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A New Role for Cortical Area MT: The Perception of Stereoscopic Depth

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ABSTRACT  Neurons that respond selectively to binocular disparity are widely assumed to play an important role in stereoscopic depth perception, but there is little direct evidence for this presumed link between neurophysiology and perception. Furthermore, it is not clear whether any of the thirty or more known cortical visual areas is specialized for stereopsis, which remains one of the most significant visual functions lacking a clear cortical substrate. We present evidence for a columnar organization of disparity-selective neurons in extrastriate visual area MT of rhesus monkeys. Nearby neurons have similar disparity tuning properties, and the preferred disparity changes smoothly across the cortical surface, suggesting that MT contains a map of binocular disparity. To test whether neurons in this map are involved in depth perception, we electrically stimulated clusters of disparity-selective MT neurons while monkeys discriminated depth in random dot stereograms. Microstimulation systematically biased perceptual judgments of depth toward the preferred disparity of neurons at the stimulation site. These results show that behaviorally relevant signals concerning stereoscopic depth are present in MT. This is the first clear demonstration of specialization for stereoscopic vision in any cortical area.

A central goal of cognitive neuroscience is to reveal how neural activity gives rise to sensory perception. Perhaps the clearest link between a specific perceptual capacity and its cortical substrate has arisen from studies of motion perception and its relation to neural activity in the middle temporal visual area (MT, or V5) of primates. Approximately 90% of MT neurons respond selectively to the direction of motion of a visual stimulus (Dubner and Zeki, 1971; Zeki, 1974), and MT neurons with similar functional properties are clustered together in "columns" such that neurons in each column respond optimally to a particular direction of motion (Albright, Desimone, and Gross, 1984). Numerous experiments have now confirmed that this "functional architecture" for motion direction reflects a prominent role for MT in mediating motion perception. For example, lesions of MT can disrupt motion perception (Newsome and Pare, 1988; Pasternak and Merigan, 1994; Orban, Saunders, and Vandenberghe, 1995), and single neurons in MT are exquisitely sensitive to weak motion signals near psychophysical threshold for motion detection (Britten et al., 1992). Moreover, electrical microstimulation of a column of MT neurons can cause monkeys to report seeing the direction of motion encoded by the stimulated neurons, even though the visual display actually contains motion in a different direction altogether (Salzman et al., 1992; Salzman and Newsome, 1994).

In this chapter, we present evidence that MT also plays an important role in stereoscopic vision. Stereopsis is the perception of depth based on small positional differences (binocular disparity) between images formed on the two retinas. Neurons that respond selectively to binocular disparity were first described three decades ago (Barlow, Blakemore, and Pettigrew, 1967; Pettigrew, Nikara, and Bishop, 1968), and have subsequently been observed in similar numbers in many primate visual areas including V1, V2, V3, MT, and MST (Hubel and Wiesel, 1970; Poggio and Fischer, 1977; Poggio, Gonzalez, and Krause, 1988; Felleman and Van Essen, 1987; Maunsell and Van Essen 1983b; Roy, Komata, and Wurtz, 1992). However, evidence for a columnar organization of disparity-selective neurons is limited. Disparity tuned neurons appear to cluster weakly in cat V1 (Blakemore, 1970; LeVay and Voigt, 1988), and preferred disparity may vary systematically within disparity-tuned subregions of V2 in monkeys and sheep (Hubel and Livingstone, 1987; Ts'o, Gilbert, and Wiesel, 1990; Clarke, Donaldson, and Whitteridge, 1976).

We now show that MT contains a columnar organization for binocular disparity in addition to its well known organization for motion direction. Disparity-selective MT neurons tend to occur in discrete patches, and preferred disparity varies systematically from column to column within these patches. Furthermore, we demonstrate that activation of disparity-tuned columns with electrical microstimulation can influence perceptual judgments of depth in a manner consistent with the disparity tuning of the stimulated neurons. Thus, disparity-selective MT neurons appear to play an important role in stereopsis.

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Clustering of disparity-selective neurons in MT

If MT contains an organized map of binocular disparity, then nearby neurons should have similar disparity tuning. To test this possibility, we measured the disparity selectivity of multiunit clusters (MU) and single units (SU) during electrode penetrations through MT. In these experiments, two monkeys (S and P) were simply required to maintain fixation on a small spot of light while a moving random-dot pattern appeared over the multiunit receptive field (RF). Location, size, direction, and movement speed of the pattern were tailored to the preferences of the neurons at each recording site. The horizontal disparity of the moving dots was varied by rendering them in depth as a red/green anaglyph on a standard CRT display (frame rate = 60 Hz). Outside the RF, the remainder of the visual display was filled with zero-disparity dots, which were replotted randomly at 20 Hz to produce a twinkling background. This zero-disparity background helped maintain the monkey's eye vergence at the depth of the fixation point. Vergence angle was monitored in monkey S with the use of binocular scleral search coils (Robinson, 1963; Judge, Richmond, and Chu, 1980), and there was no systematic dependence of vergence on the disparity of the dots.

Figure 2.1.1 shows MU (filled circles) and SU (open circles) responses measured simultaneously from a single microelectrode. Action potentials from the SU were excluded from the MU response, ensuring that the MU activity arises from several other nearby SUs. The MU response is clearly tuned for disparity, suggesting that its constituent SUs have a similar disparity preference. This conclusion is further supported by the close agreement in shape between the MU and SU tuning curves. Although the SU response is more strongly modulated by disparity, both curves exhibit peaks and troughs at similar disparities. This correspondence between MU and SU tuning curves is typical of most of our recordings in MT.

To quantify this relationship, we fitted the disparity tuning curves with a cubic spline interpolation and we extracted three parameters from each tuning curve. A disparity tuning index (DTI) was defined as $1 - (R_{\text{min}} - S)/(R_{\text{max}} - S)$, where $R_{\text{max}}$ is the maximum fitted response, $R_{\text{min}}$ is the minimum fitted response, and $S$ denotes spontaneous activity (in the absence of a visual stimulus). For sites with significant disparity tuning (one-way ANOVA, $P < .05$), the disparity at which the fitted curve reached a maximum defined the preferred disparity (PD), and the disparity difference between the largest peak and the deepest trough was considered to be the disparity tuning width (DTW).

Across our sample of 110 simultaneous recordings, DTI values for SUs and MUs were significantly corre-

![Figure 2.1.1](image-url)
by measuring MU disparity tuning curves at regularly spaced intervals along electrode penetrations through MT. Data were collected at 411 recording sites (241 in monkey P, 170 in monkey S) along penetrations from two different angles. In oblique penetrations, we approached MT from the occipital lobe, passing first through the lunate sulcus. Electrodes traveled in a sagittal plane, tilted ~20° below horizontal. Thus, our electrode passed through MT at an oblique angle, ranging from ~45° to 90° away from the surface normal. Given that MT is organized retinotopically (Maunsell and Van Essen, 1987; Albright and Desimone, 1987) and contains a columnar architecture for direction of motion (Albright, Desimone, and Gross, 1984), we expected both receptive field (RF) position and preferred direction of motion to vary systematically in these penetrations. These known variations could then be used as a reference to evaluate changes in disparity selectivity. In normal penetrations, we approached MT from the frontal lobes (near-sagittal plane, tilted ~45° below the horizontal), passing first through the central and intraparietal sulci. The electrodes thus entered MT at an angle roughly normal to the cortical surface. In these penetrations we expected RF positions and preferred directions to remain fairly constant, again providing a useful reference for comparison with disparity tuning.

Figure 21.2a shows a sequence of disparity tuning curves measured at 100-μm intervals along an oblique penetration through MT; figure 21.2b summarizes these data quantitatively. First, note that the disparity tuning was poor both at the beginning and the end of the penetration, but was quite strong in the middle. A similar patchy distribution of disparity-selective responses was observed in many penetrations, suggesting that disparity-selective and nonselective neurons are spatially segregated within MT. Patches of poor disparity selectivity were short in this penetration, but such patches extended up to 1.5 mm in other oblique penetrations (and were not always at the beginning and end of the penetration). Second, note that the PD changed systematically within the disparity-selective segment of this oblique penetration. Similar gradients of PD from "near" to "far" disparities, or vice versa, occurred along many oblique penetrations, suggesting that MT contains a systematic map of binocular disparities. Finally, as expected for an oblique penetration, the preferred direction of motion changed gradually from one recording site to the next along most of the penetration (figure 21.2b, small arrows), and RF position moved gradually from the lower left quadrant of the visual field up to the horizontal meridian (data not shown).

Figure 21.2c,d shows analogous data from a normal penetration through MT. In contrast to the oblique penetration, the disparity tuning curves were very similar from one recording site to the next (figure 21.2c). The DTI remained roughly constant throughout this penetration, except at the last recording site which was near the boundary with white matter (figure 21.2d). In addition, the PD remained quite constant within a range of near disparities between ~0.5° and ~0.9°. Both the preferred direction of motion (arrows) and the RF location in space (data not shown) changed little throughout this penetration. We obtained similar results in many of our normal penetrations, including some in which disparity selectivity was poor throughout the penetration.

To summarize these data, we analyzed changes in disparity tuning as a function of distance between recording sites. For 22 oblique penetrations, figure 21.3 (filled circles) shows the mean absolute difference in DTI (|ΔDTI|) plotted against distance. Data were pooled across the 22 oblique penetrations as follows. For each penetration, we computed |ΔDTI| for all unique pairs of recording sites. We then pooled these values across penetrations (for each distance) and plotted the mean |ΔDTI| against distance between sites. The data were then analyzed by a two-way ANOVA, with distance and penetration type as the two factors. The mean |ΔDTI| increases significantly with distance [F(9,3060) = 22.5, P << .001], indicating that nearby recording sites have more similar DTIs than distant recording sites. At large separations, |ΔDTI| for oblique penetrations approaches the value obtained from random pairings of sites (solid line). Similarly, the mean |ΔPD| for oblique penetrations (open circles) also increases with distance [F(9,2708) = 12.61, P << .001]. This confirms that there is a systematic map of preferred disparity in MT, with smooth changes from one site to the next.

Among the 14 normal penetrations, both |ΔDTI| and |ΔPD| tend to increase with distance (filled and open triangles, respectively), as is expected if our "normal" penetrations are not perfectly orthogonal to the cortical surface. At all distances, however, the data from normal penetrations lie well below those from oblique penetrations [F(1,3060) = 208.9 for DTI, F(1,2708) = 122.9 for PD; P << .001 for both]. Thus, disparity tuning stays much more constant within normal penetrations, consistent with the idea that disparity-selective neurons are organized in columns that run perpendicular to the cortical surface. A similar finding was previously reported for direction selectivity in MT (Albright, Desimone, and Gross, 1984).

To summarize, the functional architecture for disparity in MT has three main features. First, disparity-tuned neurons are clustered into columns according to preferred disparity. Second, disparity-tuned columns are themselves clustered within MT such that disparity-sensitive
Figure 21.2 MT exhibits a columnar architecture for binocular disparity. (a) Sequence of disparity tuning curves recorded at 100-μm intervals along an oblique penetration through MT in monkey S. Each graph shows the MU response as a function of horizontal disparity. Standard error bars are plotted around each mean, but are generally smaller than the data points themselves. Smooth curves are cubic spline interpolations. Dashed lines represent the spontaneous activity level, and the letters L and R give responses obtained during monocular controls. Height of scale bar = 400 events/s. (b) Quantitative summary of disparity tuning for the oblique penetration illustrated in part a. Open circles (right axis) plot disparity tuning index (DTI) as a function of distance along the electrode penetration, whereas filled triangles (left axis) plot the preferred disparity (PD) at each recording site (PD is not plotted in cases where there is no significant disparity tuning; ANOVA, P > .05). Arrows denote the preferred direction of motion at each recording site. (c) Sequence of disparity tuning curves recorded at 150-μm intervals along a normal penetration through MT in monkey P. Height of scale bar = 400 events/s. (d) Summary of disparity tuning parameters for the normal penetration in part c. Conventions as in part b.
patches of cortex are interspersed among cortex that is poorly tuned for disparity (e.g., figure 21.2a,b). Finally, in patches with good disparity tuning, preferred disparity typically varies smoothly from column to column across the surface of MT. Some aspects of the functional architecture for disparity are poorly understood at present. We do not know the actual shapes of the disparity-selective patches, nor how consistently PD is organized within these patches. In addition, we know very little concerning the alignment of maps for direction and for disparity. Optical imaging or 2-deoxyglucose functional mapping studies may help resolve these issues.

**Microstimulation of MT biases depth judgments**

We next sought to determine whether MT plays a functional role in depth perception. We tested this possibility by applying electrical microstimulation within disparity columns in MT while monkeys performed the stereoscopic depth discrimination task illustrated in figure 21.4. Two monkeys (R and T) viewed a random-dot visual display in which a fraction of the dots carried a consistent depth signal (“signal” dots), while the remaining dots were randomly scattered in depth (“noise” dots). Signal dots were presented on each trial at a disparity either “near” or “far” with respect to the fixation point. One of the two disparities was the disparity preferred by the MT neurons near the electrode tip, while the other disparity was a nonoptimal disparity. The location and size of the visual stimulus aperture, as well as the direction and speed of the moving dots, were chosen to maximize the MU response. The monkeys’ task was to report seeing near or far depth by making a saccadic eye movement to one of two small saccade targets. By varying the fraction of signal dots in the display (% binocular correlation), task difficulty could be easily adjusted. Importantly, the monkeys were rewarded for reporting the actual depth of the signal dots irrespective of the presence of microstimulation. In these experiments, random-dot stimuli were rendered in depth by presenting stimuli alternately to each eye using LCD shutters synchronized to the frame rate of the CRT display (100 Hz). Again, binocular search coils were implanted in one monkey (R) to detect possible effects of microstimulation on vergence eye movements.

We made oblique penetrations through MT to search for microstimulation sites. An adequate site was considered to be a region where the disparity tuning of MU activity was roughly constant over at least 200–300 μm. Upon identifying a suitable site, we positioned our electrode in the middle of the region of constant preferred disparity for the duration of the experiment. Microstimulation parameters were similar to those used in previous studies from this laboratory (Salzman et al., 1992; Murasugi, Salzman, and Newsome, 1993). The stimulation train consisted of 20-μA biphasic pulses, each consisting of a 200-μs cathodal pulse followed by a 200-μs anodal pulse, with a 100-μs interval between the two. If microstimulation augments the signal carried by the stimulated neurons, and if these neurons provide signals used by the monkey to perform the task, we would expect microstimulation to increase the frequency of perceptual choices toward the depth encoded by neurons at the stimulation site.

Figure 21.5 depicts exactly this result from two microstimulation experiments in MT. Figure 21.5a illustrates the disparity tuning curve for a site that responded optimally to far disparities; the arrowheads indicate the two disparities employed in the depth discrimination task. Figure 21.5b shows how microstimulation at this site affected perceptual judgments. For almost every stimulus condition, the monkey decided in favor of the preferred disparity more often on stimulated trials (filled circles) than on nonstimulated trials.
(open circles). This bias toward the preferred disparity is evident as a leftward shift of the psychometric function. We considered the magnitude of this shift to be the horizontal offset between sigmoidal curves fitted to the data points (using logistic regression). This shift was measured as the distance between the two curves at the level of 50% preferred decisions. The effect illustrated in figure 21.5b was equivalent to 22.5% correlated dots, a nearly modal effect for monkey R.

Figures 21.5c and d show similar data from an experiment performed on monkey T. Neurons at this stimulation site responded best to near disparities, as illustrated in figure 21.5c. Consistent with the MU disparity tuning, microstimulation at this site induced a strong choice bias toward the near disparity. The resulting shift of the psychometric function was equivalent to 57.6% correlated dots, the largest effect that we have observed in any of our experiments.

Figure 21.6 summarizes results from 65 microstimulation experiments. The scattergram plots the amplitude of the microstimulation effect against the disparity-tuning index measured at each stimulation site. Positive values on the ordinate correspond to leftward shifts of the psychometric function, that is, shifts toward the optimal disparity of the stimulation site. Filled symbols indicate statistically significant effects (logistic regression, $P < .05$), which occurred in 43/65 experiments. Among the significant effects, 42/43 were toward the depth preferred by neurons at the stimulation site, the one exception being a site with poor disparity tuning. The histogram at the right depicts the same data collapsed across DTI.
Role of MT in stereopsis

The experiments described here provide two new lines of evidence that primate area MT is an important processing stage for neural signals related to stereoscopic depth perception. First, MT contains a functional architecture for binocular disparity in addition to its well known architecture for direction of motion: MT neurons are clustered according to their disparity selectivity, and preferred disparities vary smoothly across the surface of MT within the disparity-tuned patches. To our knowledge, this is the first clear, quantitative evidence for a systematic map of preferred disparity in primate visual cortex [but see Hubel and Livingstone, 1987; Ts'o, Gilbert, and Wiesel, 1990]. Second, microstimulation of disparity columns in MT can bias stereoscopic judgments of depth, and the direction of the bias (near or far) is predictable from the disparity tuning of neurons at the stimulation site. Thus the disparity signals carried by MT neurons are an important part of the neural substrate for depth judgments in our task. This finding establishes the first direct link between the physiological property of disparity selectivity and the stereoscopic perception of depth. Note that the existence of disparity selective neurons alone is not sufficient to establish this link, because disparity signals can be used for other purposes such as guidance of vergence eye movements, a possibility strongly suggested by recent experiments on disparity selective neurons in V1 (Cumming and Parker, 1997; Masson, Busetta, and Miles, 1997). It is possible that disparity signals in MT are also used in the control of vergence eye movements, although careful inspection of data from monkey R revealed no effect of microstimulation on vergence.

Previous work has shown that MT is specialized for processing motion information (Albright, Desimone, and Gross, 1993). In fact, MT is often cited as one of the best examples of functional specialization in cortex. Our results show that the role of MT in vision is not limited to motion analysis. This conclusion is emphasized by the fact that many MT neurons exhibit robust disparity tuning in response to stationary random-dot patterns, and that microstimulation biases depth judgments involving stationary dots. Although the vast majority of MT neurons are selective for direction and speed of visual motion (e.g., Maunsell and Van Essen, 1983a), their activity apparently can be used to judge the depth of stationary objects as well (the retinal image is not completely stationary, of course, due to small eye movements around the point of fixation). Our findings concerning the role of MT in stereopsis are complemented by recent evidence that MT may also play a role in the perception of depth from motion cues (Bradley, Chang, and Andersen, 1998; Dodd et al., 1997).
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Under the conditions of our experiment, which involves large disparities degraded by noise, MT appears to play an important role in depth perception. This does not mean, however, that all aspects of stereopsis depend on MT, nor that any single aspect of stereopsis depends entirely on MT. Consider, for example, that monkeys are capable of discriminating differences in disparity of less than 20 seconds of arc in the fovea (Sarramanto, 1975; Cowey and Wilkinson, 1991) and 1–3 minutes of arc at 5 degrees eccentricity (Pointon, Cumming, and Parker, 1998). By comparison, the disparity tuning of MT neurons is quite coarse (figure 21.2); thus, discrimination of fine disparities in our visual stimuli may require other cortical areas where neurons are more sharply tuned for disparity. The involvement of other cortical areas may in part explain why lesions of MT have not revealed a stereo deficit (Schiller, 1993). Broadly based investigations, including single-unit recording, microstimulation, and lesion techniques in a number of visual areas, will be necessary to achieve a comprehensive understanding of the neural basis of stereoscopic vision.

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NOTE

1. SU action potentials were identified using a template-matching algorithm implemented by a spike-sorting board. MU activity was recorded by means of a time-amplitude window discriminator. SU action potentials were excluded from the MU activity by setting the upper boundary of the window discriminator well below the peak of the SU action potential. For several experiments, the effectiveness of this approach was confirmed off-line by deliberately editing out any event in the multiunit record that occurred within a 3 ms window centered on each spike from the SU response, thereby eliminating any possible “leakage” of SU activity into the MU response. Analysis of the edited MU records yielded results essentially identical to analysis of the unedited MU records.

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