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Neuronal responses to edges defined by luminance *vs.* temporal texture in macaque area V1

AVI CHAUDHURI AND THOMAS D. ALBRIGHT
The Salk Institute for Biological Studies, La Jolla

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Abstract

We examined the responsivity, orientation selectivity, and direction selectivity of a sample of neurons in cortical area V1 of the macaque using visual stimuli consisting of drifting oriented contours defined by each of two very different figural cues: luminance contrast and temporal texture. Comparisons of orientation and direction tuning elicited by the different cues were made in order to test the hypothesis that the neuronal representations of these parameters are form-cue invariant. The majority of the sampled cells responded to both stimulus types, although responses to temporal texture stimuli were generally weaker than those elicited by luminance-defined stimuli. Of those units exhibiting orientation selectivity when tested with the luminance-defined stimuli, more than half were also selective for the orientation of the temporal texture stimuli. There was close correspondence between the preferred orientations and tuning bandwidths revealed with the two stimulus types. Of those units exhibiting directional selectivity when tested with the luminance-defined stimuli, about two-thirds were also selective for the direction of the temporal texture stimuli. There was close correspondence between the preferred directions revealed with the two stimulus types, although bidirectional responses were somewhat more common when temporal texture stimuli were used. These results indicate that many V1 neurons encode orientation and direction of motion of retinal image features in a manner that is largely independent of whether the feature is defined by luminance or temporal texture contrast. These neurons may contribute to perceptual phenomena in which figural cue identity is disregarded.

Keywords: Contrast, Luminance, Flicker, Form-cue invariance, Neurophysiology

Introduction

The boundaries of objects in our visual world are generally distinguishable by spatial contrast along one or more physical dimensions, including brightness and spectral content of reflected light, texture, and distance from an observer. While the precise nature of the cue that defines a given object is crucial for generating surface representations and for object identification, there are a number of object qualities that possess no fixed relationship to the diverse sources of contrast that coincide with an object's boundaries in space. The way in which an object moves, for example, is a quality that is inherently unrelated to the sources of physical contrast that enable the object to be seen. A similar relationship holds for other object qualities such as size, location, and form. It follows that those visual system functions reliant upon such object-based qualities—motion detection, for example—must be sensitive to contrast along the multiple physical dimensions used for object definition, but they must also disregard this diversity of cues; for the nature of the cue is not pertinent to the task. In other words, because of the physical independence of cue type from certain object-based qualities, these qualities should be processed in a "form-cue invariant" fashion.

The most salient cue for figure/ground segregation is luminance (Koffka, 1935; Livingstone & Hubel, 1987) and this has served as the principal foundation for a number of theoretical approaches to spatial vision (e.g. Wilson & Bergen, 1979; Marr, 1982; Morrone & Burr, 1988). The identification of object boundaries based solely on chromatic variation can also be accomplished, although peculiarities such as transient fading and border instability are introduced (Krauskopf, 1967; Gregory, 1977). Spatial texture differences within localized regions of space can generate figure/ground separability as well (Beck, 1966; Julesz, 1981), which can be obtained with very brief presentation times, indicating that the task is preattentive (Bergen & Julesz, 1983). A powerful figural cue that emerges as a consequence of binocular vision is positional disparity between the retinal images in the two eyes. This cue is sufficient for extracting depth and shape from monocular retinal images, which are themselves devoid of any recognizable form (Julesz, 1971). Finally, and of most relevance for the present study, temporal variation or "temporal texture" differences across local regions of visual space are sufficient to elicit figure/ground segregation.

We sought to determine whether the early neural representations of certain object qualities—specifically, orientation and di-

Reprint requests to: Avi Chaudhuri, Department of Psychology, McGill University, 1205 Dr. Penfield Avenue, Montreal, QC H3A 1B1 Canada.

rection of motion—are invariant over changes in cue for figure/ground segregation. Recent psychophysical studies have shown that orientation (Regan, 1990) and shape discrimination (Regan & Hamstra, 1991) are similar for objects defined by luminance and temporal texture. Perceived motion is also qualitatively invariant for objects defined by many different figural cues (Julesz & Payne, 1968; Cavanagh & Mather, 1989; Victor & Conte, 1990; Stoner & Albright, 1992*a*). Further psychophysical evidence in support of this is provided by cross-cue interaction and adaptation effects among stimuli defined by different figural cues (e.g. Ramachandran et al., 1973*b*; Cavanagh, 1987; Cavanagh et al., 1989; Stoner & Albright, 1992*a*).

Despite the numerous and striking perceptual manifestations of form-cue invariant processing, neurophysiological investigations directly addressing the issue of form-cue invariant representations are relatively scarce. In one such study, Albright (1987, 1992) found that many neurons in the middle temporal visual area (MT) of the macaque were responsive to moving stimuli defined solely by either luminance contrast, temporal texture, or spatial texture. Most importantly, the majority of these neurons exhibited directional selectivity that was invariant over these different cues for figure/ground segregation. Albright and colleagues (Albright & Chaudhuri, 1989; Albright, 1992; Stoner & Albright, 1992*a*,*b*) noted that this form-cue invariance might develop either from convergence of cue-specific representations at the level of MT or at some earlier stage, such as primary visual cortex [striate cortex or V1]. Support for this hypothesis comes from a number of studies that collectively demonstrate a range of cue sensitivities in V1 (e.g. Poggio & Fischer, 1977; Gouras & Kruger, 1979; Livingstone & Hubel, 1984; Knierim & Van Essen, 1992), although rarely has cue invariant orientation/direction selectivity been a focus of investigation (but see Knierim & van Essen, 1992). To systematically explore the antecedents of the form-cue invariant directional selectivity seen in area MT and to address the more general issue of form-cue invariant contour representations, we have examined the possibility that the orientation and direction selectivity of V1 neurons is also invariant across a limited set of cues, specifically luminance contrast and temporal texture contrast. Our results support a scheme in which primitive representations of form are generated from multiple figure/ground cues as early as V1.

Methods

Subjects

Our subjects were two adult female rhesus monkeys (*Macaca mulatta*) of approximately 7.0 kg body weight. These animals were engaged in training or experimental sessions for no more than 5 days/week. To facilitate behavioral control, the animals were placed on a dietary regimen involving limited access to water during certain phases of training/testing. Following each training or experimental session monkeys were returned to their home cages, where they were given free access to monkey chow with fruit supplements. Body weight measurements, urine and blood chemistry analyses were performed on a regular schedule to monitor the health of each experimental animal. Monkeys were tested for myopia using standard optometric procedures and were found to have no significant refractive error.

All protocols for the use of animal subjects in these experiments have been reviewed and approved by the Salk Institute Animal Care and Use Committee and they conform to USDA regulations and NIH guidelines for the humane care and use of laboratory animals.

Surgical preparation and wound maintenance

After an initial period of acclimation to the primate chair and behavioral testing apparatus, monkeys were surgically prepared for fixation training and electrophysiological recording using conventional techniques (e.g. Albright, 1984; Dobkins & Albright, 1994). All surgical procedures were performed under strictly aseptic conditions using barbiturate anesthesia (sodium pentobarbital, 25 mg/kg i.v. initially, followed by continuous infusion of 3.5 mg/kg/h). Two weeks prior to the onset of formal fixation training, two stainless-steel recording cylinders and a post for head restraint were affixed to the skull with dental acrylic and stainless-steel screws. The cylinders were each aligned vertically, such that microelectrode penetrations were always parallel to the dorso-ventral stereotaxic axis. The cylinders were positioned bilaterally over the dorsolateral aspect of the occipital lobe and centered at approximately AP −16.0 mm and ML 15.0 mm. The cylinders were capped and the skin drawn up around the margin of the cranial implant. After healing, the cranial wound margin was treated daily for the duration of the experiment by removal of hair, cleansing with sterile saline, and by application of a topical antibiotic (Nitrofurazone, 0.2% in water soluble powder). A search coil for measuring eye position was surgically implanted in one eye using the method of Judge et al. (1980). The leads of the coil were soldered to a 2-pin mini connector (Powell Electronics, Irvine, CA) and affixed to the cranial implant with dental acrylic. Animals were given presurgical and postsurgical prophylactic antibiotics [During surgery: 30 mg/kg Keflin (Cephalothin Sodium), i.v., 3 times at 2-h intervals. Post-op: 25–50 mg/kg Keflex (Cephalexin), orally at 12-h intervals for 3 days] and postsurgical analgesics (Demerol, 1.5 mg/kg, 4 times daily for 2 days). The ophthalmic wound was treated daily for 3 days by application of an ophthalmic antibiotic (chloramphenicol, 1%).

After an appropriate fixation training period (criterion performance on visual fixation in the presence of visual testing stimuli—see below) and at least 2 weeks before the first neurophysiological recording session, the animal was again anesthetized and prepared for aseptic surgery in the same fashion as described above. One of the recording cylinders was opened and a 6-mm-diameter hole was drilled through the skull to accommodate an electrode trajectory aimed toward the region of cortex under study. Neurons in area V1 were recorded on both the dorsolateral and ventrolateral surfaces of the occipital lobe. To avoid trauma, the tip of the guide tube was only used to make a small opening in the dura, through which the microelectrode passed. The guide tube itself was not lowered into neural tissue. For ventral recordings, the guide tube was sometimes lowered through the dorsal operculum.

Behavioral training

Animals were trained to fixate a small (0.5-deg diameter) spot of light at a central location on the video display screen for periods of up to 3 s in duration. Behavioral control was achieved by administration of a small juice reward. This fixation training was carried out with the animal seated in a standard primate chair (Crist Instruments, Damascus, MD) in a quiet light-tight room facing the 60 cm distant video monitor. Head movements were prevented by bolting the implanted head-post to the frame of the primate chair. Performance on the fixation task was monitored by continuously recording eye position using the magnetic search-coil technique (Robinson, 1963). A 1 deg × 1 deg fixation window was centered on the point of ocular fixation. During each trial, eye position was constrained to this window, i.e. an eye movement that deviated

more than approximately 0.5 deg from the desired target of fixation was sufficient to abort the trial. Upon successful completion of a trial the animal was given a small juice reward. Initially, the fixation spot was simply a red square on a dark background. All aspects of data acquisition and behavioral control were managed by a PDP 11/73 computer, using software designed specifically for this purpose.

Visual stimulation

All visual stimuli were generated using a high-resolution graphics display controller (Pepper SGT, Number Nine Computer Corporation: 640 × 480 pixels, RGB analog outputs, 8 bits/gun, 60 Hz, noninterlaced) operating in an AT (80286) personal computer. Stimuli were displayed on a 19-inch analog RGB video monitor (NEC Multisync XL, phosphor B22) and were viewed at a distance of 60 cm from the nodal point of the eye. Photometric linearization tables were used to reform the highly nonlinear 8-bit voltage-luminance relationship (Watson et al., 1986). Movement was achieved by updating the position of a stimulus in synchrony with the vertical refresh of the display on alternate cycles (i.e. every 33.3 ms). This stimulus-generation computer operated under the charge of the PDP 11/73, which provided coded instructions for selection and timing of visual stimuli.

Once a neuron was isolated, the receptive field was mapped using a luminance-defined bar. The length, width, orientation, and position of this bar were under the experimenter's direct control using a joystick. Through this means we estimated receptive-field boundaries, optimal bar dimensions, as well as preferred speed and direction of motion. Following this preliminary assessment, the fixation target was repositioned such that the receptive field was located at the center of the video display. Each cell was then studied systematically using two types of visual stimuli (Fig. 1).

One stimulus was of a conventional type, which we will refer to as the *luminance* bar. This stimulus was "white" (30 cd/m^2, equal RGB activation) on a uniform black (0.5 cd/m^2) background (Michaelson contrast: 97%).

The second stimulus, which we will refer to as the *temporal texture* bar, was nearly identical to that used in our earlier neurophysiological (Albright, 1992) and psychophysical (Stoner & Albright, 1992*a*) studies of "form-cue invariant" motion processing. It was generated in the following fashion (see Figs. 1 and 2). The background was a static randomly textured pattern, which covered the full extent of the video display. Texture elements were white (equal RGB activations), element size was 0.067 deg (1 pixel), aspect ratio was square, and density was 50%. The local texture element brightness difference was constant across the display and the space-averaged luminance of the background was 15 cd/m^2. The foreground region of this display was, by contrast, a *dynamic* randomly textured pattern in a bar-shaped configuration. The spatial specifications of this foreground pattern (element size, density, etc.) were identical to those of the background. The dynamic quality of this foreground region was achieved by repetitively substituting a different random pattern (in synchrony with the vertical refresh of the video display on alternate cycles, i.e. 30 Hz). The position of the substituted pattern was shifted on successive frames to effect motion. This stimulus can also be described as a traveling square-wave of probabilistic (and nonrestorative) reversal of local element contrast. It gave the appearance of a smoothly drifting bar composed of "twinkling" or "flickering" dots moving across a static textured background. This type of stimulus is a form of "motion without correlation," as originally described by Sperling (1976) and subsequently referred to as moving "kinetic edges" (Anstis, 1980), " -motion" (Lelkens & Koenderink, 1984), "motion contrast" (Regan & Beverley, 1984), and "motion of successively generated subjective figures" (Petersik et al., 1978).

Of greatest significance for the present experiments is the fact that the space- and time-averaged luminance of the temporal texture stimulus was identical to the mean luminance of the background (i.e. 15 cd/m^2). As a consequence, there were no coherent or persistent luminance gradients that defined the foreground figure or its motion; it was detectable solely by relative temporal modulation or flicker. The absence of luminance variations between the temporal texture bar (foreground) and the static texture

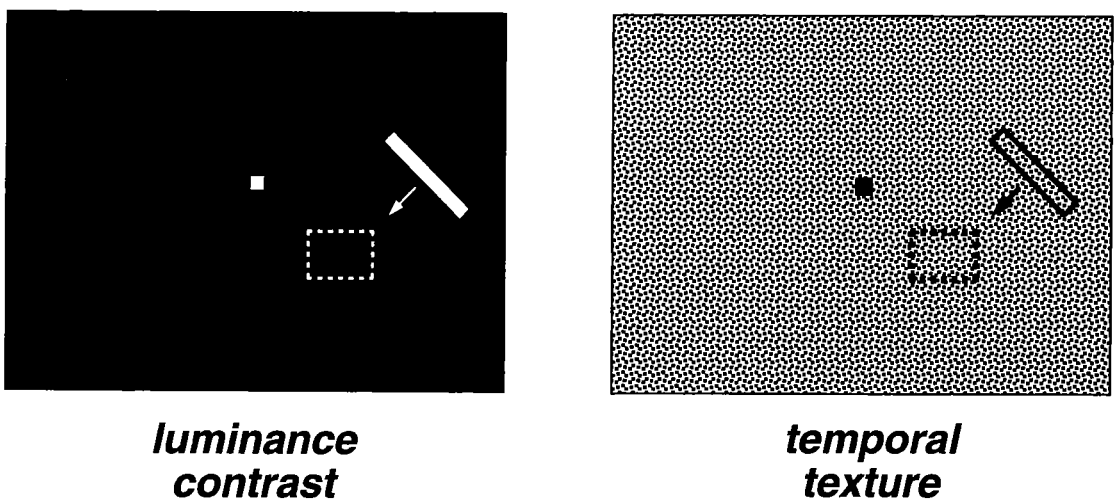


Fig. 1. Schematic depiction of luminance and temporal texture stimuli. After the monkey fixated the small square in the center of the screen, a luminance bar was used to map out the receptive field (dashed rectangle). During the recording sessions, the luminance and temporal texture bar was displayed along eight directions of motion centered on the receptive field.

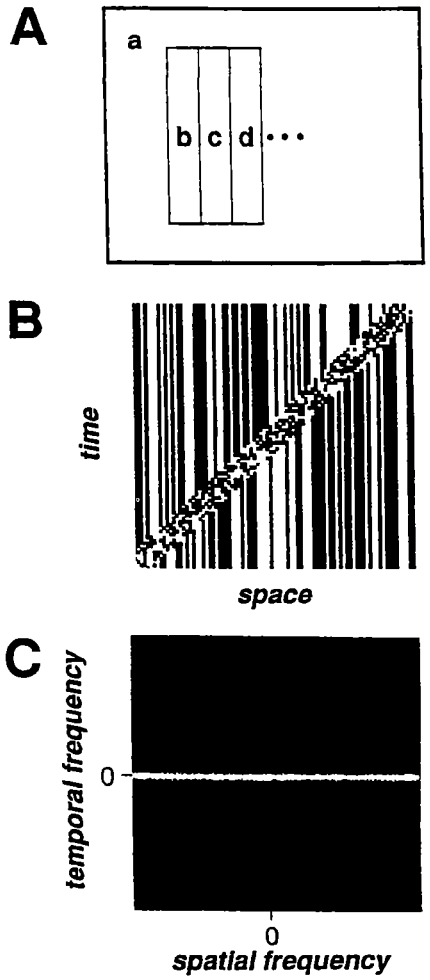


Fig. 2. The temporal texture stimulus was created by displacing a rectangular region of a random-dot pattern, where each pixel was randomly chosen to be black or white, in successive steps along a particular direction. At each step, the pattern within the rectangle is replaced by a new one (A); a stationary background is maintained at all times. A plot of the luminant energy as a function of space and time (B) shows the rightward-moving stimulus as a band of spatiotemporal noise. Spatiotemporal Fourier spectrum is broadband and devoid of any spatiotemporal frequency interaction which could be used to identify stimulus direction and speed (C). This stimulus has been referred to thus as non-Fourier motion (Chubb & Sperling, 1988).

background was verified using a standard spot photometer (United Detector Technology, Hawthorne, CA). Due to stochastic temporal fluctuations in the actual foreground ratio of black-to-white texture elements, small local space-time luminance variations occur. These random local variations, however, are devoid of spatiotemporal consistency and thus they surrender no information about the "global" motion of the foreground bar. Chubb and Sperling (1988) have applied the term "non-Fourier" to moving stimuli of this type since, in contrast to conventional motion of luminance-defined figures (such as the luminance bar used in these experiments), such motion cannot be characterized uniquely by its spatiotemporal Fourier power spectrum (Fig. 2). More generally, this stimulus is a member of the class of "second-order" motion stimuli described by Cavanagh and Mather (1989), which also includes those defined by stereoscopic and spatial texture cues.

Direction tuning for both luminance and temporal texture stimuli was assessed by sweeping these stimuli through the receptive field of each isolated neuron. The center of each sweep was located at the geometric center of the receptive field. Each of the two stimulus types was presented in eight different directions of motion with equal angular deviations between directions (45 deg). The same eight directions were used for all direction tuning assessments on all neurons. Each such assessment consisted of a series of five pseudorandomly interleaved presentations of each direction. The movement of each stimulus coincided with its appearance on the video display. Each sweep began and terminated at points outside of the classical receptive field (typically 5–10 deg beyond the receptive-field boundaries). The dimensions of the moving bar and its speed of movement were based upon values found to be optimal during preliminary hand-testing (see above). Sweep duration was constant at 2.0 s (accounting for small variations in angular sweep span that are associated with use of different sweep speeds). For each neuron, the characteristics of the luminance and temporal texture stimuli (dimensions, speed, timing, etc.) were identical in every respect, except for the obvious (and aforementioned) differences in their physical definition.

Electrophysiological recording and data analysis

Paralyene-coated tungsten microelectrodes (Frederick Haer, Brunswick, ME) with exposed tips of 10 μm or less were used to record extracellular potentials from single and multiple units. Electrodes were lowered into the brain through a stainless-steel guide tube by way of a hydraulic microdrive. The guide tube was lowered through the bone opening to penetrate the dura and the microelectrode passed down through the guide tube to the cortical area under investigation. The electrode, guide tube, and microdrive assembly were attached to the recording chamber by way of an X–Y stage (Kopf). Amplified spikes were determined to be arising from an isolated single neuron if they were of constant amplitude and waveform. Most neurons were studied until all relevant measurements were completed—typically less than 1 h. Measurements for some neurons were discontinued prematurely, however, because they became injured or poorly isolated during the course of testing.

The responses of each unit were fully characterized off-line. The responses obtained for different bar orientations were statistically evaluated by analysis of variance (ANOVA). For moving stimuli, the measure of response was the peak firing rate occurring during stimulus presentation. Direction-selective neurons were chosen from the sample that had significant ANOVA and direction-index values greater than 0.5. The strength of the relationship among the tuning curves obtained with the different sets of stimuli was evaluated by statistical correlation analysis. In addition to this direct correlational comparison of direction tuning curves across the different stimulus conditions, we used four standard measures to characterize responses and facilitate comparisons between stimulus types: (1) direction index, (2) direction tuning bandwidth, (3) preferred direction of motion, and (4) response magnitude. Direction index was computed as $[1 - (NPD/PD)]$, where PD is the firing rate of the neuron to motion of the bar along the preferred direction and NPD is the firing in response to motion along the nonpreferred direction. Computation of direction-tuning bandwidth and preferred direction of motion was preceded by fitting smooth functions to the direction-tuning data with an iterative least-squared residuals algorithm. As in our previous studies of MT direction tuning (Albright, 1984, 1992), the Gaussian model provided an excellent fit to nearly all direction-tuning data. For each

direction-tuning curve, the best-fitting Gaussian provided relatively unbiased estimates of the preferred direction of motion and the tuning bandwidth (obtainable from the mean and standard deviation of the fitted function, respectively). Response magnitude was computed as the difference between the maximum and minimum responses elicited by different directions of motion for a given stimulus type.

Results

We recorded from a total of 172 units in area V1 of two rhesus monkeys. From this sample, we were able to fully characterize the responses of 160 units to luminance and temporal texture stimuli. There were 53 units in this sample that were well isolated and considered to be single-unit responses; the remaining 107 units were composed of small multiple-unit clusters (2–3 units). We found no quantitative differences between the single- and multiple-unit samples with regard to our measures of orientation and direction selectivity and we have thus combined the results from the two samples for our statistical analyses. In our analysis of these data, we have focused on quantitative comparisons of responsivity and orientation/direction selectivity elicited by the two stimuli.

General properties

Our sample was restricted to neurons with receptive-field centers located within 5 deg of the center of gaze. Along every penetration, we encountered a restricted zone of high spontaneous activity, which occurred around the center of the region in which we were able to observe visually driven activity. We presume this to be the granular cell layer (layer 4C) (Dow, 1974) and we have used this as a criterion to distinguish and categorize the laminar position of sampled units as infragranular *versus* supragranular.

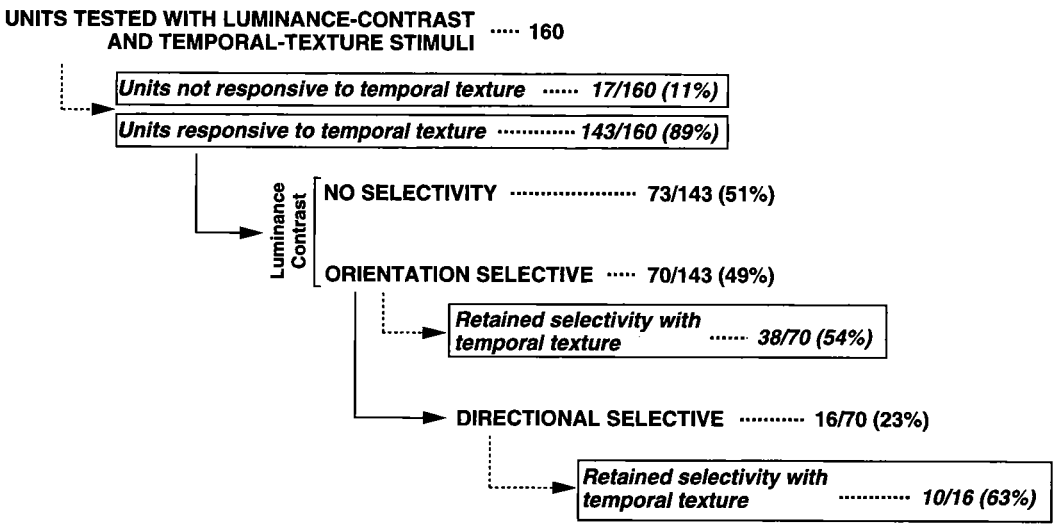
The general distribution of responses encountered in our sample is summarized in Table 1. We observed that a large majority (143/160; 89%) of the units could be activated by both luminance and temporal texture stimuli. Of those units that exhibited significant orientation selectivity when tested with the luminance bar (70/143; 49%), about one-half retained orientation selectivity when tested with the temporal texture bar. The remaining units were either unresponsive to the temporal texture stimulus or responsive to this stimulus but nonselective for its orientation. For a small number of units among those exhibiting significant orientation selectivity to both stimuli (7/70; 10%), we observed that the preferred orientation obtained using the temporal texture stimulus was shifted by as much as 90 deg relative to that obtained with the luminance contrast stimulus. Orientation tuning bandwidth was typically quite similar for the two stimuli, even for those units exhibiting a changed orientation preference.

The final category of cells was composed of those units that exhibited directionally selective responses to the luminance bar. These are indicated in Table 1 as a subset of the orientation selective sample (16/70; 23%). These units were identified as such on the basis of a criterion F value ($P < 0.05$) in an analysis of variance with direction being the measured variable. In general, we found few cells with moderate to high directional selectivity and only 10% of our total sample of 160 units had a directional index that met this criterion for the luminance bar. The responses could be broadly categorized into three types when tested for luminance contrast and temporal texture, as described in detail below.

Orientation selectivity for luminance versus temporal texture

We begin by examining the responses of those units that showed a large degree of orientation selectivity with the luminance contrast stimulus and compare their responses to the temporal texture bar. As noted in Table 1, more than half of the orientation selective cells (38/70; 54%) retained orientation selectivity when tested

Table 1. *Taxonomy of neurons within area V1 that show various properties when tested with luminance and temporal texture stimuli*[a]



[a]A large majority of our neuronal sample were responsive to the temporal texture bar. Several aspects of selectivity were then determined within this subpopulation, the results of which are displayed in this chart.

with stimuli generated using either cue. Data obtained from one unit that showed brisk responsiveness to a luminance contrast bar oriented along the 45 deg/225 deg axis is shown in Fig. 3. This unit retained orientation tuning with the same axial preference when tested with a bar generated by temporal texture. We did, however, detect a general elevation in the spontaneous firing rate, which we attribute to the presence of the textured background field. Although absolute firing rates to the two stimuli were of similar magnitude, the elevation of spontaneous activity resulted in a relative reduction in signal-to-noise for temporal texture stimuli. We found this to be a general feature of our results. The solid and dashed horizontal lines in the plot indicate the spontaneous activity in the presence of dark (luminance) and textured (temporal texture) backgrounds, respectively.

A similar proportion of units (32/70; 46%) failed to retain any discernible form of orientation tuning when tested with the temporal texture bar. In most cases, this loss was quite dramatic, as shown by the example in Fig. 4. This unit displayed a strong preference for a luminance contrast bar oriented along the 135 deg/315 deg axis. A moving bar defined by temporal texture, however, revealed no orientation preference; indeed this stimulus failed to elicit any significant response. As for the previous example, we did notice an increase in spontaneous activity associated with the presence of the textured background in the temporal texture condition.

Direction selectivity for luminance versus temporal texture

A subset of the orientation selective units (16/70; 23%) were found to exhibit significant directional selectivity when tested with luminance-defined stimuli. Among these, we were able to discern three types of responses to the temporal texture stimulus in roughly equal proportion. One set (5/16; 31% of units directionally selective for luminance bar) consisted of units that were responsive to both the luminance contrast and the temporal texture stimuli and, furthermore, displayed pronounced directional selectivity for both. An example of this is shown in Fig. 5. For this unit, the preferred direction of bar movement was to the right. Cells in this class were typically highly responsive to the luminance stimulus and less so to the temporal texture bar. Nevertheless, in this and all other such units, we observed that the preferred direction was invariant across the two stimuli used and accompanied by a similarity in the tuning bandwidths.

A second type of response (5/16; 31% of units directionally selective for luminance bar) was characterized by a loss of directional selectivity but maintenance of orientation selectivity when tested with the temporal texture stimulus. An example of this is shown in Fig. 6. Typically, such cells were quite responsive to the temporal texture bar. They were, however, far less discriminant in their responsivity to different orientations (compare cumulative

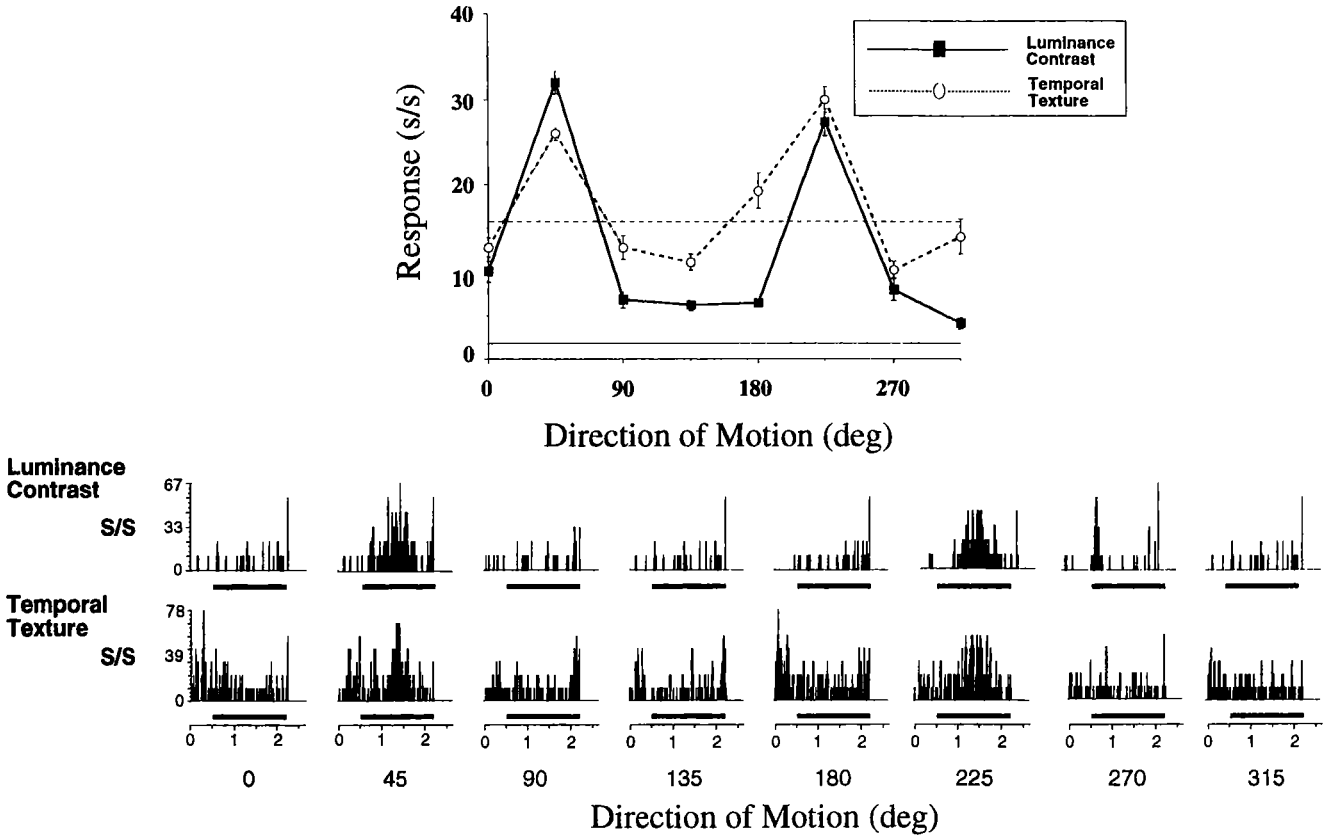


Fig. 3. Example of a V1 neuron that retained orientation selectivity when presented with temporal texture stimulus. This unit showed a strong preference for a moving luminance contrast bar oriented along the 45 deg/225 deg axis. When this stimulus was replaced with a moving bar generated by temporal texture, the unit showed the same orientation selectivity. A comparison of the background firing rates showed that spontaneous activity increased with the temporal texture stimulus, as indicated by the horizontal solid and dashed lines in the tuning curve and in the spike histograms. The bold lines under each histogram indicate the sweep duration of the stimulus.

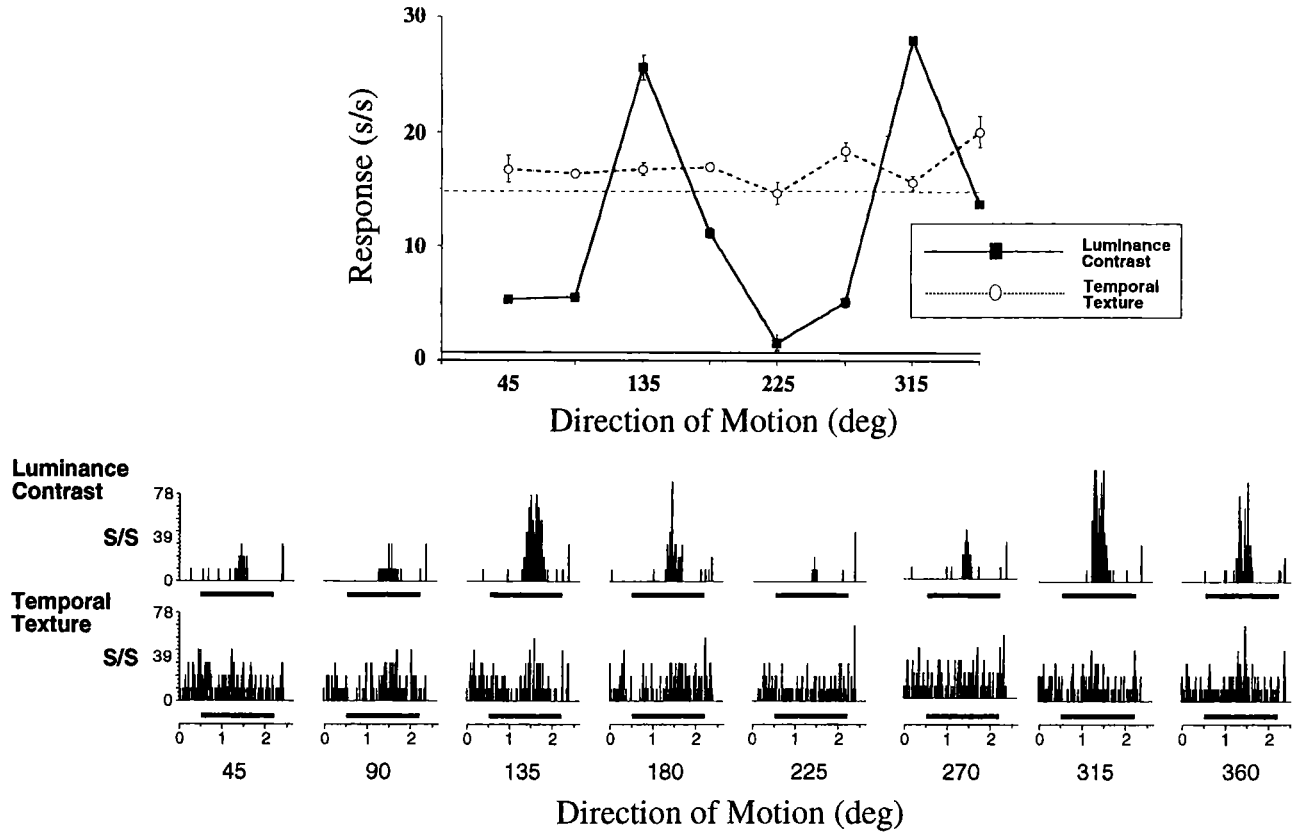


Fig. 4. Example of a V1 neuron that lost orientation selectivity when presented with temporal texture stimulus. The tuning curve for this unit shows a strong preference for a luminance contrast bar oriented along the 135 deg/315 deg axis. However, the unit failed to show selectivity for any orientation with a moving bar generated by temporal texture. Approximately one-half of the cells in our sample displayed this property. Histograms reveal the characteristically enhanced spontaneous firing rate seen with the temporal texture stimulus.

spike histograms in lower portion of Fig. 6) and, by definition, responses were nearly equal for optimally oriented stimuli moving in opposite directions.

A third type of response (6/16; 38% of units directionally selective for luminance bar) was characterized by pronounced directional selectivity for motion of the luminance bar but little or no selectivity for either direction or orientation when tested with the temporal texture stimulus. An example of this is shown in Fig. 7. This unit exhibited a peak directional response for luminance bar motion at 45 deg and a nearly uniform response at all other directions tested. Furthermore, it displayed a high firing rate at other directions of motion thereby producing a flat directional-tuning curve.

Statistical analyses

A quantification of the sample characteristics in this study has been approached with a number of measures. Because there is no unique measure of similarity in order to make the case for correlative responsiveness using multiple stimulus sets, we have made a general measure of similarity using criteria such as response magnitude, directional index, and tuning bandwidth with the understanding that each of these measures may be affected differently under the two conditions employed in this study.

Frequency histograms for directional index, tuning bandwidth, and neural responsiveness are shown in Fig. 8 for the luminance contrast and temporal texture. As Fig. 8a shows, the directional-index distribution obtained using the temporal texture stimulus tended to cluster more at the lower end (median = 0.177) when compared with the distribution obtained using the luminance stimulus (median = 0.194). However, a Median Test (Chao, 1974) showed that this difference was not statistically significant ($P < 0.05$). The tuning bandwidth distribution shown in Fig. 8b for our sample was obtained from Gaussian fits to the actual tuning curves of the cells. As this figure shows, the tuning bandwidth obtained with the temporal texture stimulus (median = 97.8 deg) tended to be larger on the whole than with the luminance stimulus (median = 87.5 deg). The Median Test also showed this difference not to be statistically significant ($P < 0.05$).

A histogram showing the distribution of angular differences between the preferred directions observed using the luminance contrast and temporal texture bar is shown in Fig. 9. As this figure illustrates, the directional differences tended to cluster around zero, with a slight bias toward negative angles (counterclockwise rotation of temporal texture direction tuning with respect to luminance contrast). The angular mean was −4.3 deg, a value that did not differ significantly from zero ($P < 0.0005$; V test of circular uniformity; Batschelet, 1965). Indeed 74% of our sample (28/38) exhibited a directional difference that was within 45 deg in either direction.

Finally, as an overall measure of the similarity between the tuning curves obtained with the two stimuli, we employed a statistical correlation test, as shown in Fig. 10. The variables in our case were the trial-by-trial responses obtained with the lu-

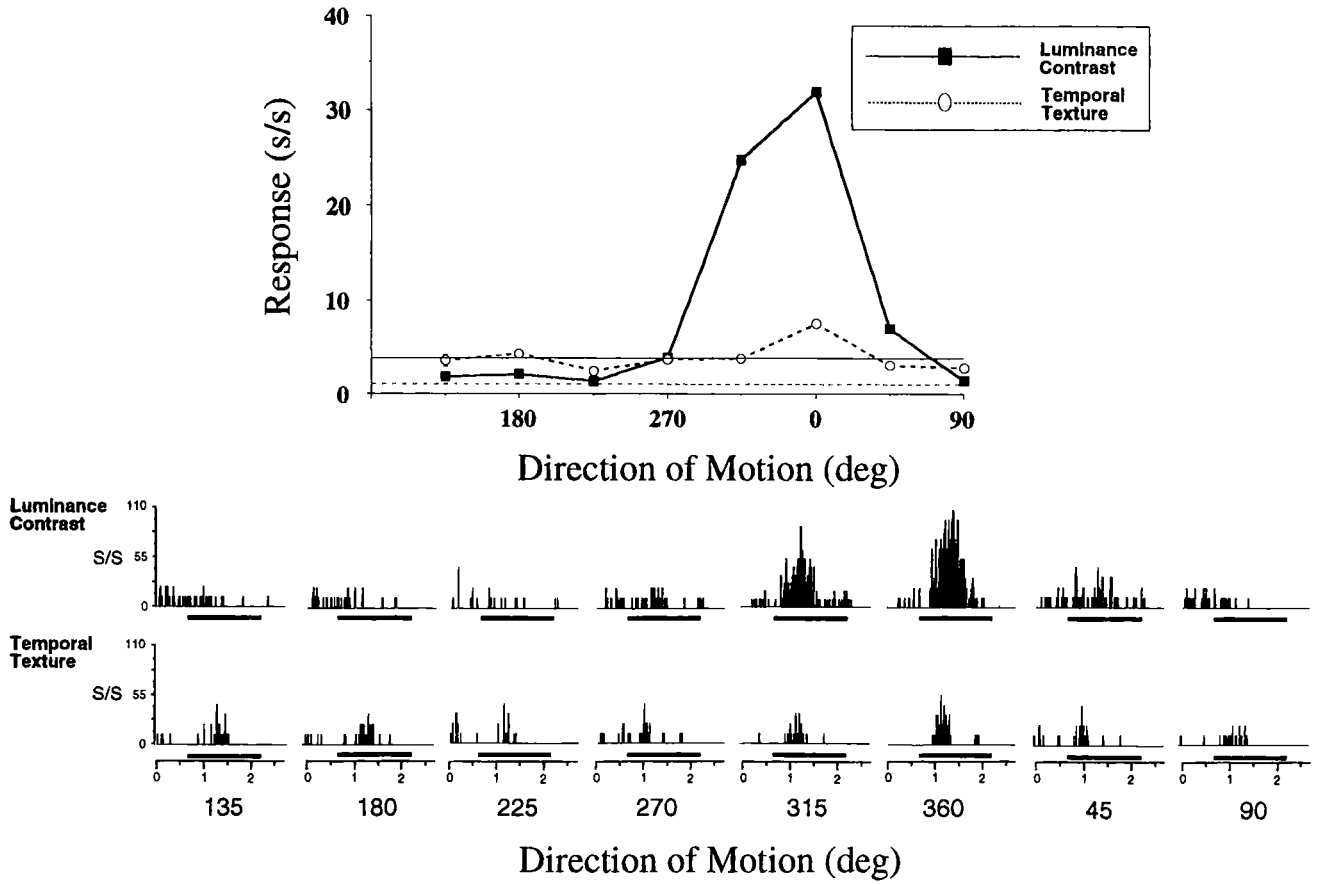


Fig. 5. Example of a V1 neuron that retained directional selectivity when presented with temporal texture stimulus. Spike histograms for eight different directions of motion show that this unit was maximally sensitive to bar motion at 360 deg, i.e. to the right. The directional selectivity, though somewhat reduced, was retained when the temporal texture stimulus was presented. About 1/3 of all directionally selective cells in our sample displayed this property. The horizontal solid and dashed lines in the tuning curve represent spontaneous firing with a black and textured background, respectively.

minance and temporal texture stimuli, paired by trial number, and direction of stimulus motion. For our sample size, a correlation coefficient value greater than 0.25 was indicative of a positive correlation at $P < 0.05$. As Fig. 10 shows, the tuning curves obtained with the two respective stimuli were statistically correlated for 28/132 (21%) of our units.

Relationship to conventional response types

We attempted to classify the units in our sample as simple or complex by examining the spike histograms for evidence of inhibitory flanking regions. In addition, we employed a narrow stationary bar flickering at 2 Hz at various locations in and around the receptive field to probe for evidence of an inhibitory response. Using both methods, we were able to reliably place half of the units in our sample into one or the other of the two categories. Although the highly directionally selective units tended to show properties associated with the simple cell type, we could not find any evidence for a simple/complex bias in units that retained selectivity with the temporal texture stimulus.

Discussion

The present experiments were designed to examine the neural bases of the perceptual phenomenon we have termed "form-cue invariance" (Albright, 1992). Using two markedly different figural cues (luminance and temporal texture), which can elicit qualitatively similar percepts of image contours, we have found that many neurons in area V1 of the macaque can be activated by stimulation with either. The existence of V1 neurons showing such similarities demonstrates that the earliest neuronal representation of image contours disregards some figural cue diversity in a manner that mirrors the qualitative perceptual invariance.

In the remainder of this discussion we will consider (1) the relationship between these results and those of previous studies of orientation/direction selectivity in macaque V1, (2) the generality of the phenomenon of form-cue invariance and evidence for its neural origins, (3) evidence for neuronal form-cue invariance in other cortical regions, (4) the concept of perceptual/neuronal "contrast equivalence" for physically nonequivalent contrast dimensions, and (5) the significance of neuronal form-cue invariance for visual perception.

Comparison with previous studies of orientational and directional selectivity in area V1

The earliest site at which orientation selectivity appears in the monkey is cortical area V1 (Hubel & Wiesel, 1968). On the whole, V1 neurons exhibit significant variability in the strength of their orientation selectivity, as made manifest by the breadth of orien-

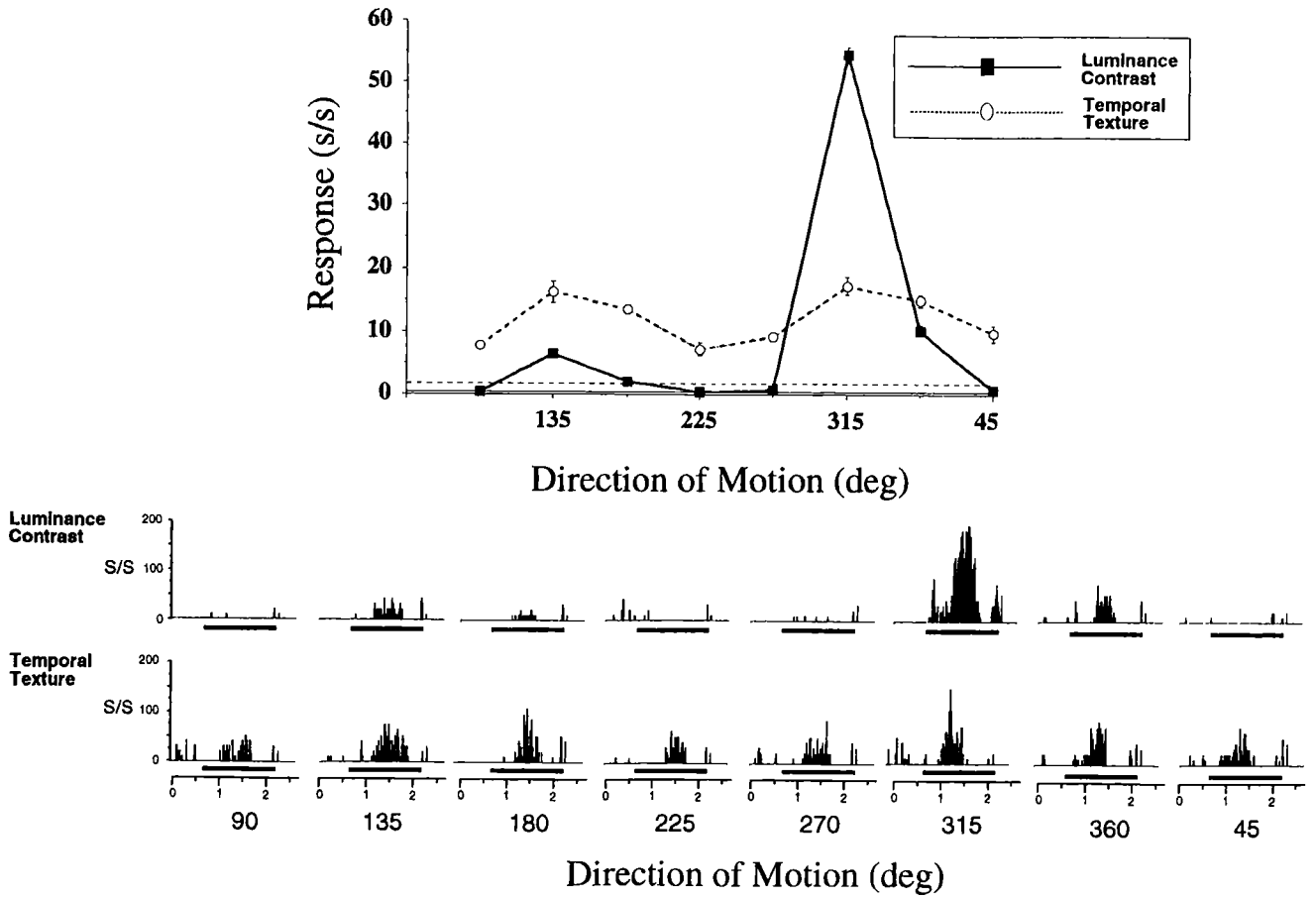


Fig. 6. Example of a V1 neuron that lost directional selectivity when presented with temporal texture stimulus. This unit was directionally selective when tested with the luminance bar, preferring motion at 315 deg. The directional bias was lost when the unit was tested with the temporal texture bar. Nevertheless, the unit maintained some selectivity for the orientation of the stimulus. About 1/3 of the directional selective units in our sample displayed this property.

tation tuning seen upon stimulation with high-contrast luminance-defined stimuli (Schiller et al., 1976*b*; DeValois et al., 1982; Albright, 1984; Parker & Hawken, 1988; Vogels & Orban, 1991). In agreement with these earlier studies, we have observed considerable variability in orientation tuning amongst our sample of V1 neurons tested with luminance-defined stimuli, ranging from sharply tuned cells to nonoriented units. Nonetheless, more than half of our oriented units were capable of encoding stimulus orientation in a form-cue invariant fashion.

Cortical area V1 is also the first site in the primate geniculostriate pathway where directionally selective neurons are found (Hubel & Wiesel, 1968). As for orientation selectivity, reports of the incidence of such cells vary (in all cases assessed with high-contrast luminance-defined stimuli). While our present estimate of the incidence of directionally selective cells (11% of all sampled cells; 23% of orientation selective) is lower than most previous reports (e.g. Schiller et al., 1976*a*; DeValois et al., 1982; Albright, 1984; Orban et al., 1986; Hawken et al., 1988) this can be attributed to differences in classification criteria as well as differences between experimental conditions. In any event, the notable and novel feature of our results bearing on directional selectivity is the fact that 63% of those found selective using luminance-defined stimuli retained similar selectivity when tested using stimuli defined by temporal texture.

The majority of directionally selective neurons in V1 have been found in layers 4b and 6 (Hubel & Wiesel, 1968; Dow, 1974; Orban et al., 1986; Hawken et al. 1988); layer 6 reportedly contains the highest proportion of neurons (72%) with a directional bias (Hawken et al., 1988). Although we did not conduct a thorough laminar analysis of recording sites, our finding that the majority of directionally selective cells were located in the lower cortical layers just prior to entering the white matter is in agreement with these previous studies. It is, moreover, consistent with the possibility that these cells were among those projecting to area MT (Lund et al., 1975)—a prospect of considerable relevance to our understanding of the mechanisms underlying form-cue invariant motion processing in area MT (Albright, 1987, 1992; see below).

Generality and neural origin of form-cue invariance

The diversity of figural cues that can define features of our visual world requires a diversity of neuronal mechanisms for their detection. Traditional views of the functions of primary visual cortex have emphasized the encoding of luminance-defined image features (e.g. Hubel & Wiesel, 1968), and there exists imposing and incontrovertible evidence for the existence of orientation detectors of this sort. Novel findings of the present study include the dem-

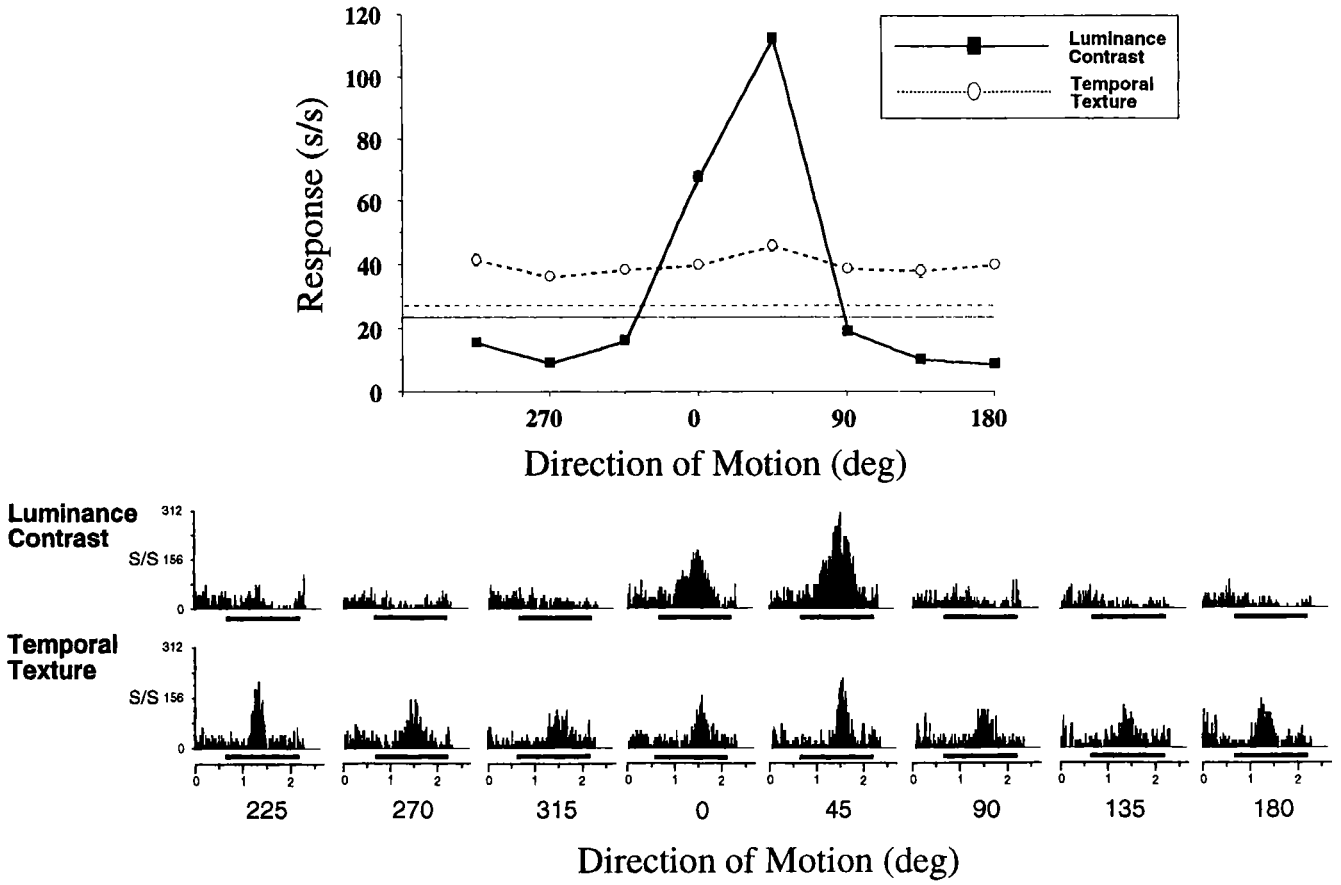


Fig. 7. Example of a V1 neuron that lost all selectivity when presented with temporal texture stimulus. This unit was highly selective for motion at 45 deg and displayed inhibition along most other directions of motion. Although the unit was responsive to the temporal texture bar, it lost all directional and orientation selectivity. About 1/3 of the directional selective units in our sample displayed this property.

onstration that (1) many V1 neurons serve as detectors for contours defined by temporal texture, and (2) these same neurons serve double-duty by detecting luminance-defined features as well. In other words, our results indicate that the valued and anticipated form-cue invariant contour representations may be present as early as area V1.

While the present study constitutes the first quantitative comparison of the responsivity/selectivity of V1 neurons to visual stimuli defined by luminance and temporal texture contrast, there have been numerous previous demonstrations that primate V1 neurons are sensitive to image variation along dimensions other than luminance contrast—a point of relevance for understanding the generality of form-cue invariance. These studies have employed figural cues such as spatial texture (Knierim & Van Essen, 1992), binocular disparity (Poggio & Fischer, 1977; Poggio et al., 1988), color (Gouras, 1974; Michael, 1978; Gouras & Kruger, 1979; Livingstone & Hubel, 1984; Vautin & Dow, 1985; Ts'o & Gilbert, 1988; Lennie et al., 1990), and illusory contours (von der Heydt & Peterhans, 1989; Grosof et al., 1993). In no case, however, have individual V1 neurons been tested for orientation/direction selectivity using more than a small subset of the potential figural cues. It would thus be premature to conclude that any single V1 neuron possesses more than a "limited" form-cue invariance. Nevertheless, in view of the computational appeal of form-cue invariance, the adaptive value that might be afforded by a truly form-cue invariant system, and psychophysical evidence bearing upon the issue (see below), it is tempting to speculate that some V1 neurons are capable of encoding orientation across a broad range of figural cues. It now becomes fitting to determine the levels of the visual system at which the individual cue contrasts are first detected.

As suggested by Chubb and Sperling (1988), "non-Fourier" temporal texture stimuli, of the sort used in the present experiment, could easily be detected using a mechanism that relies upon rectification of temporally modulated luminance inputs—a flicker detector, in other words. Indeed, some evidence indicates that this hypothesized nonlinearity forces a partial equivalence of temporal texture and luminance contrast as early as the magnocellular laminae of the LGN (Derrington & Lennie, 1984). This being the case, our demonstration of invariance for these two cues at the level of V1 should come as no great surprise. Some of the other potential figural cues may require more complicated mechanisms for their detection, however, and would not be expected to be represented in the LGN. Contours defined by stereoscopic disparity, for example, cannot not be detected prior to binocular convergence and "subjective contours" require preliminary extraction of "real" contours and are not found until areas V1/V2 (von der Heydt & Peterhans, 1989; Grosof et al., 1993).

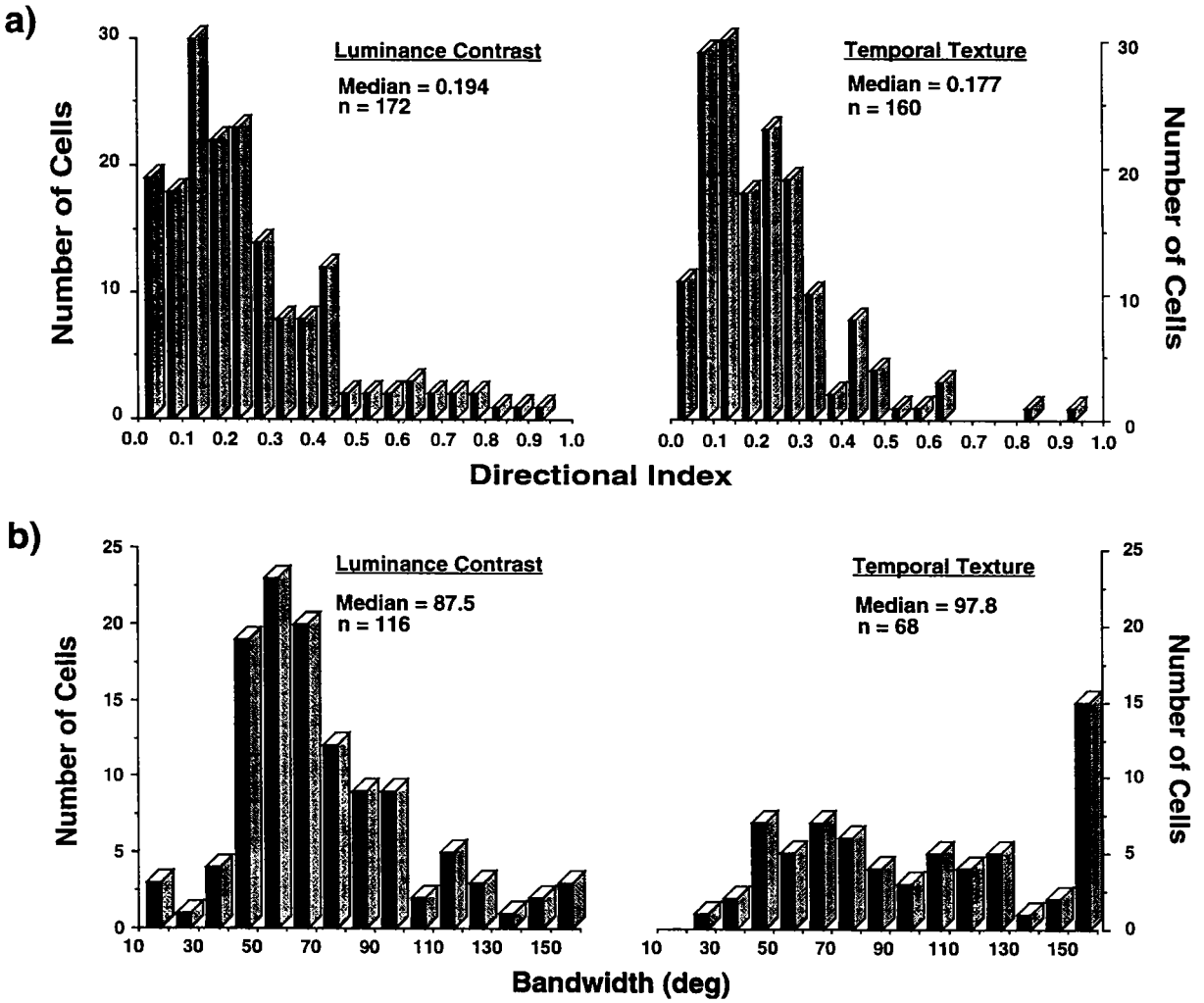


Fig. 8. Frequency histograms of the striate cortex sample using several criteria. The directional index distribution (a) was found to be more compressed toward the lower end with the temporal texture bar than with the luminance stimulus. The bandwidth (b), which was taken from Gaussian fits to the tuning curves, showed a narrower tuning for the luminance stimulus.

Form-cue invariance beyond area V1

As we have emphasized, the motion of an object is a quality that is inherently independent of the other cues that enable the object to be seen. Our perceptual experience of object motion is, accordingly, qualitatively invariant across a variety of figural cues (e.g. Julesz & Payne, 1968; Sperling, 1976; Cavanagh & Mather, 1989; Stoner & Albright, 1992*a*). Neurophysiological evidence that cortical motion detectors discard form-cue identity was first reported by Albright (1987, 1992). Many MT neurons were shown to exhibit similar direction tuning for moving contours defined solely by either spatial texture, temporal texture, or luminance contrast. In addition, some MT neurons are directionally selective for stimuli defined solely by chromatic contrast (Saito et al., 1989; Charles & Logothetis, 1989; Dobkins & Albright, 1994; Gegenfurtner et al., 1994). In view of the evidence indicating that area MT is an important component of the neural substrate for motion perception (see Albright, 1993, for review), it seems likely that form-cue invariant directional selectivity among MT neurons contributes to the corresponding perceptual invariance for motion. While the origin of form-cue invariance in area MT is unknown, it could arise by virtue of neuronal inputs from V1 that are themselves form-cue invariant (Albright, 1992). The present results, in combination with others of a similar nature, support this general hypothesis.

Form-cue invariance may well be important for visual functions in addition to motion processing. The identity of a figural cue is a manifestation of the surface properties of the object giving rise to the cue. Because object recognition can often take place in the absence of information about surface properties, i.e. on the basis of image contours alone, we infer that the neuronal mechanisms subserving object recognition express some form-cue invariance. Consistent with this hypothesis, Logothetis and Charles (1990) have reported that cells in area V4—a central component of the ventral cortical stream thought to play an important role in form vision—exhibit orientation tuning that is similar for temporal texture and luminance-defined stimuli. As for MT, this extrastriate form-cue invariance may prove traceable to the invariance we have seen at the level of striate cortex.

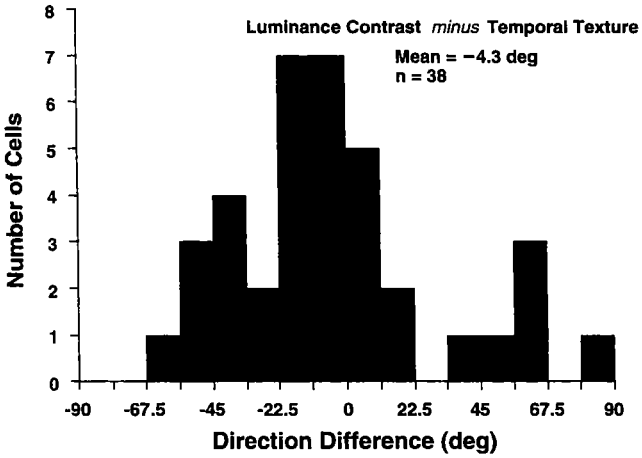


Fig. 9. Quantitative comparison of orientation tuning in the striate cortex to stimuli generated by luminance contrast and temporal texture. The histogram shows the distribution of angular differences between the preferred orientation or direction of units tested with a luminance contrast bar and then tested with one generated by temporal texture. The sample mean did not differ from zero (angular mean = −4.3 deg; $P < 0.0005$; $n = 38$; V test of circular uniformity).

Contrast equivalence

Contrast, as used in the sense described herein, refers to a physical difference in the nature of illumination falling upon spatially juxtaposed regions of the retinal surface. Two points should be borne in mind when considering mechanisms and implications of form-cue invariance. First, contrast is a measurable quantity of continuous variation, i.e. contrast has magnitude. Second, contrast may vary along multiple dimensions—luminance and temporal texture, for example—that are physically independent. Despite this independence, the fact of form-cue invariance implies the existence of a processing stage at which different contrast representations are perceptually and neuronally equivalent. This being the case, we may conclude that the different scalar dimensions of luminance and temporal texture are normalized with respect to one another such that specific paired quantities of each are of *equivalent contrast*. Perceptually, we might expect such stimuli to be of equal salience, as manifest by equivalent thresholds for detection. Regan and Beverley (1984) demonstrated the feasibility of obtaining such threshold measurements for stimuli similar to those used in the present experiments. More recently, Stoner and Albright (1992*a*) obtained direct estimates of perceptual contrast equivalence for luminance and temporal texture using a motion coherence paradigm. Although differences in task demands and stimulus configurations place some limits on the generalizability of these measurements to the present experimental conditions, results suggest that the equivalent luminance contrast for our temporal texture stimulus is relatively low (<10%). The luminance contrast used in the present experiment was, by comparison, rather high (97%). This fits well with the claim, made by most observers, that the temporal texture contours are simply harder to see than those defined by high-contrast luminance differences.

We might expect substantial quantitative differences in perceptual salience to be mirrored by differences in neuronal responsivity/selectivity. Indeed, in every instance we found the responses to temporal texture stimuli to be weaker than those to luminance-defined stimuli. Moreover, nearly one-third of the neurons in our sample expressing directional selectivity when tested with luminance-defined stimuli became bi-directional when tested with temporal texture. These two characteristic differences—weaker responsivity and weaker directionality for temporal texture versus luminance-defined stimuli—have also been reported for MT neurons studied under similar conditions (Albright, 1992; Olavarria et al., 1992). The possibility that these differences underlie differences in perceptual salience is supported by the fact that similar effects can be observed (in V1 and MT) by simply reducing the contrast of a luminance-defined stimulus, hence making it less salient (Sclar et al., 1990; Chaudhuri & Albright, unpublished data).

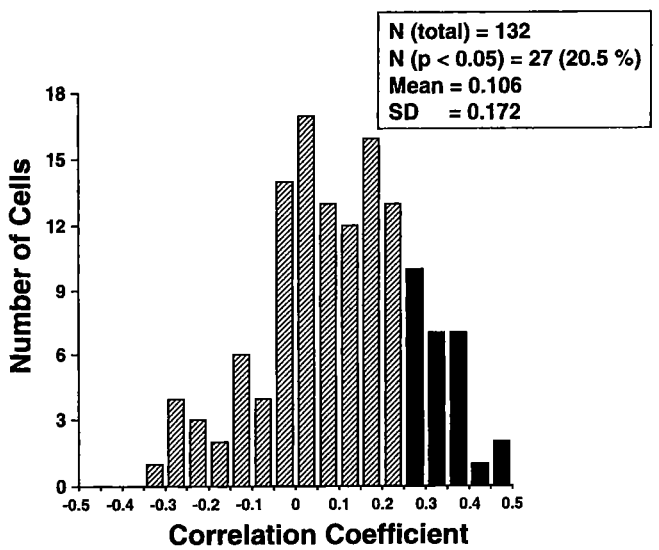


Fig. 10. Correlation coefficients for tuning curves obtained with the luminance and temporal texture bars. Correlation coefficient values above 0.25 indicate significant correlation ($P < 0.05$) among the luminance and temporal texture tuning curves. About 20% of the cells in our sample fell in this category.

Perceptual significance of neuronal form-cue invariance

There are several well-documented perceptual phenomena that would appear to be manifestations an early cue-invariant representation of image contours. For example, Regan (1989) compared orientation discrimination thresholds of human observers for luminance- and motion-defined contours (the latter are similar in critical respects to the temporal texture stimuli used in the present experiments) and found little difference—a result that agrees well with our finding of similar V1 orientation tuning for luminance and temporal texture stimuli. Similarly, shape (Regan & Beverley, 1984; Regan & Hamstra, 1991) and width (Shimojo et al., 1987) discrimination thresholds are alike for luminance- and motion-defined patterns. The qualitative form-cue invariance of human motion detection has also long been appreciated (e.g. Julesz & Payne, 1968; Sperling, 1976; Ramachandran et al., 1973*a*; Anstis, 1980; Cavanagh & Mather, 1989) and, as indicated above, may be attributable to neuronal cue-invariance in areas MT (Albright, 1992) and V1.

Evidence for form-cue invariance extends to other, more complex, perceptual constructs as well. Stoner and Albright (1992*a*) have shown that one-dimensional motion signals arising from multiple contours defined by different form-cues (luminance and

temporal texture in their experiments) are combined to render two-dimensional pattern motion using the same "rules" that govern same-cue combinations (Adelson & Movshon, 1982). Cavanagh (1987) found evidence for yet another type of form-cue invariant "featural integration"—pooling of image features defined by different cues—in perception of perspective. The evidence for form-cue invariance in stereopsis is mixed. Cavanagh (1987) reported that no depth was perceived when different form-cues were used in each eye, whereas Ramachandran et al. (1973*b*) reported that a luminance border from one eye can be fused with a disparate chromatic or texture border from the other eye.

For some perceptual tasks, form-cue identity is clearly important. As mentioned previously, form-cue identity is a direct reflection of the surface properties of the object giving rise to the cue and, by this means, can exert a direct influence over perceptual interpretation of image features. The perception of shape from shading and surface relief defined by shadows offers an illustrative example. By nature and definition, shading is a luminance-based indicant of surface properties. Perceptions of three-dimensional shape and surface relief disappear completely when cues other than luminance contrast (e.g. temporal texture or chrominance) are used to indicate shading (Cavanagh & Leclerc, 1989). The lack of perceptual form-cue invariance in this instance is not surprising since the information provided by luminance is specific to luminance. Perception of three-dimensional shape or surface relief from nonluminance cues is simply not consistent with the real world and form-cue invariance in those cases would generate spurious percepts. The computational economy afforded by form-cue invariance has apparently been weighed against veridicality in determining which perceptual tasks can operate on generalized featural information.

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