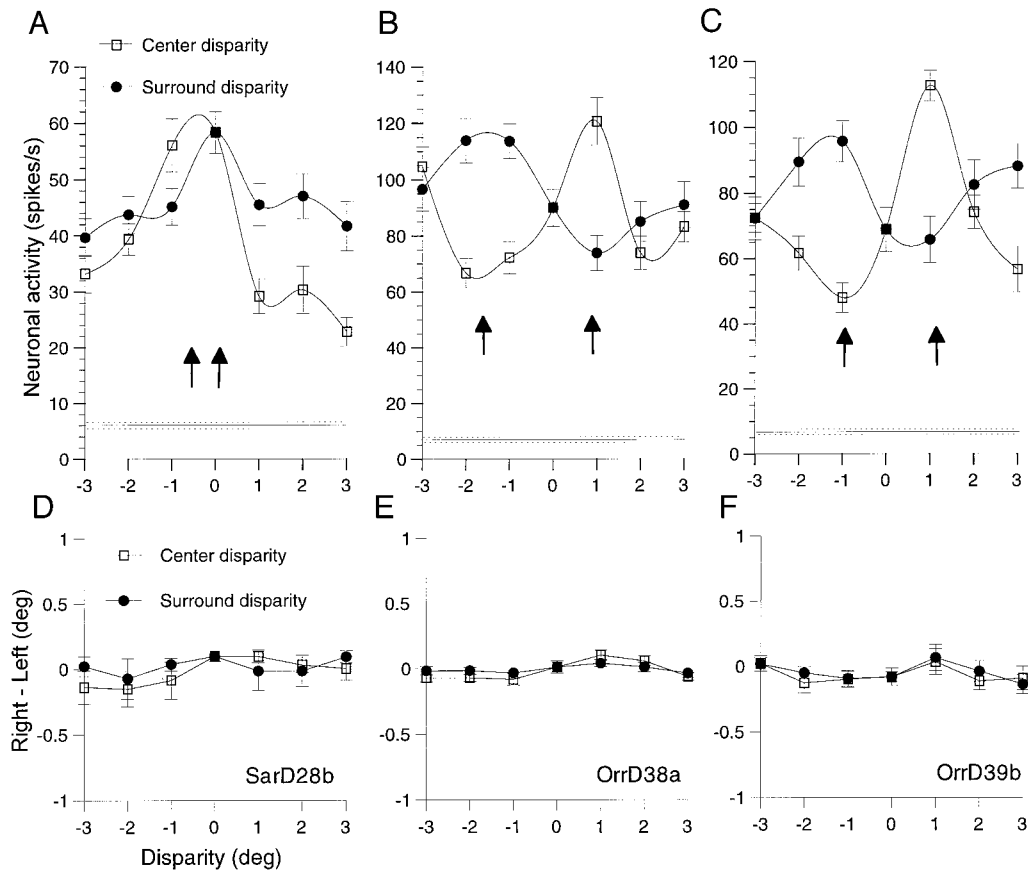


FIG. 9. Different effect of a stationary surround at different disparities on the response to motion in the RF center. A–C: 3 examples of neurons whose response to motion in the center of the field was altered by changing the disparity of the surround stimulus. Arrows indicate the location of peaks in the curves. Same conventions as in Fig. 7. B and C show a reversal of preferred disparities in the center and surround. D–F: difference in eye position during the recording in each condition for the cells in A–C as in Fig. 7.

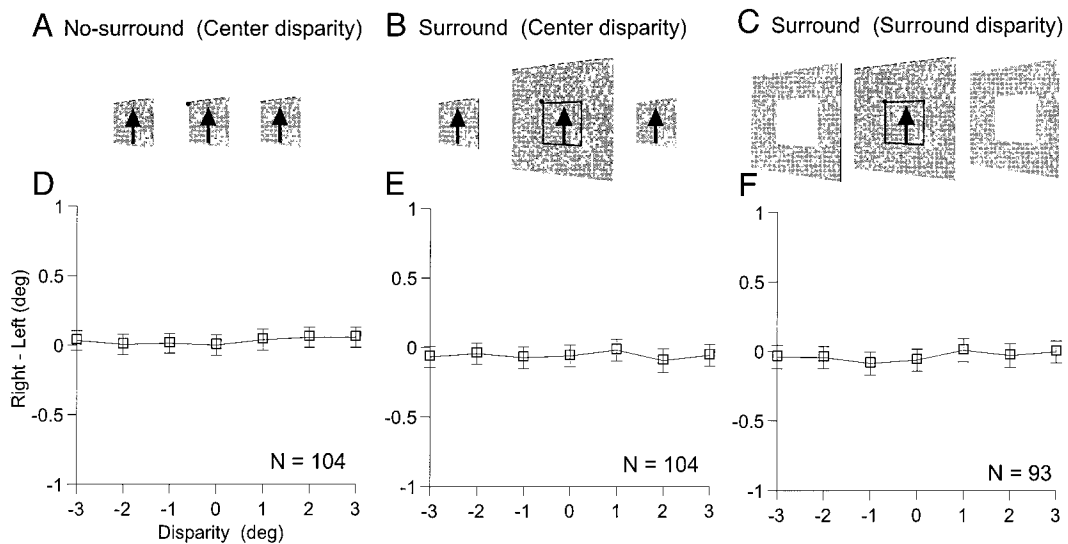


FIG. 10. Difference in position of the 2 eyes during fixation across all experiments in which only a disparity stimulus was in the RF center (A), when a disparity stimulus was in the RF center with a surround stimulus at zero disparity (B), and when the center stimulus was at zero disparity and the surround stimulus had disparity (C). The difference shown is the mean  $\pm$  SE of the horizontal eye position of the right eye minus that of the left eye during the analysis period used for neuronal activities (70–470 ms after stimulus motion onset). In all cases, the vergence was flat across disparities ( $-3$  to  $3^\circ$ ) in each condition making it unlikely that changes in vergence account for differences in the neuronal response to disparity differences.

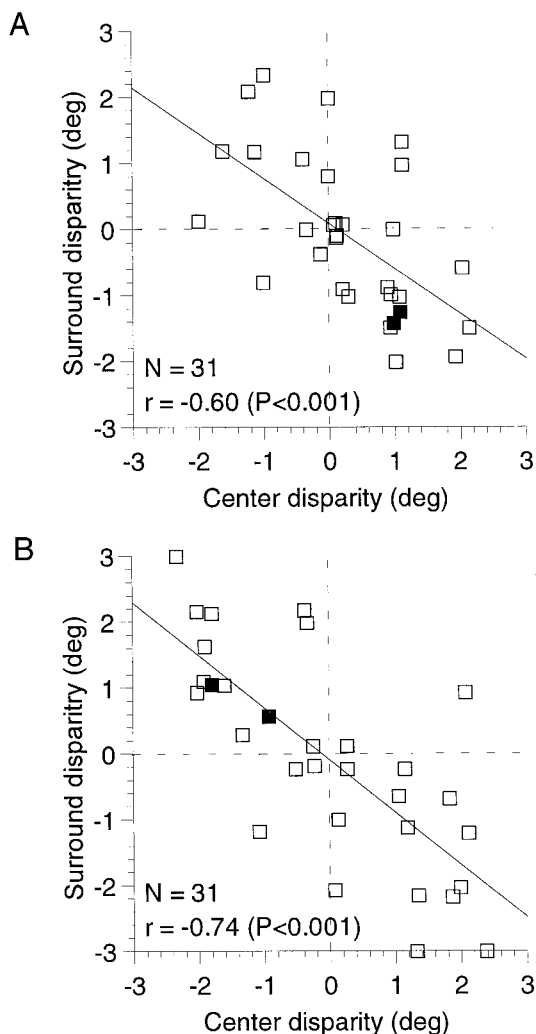


FIG. 11. Comparison of preferred disparity in RF center and surround. *A*: scatter plot showing the relation of the disparity giving the maximum response in RF center and surround for the neurons with peaked tuning curves. Each point corresponds to one neuron. The horizontal axis shows the disparity of the peak response to motion in the preferred direction and speed in the RF center tested at 7 disparities ( $-3, -2, -1, 0, 1, 2, 3$ ) with the surround at zero disparity. The vertical axis shows the disparity of the peak response to the same motion in the center at zero disparity with the surround at 7 disparities ( $-3, -2, -1, 0, 1, 2, 3$ ). The solid line is the regression line, and the filled squares show the values for the neurons in Fig. 9, *B* and *C*. Both peak locations are negatively well correlated (linear regression, slope =  $-0.68$ , intersect =  $0.09$ ,  $r = -0.60$ ,  $P < 0.001$ ). *B*: scatter plot showing the disparity giving the minimum responses in center and surround. Same conventions as in *A*. Both peak locations are negatively well correlated (linear regression, slope =  $-0.80$ , intersect =  $-0.09$ ,  $r = -0.74$ ,  $P < 0.001$ ).

Essen 1983b), although a recent study described the disparity tuning as falling along a continuum (DeAngelis and Newsome 1999). In MSTd, neurons could be largely grouped as having broad tuning to near and far disparity. The neurons in MSTl did not fit into these categories but rather had relatively broad disparity tuning. Although we identified the MSTl neurons that had a clear peak in their disparity tuning curve using an objective criteria, this was done only to convey a sense of the variation within the sample of neurons that we think have a continuum of disparity tuning functions. In both the study of MSTd and MSTl, the disparity steps used were large, to study sensitivity to a broad range of disparities, and omitted the small

steps in disparity that would be required to see fine changes in tuning. This strategy could miss fine tuning, but even if it missed a peak of fine tuning, such a peak would be superimposed on the broad tuning observed in almost all of the MSTl neurons. Such relatively broad disparity tuning in MSTl is similar to the broad tuning in MSTd (Roy et al. 1992), but the difference in the areas is the strong tendency in MSTd for neurons to be broadly tuned for near or far stimuli, and although we have seen both such neuronal types in MSTl, there appears to be no such tendency for these neurons broadly tuned for near and far disparity to predominate. Broad tuning seems to be a characteristic of both MSTl and MSTd, and this implies a function that is not related to the precise tuning of fine stereopsis but rather that related to functions more appropriately referred to as coarse stereopsis (Bishop and Henry 1971; Roy et al. 1992).

The most striking difference between MSTd and MSTl, however, relates to the disparity-dependent direction selectivity found in MSTd: the optimal direction of motion in the RF of some neurons is reversed depending on the disparity depth at which the motion occurs (Roy et al. 1992; Roy and Wurtz 1990). We saw no indication of such a reversal in any of the neurons sampled in MSTl, as indicated by a lack of response for motion in the null direction that is comparable to the response in the preferred direction (Figs. 1 and 3). The presence of disparity sensitivity in both MSTl and MSTd indicates that disparity is involved in the functional contributions of these areas, but the difference in disparity-dependent direction sensitivity suggests a difference in function between the areas.

#### *Disparity sensitivity of the surround*

In the present study, we used a stationary rather than a moving surround, because in our previous experiments (Eifuku and Wurtz 1998) we found that a stationary surround was usually as effective as a moving one. We found that a stationary surround at zero disparity simply modulated up or down the tuning curve for disparity of the moving stimulus in the RF, which was consistent with the modulatory effect of the MSTl surround reported previously (Fig. 10, Eifuku and Wurtz 1998). In contrast, when the disparity of the stationary surround was varied, the strongest modulation occurred at disparities that were frequently different from the disparity that produced the largest response for RF center stimulation.

For many neurons, the peak in the disparity tuning was the inverse of the most effective disparity in the RF center (Figs. 9, *B* and *C*, and 11*A*). This prevalence of differences between the preferred disparity in the center and surround led us to determine whether the discharge of the neurons might indicate the relative difference between the center and surround rather than the absolute disparity. We did find some neurons that responded best to the relative disparity differences between center and surround, but the discharge of other neurons was better related to the absolute difference between center and surround (Figs. 12 and 13). Our sample of neurons sensitive to relative disparity was small as was the number of disparity differences tested so that our results on relative disparity are limited. But they do suggest that at least some MSTl neurons are conveying information on the relative disparity difference between center and surround rather than the absolute difference. It may be that the indication of relative disparity seen in these MSTl neurons

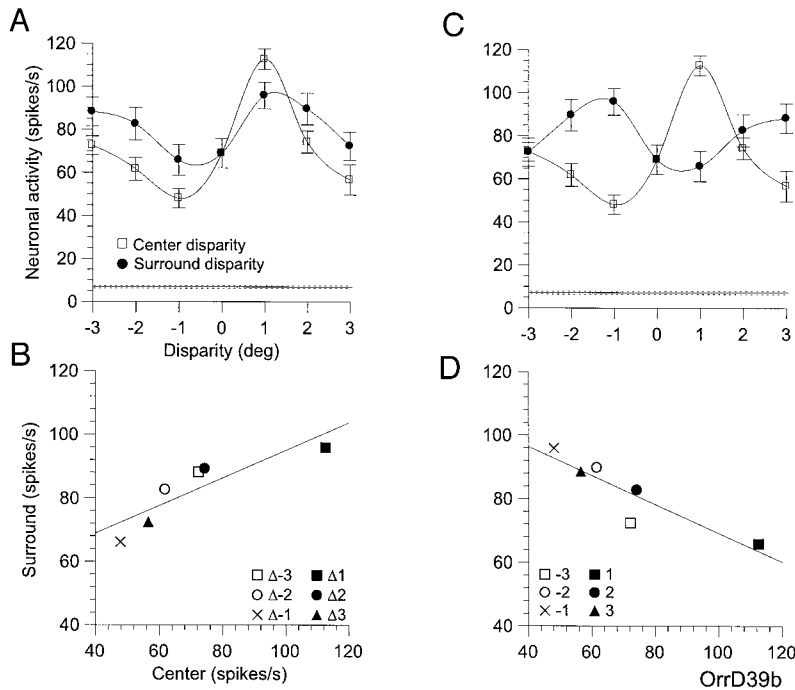


FIG. 12. Comparison of the modulation of the response to motion in the RF center as a function of the absolute differences and relative differences in disparity between center and surround. *A* and *B*: response to relative disparity differences. *A*: the relative disparity comparison (see text) is essentially the same as reversing the surround curve around the zero disparity, and the curves show this reversal of the surround values for the neuron shown in Fig. 9C. The curves are neuronal responses to disparity of the center stimulus with the surround at zero disparity (Center Disparity) and responses to surround disparity with the center at zero disparity but with the curve reversed (Surround Disparity). In both cases, motion in the center is always in the optimal direction and optimal speed and the stimulus in the surround is stationary. *B*: scatter plot for each of the 6 pairs of differences between the curves in *A*. The horizontal axis shows response with disparity in the RF center with the surround at zero disparity, and the vertical axis shows responses with surround disparity and zero center disparity. The slope of the curve is positive ( $r = 0.87$ ,  $P < 0.05$ ) indicating that the neuron changed its response with differences in relative disparity. *C* and *D*: response to absolute disparity differences. Comparison was made between the response to each disparity (*C*), which is the same as taking the difference between the 2 curves (same curves as in Fig. 9C). In *D* the horizontal axis again shows responses to different center disparities with zero surround disparity and the vertical axis shows responses to different surround disparities with zero surround disparity. The slope of the curve is negative ( $r = -0.91$ ,  $P < 0.05$ ) indicating that this neuron responded very differently to absolute disparity differences.

may become more prominent at the next higher stage of disparity processing.

So far there has been little other indication of relative disparity in extrastriate cortex, although changes in vergence did modulate the response of a few neurons in MSTd (Roy et al. 1992) and a substantial number of neurons in V1 (Trotter et al. 1996). Disparity sensitivity of V1 and V2 neurons has recently been reported to be altered by the addition of contextual stimuli, and the effect depends on the position of these stimuli in depth (Bakin et al. 1998), which suggests that the relative disparity between center and surround may be established early in cortical visual processing.

We have previously shown that the direction of motion in the center and surround of MSTl neurons can differ and that the response in the center is most strongly modulated upward when the center and surround move in opposite directions (Eifuku and Wurtz 1998). This separation produces an edge or discontinuity, such as at the edge of a moving object, that would serve to segment motion in the center from that in the surround. The difference in preferred disparities in center and surround provides a further method for segmentation of an object from the background, even if the object and its background were moving at the same direction and speed. Such an interpretation is identical to that recently put forward by Bradley and Andersen (1998) for the function of the modulatory surrounds previously reported for MT (Allman et al. 1985a,b). They showed that the modulatory surround in MT could serve the purpose of segmentation on the basis of differences in disparity, and that this segmentation was consistent with that derived from differences in direction and speed of motion between center and surround. MT centers also were reported to be mainly tuned for near disparities, followed by zero, then far (Bradley and Andersen 1998). In the present study neurons that had prominent peaks in their tuning curves were distributed across near, far, and zero disparities. Of this trilogy of segmentation mechanisms reported for MT (direction, disparity, and speed), we have now

shown both direction and disparity for MSTl in this and the preceding paper (Eifuku and Wurtz 1998).

If the disparity were to contribute to the segmentation of the object from the surround, the neurons might be expected to be sensitive to the relative difference in disparity between the object and its background (between RF center and surround) rather than to the absolute disparity of either. The presence of some neurons whose response was better related to the differences in disparity of center and surround, even though the absolute values of these disparities changed considerably over the range tested, is consistent with such a contribution for at least some of the neurons in MSTl. This relative difference in disparity would be analogous to the relative differences in direction of motion in center and surround found in the pigeon tectum (Frost and Nakayama 1983): as long as the directions of motion in the two areas are the opposite, the response in the center is modulated.

In net, we think the type of disparity processing that we have found in MSTl is more compatible with the segmentation of the visual scene than the determination of the depths of objects within the visual field. Such segmentation has been shown to be critical for the separation of one object in the field from another for perceptual discriminations (Braddick 1993; Nakayama 1985). Such separation within the field by disparity differences has also been shown to effect the control of eye movements: the amplitude of short-latency ocular following responses depends on the disparity of the peripheral visual field (Kawano et al. 1994).

#### Functional comparison of MSTl and MSTd

The type of disparity sensitivity we have observed for MSTl neurons adds to the list of differences between MSTl and MSTd. First, MSTl neurons usually respond better to motion of small spots than to large moving patterns (Komatsu and Wurtz 1988), whereas neurons in MSTd respond better to motion of



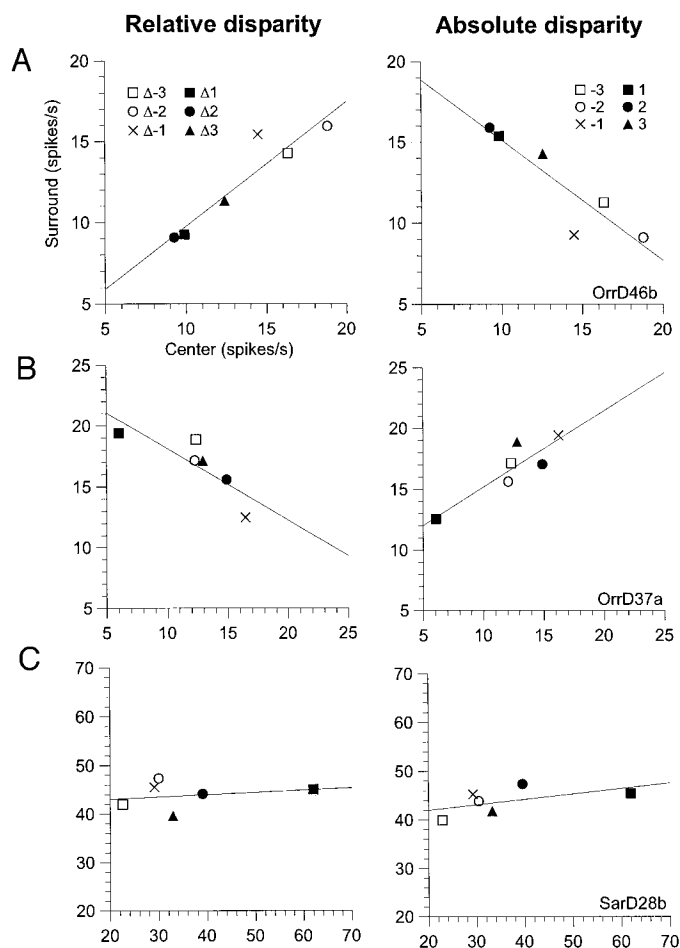


FIG. 13. Types of disparity differences between center and surround. Graphs comparing relative and absolute disparity between center and surround are the same as those in Fig. 12, *B* and *D*. *A*: the graph for this neuron had a positive slope for relative disparity; its discharge changed consistently with the relative difference between center and surround disparities. For relative disparity,  $r = 0.94$ ; for absolute,  $r = -0.90$ . *B*: a neuron whose discharge varied with absolute disparity. For relative disparity,  $r = -0.84$ ; for absolute,  $r = 0.90$ . *C*: a neuron with little difference in center and surround disparity for which a distinction between relative and absolute disparity sensitivity was not possible. For relative disparity,  $r = 0.24$ ; for absolute,  $r = 0.51$ . Slopes in *A* and *B* are significantly different from zero using a Student's *t*-test ( $P < 0.05$ ) but are not in *C*.

patterns rather than spots. The sizes of the receptive fields are also smaller in MSTl than in MSTd (Tanaka et al. 1993). Taken together, this suggests that the MSTl neurons are best suited to respond to motion in small parts of the field while neurons in MSTd respond to motion over a large part of the field. Second, many MSTd neurons respond preferentially to the components of large field optic flow stimuli such as expanding, contracting, and rotating fields of motion (Andersen et al. 1990; Duffy and Wurtz 1991; Saito et al. 1986), and there is no indication that MSTl neurons do so. Third, most MSTl neurons have a clear RF center surround organization with the effect of the surround being one of modulating the response to motion in the center rather than producing a response in the absence of center stimulation (Eifuku and Wurtz 1998). Such center surround interaction should act to segment motion in one part of the field from that in the other. Such modulatory surrounds have not been demonstrated in MSTd, and the response to large field stimuli make surrounds like those in MSTl seem unlikely in

MSTd. Fourth, the MSTl neurons have disparity sensitivity in the center, and the surround and differences in disparity preference between the center and surround provide another method of segmenting activity in one region of the field from another. Again, no such difference has been demonstrated for MSTd. In contrast, many neurons in MSTd show a change in their preferred direction of motion with changes in disparity (Roy et al. 1992; Roy and Wurtz 1990), but we found no such differences in MSTl. Finally, stimulation and lesions of MSTl alter the maintenance of smooth pursuit eye movements, whereas such stimulation and lesions closer to MSTd do not (Dürsteler and Wurtz 1988; Dürsteler et al. 1987; Komatsu and Wurtz 1989). Thus, although both MSTl and MSTd receive direct inputs from MT (Maunsell and Van Essen 1983a; Ungerleider and Desimone 1986; Van Essen et al. 1981) and respond preferentially to moving stimuli (Tanaka et al. 1986; Ungerleider and Desimone 1986; Van Essen et al. 1981), the differences in the activity of neurons in the two areas suggest that their functional contributions are different.

As indicated in this list, there are many gaps in our knowledge of the differences between MSTl and MSTd, particularly in the direct comparison of each difference in the same experiment. Given this limitation, however, the differences observed so far are striking and are made even more so with the addition of the present finding on disparity. The characteristics of MSTd neurons are consistent with a mechanism for the analysis of optic flow; they respond to a variety of flow component motions over a large field, and their sensitivity to disparity allows them to parse the visual field into depth planes to distinguish motion at different distances from the observer. This relation to optic flow is supported by recent experiments that altered judgments based on optic flow by electrically stimulating MSTd (Britten and van Wezel 1998). These characteristics led to the hypothesis that MSTd contributes to the analysis of the motion that results from the movement of an observer through the environment. In contrast, the characteristics of MSTl motion make these neurons appropriate for the segmentation of a relatively small moving object from the background (Eifuku and Wurtz 1998; Tanaka et al. 1993); they have relatively small center size, modulatory surrounds, and sensitivity to disparity differences in center and surround. These characteristics support the hypothesis that MSTl contributes more to the analysis of object motion than to optic flow.

This distinction between observer generated and object generated motion might turn out to be an oversimplification as indicated, for example, by motion parallax in the visual field that should be processed most efficiently in MSTd but could be used for object segmentation, as discussed previously (Eifuku and Wurtz 1998). But this does not alter the salient distinctions between the areas related to the processing of large field optic flow motion and small field segmentation that seems to be clearly different between MSTl and MSTd; it only alters the interpretation of what generated the motion.

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