Neural Responses to Visual Texture Patterns in Middle Temporal Area of the Macaque Monkey

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SUMMARY AND CONCLUSIONS

1. We studied how neurons in the middle temporal visual area (MT) of anesthetized macaque monkeys responded to textured and nontextured visual stimuli. Stimuli contained a central rectangular “figure” that was either uniform in luminance or consisted of an array of oriented line segments. The figure moved at constant velocity in one of four orthogonal directions. The region surrounding the figure was either uniform in luminance or contained a texture array (whose elements were identical or orthogonal in orientation to those of the figure), and it either was stationary or moved along with the figure.

2. A textured figure moving across a stationary textured background (“texture bar” stimulus) often elicited vigorous neural responses, but, on average, the responses to texture bars were significantly smaller than to solid (uniform luminance) bars.

3. Many cells showed direction selectivity that was similar for both texture bars and solid bars. However, on average, the direction selectivity measured when texture bars were used was significantly smaller than that for solid bars, and many cells lost significant direction selectivity altogether. The reduction in direction selectivity for texture bars generally reflected a combination of decreased responsiveness in the preferred direction and increased responsiveness in the null (opposite to preferred) direction.

4. Responses to a texture bar in the absence of a texture background (“texture bar alone”) were very similar to the responses to solid bars both in the magnitude of response and in the degree of direction selectivity. Conversely, adding a static texture surround to a moving solid bar reduced direction selectivity on average without a reduction in response magnitude. These results indicate that the static surround is largely responsible for the differences in direction selectivity for texture bars versus solid bars.

5. In the majority of MT cells studied, responses to a moving texture bar were largely independent of whether the elements in the bar were of the same orientation as the background elements or of the orthogonal orientation. Thus, for the class of stimuli we used, orientation contrast does not markedly affect the responses of MT neurons to moving texture patterns.

6. The optimum figure length and the shapes of the length tuning curves determined with the use of solid bars and texture bars differed significantly in most of the cells examined. Thus neurons in MT are not simply selective for a particular figure shape independent of whatever cues are used to delineate the figure.

INTRODUCTION

Most of our understanding of the neurophysiological basis of vision comes from studies in which relatively simple visual stimuli, such as spots, bars, edges, and gratings (cf. DeValois and DeValois 1988; Hubel and Wiesel 1965, 1968) were used. However, over the past 15 years, an increasing number of investigators have used more complicated visual stimuli to explore how cortical cells respond to textures and other patterns that more closely approximate the rich visual environment typically encountered in the natural world. Most objects in the natural world contain complex surface markings or irregularities that give rise to a textured appearance. Indeed, it is possible to recognize borders between objects, even when there is no overall difference in brightness or color, if the textural characteristics are sufficiently distinct. Hence it is natural to wonder how cortical cells respond to textural patterns and to what degree their characteristics can be predicted on the basis of their responses to simpler stimuli.

Various studies in cat and monkey visual cortex have revealed that texture patterns (usually some type of random dot pattern) are indeed effective stimuli for many cells in both striate and extrastriate cortex (e.g., Hammond 1981, 1985; Hammond and MacKay 1977; Poggio et al. 1988; Saito et al. 1986). In addition to this direct influence in driving cells, texture patterns can also have an indirect influence by strongly modulating the responses to conventional stimuli when presented as a surrounding background. Such modulatory influences arise from both within and outside the classical receptive field (Allman et al. 1985; Hammond and Smith 1984), and they can be either suppressive or facilitating.

In the present study, we have examined the responses of cells in the middle temporal visual area (MT) of the macaque to moving texture patterns. MT was an obvious candidate for study because of the extensive evidence implicating it in various aspects of motion analysis (Maunsell and Newsome 1987). For example, the great majority of cells in MT show a high degree of direction selectivity when tested with conventional moving stimuli (Maunsell and Van Essen 1983a; Zeki 1974). Moreover, discrete chemical lesions within MT selectively affect motion perception (Newsome and Pare 1988) and visual pursuit of moving targets (Newsome et al. 1985).

The texture stimuli that we have used differ from those most commonly used in previous neurophysiological studies. Specifically, our stimuli were not random dot patterns, but instead consisted of an array of discrete, isolated texture elements whose position, orientation, and other characteristics were under computer control. This type of stimulus, which was motivated by psychophysical studies of texture vision (Bergen and Julesz 1983; Sagi and Julesz 1985), has advantages for studying some of the specific cues that may affect neural responses. Our analysis concentrated on three general issues, some of which have been addressed in brief reports elsewhere (Olavarria et al. 1988; Van Essen et al. 1989). First, we were interested in comparing the efficacy of...
texture stimuli relative with that of conventional solid bars in terms of the magnitude of the neural responses elicited by each type of stimulus. In cat striate cortex, for example, Hammond and MacKay (1977) reported that simple cells are largely unresponsive to texture patterns, whereas complex cells are consistently responsive (but see Skottun et al. 1988). Although MT lacks the simple-vs.-complex cell dichotomy characteristic of striate cortex, it was nonetheless of interest to know how much diversity in texture responses might be present.

A second issue was whether the directional tuning profiles of MT neurons are independent of the type of stimulus used to drive the cell. Albright (1987) coined the term “form-cue invariance” for describing cells whose directional preference remains the same for identically shaped stimuli defined by different cues. Our results suggest that this property is characteristic of many, but not all, cells in MT. Some cells showed significantly reduced or altered direction selectivity when tested with moving textures as compared with conventional bright bars. We suspect that these findings are significant for understanding how MT represents motion information in the natural world.

A third issue was to understand what cues within a moving texture pattern affect neuronal response profiles. The texture patterns that we used provided for independent control of the orientation and the motion of both figure and background elements. We found that motion-related characteristics were more important than element orientation characteristics in affecting neural responses in MT.

MATERIALS AND METHODS

Animal preparation and recording

Single-unit recordings were made from three macaque monkeys (Macaca fascicularis) weighing between 2.9 and 3.6 kg. These animals were prepared for semichronic recording with the use of procedures similar to those described by Maunsell and Van Essen (1983a) and Felleman and Van Essen (1987). Under general anesthesia (Nembutal iv or 2-3% halothane in 50% Nz-O2) and aseptic conditions, a stainless steel cylinder (1.8 cm ID) was securely attached, with the use of bone screws and dental acrylic, to the skull overlying the posterior pole of the right hemisphere. The center of this chamber was positioned ~17 mm from the midline and 13 mm anterior to the occipital ridge, thus providing a posterior, parasagittal approach to MT.

After 3-8 days of recovery, semichronic recordings were conducted in twice-weekly sessions for up to six sessions, each of which lasted ~12 h. For each animal, a substantial portion of the data came from a final acute session lasting between 6 and 8 days. During recording sessions, animals were paralyzed by continuous intravenous infusion of pancuronium bromide (3-8 μg·kg·h) or gallamine triethiodide (11 mg·kg·h), and were resuscitated through a tracheal cannula with a mixture containing 2.5% CO2 in air. Anesthesia was maintained with sufentanil citrate (3-8 μg·kg·h) administered through the infusion. The level of anesthesia was adjusted for each animal by: 1) assessing the adequacy of anesthesia before starting the infusion of paralytic; 2) monitoring the electrocardiogram (EKG) continuously to insure it was in an appropriate range (<200 beats/min), and 3) periodically testing for the absence of transient EKG responses to noxious stimuli. In addition, at the end of one 7-day recording experiment, we halted the infusion of paralytic while maintaining the sufentanil infusion. After the paralytic had worn off, the animal did not give coordi-

nated or purposive movements either in the resting state or in response to noxious stimuli. This variation in the “trial preparation” indicated that the level of anesthesia remained adequate even after many days of continuous infusion.

The infusion solution contained sodium chloride (0.45%), glucose (2.5%), and dexamethasone (0.05 mg·kg·h), and it was supplemented by periodic intravenous injections of amino acids (Vet Labs Oral Solution, 3 ml/4 h) and vitamin B complex (0.75 ml/day). Expired CO2 was monitored throughout the experiment, and the body temperature was maintained at 37-38°C with a water heating pad. At the end of each semi-chronic recording session, the infusion of the anesthetic and paralytic drugs was stopped. Shortly after spontaneous movements were observed, atropine (0.15 mg/kg im) and pyridostigmine bromide (0.33 mg/kg im) were administered to facilitate rapid recovery.

Extracellular recordings of single-unit activity were made with glass-coated platinum-iridium microelectrodes (1-2 MΩ), which were advanced through a small duralotomy with the aid of a microdrive mounted on the skull chamber. This microdrive was equipped with an X-Y stage that allowed accurate positioning of the electrode within the chamber. Selected recording sites were marked by small electrolytic lesions (7 μA for 7 s) to aid in the subsequent histological reconstruction. Atropine (2%) and neosynephrine were administered to the eyes to produce mydriasis and cyclopegia. The eyes were then fitted with zero-power contact lenses and focused onto a tangent screen (114 cm distant) with appropriate trial lenses determined by retinoscopy. Eye shutters attached to artificial pupils (8 mm diam) were placed in front of the eyes. The projections of both foveas on the tangent screen were determined with a reversing-beam ophthalmoscope, and a prism was used to align them within 0.5-1.0°. The alignment was further improved by using an adjustable (Risley) prism to superimpose left eye and right eye receptive fields from binocular cells encountered while traversing V1 and V2.

Histology

At the end of the acute session, animals were deeply anesthetized by administering an overdose of pentobarbital sodium, and then perfused with normal saline followed by glutaraldehyde and/or formaldehyde in concentrations appropriate for anatomic experiments carried out in the hemisphere opposite to the recordings. Blocks of tissue containing the electrode tracks were equilibrated in 30% sucrose, frozen, and sectioned at 31 μm. Reconstructions of electrode penetrations were made from analyses of series of sections stained for Nissl substance, myelin (Gallyas 1979), and cytochrome oxidase (DeYoe et al. 1990; Wong-Riley 1979). The location of MT was determined primarily from myelin-stained sections (Van Essen et al. 1981).

Visual stimulation

Once a cell was isolated, stimuli generated with an optical projection system were projected onto a tangent screen and used for mapping receptive fields and qualitatively assessing other receptive field characteristics. The basic stimulus was a stationary or moving bar whose luminance, length, width, orientation, velocity, direction, binocular disparity, and wavelength could be controlled either manually or by computer. An optimal stimulus selected by varying these parameters was used to plot monocular and binocular receptive fields and to make an initial estimate of the cell’s preferred direction of motion. For most MT cells (81 of 111) the direction tuning was then determined quantitatively with the use of the optical projection system (Maunsell and Van Essen 1983a).

For presenting texture stimuli, the central 60 × 60 cm area of the tangent screen contained a hinged panel that could be swung open to expose the 66-Hz monitor (noninterlaced) of a Masscomp
Aurora Graphics display. The animal's direction of gaze was positioned by rotating the head within a flexible head-holder or by placing prisms in front of both eyes, so that the receptive fields of MT neurons in a given penetration were well within this window. The 19-in. monitor rested on a hydraulic platform and could be positioned anywhere within the window as needed for the particular cell under investigation.

Computer graphics stimuli were generated with the use of customized software modified from that developed previously for psychophysical studies (Julesz et al. 1976; Sagi and Julesz 1985). Figure 1 illustrates some of the key characteristics of the texture patterns that we used. Each stimulus consisted of a sequence of seven frames presented in rapid succession to generate apparent motion. The speed of motion was determined by the interval between frames (usually 50–150 ms) and by the spatial offset of whatever portion of the pattern was moving, both of which could be independently specified. Each frame consisted of two rectangular regions (a central rectangular figure surrounded by a larger background region). The central figure could be either a texture bar (made up of discrete, elongated texture elements, as in Fig. 1) or a solid bar of uniform luminance (equal to the mean luminance of the texture patterns). The background could be either completely blank or composed of a texture field whose texture elements could be identical in orientation to those in the center or, as in Fig. 1, orthogonal in orientation. During successive frames in which the figure was displaced across the screen, the texture elements within the figure retained their positions relative to one another, rather than taking on the positions of the other elements in the background. In effect, the result was equivalent to a texture pattern that had been painted on a piece of cardboard and moved stepwise across the screen, progressively occluding a new region of the textured background while restoring the original background pattern in the region it just left. Individual texture elements were never partially occluded, however; they were always fully present or completely absent. A similar procedure was used to simulate motion of the background, which appeared as a rigid texture pattern moving across the screen. Unlike the net translation across the receptive field that took place for the figure, the borders of the background pattern remained fixed as the internal pattern translated.

By their nature, these stimuli were characterized by coherent motion of the collection of texture elements in the figure and/or background. In this respect, they differed from the "drift-balanced" stimuli exploited by Chubb and Sperling (1988) and Albrecht (1992), in which the motion of local elements is uncorrelated with one another or with the direction of figural motion. Our stimuli contained components of motion energy in many directions, because the displacement of individual texture elements could occur in any direction as the moving texture bar occluded the background pattern. However, coherent motion of the figure pattern occurred only in one direction (see Discussion).

Numerous parameters were needed to specify the exact composition of the texture stimuli, and all of these could be independently adjusted at the time of the experiment. Before undertaking any quantitative analyses, we routinely carried out a preliminary qualitative assessment aimed at finding a type of texture stimulus that was effective in driving the cell under study. The texture pattern was centered on the receptive field of the cell under study, the direction of motion was matched to the best direction determined with the use of the optical projection system, and various other parameters were then adjusted in an attempt to elicit a vigorous response from the cell. Additional information on stimulus characteristics is given in the legend to Fig. 1.

For practical reasons, our main quantitative analysis was divided into three separate stimulus series (A–C), each of which addressed a particular set of issues. When possible, all three series were run on each cell, but owing to the limitations of recording stability and the fact that each series required 10–30 min to com-

![Frame 1](image1)

![Frame 7](image2)

**FIG. 1.** Characteristics of computer-generated texture patterns used in this study. This figure shows the first and last frames of a 7-frame sequence that simulates motion of a texture bar. Each frame contained a rectangular array of elements (20 × 20 in this example, but up to 25 × 25 in size). Most series were run with the use of white elements on a dark background, but in some instances we used dark elements on a light background, as shown here. The mean spacing between element centers was adjusted according to the size and eccentricity of the receptive field; it was usually between 0.27 and 0.5°. The overall stimulus size was typically 6–12° across and was adjusted to be 2–3 times the receptive field size. The array was divided into a rectangular figure surrounded by a background pattern. The figure size was based on the optimal bar size determined during preliminary testing and typically ranged from 1 × 4 to 4 × 12 elements in size. Each texture element was a short line segment 0.05–0.08° in width and 0.15–0.2° in length. Their orientation was always ±45 degrees oblique to the axis of the figure, which minimized any luminance artifacts at the border between figure and background. The exact position of each texture element was locally displaced ("jittered") relative to a precise geometric array to minimize alignment artifacts. Each element was randomly displaced <70% of the distance between geometric array centers along both axes of the array. Motion was simulated by displacing the figure (and sometimes also the background) by a discrete number of element spacings at time intervals that were integral multiples of the 15-ms refresh period for the 66-Hz monitor. Owing to hardware limitations of the computer, only 7 frames of motion could be presented in rapid succession. We commonly used interframe displacements of 30–130 ms and interframe displacements of 1 (or occasionally 2) element spacings, resulting in apparent motion at speeds usually between 3 and 20 deg/s. This was in the low half of the range of preferred speeds for middle temporal visual area (MT) neurons (Maunsell and Van Essen 1983a), and, except at the longest intervals, it gave an appearance of relatively continuous motion to human observers.
plete, many cells were lost after running only one or two series. Moreover, some cells failed to give a significant response to any of the stimuli used in a series, in which case they were rejected from further analysis for that series. The number of cells tested and accepted for subsequent analysis in each series is indicated in Table 1. A total of 111 cells were tested with at least one series, and 80 of these gave significant responses to at least one texture condition. Black-on-white stimuli were used in quantitative tests for the further analysis for that series. The number of cells tested and the stimuli used in a series, in which case they were rejected from complete, many cells were lost after running only one or two series.

Calibration of stimulus luminance

Several precautions were taken to ensure that no difference in average luminance was caused by the shape, orientation, or motion of the figure. We found that on our video monitor (in fact, on all raster monitors we tested), the luminance of line segments at different orientations varied substantially, especially for thin lines (1 or 2 pixels wide). This may reflect both aliasing of oblique lines and the limited temporal bandwidth of the z axis (brightness) amplifiers. The former tends to make oblique lines less bright, whereas the latter makes vertical lines less bright. The resulting relationship between luminance and line orientation was neither simple nor smooth. Consequently, a lookup table was used to specify the gun values needed to achieve equal luminance (±3%) for each orientation, element width, and length available for use. The semiautomated calibration process used to create these lookup tables was repeated periodically to compensate for any drift in the system. Relative luminance matches were established with a United Detector Technologies photometer equipped with a sensor calibrated to measure photopic luminance. Absolute luminance values were measured with a Pritchard telephotometer (Spectra). Luminance of the blank video screen, including reflection of ambient illumination, was ~0.2 cd/m², and the Michaelson contrast between the blank screen and the white texture elements was ~95%.

Anway another way that luminance artifacts might occur is at the boundary between adjacent rows of orthogonally oriented texture elements. If the elements were regularly spaced and aligned with the row-column axes, the gap between rows would be different along the figure boundary than elsewhere in the display. Because this irregular gap is correlated with the orientation and motion of the texture figure, it could produce a spurious luminance cue for figural motion. This was avoided by using figure and surround elements that were oriented at 45° relative to the figure axis (which was either orthogonal to or parallel to the cell's preferred direction of motion) and were randomly displaced relative to an array of regularly spaced grid positions (see Fig. 1). Also, a different random distribution was used to calculate the element positions on successive presentations of the same stimulus condition. A useful way to check for luminance artifacts was to view the video display through a sheet of translucent tracing paper placed over the screen. Low-pass filtering the image in this way eliminates the orientation information carried by the relatively fine (high-frequency) grid of texture elements. We found that after completion of the luminance calibration process, the static and moving figures used in this study were invisible against the textured background when viewed through the paper. Hence any differential responses to the moving patterns could be attributed to relatively high spatial frequency information in the images (i.e., textural differences) rather than to low spatial frequency artifacts.

Data analysis

The spike data were stored and processed on a PDP 11/34 computer as described previously (Maunsell and Van Essen 1983a). For each series, data were averaged from 3 to 10 (usually 5) pseudorandomly interleaved presentations of each stimulus. After each test series, the average impulse rate and standard error for each stimulus condition were printed, which helped in directing the course of further testing. Additional calculations of peristimulus time histograms, average response curves, and direction selectivity indexes for the various stimulus conditions were done off-line.

At the beginning of each trial, the first frame in the stimulation sequence was presented as a stationary pattern for a period of 1 s. The figure pattern generally appeared within the classical receptive field, but near its margin. In most MT cells, this caused no obvious change in background activity, but some cells responded to this static pattern with a transient or even a prolonged change (either elevation or suppression) of background firing. After this initial period, the target moved across the classical receptive field at a speed and duration determined as described in the legend to Fig. 1, terminating at a position opposite to the starting point (relative to the receptive field center). Response magnitudes were calculated as the mean firing rate during the period of stimulus motion (starting 40 ms after motion onset and stopping 40 ms after offset to compensate for response latencies) minus that during the initial 1-s static frame (Eq. 1)

\[ R_i = F_i - F_{bi} \]

where \( R_i \) is the net motion-elicited response in direction \( i \), \( F_i \) is the mean firing rate during stimulus motion in direction \( i \), and \( F_{bi} \) is the mean firing rate in the 1-s period immediately before motion in that direction. Differences between response averages for stimulus onset and stimulus movement were evaluated with the Student's t test. A cell was considered to respond significantly to stimulus movement if these averages differed at the 5% level (one-tailed). To estimate the standard error of the mean for the individual "before" periods as needed in this analysis, we used the standard deviation calculated across all stimulus presentations. (The individual standard errors were not available from our computer analysis program, and this alternative strategy provides a conservative basis for assessing the statistical significance of evoked responses.) When the response to two different types of stimulus (e.g., solid bar vs. texture bar) were compared, only cells that responded significantly to at least one of the stimuli were considered. To analyze the direction selectivity of MT cells for various stimuli, we calculated a direction index (DI) using the formula (Maunsell and Van Essen 1983a)

\[ DI = 1 - R_{o} / R_{p} \]

where \( R_{o} \) and \( R_{p} \) represent the net motion-elicited responses to the opposite and preferred directions, respectively. For comparisons of direction selectivity between two types of stimuli, only cells that responded significantly to at least one direction for both stimuli were considered. The direction index is a common and useful measure of the direction selectivity of a cell. However, because it is
based on a ratio of two values, it is difficult to assess the statistical significance of a difference in a cell’s direction index for two stimulus types. We therefore chose to use a two-factor analysis of variance (ANOVA) to test the statistical reliability of differences in responses of single cells to different stimulus types and different directions. The two levels of factor 1 were the stimulus type (e.g., texture bar vs. solid bar), and the two levels of factor 2 were the preferred and opposite directions of motion. As with the direction index, the measurements used to calculate the ANOVA were the response magnitudes calculated with the use of Eq. 1. Cells were considered to have a statistically significant difference in directionality if there was a significant ($P < 0.05$) interaction between the stimulus type and the direction of motion. It is important to note that the ANOVA does not measure the statistical significance of differences between direction indices, for $DI$ is based on a ratio between two responses, whereas the ANOVA is based on absolute differences in response magnitudes. Nevertheless, the ANOVA provides the cleanest test that we are aware of for assessing whether the difference in a cell’s directionality for different stimulus types is statistically reliable or is the result of chance fluctuations.

RESULTS

Assignment of recording sites

Entrance into MT during an electrode penetration was manifested by clusters of directionally selective cells having appropriately sized receptive fields at depths between 10.5 and 12 mm from the entry site in V1. Our results are based on data from cells that were judged to be in MT by their receptive field properties and by the histological reconstructions of electrode penetrations. Figure 2 shows a parasagittal section through the superior temporal sulcus stained for myelin. The path of an electrode penetration and two electrolytic lesions are visible within the boundaries of MT. Figure 3 shows a plot of receptive field size (square root of receptive field area) as a function of the eccentricity of MT. Figure 3 shows a plot of receptive field size (square root of receptive field area) as a function of the eccentricity of the center of the receptive field in the population of 110 units for which borders were mapped. These data were fit by a least-squares regression line in which the relationship between receptive field size ($S$) and eccentricity ($E$) is $S = 1.10 + 0.72E$. This relationship is similar to that reported by others for MT (Albright and Desimone 1987; Desimone and Ungerleider 1986; Gattass and Gross 1981; Maunsell and Van Essen 1987; and Tanaka et al. 1986).

Solid bar versus texture bar stimuli (series A and B)

One of our primary objectives was to compare the responses to a moving texture bar (TB) with those to a solid bar (SB) having the same size and velocity. This comparison was provided by stimuli 1 and 2 of series A, as illustrated schematically in Fig. 4. As shown below, these responses were not always identical, and the remaining stimulus in series A and those in series B were designed to explore the basis for these differences in tuning profiles. Specifically, stimulus 3 (series A) contained a moving texture bar, but without any textured background (texture bar alone, TBA); series B contained a moving solid bar in the presence of a stationary textured background (stimulus 1, texture/solid bar, TSB) or in its absence (stimulus 2, solid bar, SB).

Response magnitude comparison

We found that texture bars elicited robust responses in most, but by no means all, cells in MT. The diversity of results obtained is illustrated in Fig. 5 with data from three cells. Each plot shows response magnitude (spikes/s exceeding the before period, when the first frame of the sequence was present but not moving) in each of four orthogonal directions. Peristimulus spike histograms for each cell are shown at the bottom of the figure. Filled squares and solid
There was a significant response of a neuron to texture bars, which was a solid bar with a texture surround of equal mean luminance, and solid bar alone. For clarity, these illustrations contain fewer texture elements (12 × 12) than the 20 × 20 or larger arrays used in the actual experiments (cf. Fig. 1). Four different directions of motion were presented for each stimulus, for a total of 12 conditions in series A and 8 conditions in series B. An optional extension sometimes used in series A included an additional 12 conditions in which the figure was rotated by 90°, so that motion was parallel to the long axis of the figure. For the great majority of cells studied, the actual stimuli presented were bright texture elements on a dark background, i.e., the reverse of the contrast illustrated here.

On average, MT cells responded less strongly to texture bars than to solid bars. This is illustrated by the population analysis in Fig. 6, which shows a scatter plot of mean responses to the most effective solid bar versus responses to the most effective texture bar (top right), as well as separate histograms for the solid bar maximal responses (inverted histogram, bottom right) and texture bar maximal responses (sideways histogram, top left), for all 51 cells that gave a significant response to one or the other stimulus type. In the individual histograms, cells giving significant responses above that to the initial stationary pattern are represented in black; those with nonsignificant responses are represented by open bars. The response in the preferred direction for texture bars (14.7 ± 1.9 spikes/s, mean ± SE) was on average about two-thirds of that for solid bars (mean = 23.2 ± 2.3 spikes/s), a difference that is statistically significant (t = 2.8, P < 0.05). There was a significant positive correlation between the maximum response magnitudes obtained from single cells for solid bar and texture bar stimuli (r² = 0.50, P < 0.05). Thus the magnitude of maximum response of a neuron to texture bars is only partially predictable from the neuron’s maximum response to solid bars. In about a third of the sample (19/51, 37%, solid squares in scatter plot), the maximum responses to texture bars and solid bars were significantly different (P < 0.05). In all of these except the one case shown in Fig. 5C, the texture bar response was significantly less than the maximal solid bar response. These differences are not attributable to the effects of the stationary patterns on the firing rate before stimulus motion. During the period before the onset of stimulus motion, the mean firing rate in the presence of the stationary texture pattern was lower than that in the presence of the stationary solid bar (4.5 vs. 6.7 spikes/s). On an individual cell basis, the rate was lower for texture patterns than for solid bars in 43 cells and higher in 8 cells, a difference that is significant at the P < 0.05 level (sign test). This difference in firing rate was statistically significant in 27 cells (P < 0.05, t test), 26 of which had the lower rate with the stationary texture bar. Consequently, if we were to compare the absolute firing rate rather than the firing rate relative to the stationary before period, the disparity in response magnitude for solid bars versus texture bars would be even greater.

Direction selectivity

The examples already illustrated (Fig. 5) indicate that directional tuning curves were not always identical for solid bar and texture bar stimuli. Figure 7 shows several additional examples to illustrate the diversity in directional tuning profiles that we encountered. As in the earlier example, firing rates in each of the four directions tested are shown for solid bars (solid squares, continuous lines) and texture bars (open squares, dashed lines). The cell in Fig. 7A was highly direction selective for both types of stimulus, and the tuning curves differ rather little. In contrast, the cell in Fig. 7B was highly direction selective for solid bars but showed only a slight directional bias for texture bars. This difference in directional tuning was attributable to a combination of decreased responsiveness for downward movement of the texture bar (the preferred direction for solid bars) and enhanced responsiveness for the upward direction. The cell in Fig. 7C responded most strongly to upward movement for the solid bar but was essentially pandirectional for the texture bar, showing, if anything, a slight bias for downward movement.

To analyze the results for the entire population of cells, we computed a direction selectivity index (DI) using a standard formula in which values near zero reflect low direction selectivity and values near unity reflect strong direction selectivity (see Methods). Because the direction of maximal response was often different for solid bars and texture bars, there were two ways in which the comparisons could be carried out. One was to calculate the direction index on the basis of independent determinations of the preferred direction for each stimulus type, irrespective of whether the preferred directions happen to be the same or different. This measure, which we call the “absolute directionality,” indicates the overall degree of directionality associated with each stimulus type. Another approach was to use the direction of maximal response for one stimulus type as the reference direction for comparing preferred directions and for
FIG. 5. Response magnitude comparisons for solid bar and texture bar stimuli presented to three different cells. Each plot in the upper portion shows response magnitude (spikes/s) in each of the four orthogonal directions tested for texture bar (open squares, dashed lines) and solid bars (filled squares, solid lines). The direction giving the highest response is shown at left in each plot. Peristimulus time histograms are shown below. These examples illustrate cells whose highest response to solid bars was larger (A: 88C07E), about equal (B: 88D14D), or smaller (C: 88B15J) than to texture bars. For C, none of the stimulus directions gave a statistically significant response above background for solid bars, but there was significant suppression opposite to the preferred direction. In this and later figures, standard errors are indicated for the responses to individual conditions and for the baseline activity before motion onset (horizontal dashed lines).

FIG. 6. Response magnitude comparison for solid and texture bars. Histograms show the distributions of magnitude of best responses to texture bars (sideways histogram on left) and solid bars (histogram on bottom). Filled portions represent cells giving statistically significant responses; open portions represent nonsignificance above the background. Responses of each cell to both stimuli are shown in the scatter plot. Filled squares represent responses that differ significantly from one another.

FIG. 7. Direction selectivity comparison for solid bars (m, - - -) and texture bars (0, - - - -). Data from 3 cells are shown to compare direction selectivity to solid and texture bars when the preferred direction for solid bar is taken as a reference. All responses are normalized to the response for the solid bar in the preferred direction. A (cell 88C10F): similar direction selectivity for solid and texture bars. B (cell 88C13D): a cell highly selective for solid bars but nonselective for texture bars. C (cell 88B16M): a cell highly selective for solid bars and slightly (but not significantly) biased in the opposite direction for texture bars.
calculating both direction indices. This measure, which we call the "relative directionality," indicates the degree to which the population of cells can signal the particular direction in which a target is moving independent of the cues with which it can be distinguished. We carried out both types of analysis, because they provide complementary types of information.

**Absolute directionality**

Figure 8 shows histograms of the direction index as calculated independently for solid bars (bottom right) and texture bars (top left). Each histogram includes only cells showing a statistically significant response for the stimulus in the preferred direction (45 cells for solid bars, 35 cells for texture bars). In addition, the scatter plot in the top right includes data from the 29 cells that responded significantly to both solid and texture bars (shown by solid bars in the individual histograms). As expected, most MT cells were highly selective for the direction of motion of solid bars. The mean direction index for our sample of 45 cells was 0.8 ± 0.05 (SE), similar to but slightly lower than previous reports (Albright 1984; Maunsell and Van Essen 1983a; Rodman and Albright 1987). For texture bars, the distribution was skewed toward lower values; the mean direction index was only 0.4 ± 0.04, which was significantly lower than that for solid bars (t = 7.0, P < 0.01). Fewer than half of the cells (15 of 35) had a direction index >0.5, which is a common criterion for a direction bias, and only 4 cells (11%) had an index >0.7, a common criterion for strong direction selectivity.

Another way of summarizing these results is by way of the population tuning curves shown in Fig. 9. These plots were prepared by aligning the tuning curves from individual cells along the direction of maximum response for each stimulus type (i.e., as if the best responses for all cells were in the same direction). The response magnitudes (spikes/s minus the before period) were then averaged for each of the four directions and plotted separately for solid bar stimuli (Fig. 9A) and texture bar stimuli (Fig. 9B). For solid bars, the mean response 180° from the best direction was 3.6 ± 1.3 spikes/s, only 16% of the maximum. The corresponding value for texture bars was 8.3 ± 1.0 spikes/s, which was 56% of the texture bar maximum and was significantly greater than that for solid bars.

**Relative directionality**

In only about half of the cells (15/28) for which a valid comparison could be made were the directions of maximal response identical for solid bar and texture bar stimuli. For the remaining 13 cells, the maximal texture bar response was either in the direction opposite to that for the solid bar (11 cells) or in one of the two orthogonal directions (2 cells). If shifts in preferred direction had occurred randomly, one would expect twice as many cells in the "orthogonal" group as in the "opposite" group, rather than a small minority (because there are two possible orthogonal directions). This bias might be related to the shapes of the population response curves in Fig. 9, where the minimum response occurs at 180° for solid bars but at 90 and 270° for texture bars. However, these tendencies within each population curve are not statistically significant, and the correlation might be coincidental.

Figure 10 illustrates a quantitative comparison of direction indices when both calculations were based on the preferred direction determined for solid bars. We chose solid bars rather than texture bars as the reference stimulus because, as already shown, they gave stronger responses on average. Consequently, direction indices for solid bars (abscissa) are all positive, whereas those for texture bars (ordi-
nate) are either positive or negative depending on whether the maximum response agreed with or differed from that for the solid bar (see legend). There was no significant correlation between the direction indices for solid bars and texture bars ($r^2 = 0.0006$). For 11 of the 28 cells, the measured direction index was opposite in sign for texture bars versus solid bars; for 7 cells (black squares) the differences in direction selectivity were statistically significant ($P < 0.05$, ANOVA). Thus our results demonstrate a clear loss of directionality in many cells when texture stimuli were used, but convincing reversals of direction preferences in individual cells were rare.

**Effects of the texture surround**

The differences in directional tuning profiles for texture bars versus solid bars were initially unexpected. An obvious question is whether this difference is attributable to the textured nature of the moving target or to the presence of a static texture surround. Two types of comparison were used to address this issue. One comparison involved the use of a texture bar alone, which contained the same distribution of texture elements as in the standard moving texture bar, but which lacked any texture surround (stimulus 3, series A, Fig. 4). We found that the texture bar alone was on average more similar to the solid bar than to a standard texture bar in terms of the magnitude and directionality of the responses elicited. The average response magnitude for the most effective texture bar alone (25.0 $\pm$ 2.5 spikes/s) was not significantly different from that to the most effective solid bar (24.0 $\pm$ 2.4 spikes/s) for the 48 cells in the comparison group, and the correlation in response magnitudes for individual cells was strong ($r^2 = 0.69$). Figure 11 illustrates the results on directionality by showing a scatter plot of direction indices for texture bar alone versus solid bar (Fig. 11A), where the correlation is high ($r^2 = 0.53$), and a separate scatter plot for texture bar versus texture bar alone (Fig. 11B), where the correlation coefficient is low ($r^2 = 0.07$); in the latter comparison, nine cells showed statistically significant differences in their direction preference. The fact that the texture bar alone acts very much like a solid bar stimulus is not surprising, because there is a strong luminance difference between target and background for both stimuli.

To test more directly for the effects of a textured surround, we generated a hybrid stimulus consisting of a solid bar for the moving target and a texture pattern of equal average luminance for the stationary background (stimulus 1, series B, Fig. 4). In terms of response magnitudes, there was a high positive correlation ($r^2 = 0.64$) in the maximum response to a solid bar with texture surround versus that to a standard solid bar for the 25 cells that responded significantly to at least one stimulus. The average response to the most effective solid bar with texture surround (24.1 $\pm$ 4.5 spikes/s) was not significantly different from that to the most effective solid bar (26.8 $\pm$ 5.0 spikes/s).
spikes/s). Five cells (20%) responded significantly differently ($t > 3.35; P < 0.01$) to the solid bar versus the solid bar in texture surround. In three cells, the texture surround reduced the maximum response, whereas in two, it enhanced the response.

Figure 12 shows directional tuning curves for three cells that represent the spectrum of results we encountered for the 19 cells giving significant response to both the standard solid bar and the solid bar in the texture surrounds. Direction selectivity for a solid bar stimulus was not affected by the static texture surround for the cell in Fig. 12A, but it was abolished for the cell in Fig. 12B. For the cell in Fig. 12C, direction selectivity was reversed for the two stimulus types. As with the comparisons between texture bars and solid bars, these effects were attributable to a combination of reduced responsiveness in one direction and enhanced responsiveness in the opposite direction. The mean direction index for the solid bar in texture ($0.68 \pm 0.07$, SE) was significantly smaller than that for the standard solid bar ($0.93 \pm 0.05$, SE), suggesting that the texture surround accounts in large part for the reduced direction selectivity to texture bars.

Results for the entire population of cells studied with series B are shown in a scatter plot of direction indices for solid bar versus solid bar in texture surround (Fig. 13), using the preferred direction for the solid bar as the reference. More than half of the population showed a comparably high degree of direction selectivity for both stimulus types. However, the correlation was poor for the remaining cells, and the overall correlation coefficient was low ($r^2 = 0.04$). When comparing relative directionality of individual cells, the differences were statistically significant for 5 of 19 cells. There was no significant reduction in average response magnitude accompanying the partial reduction in direction selectivity caused by the texture surround.

The effects of a texture surround might, in principle, be a consequence of the presence of texture per se in the background pattern. Alternatively, it might reflect the loss of luminance contrast between the figure and surround. To address this issue, in three cells we increased the luminance of the solid bar by $\sim0.5$ log units above the average luminance of the surround. In two of the three cases, this resulted in significantly increased direction indices (from 0.15 to 0.6 and from $-0.24$ to 0.5) for the solid bar in texture surround, but no significant change in directionality for the solid bar on a blank background. This preliminary observation suggests that the degree of luminance contrast between figure and surround may be an important factor affecting direction selectivity.

To summarize, the results obtained using the stimuli in series A and B revealed three important findings. 1) Texture bars often elicit vigorous responses from MT neurons, but the magnitude is usually less than for a solid bar stimulus. 2) The degree of direction selectivity is, on average, markedly lower for texture bars than for solid bars. This occurs as a result of enhanced responsiveness to texture bars moving in the null direction of solid bars as well as a reduced responsiveness to texture bars moving in the preferred direction, with little change in the two orthogonal directions. 3) The differences in direction selectivity for texture bars versus solid bars are in part attributable to the presence of the textured surround rather than the textured nature of the moving target. However, this does not reveal what aspect of texture is important, or whether all texture patterns would have the same effect. This issue is addressed in the next section.

**Contributions of specific textural characteristics to neural responses (series C)**

In the standard texture bar stimulus discussed in the preceding section (stimulus 1, series A), the central figure differed from the background in the orientation of its texture.
elements and also because the bar was moving while the background was stationary. To explore the relative importance of different textural characteristics in shaping the responses of MT neurons, we used the collection of six stimuli contained in series C (Fig. 14). In stimulus 1 (texture bar, TB1), the figure and background differed in both orientation and motion; this stimulus was equivalent to the texture bar of series A. In stimulus 2 (orientation bar, OB1), the figure and background differed in orientation, but there was no differential motion because the background moved along with the figure. In stimulus 3 (motion bar, MB), there was differential motion between figure and background but no difference in element orientation. Stimulus 4 (texture bar, TB2) was like stimulus 1 except that the element orientations between figure and background were reversed. Similarly, stimulus 5 (orientation bar, OB2) was like stimulus 2 except for the reversal of element orientation. Finally, stimulus 6 (motion field, MF) was a uniformly moving texture field, with no differential motion and no orientation contrast.

In analyzing the results from this series, we focused on a set of eight pairwise comparisons involving stimuli differing in a single characteristic. In Table 2, these have been grouped according to the particular characteristic that differs between the two members of each pair. The first column indicates which pair of stimuli (identified as in Fig. 14) are compared. The next two columns indicate whether orientation contrast (column 2) or background motion (column 3) was present in both pairs (+), absent in both (0), or was the characteristic that differed between members of the pair (Δ). The last two columns indicate the orientations of the texture elements in the figure and background, which were either clockwise (/) or counterclockwise (\) relative to the long axis of the figure, or which changed between members of the pair (Δ).

**Table 2. Pairwise comparisons between texture stimuli differing in only a single cue**

<table>
<thead>
<tr>
<th>Stimulus Comparison</th>
<th>Orientation Contrast</th>
<th>Background Motion</th>
<th>Figure Orientation</th>
<th>Background Orientation</th>
</tr>
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<tbody>
<tr>
<td>1 vs. 2</td>
<td>+</td>
<td>Δ</td>
<td>/</td>
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<td>4 vs. 3</td>
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<td>3 vs. 6</td>
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<tr>
<td>1 vs. 3</td>
<td>Δ</td>
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<td>2 vs. 6</td>
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<td>1 vs. 4</td>
<td>+</td>
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<td>2 vs. 5</td>
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<td>0</td>
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</tbody>
</table>

Stimuli compared are from Fig. 14. +, present; Δ, present in one but not the other; /, clockwise; \, counterclockwise; 0, absent.

**Effects on response magnitude**

Many cells responded comparably well to all four types of moving texture stimulus in series C (motion field, motion bar, orientation bar, and texture bar). The orientation of texture elements in either the figure or the background generally had little effect on neural responses, but the presence or absence of background motion was an important factor for a significant minority of cells. Figure 15 illustrates these findings by showing scatter plots of response magnitudes for selected comparisons—one from each of the three groupings listed in Table 2. Figure 15A plots the maximal orientation bar response. Similar results were found for the other two comparisons of this type (stimuli 3 vs. 4 and 2 vs. 6). The mean responses differed by ~5% for all three comparisons.

Figure 15B compares responses to the two texture bar stimuli that differed only in the absolute orientation of their texture elements (stimuli 4 vs. 1). Not surprisingly, both types of stimulus were equally effective, on average. A few cells (4 of 57) showed a significantly greater response (P < 0.05) to one stimulus than the other, suggesting that they were sensitive to the absolute orientation of elements in the center and surround. Likewise, a pronounced effect of absolute element orientation occurred for a few cells in comparing stimuli 5 vs. 2 (data not shown). Although these effects appear genuine, they occur in only a small minority of the overall MT population.

Figure 15C compares responses to an orientation bar (stimulus 2, with background motion) to a texture bar (stimulus 1). For most cells, the two stimuli were comparatively effective, as evidenced by the clustering of data points near the 45° (equal effectiveness) diagonal. However, about a third of the cells (18 of 57; filled squares) showed a statistically significant difference (P < 0.05) between their peak responses to the two stimulus types. In most of these cases (15 of 18), the texture bar response was greater than the orientation bar response. Similar results were found for the
TEXTURE RESPONSES IN MT

A Stimuli 3 vs. 1
± Orientation Contrast

B Stimuli 4 vs. 1
Different Element Orientation

C Stimuli 2 vs. 1
± Background Motion

Response Magnitude (Spikes/Sec)

FIG. 15. Scatter plots of maximal response magnitudes for cells tested with motion bars vs. texture bars (A; stimulus 3 vs. 1 of Fig. 14), texture bars with element orientations changed (B; stimulus 4 vs. 1), and orientation bars vs. texture bars (C; stimulus 2 vs. 1). Response magnitudes are strongly correlated for texture bars vs. motion bars and for the 2 types of texture bar, but are less well correlated for orientation bars vs. texture bars.

other two comparisons of stimuli with or without background motion (stimuli 4 vs. 5 and 3 vs. 6). Taking all three comparisons together, the maximum response to stimuli with a moving background was, on average, 30% smaller than the maximum response to stimuli with a stationary background. Thus background motion on average caused moderate decrement in neural responses.

Previous studies have shown that responses of MT neurons can be modulated by the direction of motion of background patterns lying completely outside the classical receptive field (Allman et al. 1985). In our stimulus displays, the figure was usually contained entirely within the classical receptive field, whereas the background covered the remainder of the classical receptive field and extended well into the modulatory surround. As suggested by Tanaka et al. (1986), both parts of the background pattern (inside and outside the classical receptive field) may contribute to the modulatory effects reported here, but we did not attempt to dissect their relative importance.

Effects on direction selectivity

We noted previously that directional tuning profiles are often different for solid bar and texture bar stimuli. The same issue arises in relation to the various types of textural motion presented in series C: to what extent do the preferred direction and the degree of direction selectivity agree for different texture stimuli? Altogether, series C contained six different stimulus patterns, for which there are 15 pairwise comparisons that are combinatorically possible. Figure 16 shows comparisons of direction indices for three such comparisons: orientation bars versus uniform motion fields (A, stimuli 2 vs. 6), texture bars versus motion bars (B, stimuli 1 vs. 3), and texture bars versus texture bars with element orientations interchanged (C, stimuli 1 vs. 4). For all three pairwise comparisons, there is a positive and statistically significant correlation between the two sets of direction indices ($r^2 = 0.40, 0.24$, and $0.23$, respectively). However, the correlations are far from perfect, even though only two cells showed statistically significant differences, which is no greater than the number expected by chance.

Effects of target dimensions

Previous studies have reported that most MT neurons are relatively nonselective for stimulus dimensions, although a minority of cells are quite selective (Maunsell and Van Essen 1983a; Zeki 1974). At the outset of studying each cell, we made an initial qualitative assessment of the preferred size, if any, of the solid bar, and we also tested several sizes of texture bar. In these preliminary tests, most cells did not appear sharply tuned for stimulus dimensions, but some were moderately or strongly selective for stimulus length and/or width. In the quantitative analyses discussed in preceding sections (series A–C), we used the figure dimensions that seemed most effective in driving cells with the texture patterns. For 28 cells, we carried out a quantitative analysis of the response versus bar length for texture bars and solid bars moving in the cell’s preferred direction. For each stimulus type, responses were measured for four or five stimulus lengths, usually ranging from 20 to 30% of the classical receptive field size at the shortest to 150–200% at the longest.

In the majority of cells examined, the quantitative analysis revealed a significant degree of length tuning for one or both types of stimulus, in that the response at the preferred length was significantly greater than at one or more other lengths. In the majority of these cells, the preferred length and the type of length tuning differed for texture bars versus solid bars. Figure 17 shows results from four cells to indicate the diversity in this population. The cell in Fig. 17A showed pronounced length summation for both texture bars and solid bars; the only significant difference was the greater overall efficacy of the solid bar stimulus. In Fig. 17B, the texture bar response again showed length summation; in fact, only the longest bar elicited a statistically significant response. In contrast, the solid bar response clearly declined for the two longest stimuli, indicating significant end inhibition. In Fig. 17C, the only effective texture stimu-
A Stimuli 2 vs. 6 B Stimuli 1 vs. 3

Direction Index: Orientation Bar

Direction Index: Textured Bar

Direction Index: Uniform Moving Field

Direction Index: Motion Bar

FIG. 16. A: effects of contrast and absolute orientation cues on directionality. Effect of orientation contrast on uniformly drifting patterns. Scatter plot comparing direction indices to orientation bars (drifting bar and surround) and uniform moving fields (see Fig. 14) from 25 cells that responded significantly to both stimuli. Direction indices for uniform moving fields were computed along the axis determined by the maximal responses to orientation bars. B: scatter plot comparing direction indices to texture bars and motion defined bars (see Fig. 14) from 45 cells that responded significantly to both stimuli. Direction indices for motion defined bars were computed along the axis determined by the maximal response to texture bars. C: scatter plot comparing direction indices for the two types of texture bar (TB vs. TB1), using TB1 to define the preferred direction.

lus was the shortest bar. In contrast, for the solid bar, all lengths were effective, but there was a clear peak for an intermediate length, indicating length summation for short stimuli and end inhibition for longer ones. Finally, in Fig. 17D, the texture bar response showed a peak at an intermediate length, whereas the solid bar response was best for the shortest bar and showed substantial (albeit incomplete) end inhibition.

For each cell, the responses to both texture bars and solid bars were categorized as follows: 1) a flat response, 2) length summation, 3) end inhibition, 4) peaked response (i.e., significant length summation as well as end inhibition), and 5) nonresponsive or uncertain categorization. The most common category for texture bars was length summation (10 cells); only a few showed end inhibition (3 cells) or peaked responses (2 cells). For the solid bar responses, end inhibition was more common (8 cells); 5 showed peaked responses and 3 showed length summation. Of the 18 cells that were assigned to the first four categories for both solid bars and texture bars, only 6 cells (33%) were in identical categories for both stimulus types. We conclude that the preferred stimulus dimensions and the length tuning profiles for stimuli differing in textural characteristics are often not in close concordance.

In some tests, we used stimuli in which the motion was parallel to the long axis of the texture bar as well as stimuli in which the motion was orthogonal to the bar. We then assessed whether the shapes of the directional tuning curves were similar for the two types of stimulus motion. In general, this was indeed the case; the preferred direction for a bar moving lengthwise (parallel to the long axis) was usually the same as that for a bar moving sideways (orthogonal to the long axis). However, in a few cells, the directional tuning curves were strikingly sensitive to bar orientation, because the preferred direction for parallel motion differed from that for orthogonal motion by 90°.

FIG. 17. Length tuning curves for texture bars (o) and solid bars (□). A: cell showing length summation for both stimulus types (cell 88Bi4U). B: cell showing length summation for texture bars and end inhibition for solid bars (cell 88C07I). C: cell showing end inhibition for texture bars and a peaked tuning profile for solid bars (cell 88C07L). D: cell showing a peaked tuning profile for texture bars and end inhibition for solid bars (cell 88Bi4R).

DISCUSSION

Processing of motion and textural information in MT

The suggestion that area MT is involved in motion analysis was first prompted by physiological studies showing that it contains a high incidence of direction selective cells in alert (Mikami et al. 1986) as well as anesthetized monkeys...
More direct evidence on this issue has come from recent studies in which lesions and focal electrical stimulation were used to implicate MT directly in contributing to pursuit eye movements and to the perception of motion direction (Newsome and Pare 1988; Salzman et al. 1990). However, there is much more to motion analysis than simply computing the two-dimensional direction of motion of isolated targets in the visual world. Motion information is used for computing complex three-dimensional trajectories and also for various purposes unrelated to motion perception per se. These include figure-ground segregation, estimating the relative distance of different objects, and inferring the three-dimensional structure of objects, all using cues of relative motion in the visual field. Thus one might expect diversity and richness in the physiological properties of MT neurons, and indeed this has been reported in studies from several laboratories. Many MT neurons are selective for speed and/or binocular disparity (Maunsell and Van Essen 1983a,b), which indicates that tuning along multiple dimensions is common. Responses to motion within the classical receptive field are often modulated by motion in the far surround, suggesting that relative motion, rather than just absolute retinal motion, is an important factor for MT neurons (Allman et al. 1985; Tanaka et al. 1986). Responses to combinations of gratings (“plaid” patterns) are not always equal to the sum of the individual component gratings, suggesting that important nonlinear interactions contribute to motion responses (Movshon et al. 1986; Rodman and Albright 1989).

In the present study, we extended this general approach by analyzing the responses of MT neurons to a variety of texture patterns and comparing them to the responses to conventional moving bars. Our analysis focused on three basic issues, two of which are relatively straightforward to interpret. First, we found that most MT neurons responded well to both solid bars and texture bars, but that, on average, solid bars were a more effective stimulus. This is not surprising given our subjective impression that the moving texture bars were perceptually less salient than the solid bar stimuli for the particular stimulus conditions we used. Although the relative responses to texture bars versus solid bars varied over a wide range, we found no indication of a distinct class of texture-prefering cells.

A second issue was to analyze the relative importance of different cues in eliciting responses to moving textures. We found that neither the absolute orientation of the texture elements nor the relative orientation between figure and background elements had much effect on neural responses. Also, the stimuli containing differential motion between figure and background were often more effective than uniformly moving patterns. These observations correlate with our subjective impression about the perceptual salience of our stimuli for human observers. With the parameters used in this study, bars defined by orientation contrast appear less salient than bars that are equivalent in other respects but are defined by differential motion. It would be of interest to compare neural responses generated by stimuli that were matched for their perceptual salience, but we are not aware of any studies done along these lines. Another unresolved issue is whether the presence of a figure per se affects neural responses in MT. This could be tested using stimuli containing a smooth velocity gradient between center and surround as well as stimuli with a sharp velocity discontinuity as in the present study. The finding that optical blurring of a motion discontinuity can strongly affect neural responses in area MST (Sugita and Tanaka 1992) suggests that this is an important issue to address.

A third issue is the degree to which directional tuning curves depend on the type of stimulus used. The present study yielded some unexpected findings that merit detailed consideration. In general, most neurons in visual cortex respond to a wide variety of stimuli and are tuned along multiple stimulus dimensions. An important question is how the tuning profile along one dimension depends on other characteristics of a visual stimulus.

**Cue dependence and cue independence**

When a cell is reported to be selective for a certain parameter (say, orientation or direction), it is often assumed, implicitly or explicitly, that the preferred value (say, vertical) and the sharpness of tuning are not critically dependent on the nature of the stimulus used to elicit the responses. This has occasionally been documented by showing, for example, that orientation tuning curves change in magnitude but not in shape when stimulus contrast is raised or lowered (Sclar and Freeman 1982). However, there is no a priori reason why this assumption should always be valid, and, in addition to the counterexamples illustrated in the present study, there are others documented in the literature (see below).

We have adopted the general terms cue dependent and cue independent to describe whether a cell’s tuning curve for a given parameter depends on the particular characteristics of the stimulus. For example, Fig. 18A shows a hypothetical tuning curve for direction of motion that has the same shape for stimuli defined by two different texture patterns (T1 and T2), even though the amplitudes of the curve differ. The cell can be regarded as cue independent for stimulus direction when those particular textures are used. In contrast, the hypothetical cells of Fig. 18, B and C, have directional tuning profiles for the two textures that differ either in shape (Fig. 18B) or in the location of the peak (Fig. 18C). They are therefore cue dependent for stimulus direction when these textures are used. Our terminology is similar to Albright’s (1992), who used the expression “form-cue invariant” to describe MT neurons whose preferred direction did not depend on the type of stimulus used to define a moving bar-shaped region. However, the directional tuning that we studied was not necessarily related to figure-ground segregation and the shape per se of the moving target. Therefore, we prefer to avoid the term form-cue and any misleading connotations it might have in the context of our results.

Parenthetically, it is worth mentioning an alternative nomenclature, separability versus inseparability, that relates to this issue. Suppose that the responses \(R\) of a neuron are measured as a function of two continuous parameters, say, the direction \(d\) and speed \(s\) of motion. One can ascertain whether the function \(R(d,s)\) can be expressed as the product of two simpler functions, \(F(d)\) and \(G(s)\), each of which depends on only a single parameter. If this is indeed the case, then \(R\) is a separable function of \(d\) and \(s\) over the region of
The issue of cue dependence versus cue independence is important for understanding the strategies that might be used to compute motion trajectories on the basis of neural activity patterns in MT. Suppose, for example, that the directional tuning profiles of all cells in MT displayed perfect cue independence when tested with various types of moving stimuli. This would make it relatively straightforward to compute the actual direction of object motion by comparing the relative activity in a population of cells having different preferred directions. One specific strategy that would be attractive is the type of population coding strategy that has been successful in relating motor performance to neural activity patterns in motor cortex (Georgopoulos et al. 1988). In their model, each neuron "votes" for a particular direction of movement (the cell's preferred direction), but the strength of its vote depends on the firing rate of the cell. They found that the predictions of the model were more
accurate when the strength of a cell’s vote also depended on how strongly directional the cell was (e.g., weakly directional cells contribute less and highly directional cells contribute more). Applied to MT and motion analysis, the idea would be that each neuron votes for a particular direction of object motion (its preferred direction), but the strength of its vote is weighted according to the neuron’s firing rate and how strongly directional the cell is. Each neuronal vote would be represented as a vector of appropriate direction and magnitude; the vectorial sum of all the individual neuronal contributions yields an overall population vector that would represent the perceived direction of object motion. However, to the extent that directional tuning profiles are strongly cue dependent, this simple population coding strategy would run into difficulty. This is because the strength of each neuron’s vote could no longer be computed on the basis of a fixed direction preference and degree of directionality. Rather, it would be necessary to take into account the type of stimulus being viewed to compute the vectorial contribution of each cell. This would not be impossible, but it adds greatly to the computational complexity of the problem.

Given that a significant degree of cue dependence indeed exists in MT, there are several possible implications relating to the above analysis. One is that computation of motion trajectories may involve a more sophisticated population coding strategy than that just outlined. Alternatively, it might be that the visual system relies on a relatively simple but imperfect strategy, accepting that performance will deteriorate when viewing more complex motion patterns. This raises the question of how various aspects of performance such as motion discrimination depend on stimulus composition. In general, discrimination thresholds are not always identical to detection thresholds in various psychophysical tasks. For example, the threshold for discriminating the direction of motion of certain grating patterns (low temporal frequency and high spatial frequency) is higher than the threshold for detecting the presence of the grating (Watson et al. 1980). In other words, an observer may reliably see the presence of a target but be wrong about the direction in which it is moving. Anecdotally, it is our impression that such perceptual misjudgments can easily occur when viewing the texture patterns used in the present study. In future studies, it will be of particular interest to use stimuli that are matched for equal detectability when making comparisons of perceptual discrimination or of neuronal tuning curves. Relevant to this is a striking illusion that was recently reported, in which the perceived direction of a bar moving against a textured background can deviate from its actual trajectory by up to 90° (Cormack et al. 1992). The illusion can plausibly be explained in relation to spatiotemporal filtering mechanisms discussed in the next section.

Relation to spatiotemporal filtering mechanisms

Ours is not the first study to provide evidence for cue dependence of direction selectivity in visual cortex. Hammond and Smith (1983) reported that many complex cells in V1 of the cat have a simple, unimodal directional tuning curve when tested with solid bars and with slowly moving texture bars, yet, when tested with rapidly moving texture bars, the same cells have bilobed tuning curves with preferred directions oblique to that for the solid bar. Movshon (cited in Hammond and Smith 1983) suggested that the change in directional tuning profile might simply reflect sensitivity for components of motion in the preferred direction and at the preferred speed by a conventional spatiotemporally tuned cell. However, this apparently cannot account for all of the findings of Hammond and Smith, because they reported bilobed tuning curves even when testing at the cell’s preferred speed.

A related set of issues arise in our experiments, because incoherent motion energy was distributed broadly in our displays, even though coherent motion of texture elements occurred in only a single direction in a given stimulus. To appreciate why there should be components of motion energy in many directions, consider the array position associated with a single texture element. On any given frame, the position of the element is randomly displaced from the intersection of row and column lines in the array. As a texture bar moves by, the texture element jumps to another random displacement, thereby simulating apparent motion of a single element in a random direction. Direction-selective neurons in V1 that have conventional spatiotemporal tuning would be responsive to small displacements of a texture element within their receptive fields. Hence the moving texture bar would activate a random subset of such neurons, representing a variety of preferred directions. A higher center such as MT getting inputs from such cells would receive conflicting signals in terms of the preferred directions of cells activated by different elements in the stimulus. Conflicting signals of this type may contribute to the reduction in direction selectivity seen for texture bars relative to solid bars. The fact that many MT neurons are nonetheless direction selective for texture bars suggests that there are mechanisms for integrating across space and taking advantage of either the progressive spatial sequence of frame-by-frame changes (cf. Mikami et al. 1986) or the coherent movement of nearby texture elements. However, this integration need not take place primarily or even exclusively within MT. Cells in V1 are strongly affected by patterns outside the classical receptive field (cf. Allman et al. 1990; DeYoe et al. 1986; Knerim and Van Essen 1992) and can show direction selective responses to moving texture bars akin to that documented in the present study (DeYoe et al. 1986; Van Essen et al. 1989). It may be that this type of processing is not restricted to any single area. Instead, it might take place at different spatial scales in different areas, and it might reflect the powerful feedback influences known to project from higher to lower areas.

Concluding remarks

The transition from bars and gratings to visual textures represents a large step upward in the intrinsic complexity of the stimuli used to study neural responses. Inherent in the notion of texture is the idea of fluctuations in the spatial luminance pattern that can only be analyzed statistically, rather than by tracking the exact positional relationships of every single feature. The present study adds to the growing knowledge about which of these statistical characteristics are important in determining neural responses in different
REFERENCES


TEXTURE RESPONSES IN MT


