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Neural correlates of boundary perception

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Abstract

The responses of neurons in areas V1 (17) and V2 (18) of anesthetized and paralyzed rhesus monkeys and cats were recorded while presenting a set of computer-generated visual stimuli that varied in pattern, texture, luminance, and contrast. We find that a class of extrastriate cortical cells in cats and monkeys can signal the presence of boundaries regardless of the cue or cues that define the boundaries. These cue-invariant (CI) cells were rare in area V1 but easily found in V2. CI cortical cells responded more strongly to more salient boundaries regardless of the cue defining the boundaries. Many CI cortical cells responded to illusory contours and exhibited the same degree of orientation and direction selectivity when tested with boundaries defined by different cues. These cells have significant computational power inherent in their receptive fields since they were able to generalize across stimuli and integrate multiple cues simultaneously in order to signal boundaries. Cells in higher order cortical areas such as MT (Albright, 1992), MST (Geesaman & Anderson, 1996), and IT (Sary et al., 1993) have previously been reported to respond in a cue invariant fashion. The present results suggest that the ability to respond to boundaries in a cue-invariant manner originates at relatively early stages of cortical processing.

Keywords: Cue invariant, Visual perception, Monkey, Extrastriate cortex

Introduction

The perception of boundaries relies on many visual cues in addition to luminance. Recent computational theories suggest that the visual system must extract information about boundaries from differences in cues such as color, motion, texture, perspective, and shading (Brady & Grimson, 1981; Grossberg, 1994) regardless of whether luminance differences exist or not. Information from these different attributes are combined by the visual system in order to localize boundaries. In fact, psychophysical studies indicate that boundary localization is more precise when multiple attributes are combined at a common site prior to making the decision to localize a boundary (Rivest & Cavanagh, 1996). Indeed, the strategy underlying camouflage is to minimize the number of visual cues that distinguish an organism from its environment. Chameleons sitting on branches, hunters, and camouflaged soldiers all employ this strategy.

The purpose of this study was to determine if certain classes of cells in cortical areas V1 and V2 of cats and monkeys can detect and/or combine multiple visual cues in order to signal the presence of a boundary (see Methods for our classification of these cue-invariant cells). Indeed, it has already been shown that cells in monkey area V2 respond to illusory contours (ICs) (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989). Even in V1 some cells are reported to respond to ICs (Redies et al., 1986; Grosof et al., 1993) and to be cue invariant (Zipser et al., 1996). Cue-invariant (CI) cells have also been reported to exist in higher order cortical areas such as MT (Albright, 1992), MST (Geesaman & Anderson, 1996), and IT (Sary et al., 1993). The first level within the visual pathways at which the ability to respond in a cue-invariant fashion arises is not clear. The results presented here indicate that such cells exist in cortical area V2 and to, a lesser extent, in area V1. CI cells in these two lower order cortical areas are likely to represent the first stage of cue-invariant boundary perception.

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Methods

Physiological recording procedures

Cats and monkeys were prepared for electrophysiological recording as described previously (Leventhal et al., 1995). Subjects were sedated with Ketamine HCl (Ketalar; Parke-Davis, Berlin, Germany) and then anesthetized with halothane (2%) (Fluothane; Ayerst Laboratories, La Jolla, CA) in a 70:30 mixture of N_2O:O_2. Intravenous and tracheal cannulae were inserted. Animals were placed in a stereotaxic apparatus, and all pressure points and incisions were infiltrated with a long-acting anesthetic (1% lidocaine HCl; Elkins-Sinn, Cherry Hill, NJ). A mixture of *d*-tubocurarine (0.4 mg/kg/h; Abbott Laboratories, North Chicago, USA) and gallamine triethiodide (7 mg/kg/h; Sigma Chemical Company, St. Louis,

MO) was infused intravenously to induce and maintain paralysis. Animals were ventilated and anesthesia was maintained with a mixture of nitrous oxide (75%), oxygen (25%), and halothane (0.5–1%) as needed. Expired pCO_2 was maintained at approximately 4%. Body temperature was maintained at 38°C. Heart rate and EEG were monitored throughout the experiment to assess the level of anesthesia.

A cylindrical chamber was positioned over a craniotomy above area V1 or V2, filled with a 4% solution of agar in saline and sealed with wax. The eyes were protected from desiccation with contact lenses. When necessary, spectacle lenses and artificial pupils (3 mm in diameter) were used to focus the eyes on a tangent screen positioned 114 cm (cat) or 228 cm (monkey) from the retina. The optic discs, blood vessel patterns, and central areas were visualized directly by back-projections of the retina onto the tangent screen. These projections were determined repeatedly during the course of each recording session and were used to determine the positions of the central area (Fernald & Chase, 1971).

Receptive-field mapping procedures

Extracellular action potentials of isolated cortical cells were recorded with tungsten microelectrodes or microcapillary glass electrodes containing 4 M NaCl. Impedances were approximately 2–5 MΩ. The electrode was advanced using a hydraulic microdrive (Kopf) and was moved 75 to 150 μm between units to reduce sampling bias and to record from a large region of cortex in each animal. Cells in areas V1 and V2 of cats and monkeys were recorded from the cortical representations of the central and paracentral regions of the visual field.

Visual stimuli were generated on a Tektronix (Beaverton, Oregon) 608 display driven by a Picasso (Cambridge, MA) image synthesizer. The Picasso was controlled by computer in conjunction with a specially designed hardware and software package developed by Cambridge Electronics Design, Ltd. (Cambridge, England). Our system is able to randomly generate a broad spectrum of visual stimuli under computer control, collect the data, and perform on-line statistical analyses. The oscilloscope display was mounted on an apparatus which allowed it to be moved to any point in the animal's visual field while at the same time maintaining a fixed distance between the display and the animal's retina. In experiments employing cats, the center of the display screen was always 57 cm from the animal's retina. In experiments employing monkeys, the display was 171 cm from the animal's retina. The different distances were required because the receptive fields of monkey cells are much smaller than those of cat cells.

The eccentricity of each cell's receptive field was defined as the distance from the center of the receptive field (determined by presenting stimuli to the dominant eye) to the projection of the central area for that eye. For all units studied, the most recent determinations of the projections of the optic disks (Fernald & Chase, 1971) and central area (Pettigrew et al., 1979) were used to determine eccentricity. Since receptive fields were first plotted on a tangent screen, appropriate corrections were made for all receptive fields to convert receptive-field size and distance from the projections of the central area to degrees of retinal angle. Receptive-field size was defined as the minimum response field using the method of Barlow et al. (1967). The calibrations on our optical display apparatus provided a means of determining each unit's eccentricity and receptive-field size directly since the center of the display was always the same distance from the animals' retina regardless of the region of the visual field being studied.

Procedures for the generation of visual stimuli

The visual stimuli in this study included computer generated isoluminant grating-induced boundaries (GIBs, as in Figs. 1, 5, and 6), isoluminant texture-induced boundaries (TIBs, Figs. 1, 5, and 6), isoluminant motion-induced boundaries (MIBs are boundaries defined by coherently moving texture elements within a field of identical texture elements [Fig. 5A]), illusory contours (ICs) induced at the border of two square-wave gratings differing only in spatial phase as well as luminance induced boundaries (LIBs) such as drifting sinusoidal gratings, spots, and bars. Descriptions of how various types of boundaries producing stimuli are defined can be found in Cavanagh and Mather (1989; motion) and Bergen (1991; texture). At maximum contrast, the luminance of the light bars presented was 8.37 cd/m^2 and the luminance of the dark bars presented was 0.91 cd/m^2. Colored stimuli were generated using the foregoing procedures in conjunction with appropriate Kodak wratten filters (red, green, blue, and yellow). In this study, wavelength selectivity was only studied qualitatively in order to determine whether the CI cells studied quantitatively were wavelength sensitive. The display was calibrated at the start of all experiments. This was done using Cambridge electronics software in order to assure stimulus clarity, size, centering, and timing. Luminance was measured using a Tektronix J17 lumacolor photometer to assure that the stimuli were comparable across studies.

Orientation and direction sensitivity

The physiological orientation and direction biases of cortical cells were studied quantitatively. The orientation of each boundary was orthogonal to its direction of motion (the orientation is 90 deg less than the direction). Initially, 15 presentations of moving sinusoidal gratings (temporal frequency of 2–4 Hz) at each of 24 to 36 randomly generated orientations from 0 deg to 360 deg were used to compile the orientation tuning curves for the cells studied. The spatial-frequency tuning of the cells was studied using optimally oriented stimuli. The orientation biases of the cells were then studied at spatial frequencies close to both the cell's optimal and cutoff spatial frequencies. The various orientations and spatial frequencies were presented to the cell in random order to reduce sampling bias. The length and width of the stimulus used was the one judged optimal for the cell. The temporal frequency employed was also the one judged optimal for the unit. After determining the cell's orientation and direction selectivity using sinusoidal gratings, the orientation and direction selectivities were tested again for GIBs, MIBs, TIBs, and ICs of comparable length, width, and velocities. Cells were judged to be cue invariant only if they exhibited the same orientation and direction preferences to these stimuli as they did to sinusoidal gratings. Only cells that were judged to be cue invariant were tested further.

The responses of the cells to the visual stimuli presented were stored to disk for later analysis. The responses to the sinusoidal gratings were defined as the amplitude of the fundamental Fourier component of the poststimulus time histogram. For the maps employing nonsinusoidal stimuli, the responses were defined as the peak response of the poststimulus time histogram. The total analysis time after stimulus onset was 150–300 ms depending upon the time course of the visually evoked response. Background activity was subtracted in order to study the strength of the evoked response.

The orientation and direction preferences and sensitivities were calculated for each cell using the statistical methods described in detail in Batschelet (1981) and Zar (1974). These methods have

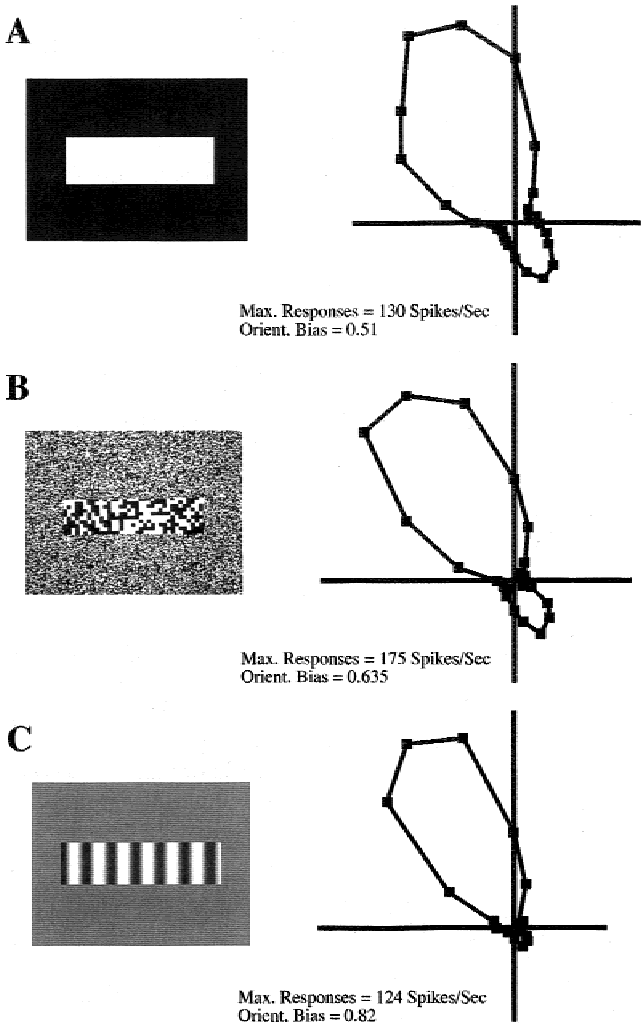

Fig. 1. Orientation-selective responses of a cue-invariant complex cell in cat area 18. The orientation biases and maximum responses are shown for each stimulus condition. Notice that this cell responded more selectively to equiluminant boundaries (B, C) than to a light bar. The stimuli shown in A–C are a luminance boundary, a texture-induced boundary (TIB), and a grating-induced boundary (GIB), respectively. The GIBs were generated using sinusoidal gratings within a uniform background of the same mean luminance. GIBs such as those employed in this study are known to evoke responses from some cells in monkey area V1 (Grosof et al., 1993). These authors regard GIBs as a type of illusory contour. There is some question, however, as to whether grating-induced boundaries, such as those produced by abutting, out of spatial phase sinusoidal gratings, are illusory contours in the same sense as, for example, the Kanisza triangle (Kanisza, 1979). The latter stimulus, but not the former, contains clear gaps that must be filled in perceptually. On the other hand, abutting out of spatial phase square-wave gratings that were also employed in this study, clearly produce illusory contours since gaps in the stimulus must also be filled in perceptually. In this and the following figures, the spatial frequencies of the grating induced-boundaries shown are not necessarily the same as the ones used to test the cell. They are provided to show the reader the type of stimulus used in each case. In general, the gratings employed to generate the GIBs were close to the spatial frequency cutoffs (as tested with drifting sinusoidal gratings) for the cells. When tested with drifting sinusoidal gratings this cell responded best to 0.2 cycles/d. Its cutoff spatial frequency was 0.8 cycles/d.

been previously used in the calculation of orientation and direction selectivities of retinal ganglion cells (Levick & Thibos, 1982; Thibos & Levick, 1985), LGNd relay cells (Shou & Leventhal, 1989), and cortical cells (Wörgötter & Eysel, 1987; Wörgötter et al., 1990). Briefly, the responses of each cell to the different directions of motion of the stimulus presented were stored in the computer as a series of vectors. The vectors were added and divided by the sum of the absolute values of the vectors. The angle of the resultant vector gives the preferred orientation or direction of the cell. The length of the resultant vector, termed the orientation or direction bias, provides a quantitative measure of the orientation or direction selectivity of the cell. Because the periodicity of orientation is 180 deg, the angles of the direction of the various stimuli were multiplied by a factor of two when calculating orientation preferences. However, direction is cyclic over 360 deg, therefore the actual directions of the moving boundaries were used to calculate the direction preferences of the cell. Orientation and direction biases ranged from 0 to 1 with 0 being completely unselective and 1 responding only to one orientation or one direction, respectively.

Since the vector analysis described in the previous paragraph takes into account the responses at all directions of stimulus motion and it can account for lopsided (non-Gaussian) (Thompson et al., 1989) orientation and direction tuning, it is more accurate than some previously used methods (i.e. half-width-at-half-height, direction index, and maximum-to-minimum response ratio; see below) to predict the orientation and direction preferences of visual neurons (Wörgötter et al., 1990). Therefore this method of analysis is preferred and was used in this study to determine the orientation and direction selectivities of cortical cells.

In addition to orientation and direction sensitivity, the contrast sensitivity and spatial-frequency tuning of most cells were also determined. We also studied the effect of increasing stimulus salience on cell response. The salience of TIBs was studied by varying the sizes of the texture elements inducing the boundary while keeping the background texture element constant (Fig. 5). The salience of GIBs was varied by varying the contrast and spatial frequency of the grating-inducing elements inducing the boundary. The salience of ICs was varied by varying the number of inducing elements that induced the illusion. Finally, the responses of CI cells were also studied when the salience of the stimulus was increased by combining qualitatively different boundary types.

Reliability of mapping procedures

We tested whether or not the preferred orientation and directions of the cells studied can be determined accurately and consistently over time. To this end, we studied many cells for 1 h or more and compiled multiple tuning curves. Using our techniques, an orientation or direction bias of 0.08 or greater indicated that the circular distribution of the cell's responses to moving stimuli was nonrandom (Rayleigh test, $P < 0.05$; described below) (Zar, 1974) while an orientation or a direction bias of 0.1 or greater indicated significance at the $P < 0.005$ level (Rayleigh test). Cells with biases of 0.1 or greater exhibited preferred orientations and directions that differed by less than 10 deg with repeated testing; their degree of bias varied very little with repeated testing. Thus, in this study, a cell exhibiting a bias of 0.1 or greater was considered to be orientation or direction selective; cells with biases less than 0.1 were defined as being nonorientation or nondirection selective. Our results indicate that a bias of 0.1 corresponds to a preferred orientation to nonpreferred orientation response ratio of about 2:1, and

a preferred direction to nonpreferred direction response ratio of about 1.5:1.

Contrast sensitivity

The dependence of cortical cell responses upon stimulus contrast was studied using optimally oriented and directed equiluminant boundaries, sinusoidal gratings, bars, and spots. The actual contrast for bar and spot stimuli was defined as the ratio of the luminance of the spot or bar to its background. The actual contrast for sinusoidal gratings was defined as the ratio of the luminance of the center of the light and dark cycles of the gratings. The maximal contrast was 80% [$(8.37 - 0.91\ cd/m^2)/(8.37 + 0.91\ cd/m^2)$]. The contrast of the stimuli was systematically varied *via* computer control from 0.01 to 1.0, where 1.0 = maximal contrast, or 80%, and 0.01 = 1% of the maximal contrast, or 0.8%. Ten contrast levels were employed. The responses of each cell to the different contrast levels were determined and compared for the different stimuli.

Definition of cue-invariant (CI) cells

To be considered cue invariant a cell in our sample had to meet a number of criteria. These are as follows:

1. The cell had to exhibit the same preferred orientation and direction when tested with LIBs, TIBs, GIBs, and/or MIBs.
2. The response of the cell did not change when the preferred GIB stimuli were phase shifted (see Grosof et al., 1993). This assured that the cell was responding to the different types of boundaries and not to the inducing elements that defined the boundaries.
3. The receptive fields of CI cells were large (usually 6–12 deg width in cats and 3–6 deg width in monkeys). We took care to use stimuli that were shorter than the cell's receptive field (RF). CI cells still exhibited the same stimulus preferences regardless of cue even when the stimuli were shorter than the cells' receptive field. This further confirmed that the cell was actually responding to the equiluminant boundaries, not to the inducing elements defining the boundaries.
4. The spatial frequencies of the elements defining the equiluminant boundaries were varied for each cell. A cell was not considered cue invariant unless its stimulus selectivity remained unchanged. In fact, the spatial frequency, texture size, boundary length, velocity, etc. of the stimuli employed appeared not to change whether or not a cell was cue invariant. However, changes in these same parameters could affect the strength of a cell's responses to all types of boundaries.

Histology and histochemistry

At the conclusion of each experiment the animal was deeply anesthetized and perfused through the heart with 700 ml of lactated Ringer's solution containing 0.1% heparin, followed by 1000 ml of 1% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer at pH 7.4, followed by 600 ml of lactated Ringer's solution containing 5% dextrose. Brains were removed, and the portions containing the electrode tracts were blocked and stored for 2–4 days in 30% sucrose solution and then frozen sectioned at 50 μm. The sections were mounted on gelatinized slides and stained with thionin, and coverslipped. Cells are assigned to areas V1 and V2 based upon the locations of the electrode tracts.

Results

This study contains a quantitative description of the responses of cortical cells to boundaries defined by a variety of cues. The results provide evidence for a class of complex cells in areas V1 and V2 of monkeys and cats that respond strongly and reliably to boundaries induced by motion (MIBs), texture (TIBs), gratings (GIBs), and luminance (LIBs) (Figs. 1–5). We refer to these cells as cue-invariant (CI) cortical cells. CI cortical cells were most frequently encountered in area V2 of monkeys and cats. They were rare in V1 of monkeys and cats. For this reason our V1 cell sample is not large enough to analyze statistically. An example of a CI cell recorded from cat area 17 (V1) is, however, shown in Fig. 5. Other than Fig. 5, the results presented here are based upon cells recorded from area V2. A total of 156 CI cells were recorded from

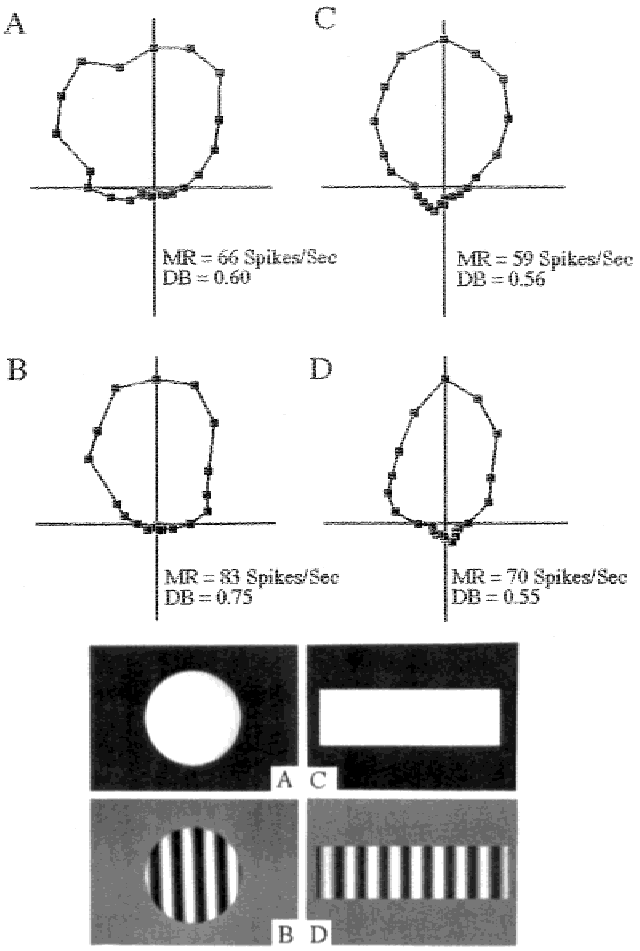

Fig. 2. Direction-sensitive responses of a cue-invariant (CI) cortical cell recorded from area V2 of rhesus monkey visual cortex to spots (A), bars (C), and to grating-induced boundaries (GIBs) (B, D). The maximum responses (MR) and direction biases (DB) are shown. Notice that this cell responded more strongly to the grating-induced boundaries than to the luminance-induced boundaries. When tested with drifting sinusoidal gratings, this cell responded best to gratings of 1.2 cycles/d and ceased responding at 5.0 cycles/d.

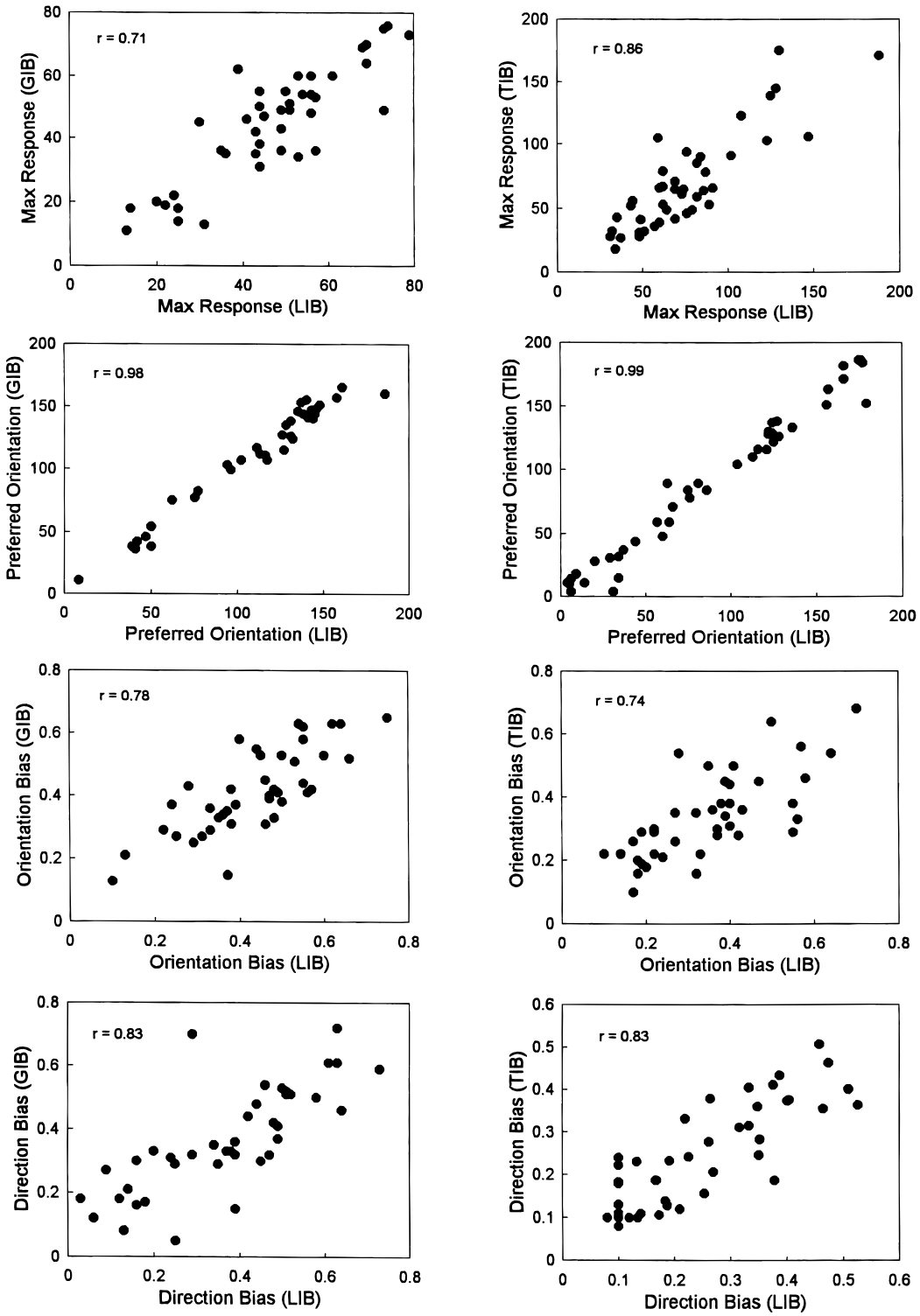

Fig. 3. The maximum responses (spikes per second), preferred orientations, orientation biases, and direction biases of CI cells in cat V2. Cells were tested with LIBs (light bars—ordinate), GIBs, and TIBs (abscissa). For this figure, the GIB was a sinusoidal grating within a blank field of the same mean luminance (see Fig. 1C). The TIB employed is shown in Fig. 6C. The cells used to compile this figure and Fig. 4 were studied in the greatest detail using LIBs, TIBs, and GIBs. The remaining cells included in our sample were studied stressing various other parameters. All of the cells included in Figs. 3 and 4 exhibited orientation and direction biases ≥ 0.1. Cells exhibiting lower biases were considered unselective and, therefore, omitted. For each scatter plot, the correlation coefficient (r value) is indicated. Notice that regardless of the stimulus employed, cat CI cortical cells exhibited similar degrees of selectivities, orientation preferences, and maximum responses.

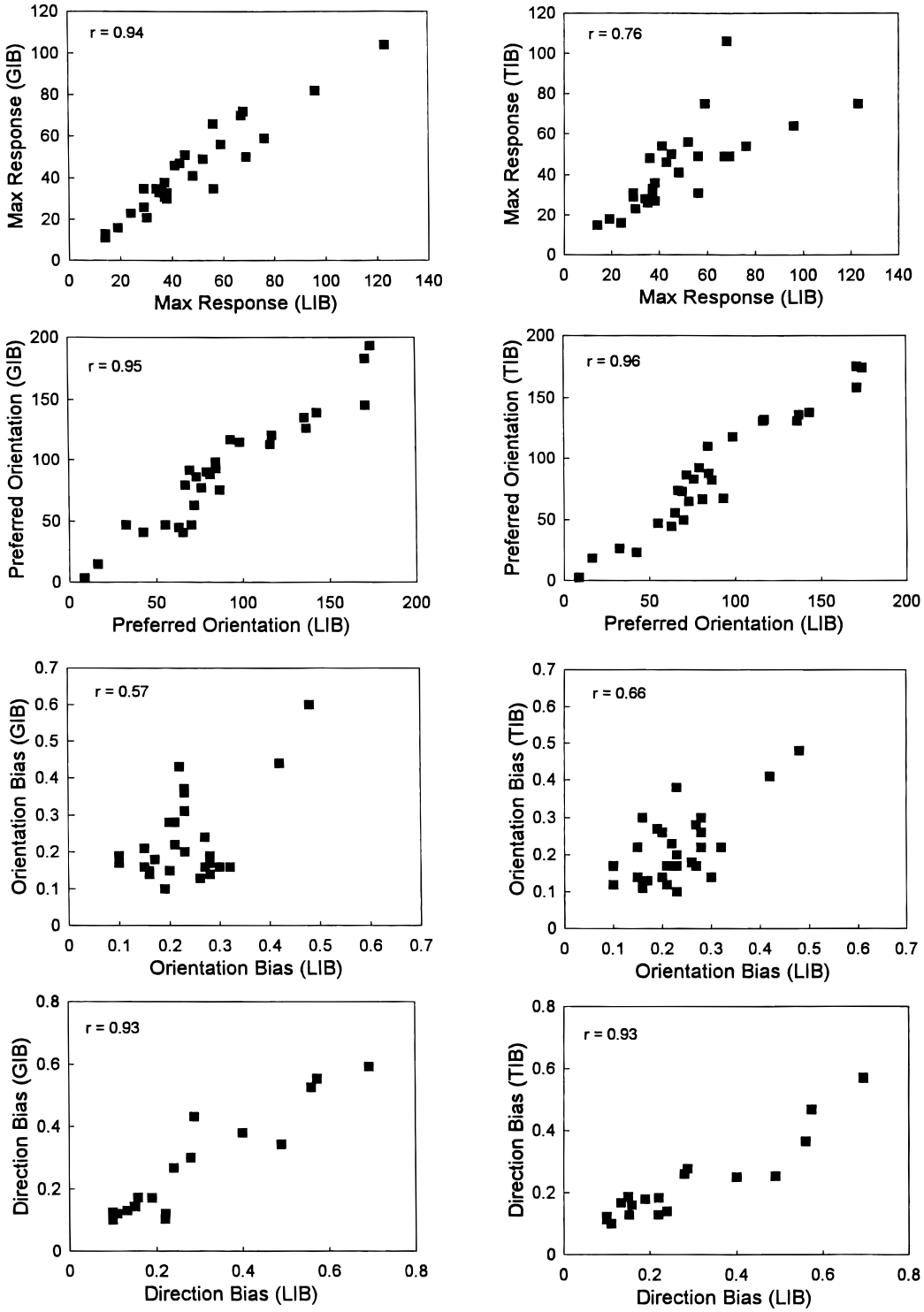

Fig. 4. The maximum responses, preferred orientations, orientation biases, and direction biases of V2 complex cells in rhesus monkeys. Conventions are as in Fig. 3. Regardless of the stimulus employed, monkey CI cortical cells exhibited similar degrees of selectivity, preferred orientations, and maximum responses.

area V2 of 11 cats and 89 CI cells were recorded from area V2 of four rhesus monkeys. It is difficult to judge the exact percentage of CI cells in area V2 since we specifically searched for them. Our qualitative determination of color selectivity suggested that CI cells tended to be wavelength insensitive in monkey area V2. In cats and monkeys, CI cells exhibited clear orientation and direction selectivity when tested with all types of boundaries (Figs. 1–5). Most responded selectively to TIBs, GIBs, MIBs, and LIBs that were shorter than their receptive fields. These cells, therefore, must have been responding to the boundaries that were induced by the various stim-

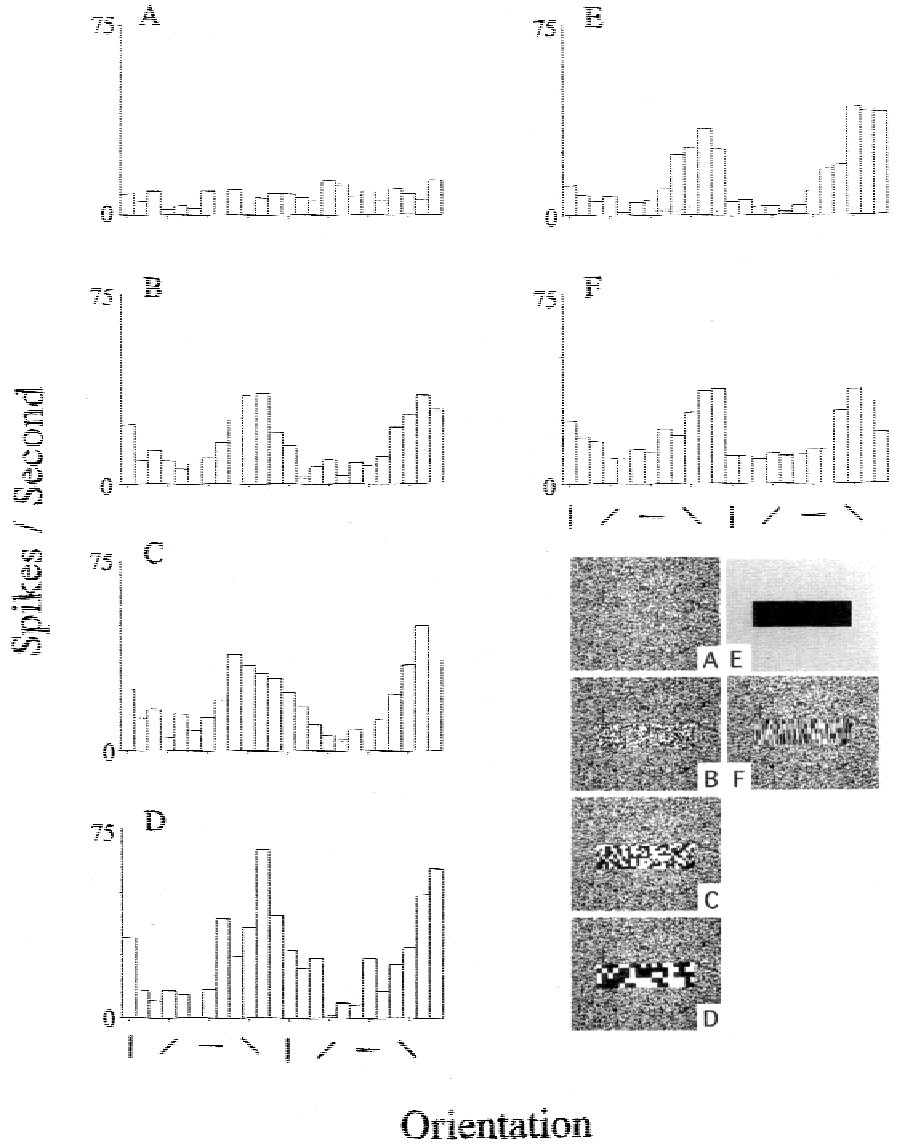

Fig. 5. Histograms illustrating the responses of a cat area V1 CI cortical cell to boundaries produced by isoluminant motion-induced boundaries (A), isoluminant texture patterns (TIBs) (B–D), a dark bar (E), and an isoluminant texture pattern consisting of elements oriented orthogonal to the cells' preferred orientation (F). The stimulus in A appears to be a uniform field since a boundary is only visible when a rectangular area of the texture elements is moved coherently through a background of the same texture elements. The receptive field of this complex cell exhibited strong OFF and weaker ON responses. The receptive field of this cell was longer than the test stimulus (9 deg). Thus, the cell's responses are likely to have resulted from an array of nonlinear subunits that responded to local luminance differences within the receptive field. The boundary in A was the least salient and the cell did not respond. Salience increased in B, C, and D. The magnitude of response increased with increasing salience of the stimuli. The responses of the cell to an isoluminant texture pattern consisting of subunits oriented orthogonal to the cell's preferred orientation are shown in F. Notice that the orientation of the texture elements did not affect the cell's response. Also notice that the cell responded more strongly to certain TIBs (C, D) than to a luminance boundary (dark bar in E). The two peaks in the histograms illustrate the responses to stimuli of the same orientation moving in opposite directions. When tested with drifting sinusoidal gratings, this cell responded best to 2.5 cycles/d and ceased responding at 5.0 cycles/d.

uli, not the individual inducing elements of the stimuli. It is noteworthy that CI cells tended to have relatively large receptive fields (1–3 deg in width in monkeys, and 2–10 deg in width in cats).

We tested the orientation and direction-selective responses of samples of cat and monkey CI cells using boundaries defined by gratings, texture, and luminance. In general, these cells exhibited the same preferred orientations and directions regardless of the stimulus used. CI cortical cells also exhibited similar degrees of selectivity regardless of the stimulus employed (Figs. 3 and 4).

It is noteworthy that the degree of orientation bias exhibited by CI cortical cells ($n = 28$) in monkeys was, on average, lower than the degree of bias exhibited by other types of orientation-selective cortical cells ($n = 91$; Mann-Whitney U test, $P < 0.001$). In monkeys, virtually all CI cortical cells exhibited biases in the range of 0.1–0.4. Using identical techniques to those employed in this study, we find that other types of monkey cortical cells, such as simple cells, often exhibit biases in the 0.4–0.8 range (Leventhal et al., 1995; Zhou et al., 1995). In cats, some CI cortical cells did exhibit biases in the 0.4–0.8 range. Their biases still tended to be lower than those of other types of selective cells such as simple cells.

Virtually all CI cortical cells responded more strongly to more salient (visible) stimuli (Figs. 5 and 6). The salience of the boundaries was changed by varying the texture differences, contrast, and luminance levels that defined the boundaries. The firing rates of most CI cortical cells increased when the salience of a boundary defined by one attribute increased (i.e. a more salient texture *vs.* a less salient texture) (Figs. 5 and 6). The firing rates of CI cortical cells also increased if multiple cues were combined to define a boundary. In fact, clear orientation and direction-selective responses could even be evoked when a subthreshold TIB was superimposed upon a subthreshold MIB or LIB (Fig. 7). Similarly, when a subthreshold LIB was combined with an IC or GIB, the response of CI cortical cells increased relative to the response to the IC alone. Thus, CI cortical cells are able to integrate multiple cues in order to signal the presence of a boundary.

The responses of CI cortical cells suggest that their receptive fields consist of an array of unoriented, nonlinear subunits that are

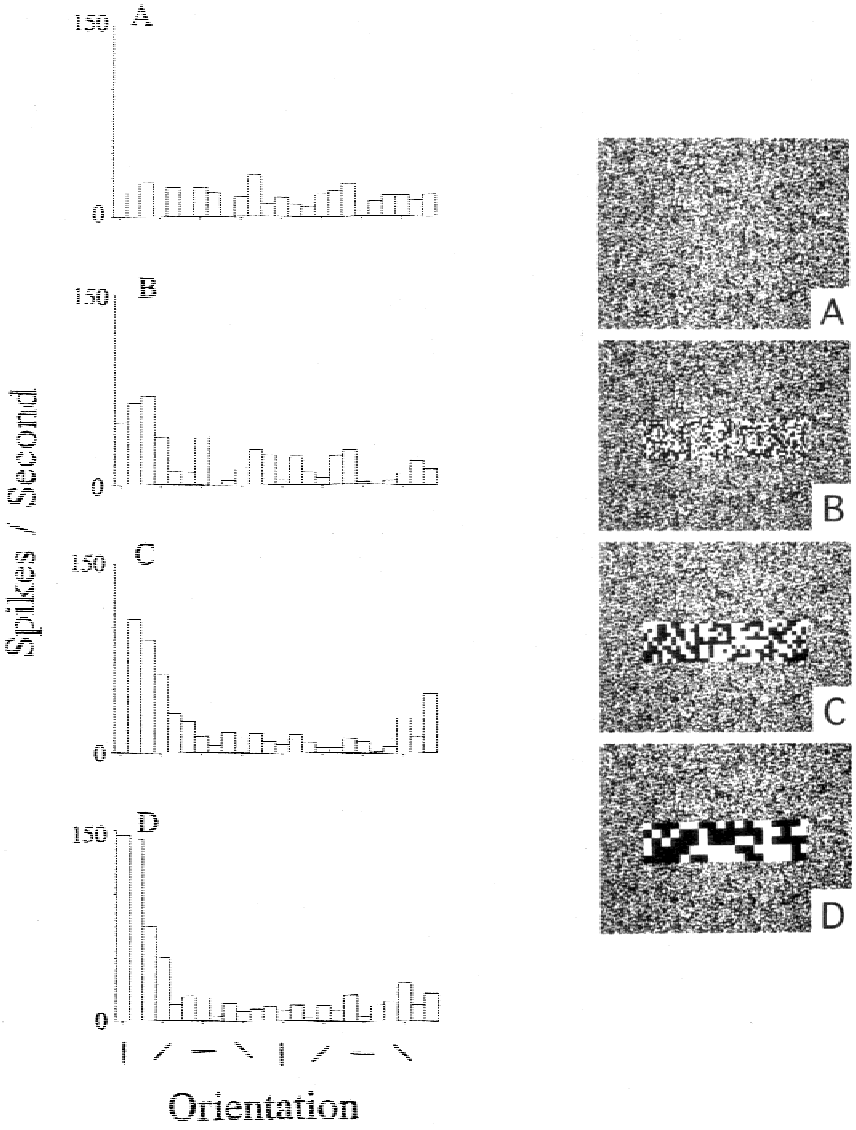

Fig. 6. Histograms illustrating the response amplitude, orientation, and direction selectivity of a CI cortical cell recorded from area V2 of rhesus monkey visual cortex. The stimuli employed are shown in A–D. In all cases, the equiluminant boundaries were shorter than the receptive fields. Notice that the cell's response increased as the salience of the isoluminant texture-induced boundaries (TIBs) increased. When tested with drifting sinusoidal gratings, this cell responded best at 1.5 cycles/d and ceased responding at 5.0 cycles/d.

linked cooperatively along the axes of the cells' preferred orientation and direction (Victor & Conte, 1991; Grosof et al., 1993). Our results support the idea that the subunits are unoriented because the responses of CI cortical cells were unaffected by the orientation of the texture elements used to generate a TIB. For example, a horizontal TIB generated using vertical texture elements and a horizontal TIB generated using unoriented or horizontal texture elements evoked the same responses from a CI cortical cell that was selective for horizontal (Fig. 5F). Our results support the idea that cooperative linkage of the subunits occurs only along the cell's preferred axes. Evidence for this comes from the observation that an increase in the number of inducing elements flashed or moved parallel to the cell's preferred orientation results in clear summation while increases in the number of elements flashed or moved orthogonal to the preferred orientation does not (Figs. 8 and 9).

Illusory contours can be defined as contours that are perceived in the absence of a continuous luminance boundary. Illusory contours, thus, contain gaps that must be filled in perceptually. A number of studies have provided evidence that illusory contours (ICs) can evoke responses from cells in visual cortex of monkeys and cats (von der Heydt et al., 1984; Redies et al., 1986; von der Heydt, 1987; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; Grosof et al., 1993). We find that CI cortical cells in monkeys and cats respond selectively to ICs. They also respond to GIBs that some authors regard as illusory contours (Grosof et al., 1993; see legend to Fig. 1). The responses of these cells to ICs appear to be a result of the computational ability inherent in their receptive fields. Our observations provide a neural basis for psychophysical results that indicate that the visibility of an IC is increased if it is combined with a subthreshold luminance boundary (Dresp & Bonnet, 1995). The present results can also explain the oblique effect in the perception of illusory contours since more CI cortical cells responded to horizontal and vertical than to oblique orientations (Soriano et al., 1996). CI cortical cells were divided into four groups. These groups contained cells with preferred orientations within 22.5 deg of horizontal, vertical, 45 deg or 135 deg. Overall, 61% of the CI cells in cat V2 and 65% of the CI cells in monkey V2 preferred orientations within 22.5 deg of horizontal and vertical.

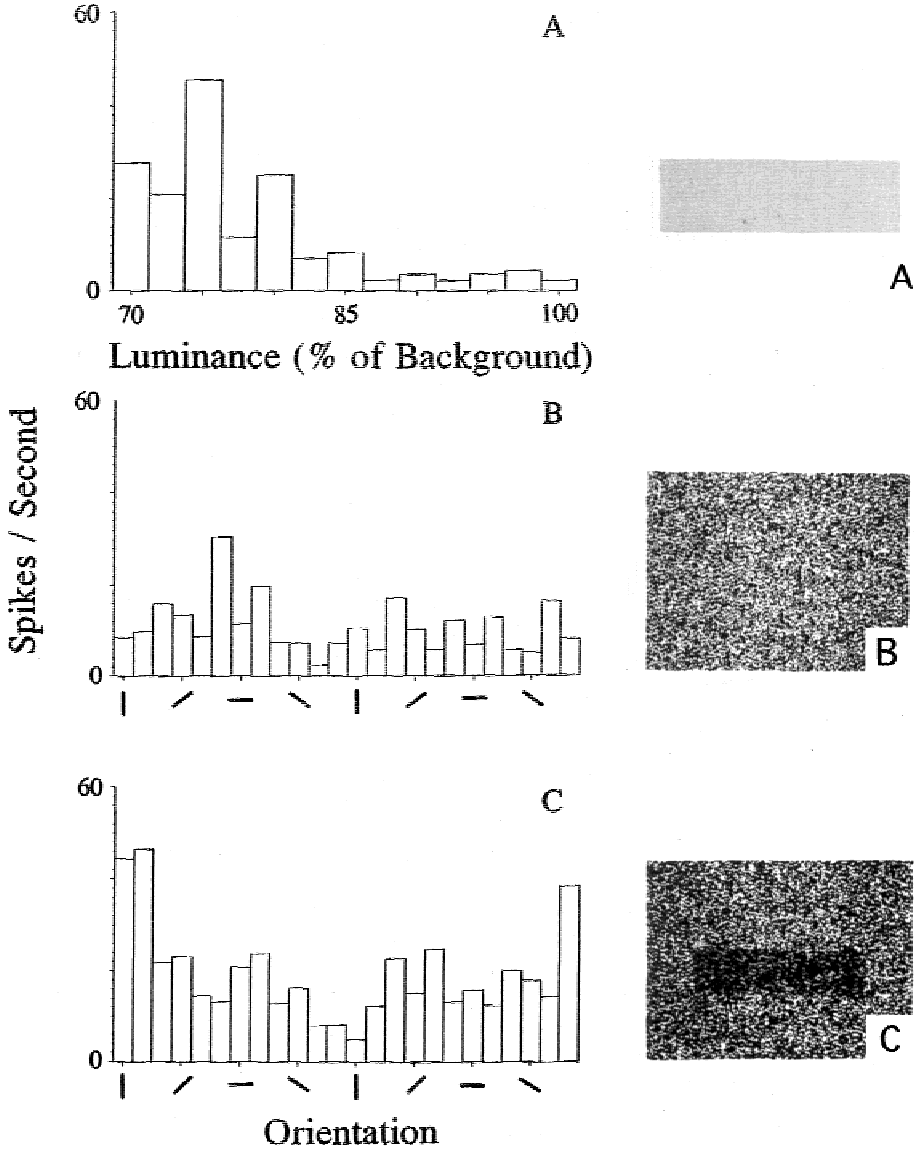

Fig. 7. Responses of a CI cortical cell in area V2 of rhesus monkey visual cortex to luminance-induced boundaries of different salience (A), a texture-induced boundary that was not salient enough to elicit a response (B), and the subthreshold texture boundary in B upon which a subthreshold luminance boundary was superimposed (the boundary and the background differed in luminance by $<10\%$) (C). Notice that this CI cortical cell responded strongly and selectively in C. Thus, it has the computational power to combine different attributes of visual stimuli and signal the presence of a boundary defined by two subthreshold cues. When tested with drifting sinusoidal gratings, this cell responded best at 1.0 cycles/d and ceased responding at 2.0 cycles/d.

Discussion

Since the early work of Hubel and Wiesel (Hubel & Wiesel, 1962, 1968), LIBs such as bars, spots, and gratings have been the standard stimuli used to study the receptive-field properties of cortical cells. The sorts of equiluminant visual stimuli employed in this study are poor stimuli for most linear cortical cells. On the other hand, some CI cortical cells actually respond more strongly to MIBs, TIBs, GIBs, and ICs than to LIBs, even if the contrasts of the LIBs are optimized. This is especially true when multiple visual cues define a boundary simultaneously. The responses of CI cortical cells to LIBs therefore appear to result because these stimuli excite the mechanism that mediates the cells' cue-invariant response, not because LIBs are necessarily the preferred stimuli of the cells.

In both cats and monkeys, parallel pathways exist that begin in the retina and continue into extrastriate visual cortex. One of the pathways in the monkey (P pathway) is wavelength sensitive while the other is predominantly wavelength insensitive (M pathway) (Stone et al. 1979; Shapley & Perry, 1986). These pathways terminate in different regions of cortical area V1 and this segregation is largely maintained in area V2. It is tempting to speculate that CI cortical cells in area V2 will prove to be most common in the M pathway since their responses tended to be wavelength insensitive. Some cells in higher cortical areas of monkey such as MT (Albright, 1992) and MST (Geesaman & Anderson, 1996) also respond in a cue-invariant manner. These areas are also thought to be part of the M pathway (Van Essen et al., 1992).

This study shows that CI cortical cells can extract and integrate orientational and directional information about boundaries using multiple cues simultaneously. The responses of these cells increase when the salience (visibility) of boundaries increases regardless of the cue or cues defining the boundary. Thus, CI cortical cells seem well suited to contribute to the sorts of cue-invariant boundary perception revealed by psychophysical studies (Yeh et al., 1992; Landy, 1993; Rivest & Cavanagh, 1996). The fact that they are found principally in area V2, but even in V1 in a small proportion indicates that the ability to respond to boundaries in a cue-invariant manner originates at the earliest stage of cortical processing.

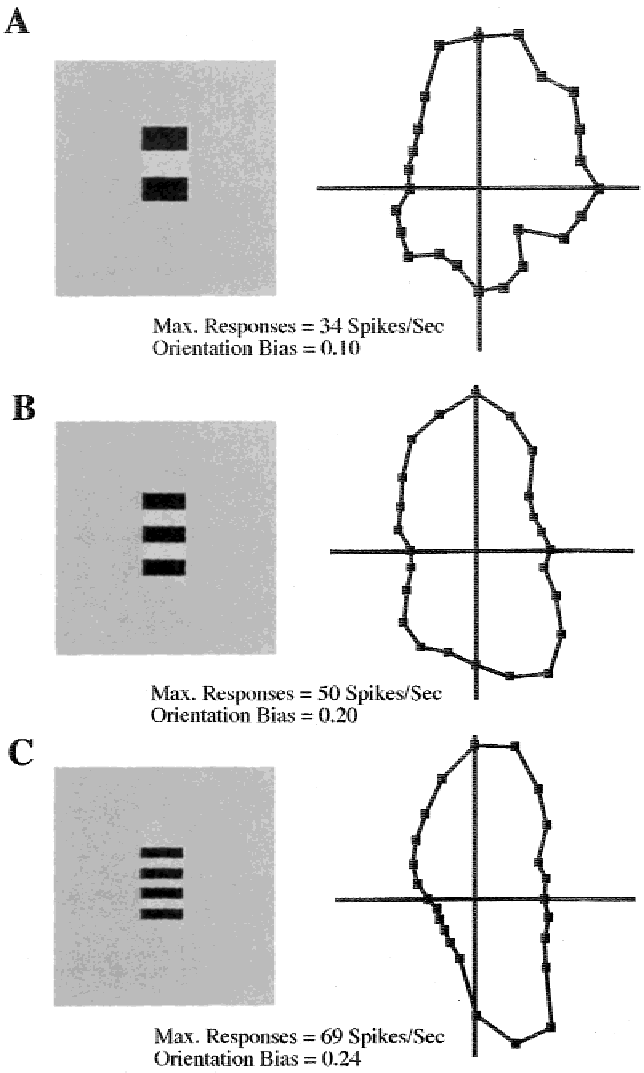

Fig. 8. Orientation-selective responses of a cue-invariant complex cell in cat area 18 to boundaries defined by different numbers of inducing elements. Notice that this cell responded more strongly and selectively to moving boundaries induced by multiple, closely spaced elements than to boundaries induced by fewer, widely spaced elements. When tested with drifting sinusoidal gratings, this cell responded best at 0.2 cycles/d and ceased responding at 0.8 cycles/d.

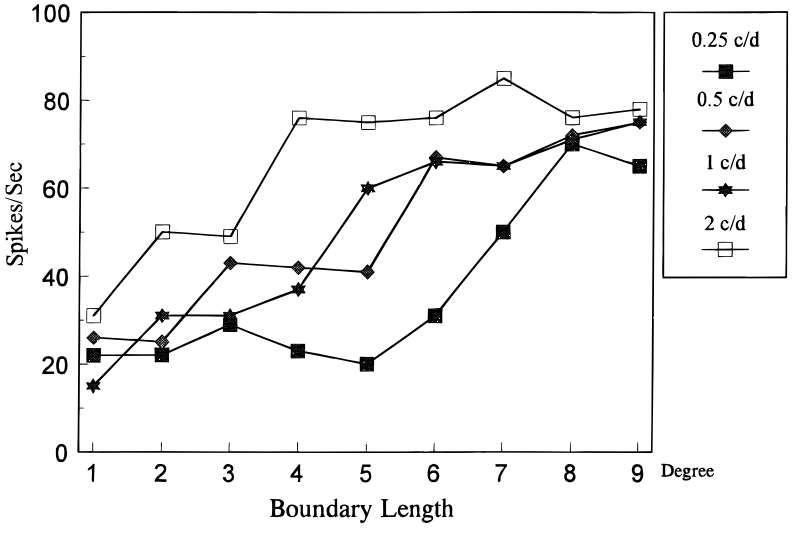

Fig. 9. Responses of a CI cortical cell recorded from area V2 of rhesus monkey cortex. Boundaries induced by gratings (as in Fig. 1C) of different lengths and spatial frequencies (cycles/degree [c/d]) were employed as test stimuli. Overall, longer GIBs (consisting of more grating cycles) elicited stronger responses than did shorter GIBs of the same spatial frequency. Also, boundaries induced by higher spatial-frequency gratings (2 c/d) equal in length to boundaries induced by lower spatial frequencies (0.25 c/d) elicited stronger responses. This is because the higher spatial-frequency GIBs contained more inducing elements than did the lower spatial-frequency GIBs.

The ability of humans to perceive boundaries that are defined by attributes other than luminance, such as illusory contours, has been formally recognized for nearly a century (Schumann, 1900). Westheimer and Li (1997) have recently studied orientation discrimination in humans using illusory contours and luminance boundaries as stimuli. They find that orientation discrimination is poorer by a factor of 2 when illusory contours are used as the stimuli. We find that many CI cortical cells respond selectively to the orientations and directions of ICs. However, their orientation biases are, on average, weak compared to other types of cortical cells. The weak selectivity of CI cells could explain why the orientations of illusory contours are more difficult to discriminate than are the orientations of luminance boundaries that can be encoded by highly orientation-selective cells such as most simple cells that are not cue invariant. Even though CI cells may be ill suited to signal the precise orientations and directions of luminance boundaries, the fact that they respond to a wide range of cues does make them better suited than non-cue-invariant cells to signal the presence of other types of boundaries.

Recent studies in humans employing functional magnetic resonance imaging (fMRI) have provided evidence that specific regions of extrastriate visual cortex, including area V2, are active during the viewing of illusory contours (Hirsch et al., 1995). The CI cortical cells we described here are relatively common in monkey area V2. These cells respond to illusory contours as well as to boundaries defined by cues such as motion, texture, and gratings. Equiluminant stimuli of the type studied here have not been employed in fMRI studies of human extrastriate cortex. It is tempting to speculate that illusory contour-sensitive regions of human extrastriate cortex are not specialized only for the detection of illusory contours. Rather, these regions may contain CI cortical cells of the type described in this study. Such cells can provide the capacity for boundary perception in the face of a dynamic visual world in which visual cues routinely and rapidly change in number and salience.

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