INTRODUCTION

The recognition of a particular object in a real scene is frequently plagued by the presence of shadows or surface markings that generate clear luminance contrast boundaries but do not correspond to the border of an object. Rather than facilitating object recognition, some luminance contrast boundaries may therefore make the differentiation of an object more difficult. The ability to integrate boundaries based on discontinuities other than luminance contrast, such as those resulting from chromatic, texture, or motion differences, would provide the visual system with additional information with which to overcome the difficulties created by such shadows or surface markings.

While it may seem incontrovertible, both on the basis of everyday experience and psychophysical experiment (Regan 1989; Regan and Hamstra 1992) that shapes can be resolved from motion cues, the mechanism for resolving boundaries from motion remains nonetheless something of a visual phenomenon in search of a cortical substrate. Single-cell recordings have established that neurons in the infero-temporal cortex of the primate visual system respond to preferred shape irrespective of whether its boundaries are defined by luminance, texture, or motion contrast (Sáry et al. 1993). Information about static, albeit motion-defined, boundaries is thus clearly present in, and utilized by, higher-order areas, but this tells us nothing about the actual origin of that information. It should be emphasized at this point that we refer to stationary boundaries formed by moving planes. Moving kinetic boundaries are apparently quite another phenomenon: perceptually, moving boundaries are difficult to discern and are not even perceived by some individuals, whereas static boundaries appear distinct and are universally perceived (Regan 1989; Regan and Hamstra 1992; Sáry et al. 1994). Recent PET studies in our laboratory (Dupont et al. 1997) have moreover shown that moving kinetic boundaries elicit only weak activation, whereas static boundaries produce strong, specific activations (Dupont et al. 1997; Orban et al. 1995; Van Oostende et al. 1997). This distinction is particularly relevant considering that Leventhal et al. (1998) have recently shown that cue-invariant selectivity for static boundaries, including those generated by moving planes, is a property that appears early in visual processing and may thus represent a rather basic aspect of vision on a par with orientation selectivity itself.

There are at least two conceivable schema for producing selectivity for kinetically defined boundaries as suggested by the organization of the primate visual system. Visual cortex can be considered as consisting of two distinct pathways, the ventral pathway dealing with color and form perception and the dorsal pathway dealing with spatial and motion processing (DeYoe and Van Essen 1988; Maunsell 1987; Ungerleider and Mishkin 1982). Therefore one possibility is that motion information from motion remains nonetheless something of a visual phenomenon in search of a cortical substrate. Single-cell recordings have established that neurons in the infero-temporal cortex of the primate visual system respond to preferred shape irrespective of whether its boundaries are defined by luminance, texture, or motion contrast (Sáry et al. 1993). Information about static, albeit motion-defined, boundaries is thus clearly present in, and utilized by, higher-order areas, but this tells us nothing about the actual origin of that information. It should be emphasized at this point that we refer to stationary boundaries formed by moving planes. Moving kinetic boundaries are apparently quite another phenomenon: perceptually, moving boundaries are difficult to discern and are not even perceived by some individuals, whereas static boundaries appear distinct and are universally perceived (Regan 1989; Regan and Hamstra 1992; Sáry et al. 1994). Recent PET studies in our laboratory (Dupont et al. 1997) have moreover shown that moving kinetic boundaries elicit only weak activation, whereas static boundaries produce strong, specific activations (Dupont et al. 1997; Orban et al. 1995; Van Oostende et al. 1997). This distinction is particularly relevant considering that Leventhal et al. (1998) have recently shown that cue-invariant selectivity for static boundaries, including those generated by moving planes, is a property that appears early in visual processing and may thus represent a rather basic aspect of vision on a par with orientation selectivity itself.

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Kinetic boundaries in V1 and V2

Response to motion from the dorsal stream may at some point be introduced into the ventral stream where it is combined with information about color and luminance boundaries. A second possibility is that the initial processing takes place entirely within in lower-order areas such as V1 or V2 where various compartments containing cells selective to either orientation, motion, or color (Coogan and Van Essen 1996; Hubel and Livingstone 1987; Olavarria and Van Essen 1997) lie in close juxtaposition to one another. Kinetic edge information might therefore be extracted at these early levels, then passed along to higher areas, with no need for information originating in the dorsal stream.

Previous work has focused on the role played by the dorsal stream, particularly area MT/V5, in extracting motion boundaries. However, there are conflicting reports concerning the effect of lesions in area MT/V5 on the discrimination of figures defined by kinetic boundaries. Marcar and Cowey (1992) reported some deficit in the ability of monkeys to discriminate figures defined by kinetic boundaries following a large lesion of area MT/V5 and surrounding cortex, whereas Lauwers and colleagues found at most modest impairment in the ability of monkeys to discriminate the orientation of a kinetic grating in a systematic comparison of extensive and limited lesions in the STS (Lauwers et al. 2000). An investigation into the orientation selectivity of area MT/V5 for kinetic boundaries (Marcar et al. 1995) revealed that neurons in this area respond only to the local motion in the kinetic boundary stimulus, casting further doubt on the possibility that MT/V5 may be directly involved in the extraction of kinetic boundaries. In human visual cortex, the kinetic-occipital region, or KO, has been shown to be selectively activated by stimuli containing kinetic boundaries using both positron emission tomography (PET) imaging (Dupont et al. 1997; Orban et al. 1995) and functional magnetic resonance imaging (fMRI) (Van Oostende et al. 1997). Unfortunately, KO is not an option for single-cell recording in the monkey because the homologous area has yet to be identified in other primate species.

Because the primary motion area, MT/V5, does not appear to be directly involved in the encoding of the orientation of kinetic boundaries, the next logical step is to look in lower-order areas, particularly V1 and V2. Area V2 has been associated with orientation selectivity for nonluminance contrast boundaries for some time (Leventhal et al. 1998; Peterhans and von der Heydt 1989; von der Heydt and Peterhans 1989) and thus represents a good candidate for the area where motion-based form processing first emerges. The work of the Leventhal group provides convincing evidence for neurons with cue-invariant edge selectivities in V2 and describes a selectivity for motion boundaries but details of the motion stimulus are unfortunately sketchy, and no motion boundary responses are illustrated for the monkey (Leventhal et al. 1998). These workers found relatively few cells in cat and monkey striate cortex with cue-invariant selectivity for edges, but earlier reports (Grososf et al. 1993; Redies 1989; Redies et al. 1986) have described cells in area V1 that were responsive to the orientation of boundaries defined by edges other than luminance boundaries. Because these reports indicate at least some coding of other types of boundaries takes place in primary visual cortex, we extended our investigation to include area V1 as well as V2.

In any response to motion boundaries found at these early stages of visual processing, a comparison of response latencies to those elicited by luminance edges could provide some measure of insight as to the origin of such signals. This is possible because objects defined by either type of boundary elicit responses in area IT with delays in the same 80- to 120-ms range (Sáry et al. 1995). Although it is possible to invoke a number of schemes to explain this coincidence, a simple and likely scenario is that motion- and luminance-boundary information are integrated within single neurons at some fairly early point during processing and thence travel to further destinations via the same neural substrate as a sort of generic edge signal. From that hypothetical entry point forward, all information signaling edges will have the same latency whether originally derived from motion or luminance. At ventral stream components prior to the emergence of motion boundary information, selectivity for these boundaries will not exist if the motion boundary information is transmitted exclusively to higher cortical areas. If, on the other hand, it is also relayed retrogradely along the ventral stream, then responses to such boundaries will become increasingly longer in latency compared with the luminance response, at successively lower hierarchical levels. The existence of specific responses to motion-defined boundaries within V1 and V2 and the latency of those responses with respect to luminance boundaries can thus provide valuable clues regarding the circuitry involved in extracting that information.

METHODS

We recorded from single cells in areas V1 and V2 of 10 anesthetized (sufentanil; Sufenta Forte, 5 μg · kg⁻¹ · h⁻¹) and paralyzed (pancuronium bromide: Pavulon, 0.4 mg · kg⁻¹ · h⁻¹) adult male macaque monkeys (Macaca fascicularis) weighing between 3 and 5 kg. In most subjects, additional experiments reported elsewhere (Marcar et al. 1995) were simultaneously carried out to minimize the total number of animals required. Monkeys were prepared for acute extracellular electrophysiological recording using procedures standard in our laboratory (see Lagae et al. 1994; Marcar et al. 1995; Raiguel et al. 1995). Electrolytic lesions were made during the course of each penetration, and the cortical area and laminar location of cells that were recorded were later confirmed on sections stained with cresyl violet or for cytochrome oxidase (Livingstone and Hubel 1982, 1987) to identify subcompartments of areas V1 and V2.

Stimuli

The basic stimulus was a texture pattern of random pixel noise moving in the frontoparallel plane at optimum speed for the cell being tested, and were identical to those used by Marcar et al. (1995). Each white (47 cd/m²) pixel subtended an angle of 3 arcmin at the standard testing distance of 57 cm, with a density of 25% on a dark background (0.2 cd/m²). The minute size of the individual elements of this pattern was chosen so as to curtail edge artifacts. Dot lifetime was not limited except where dots scrolled off the edges of the stimulus or encountered the kinetic boundary. Stimuli were stored as sequences of 512 × 512-pixel images on a Microvax II Workstation that were displayed at 100 Hz using a Gould IP 9545 image computer, and presented in pseudorandom order. The texture pattern filled the entire 25.6 × 25.6° (at standard testing distance of 0.57 m) area of the monitor at all times. In this investigation, a kinetic edge was always defined by two texture patterns moving in opposite directions while the kinetic edge itself remained stationary. We opted for a stationary edge as we were interested in the coding for the orientation of the edge rather than for higher-order motion (Albright 1992). At least five complete runs of the testing sequence in both the forward and backward directions.
were presented, that is, with the directions of movement in the two halves of the stimulus reversed.

We employed two classes of kinetic edges (KEs), as in Marcar et al. (1995): one in which the direction of motion was parallel to the orientation of the edge (KEP) and one in which the direction of motion was orthogonal to the orientation of the edge (KEO). By comparing the apparent orientation selectivity to these two stimuli, we were able to distinguish orientation selectivity for KEs from direction selectivity for the local motion (Fig. 1). Our assumption was that a cell that responded to the local motion within the stimulus would shift its apparent orientation selectivity by 90° between the two classes of KEs. Cells that responded to the orientation of the KE, on the other hand, would exhibit the same apparent orientation selectivity for both classes of KEs. In addition to the single KE, we also examined the response to a kinetic grating, that is, a stimulus in which multiple KEs were present at 0.8° intervals. Each KE stimulus was presented for 300 ms, was preceded by a 250-ms prestimulus period during which the first frame of the sequence was visible on the screen, and was followed by a 500-ms poststimulus period during which the last stimulus frame remained visible on the screen. Because the random dots were already present over the receptive field when motion began, motion onset coincided with the appearance of the first frame of the motion sequence.

Static luminance-contrast stimuli (Lum) consisted of stationary square-wave gratings (0.8, 1.6, and 3.2 cycles/° at 57 cm), and single, 0.6°-wide light (47 cd/m²) and dark light (0.2 cd/m²) bars on a gray background of 24 cd/m². For neurons responding like complex cells, light- and dark-bar responses were averaged, otherwise the polarity giving the best response was used. Static stimuli were presented at orientations encompassing a full 180° at 22.5° (V2) or 11.25° (V1) intervals. These stimuli were flashed onto a uniform screen of equal mean luminance for a 300-ms presentation time with 750 ms between presentations. The grating or bar giving the strongest response was selected for comparison with the KE response.

Testing procedure

Following hand plotting of the receptive field, including qualitative assessment of speed and direction characteristics, cells were tested monocularly with computer-generated stimuli using the eye giving the stronger response. A series of three preliminary tests were first carried out to determine the optimum orientation and length for stationary, flashed bars and to center the stimuli over the receptive field. Optimum static orientation (Fig. 2A) was determined using stationary, flashed light and dark bars and gratings of optimum length, based on hand plotting, at 8 orientations in V2 or at 16 orientations in steps half as great in V1. Comparing the orientation determined during handplotting with the orientation obtained in this test served as a preliminary control on the centering of the monitor, which was crucial for obtaining accurate orientation tuning (see following text). In the position test that followed, we mapped the receptive field (RF) quantitatively with small light and dark bars, at optimum orientation, presented in 25 locations in a 5 × 5 grid (Fig. 2B). In V2, these bars measured 2.4, 1.2, or 0.6 × 0.3°, depending on the size of the handplotted RF, with corresponding grid spacings of 2.4 × 1.2, 1.2 × 0.6, and 0.6 × 0.3°. In area V1, where RFs tended to be smaller, bars measured 1.2 × 0.3, 0.6 × 0.3, or 0.3 × 0.2° with center-to-center grid spacings of 1.2 × 0.6, 0.6 × 0.3, and 0.3 × 0.2°. A great deal of effort was expended in insuring accurate centering of the stimuli because a static bar that is not precisely centered can produce misleading orientation tunings. It was almost always necessary to reposition the monitor and repeat the position test several times, with increasingly smaller bar sizes of both polarities, to achieve the desired level of precision. If the position test revealed that the initial orientation test had been slightly off center, then it was necessary to repeat that test as well and to begin the alignment process anew. The use of a laser alignment system, and a grid displayed on screen between tests that corresponded to the center-to-center bar spacings, enabled us to achieve an eventual centering accuracy of better than 0.2°. Since this error is much less than the extent of even the very smallest RFs in V1, we feel confident that the centering was at least sufficient for the purposes of our analysis. As a further control, if we still held the cell at the end of the testing procedure, then a second position test would be carried out to confirm that the results of the KE test were consistent and not due to any shift in eye position or other positional artifact.

With the monitor positioned so that its center precisely matched the RF, the optimum stimulus length was determined from a length-response curve (Fig. 2C) created by presenting light and dark bars of increasing length at the optimum orientation. In all tests, on-line graphic analysis of the test results, similar to the illustrations in Fig. 2, assisted in determining optimum stimulus orientation, size, and centering.

Following these optimization measures, we again tested the orientation selectivity of the cells but now using the parallel and orthogonal KE stimuli in both the forward and backward motion directions (see Fig. 1). This stimulus was positioned over the RF using the center determined in the pretesting, and the diameter was adjusted to the optimum edge length using a black paper cutout placed over the screen. The test was first carried out using a single KE, then in many instances, was repeated using the kinetic grating (KG) stimulus.

FIG. 1. Diagram showing how neurons respond selectively or nonselectively to a kinetic edge. Top: filled and open arrowheads represent “forward” and “backward” motions. Stimulus was normally masked during testing so that the edge of the stimulus corresponded with the edge of the receptive field (shading and dashed circles). Filled polygons inside bottom 4 circles represent polar plots of responses to the various kinetic stimuli shown schematically at the periphery of each plot. Arrowheads in these circles illustrate the specific motion directions tested. Boundaries generated by pixels moving parallel (left column) or orthogonally (right column) with respect to the boundary will generate preferred orientations that are 90° out of phase in nonselective neurons (top) responding to local motion, but which match in kinetic edge- (KE)-selective neurons (bottom) responding to the orientation of the boundary.
orientation of 22.5° was obtained by rotating the monitor to match the pre-
stimulus was a light bar measuring 1.2 by 0.6°, tested at 0.6° steps. The optimal
optimum orientation and, in the case of luminance-defined edges,
spontaneous discharge rate by 2 SD and that was followed by at least
the onset of the response was then defined as the first bin
and the selectivity index (SI) for kinetic or static edges, which is a
measure of the strength of orientation selectivity, was determined by
the formula
\[
SI = \frac{\sqrt{\sum_{i=1}^{n} S_i \cdot \sin \alpha_i} + \sqrt{\sum_{i=1}^{n} S_i \cdot \cos \alpha_i}}{\sum_{i=1}^{n} S_i}
\]
where \(n\) is the number of orientations tested, \(S\) is the response elicited by stimulus \(i\), and \(\alpha\) is the angle specifying the orientation of a given stimulus (Batschelet 1981). The latency of the responses were deter-
mined using a CUSUM analysis (Ellaway 1978; Maunsell and Gibson 1992; Vogels and Orban 1994) to identify the time of response onset. First the mean and standard deviation of the spontaneous spike rate was determined from the 150-ms periods preceding stimulus onset of all runs. The onset of the response was then defined as the first bin after motion or flashed stimulus onset where the bin exceeded the spontaneous discharge rate by 2 SD and that was followed by at least two successively increasing bins. All latencies were determined at the optimum orientation and, in the case of luminance-defined edges, polarity.

**Image analysis of cytochrome histology**

To reconstruct the compartmentalization of area V2 as revealed by the cytochrome oxidase activity (Livingstone and Hubel 1982, 1987;
Olavarria and Van Essen 1997), we applied the technique of Peterhans and von der Heydt (1993). The histological preparation was first converted to digital images using an image analysis system (Komtron) so that commercial image processing software could then be used to create montages of contrast-enhanced images. Successive images were juxtaposed and precisely aligned until the entire cortical area was included. By aligning successive cortical sections in this manner, it becomes possible to distinguish the subtle differences between thick and thin stripes (Peterhans and von der Heydt 1993), and recorded cells could be localized according to thick, thin, and interstripe compartments using electrode tracks and lesions.

RESULTS

Database

We recorded KE responses from 127 neurons in area V2 and 122 in V1. In addition, 58 of these V2 neurons in were also tested with a kinetic grating (KG). Neurons that completely failed to respond to the parallel or orthogonal KE stimulus (10/127 in V2, 6/122 in V1) were not considered further and were removed from the database. Similarly, a few neurons for which the corresponding luminance edge tests (4/127 in V2, 9/122 in V1) produced no response were not included in the analysis. The eccentricities of the remaining 113 neurons in V2 and the 107 in V1 ranged from 0.7 to 22° (median 6°) and from 1 to 16° (median 9°), respectively.

KE responses in area V2

In Figs. 2–4, we trace the entire testing procedure for cell 7110, which responded particularly well to the KEs. Preliminary testing (Fig. 2, A–C) showed that this neuron responded vigorously to either a light or dark bar oriented at 22.5° with respect to the horizontal. Because this neuron was a complex cell the responses to light and dark bars were nearly equal, thus these responses were averaged when later compared with the KEs. The position test (Fig. 2B) that followed was used to center the monitor on the RF of the neuron and also shows that the RF had an approximate half-height diameter of 2°, typical for V2 at this eccentricity (9°). Neither the light nor dark bar (Fig. 2C) showed any evidence of end-stopping so that response increases with bar length, up to a diameter of about 3°, then levels off. Because no end-stopping was apparent, no mask was used to limit the stimulus size in the subsequent KE and KG tests, and thus those stimuli covered the full 25° diam of the monitor.

Figure 3 illustrates the peristimulus time histograms (PSTHs) for the responses (response significance P < 1.0 × 10−5 for both KEP and KEO, ANOVA) of cell 7110 to the four types of KEs tested: those containing a single edge (KEP and KEO) and those consisting of multiple KEs (KGPs and KGO) forming a grating pattern. The histograms indicate that in either case, the cell essentially ignored the direction of motion, responding best when the motion boundaries were oriented at about 23°. Responses are illustrated as a function of orientation in Fig. 4A, adding the Lum response for comparison. Regardless of how the edge is generated, whether with orthogonal or parallel KEs or gratings, or with a luminance edge, all stimuli have preferred orientations near 22.5°. Orientation selectivity is evident for all stimuli, with SIs of 19, 35, 20, 17, and 60 for KEP, KEO, KGPs, and Lum, respectively, and by the significance of the factor orientation for both KEP and KEO (P = 0.05 and 0.02, ANOVA). As with all selective cells, no statistical difference was found between forward and backward directions of motion (P = 0.11 and 0.38 for KEP and KEO, median P for the entire sample = 0.56, ANOVA) so the data for the two directions of motion were combined. Of the cells...
meeting the response criterion in the KE tests, the forward and backward conditions were statistically equivalent in all but four. None of these were later determined to be KE selective.

However, it was obvious that the majority of V2 neurons did not respond to the orientation of the KE stimuli as 7110 (Fig. 4A) did but reacted instead in patterns characteristic of a local motion response. An example of such a cell, 5604, is shown in Fig. 4B. As with cell 7110, this cell gave strong responses to the KE stimuli (P < 1.0 × 10⁻⁶ for both KEP and KEO) and the factor orientation was again significant (P = 3 × 10⁻⁵ and 2 × 10⁻³, ANOVA for KEP and KEO, respectively). Again, forward and backward directions were statistically indistinguishable (P = 0.88 and 0.35, ANOVA) and were combined for further analysis. In contrast to cell 7110, the parallel and orthogonal responses of 5604 display maxima which are 90° out of phase with one another, just as MT/V5 neurons typically do in responding to local motion (Marcar et al. 1995).

Of the 113 neurons tested in V2, 13 failed to give a statistically significant response in one or both of the KE tests. In an additional 66, orientation was not a significant factor, indicating that the majority of V2 neurons do not show strongly directional- or orientation-selective responses toward the KE stimulus and are probably specialized for other, unrelated tasks. This left 34 neurons with statistically significant responses and orientation selectivity toward the KE stimulus. We were now presented with the task of determining which cells of the neurons in this subgroup were actually responding selectively to the orientation of a kinetic boundary and which were merely responding to local motion as outlined in Fig. 1. Because we essentially wanted to determine whether the actual response of the KEO test is more like that of the KEP or like the KEP rotated 90°, we compared the correlation between the eight positions of the KEP with the eight positions of the KEO and with the KEO shifted by four positions, or 90° (Movshon and Newsome 1996; Movshon et al. 1985). Figure 5A illustrates the results of this analysis for all cells with significant responses and orientation selectivities and plots the correlation coefficient between the KEP and KEO responses along the abscissa. On the ordinate are the correlation coefficients between the KEP responses with the KEO responses rotated by 90°, corresponding to the nonselective condition where preferred KEP and KEO orientations are at right angles to one another. Neurons selective for the orientation of the KE will fall into the bottom right-hand corner of this plot, whereas those responding only to local motion will congregate in the top left. The selective and nonselective cells did indeed occupy well-defined groups in their respective corners of this plot with relatively few lying in the center and thus remaining unclassified. The KEP-KEO correlations of all but 3 of the 13 cells in the selective group proved statistically distinct from the nonselective (shifted) correlation. All 15 of the nonselective cells’ KEP-shifted KEO correlations were statistically distinct from a nonshifted condition. Figure 5B (discussed in the following text in comparing V1 with V2) presents a similar plot of the data obtained from the KE tests in V1.

Figure 6A illustrates the relationship between the preferred orientations of the KEP and KEO stimuli across the population. This figure shows the distribution of the angular differences between the mean angles of the KEP and KEO responses for all 34 V2 cells meeting statistical criteria for response and orientation selectivity. Many differences cluster around 90°, corres-

FIG. 5. Comparison of KEP and KEO responses in V2 (A) and V1 (B). The abscissa represents the correlation coefficient between the KEP responses and the KEO responses at the 8 tested orientations for a given cell. The ordinate represents the correlation coefficient for that cell between the KEP responses and the KEO responses at orientations shifted by 90°. The KEO and the shifted-KEO correspond to the 2 response predictions for selective vs. nonselective neurons (see Movshon and Newsome 1996). In selective cells, the KEP response will strongly correlate with the KEO response at each orientation; in nonselective cells, these two responses will be 90° out of phase. - - - , boundaries of correlations that are significantly different from the opposite correlation; · · · , boundaries of correlations significantly different from 0 (Movshon et al. 1996; Zar 1974). □ (bottom right and top left), arbitrary boundaries encompassing the “selective” group and “nonselective” neurons, respectively. These same criteria were then applied to V1. Response patterns in the 2 cortical areas were compared by taking the absolute value of the difference between the KEP-KEO correlation coefficient and the KEP-KEO (shifted) correlation coefficient for each cell. The distributions of these values proved extremely different (P < 0.10⁻⁶, Student’s t-test).

The 13 cells meeting all our criteria for KE selectivity appear to demonstrate a generalized selectivity for a particular boundary orientation, extending to boundaries defined by lu-
Response properties of V1 and V2 neurons to KE and Luminance stimuli

Logically a neuron that is selective for orientation of a kinetic boundary should respond to such boundaries regardless of the stimulus containing that boundary, although there is some indication that multiple luminance edges may produce responses quite different from those of single edges in some V1 and V2 neurons (von der Heydt et al. 1992). To test the generality of KE selectivity in our sample, 58 neurons were also tested with a grating pattern created by moving random pixel noise. Thirteen of these grating tests met statistical response criterion, including example 7110 (Fig. 4A). It is apparent that selectivity was almost entirely retained for the kinetic gratings in this neuron although the tuning is a bit broader for the grating, particularly in the orthogonal condition, than for the single motion-defined boundary. Of the original 13 selective cells, 7 were also tested with kinetic grating stimuli. While only three of these seven were selective for the KEs of the grating pattern using the same criteria (that is, response, orientation selectivity, and KEP-KEO correlations), as for the single KE, four of the seven had a preferred orientation for the kinetic grating that fell within 15° of that for the single edge and only 1 exceeded 30°. Neurons selective for the single KE thus generally retained their orientation selectivity when presented with kinetic gratings, although selectivity was generally not as strong as that for the single edge. This observation is illustrated by the lower SI values (Table 1) for gratings compared with single edges. Because only a single spatial frequency was tested, however, it may be that this parameter was suboptimal for many of the neurons tested.

KE responses in area V1: a comparison with V2

While a number of neurons in area V2 appeared to be able to respond to the orientation of both kinetic and luminance-defined boundaries, applying the same criteria to the responses of V1 cells yielded far fewer selective cells. Although fully 50 of 107 cells in the V1 sample met the statistical criteria for response rate and orientation selectivity, only 4 neurons proved selective when correlations of KEP and KEO responses were compared with one another (Fig. 5B). It is obvious from Fig. 5 that there is a fundamental difference in the responses of V1 and V2: in the plot of V2 correlations (Fig. 5A), the data points tend to cluster in the top left and bottom right corners, indicating a predominance of neurons that were strongly selective for either the direction of motion or the orientation of the KE, respectively. In contrast, data points tend to cluster in the center of the V1 plot, indicating strong selectivity for neither property. We can quantitatively compare responses in the two cortical areas by taking the absolute value of the difference

![Table 1](http://jn.physiology.org/lookup/suppl/doi:10.1152/jn.1992.711.3.2792/-/DC1/Supplemental_Table1.png)

**Table 1. Response properties of V1 and V2 neurons to KE and Luminance stimuli**

<table>
<thead>
<tr>
<th>Class†</th>
<th>KEP*</th>
<th>KEO</th>
<th>KGP</th>
<th>Lum</th>
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<tr>
<td></td>
<td>All</td>
<td>Sel</td>
<td>NS</td>
<td>NC</td>
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<tr>
<td>V2</td>
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* Definitions for tests are KEP (kinetic edge, parallel), KEO (kinetic edge, orthogonal), KGP (kinetic grating, parallel), and Lum (luminance edge) tests. † All, all cells tested, including those not meeting basic response criteria; Sel, NS, neurons classified as selective and nonselective; NC, those failing to reach minimum response and tuning criteria. ‡ FR indicates median net average firing rates; SI is the median selectivity index. § Kinetic gratings were not tested in area V1.

![Figure 6](http://jn.physiology.org/lookup/suppl/doi:10.1152/jn.1992.711.3.2792/-/DC1/Supplemental_Figure6.png)

**Figure 6.** A: distribution of the angles between the preferred orientations of the KEP and KEO for all cells in V2 (●) and V1 (□) meeting the minimum firing rate and orientation selectivity criteria. V2 displays a bimodal distribution, with narrow peaks at 90° and 0°, whereas V1 shows no particular pattern save perhaps a slight tendency to cluster toward the high end of the range. B: comparison of distributions of the angle between the preferred orientations for the KEP and Lum stimuli in KE-selective cells in V1 and V2. There is a strong preference in V2 for luminance edges that are close to the preferred KE orientation, but no particular pattern is evident in V1.
between the two correlation coefficients for each cell, which in effect, quantifies the tendency of the neuron to show some kind of selectivity. V1 proved quite distinct from V2 in this regard ($P < 1.0 \times 10^{-6}$, Student’s $t$-test).

Differences between areas V1 and V2 are also apparent in the tuning curves of V1 cells, even those that met the criterion for selectivity. Figure 7A illustrates the KEP, KEO and Lum tuning curves for cell 8102, one of the most selective neurons in V1. If we compare these response curves with the V2 responses illustrated in Fig. 4A, the generally lower quality of orientation tuning in V1 is evident from the broader and relatively poorly defined peaks. Nonselective cells in V1, like the example shown in Fig. 7B (cell 5008), on the other hand, tended to resemble those in V2, giving tuning curves for parallel- and orthogonally defined KEs that were $90^\circ$ out of phase with one another.

As well as by the quality of the KE orientation tunings in individual cells, however, V1 and V2 were also distinguished by the relative lack of KE-selective neurons in V1, a distinction confirmed by a $\chi^2$ test ($P < 0.03$) comparing the proportions of such cells in V1 and V2 (13/112 vs. 4/107). The paucity of cells in V1 strongly tuned for kinetic boundaries is illustrated from another standpoint by Fig. 6A, which shows the distribution of the angles between the preferred KEP and KEO orientations. While area V2 showed a pronounced biphasic distribution with a peak at a KEP-KEO angle of zero, this peak was absent from the V1 distribution. Instead there was a broad pattern of responses with a slight bias toward $90^\circ$. Although there were many cells in both area V2 and that appear to respond to local motion (the peaks at $90^\circ$), V2 contains a higher proportion of neurons that are selective for the orientation of the KE, with KEP-KEO angles near $0^\circ$. The preferred orientation of the KEP also exhibited a much higher degree of correspondence to that of the Lum in V2 compared with V1, where the preferred Lum orientation came close to that of the KEP in only one of the four selective neurons (Fig. 6B).

**Properties of KE-selective cells**

Many of the distinctions between V2 and V1 cells are summarized in the average tuning curves (Fig. 8) of the KE orientation-selective and -nonselective cells in the two areas. To create these average curves, the KEP stimulus showing the maximum response for a given neuron was first assigned an orientation of $0^\circ$. All responses to the various orientations of the KE and Lum stimuli were then expressed relative to this orientation. Population averages for each orientation of each stimulus type could now be calculated on the basis of values aligned in this manner. In V2, the average selective cell response showed unequivocal and relatively narrow tunings that shared the same preferred orientation for all boundary types, including the luminance edge. This argues that KE selectivity as we have defined it is a robust property of these neurons and may indicate an ability to extract or combine multiple properties associated with object boundaries. In contrast, the response to a luminance edge was much weaker in nonselective cells with a broad tuning that approximates that of the KEP, but not the KEO, stimulus. The V1-selective cells showed much weaker responses than V2-selective cells, with broad, poorly defined tunings and imperfect alignment of the preferred orientations, particularly with regard to the KEO stimuli. These results substantiate the report of Leventhal et al. (1998) that cells combining multiple edge selectivities are present in V2 but relatively sparse in striate cortex.

Table 1 summarizes the median responses and orientation selectivities of V1 and V2 to the KEP, KEO, KEG, and Lum stimuli. The strong selectivity for the luminance edge in V2-selective cells compared with nonselective cells is again reflected in these median values, which show both a higher firing rate ($P = 0.05$) and a somewhat sharper orientation tuning ($P = 0.07$, Mann-Whitney $U$) as shown by the SIs. This observation perhaps more remarkable considering that neurons were classed as selective or nonselective on the basis of responses to the kinetic stimuli, which have little in common with the luminance edge except the presence of an oriented boundary. No consistent differences were apparent between selective and nonselective cells in V1 with regard to the sharpness of tuning. In V1, Lum responses of KE-selective neurons were about equal to those of nonselective cells and were no more sharply tuned.

From Table 2, it may be seen that KE-selective neurons in V2 showed no obvious clustering in any single cortical layer, although there was significant ($P = 0.01$, $\chi^2$ analysis) tendency
for the deeper layers to be have higher proportions of selective cells compared with layer 2–3. The picture was less clear regarding specific cytochrome oxidase compartments, however, because both selective and nonselective neurons were distributed roughly equally within each of the thick stripe and interstripe compartments. None of the cells lying in the thin-stripe compartment could be classified as either selective or nonselective and may therefore be concerned with attributes not present in our stimuli. No significant differences were observed between V2-selective and -nonselective cells with regard to eccentricity (medians, significant and NS, respectively, $5.95$ and $5.4°$) or the degree of end-stopping (medians, 80 and 92% of maximum response, respectively, at maximum bar length).

Response latencies in V2 neurons

As outlined in the introduction, we had considerable interest in examining the latencies of responses to kinetic and luminance edges because the latency could have much to tell us about the circuitry involved in extracting motion-defined boundaries. CUSUM analysis shows us that the median response latency for the KEP stimulus in V2 neurons is 120 ms for KE-selective neurons, but only 90 ms for nonselective ($P = 2.310^{-2}$, Mann-Whitney $U$). The response to the KEO stimulus gives exactly the same median latencies, 120 and 90 ms, for the two classes. No statistical difference in firing rates for selective and nonselective cells ($P = 0.56$, Mann-Whitney $U$) could be detected that might indicate that relative response strengths contributed to this difference in onset time. Thus there appears to be an inherent difference in the time required for selective and nonselective cells to respond to a stimulus containing a KE.

It could be, though, that the population of cells found to be selective might have inherently longer latencies for some trivial reason having little to do with their selectivity. The median response latency for a luminance edge in both selective and nonselective cells proved to be 60 ms, however, demonstrating that these two classes thus have identical latencies where the extraction of a KE is not involved. The distinction between
KE-selective and -nonselective cells becomes apparent in the length of the time interval required to respond to a KE above that required to respond to a simple static luminance edge. The median difference was only 20 ms in nonselective cells but was 40 ms in selective cells. This “difference of differences” was statistically highly significant ($P = 6 \times 10^{-3}$, Mann-Whitney $U$). The former probably represents the time required to extract simple local motion over that required for the static luminance edge, whereas the latter also includes the additional processing time required to extract the kinetic boundary.

Figure 9 compares the normalized average PSTH for the response to a luminance bar with those to the KEP in KE-selective and -nonselective cells in V2. Actual mean firing rates were 21, 30, and 23 spikes/s for selective, nonselective, and Lum responses, respectively. This figure reiterates the findings using the CUSUM method: the average response to a static luminance bar clearly preceded the response to the KEP stimulus in both selective and nonselective neurons, with longer average delays, totaling about 50 ms later, in the selective neurons. The slower responses to KE stimuli compared with the Lum stimuli in the V2 population again suggest that the KE response requires feedback from higher areas, particularly in cells that must also signal the orientation of a KE.

**DISCUSSION**

We have shown that area V2, an early component of the ventral stream, contains neurons that appear to be able to extract a boundary defined exclusively by motion and that are tuned for the orientation of that boundary. At the other extreme of the ventral pathway, area IT has been found to contain neurons that are able to respond selectively to shapes defined solely by motion attributes (Sáry et al. 1993) or that are tuned for the orientations of kinetic gratings (Sáry et al. 1995). Selectivity for motion-defined boundaries may thus be a general property of neurons throughout the length of the ventral stream.

**Orientation selectivity for KEs in areas V1 and V2**

Our results show that area V2 is distinguished from other early visual areas, such as V1 and MT/V5, in possessing neurons with a clear selectivity for kinetic boundary orientation. While investigations using visually evoked potentials (Lamme et al. 1993) and fMRI (Reppas et al. 1997) have shown that area V1 can be activated by stimuli containing kinetic boundaries, an activation by stimuli containing such boundaries does not necessarily imply that individual cells in V1 are capable of signaling their orientations nor even that V1 is responding in any specific way to those boundaries. Indeed the activations obtained in V1 (Reppas et al. 1997) do appear distinct from those in V2, V3, and V3A, insofar as V1 was maximally activated by highly segmented stimuli containing up to 40 boundaries at as many different orientations, whereas the other three areas preferred stimuli containing a limited number of such boundaries. This further suggests that the weak KE-orientation selectivity we observe in V1 may be qualitatively as well as quantitatively different from that we observe in area V2. A recent study comparing boundary perception in V1 and V2 (Leventhal et al. 1998) has confirmed the existence of neurons, abundant in extrastriate regions but rare in striate cortex of both cats and monkeys, that are capable of integrating multiple cues to signal boundaries in a cue-invariant manner. It is difficult to compare percentages of cue-invariant cells in that study to our KE-orientation selective cells, however, because exact percentages were not reported.

There is widespread agreement that high proportions of orientation-selective cells occur in both the thick-stripe and interstripe compartments of V2 with relatively few in the thin stripes (DeYoe and Van Essen 1985; Gegenfurtner et al. 1996; Hubel and Livingston 1987; Peterhans and von der Heydt 1993; Roe and Ts’o 1995; Schoups et al. 1995; Shipp and Zeki 1985; Tootell and Hamilton 1989; Ts’o et al. 1990). This would seem to fit the pattern we find because all selective (and nonselective) cells were confined to the thick- and interstripe compartments. It is interesting to note that the highest proportion of KE-selective neurons were observed in the interstripe regions, which send projections further into the ventral stream where kinetic and luminance boundary orientation information characteristically associate to produce shape selectivity (Sáry et al. 1993). Even within the interstripe subcompartment, however, it appears unlikely that all the neurons are concerned with processing KE attributes. Of the 48 neurons recorded in the interstripe regions, the response to a luminance edge of 18 could be considered as orientation selective (SI > 15), but only 9 of these were also selective for the corresponding KE. The remainder of the orientation-selective interstripe neurons may be concerned with comparing luminance boundaries with those defined through other means, such as texture or color, or may deal with some other aspect of orientation.

**Response onset latencies in V2**

The long latencies of KE responses in KE-selective cells compared with those of nonselective cells are consistent with the notion that such selectivity entails additional signal processing, involving either feedback from higher areas, or complex local circuits and lateral interconnections within V2 itself. In this regard, Tomita et al. (1999) have shown in single-cell recordings of monkey inferior temporal cortex that increased latencies are characteristic of a top-down, driving input of the sort we propose here. The term top-down denotes feedback initiating spike events in a given area that arrives from hierar-
chichically higher areas as opposed to the more common bottom-up input elicited by hierarchically lower areas. Feedback consisting of driving input should not be confused with modulatory feedback that modifies only the amplitude of an existing response without altering the onset latency (Hupe et al. 1995; Lamme 1995; Lamme et al. 1998). The 30- to 40-ms delay that we observed in KE-selective over -nonselective responses in V2 visual cortex is shorter than the 50–100 ms reported by Tomita et al. for feedback from frontal to inferior temporal cortex, but this may simply relate to the shorter physical or synaptic distances involved. An argument that the KE-selective responses are driven by the same sort of top-down feedback, rather than by local circuit interactions within V2, is that locally produced delays would tend to be perpetuated up the hierarchy and should still be present at the level of IT. Were this to be the case, then different boundary types would result in different latencies at that level, contrary to actual observations in IT (Sáry et al. 1995).

Other factors, such as firing rate (Maunsell and Gibson 1992; Raiguel et al. 1999) and stimulus contrast (Gawne et al. 1996) have been shown to affect response latencies under some circumstances. Methodological errors in the CUSUM method, where signal (response)-to-noise (spontaneous firing rate) ratios might influence the calculation of onset times, can be ruled out immediately: the luminance edge produces response levels twice as high in KE-selective cells compared with nonselective, yet give identical median latencies of 60 ms. It will also be noted that the histogram data (Fig. 9), which is independent of such artifacts, shows results virtually identical to those obtained by the CUSUM method. While the relatively high contrast of the luminance stimulus might partially explain why this stimulus generates a shorter response time than the KE stimulus, it cannot explain the statistically significant 20-ms difference between selective and nonselective cells with regard to the length of the delay between the onset of a luminance response and the onset of a KE response.

**Possible site of KE extraction**

Because we observed very few KE-selective cells in V1 and latencies suggest that the KE selectivity in V2 arrives there via feedback, it is unlikely that kinetic boundary information is actually extracted in either of these early visual areas. This points to the alternative interpretation, whereby motion information is introduced into the ventral pathway at some point from the dorsal pathway. Certainly there is abundant anatomical (Colbey et al. 1988; Distler et al. 1993; Hof et al. 1996; Perkel et al. 1986; Rockland et al. 1994; Shipp and Zeki 1989; Ungerleider and Desimone 1986; Zeki and Shipp 1989) and physiological (Hupe et al. 1998) evidence for feedback to V2 from a number of higher extrastrate areas, including area MT/V5 (Shipp and Zeki 1989; Ungerleider and Desimone 1986). MT/V5 seems an unlikely source of this information, however, since previous studies have shown area MT/V5 is not crucial for the extraction of kinetic boundaries (Lauwers et al. 2000; Marcar et al. 1995). Another dorsal stream component, such as area V3, may carry out the initial motion analysis. V3 does in fact contain many direction-selective cells (Gegenfurtner et al. 1997), and has been shown to project to area V4 (Felleman et al. 1997), a dorsal-stream component. Human area V3A responds to motion (Tootell et al. 1997) and both V3 and V3A have been reported to be activated by motion boundaries (Reppas et al. 1997). However, human V3 and V3A are clearly distinct from KO (Van Oostende et al. 1997). Thus the ultimate source of the kinetic boundary signals may have to await the identification of the lower-primate homologue of area KO, whatever that may prove to be. In lower primates, V4 performs many form-related tasks (Desimone et al. 1985) and may have a modular organization (Zeki and Shipp 1989) thus could conceivably contain a proto-KO, which appears in fully differentiated form only in humans. Recent work using fMRI and double-label 2-deoxyglucose autoradiography in monkeys suggests that this may indeed be the case (Nellissen et al. 2000).

Whatever its source, the absence of any real difference in the latencies of IT neurons responding to either motion- or luminance-defined boundaries implies that KE information must be integrated into the ventral pathway at a point (Y in Fig. 10), where its latency is similar to that of the luminance response. Moreover, this point must lie downstream from area V2 where we find that the latency of the KE response is greater than that of the luminance, presumably as a result of having been relayed back upstream to V2 from the entry point. This entry point must also lie somewhere in the “middle level” of visual cortex that includes V4 and surrounding areas. Hypothetical pathways between the area extracting kinetic boundary information and V2 may thus comprise other areas in addition to V4. The fact that the latency difference between KE and Lum latency for KE selective V2 neurons is relatively small indicates there could be only one or two such areas. There remains at least one other possibility that cannot be entirely dismissed. It is possible that local interactions within V2 could account for latency differences in KE and luminance responses and that circuitry downstream could later compensate for the timing disparities between the two so that both types of boundaries ultimately produce similar latencies in IT. Although we have speculated that mechanisms may exist that fine-tune the temporal relationships of moving stimuli to preserve their proper spatial relationships despite processing delays (Raiguel et al. 1999), it is difficult to see the utility of a similar system for static edges.
Role of KE information in lower-order visual areas

At this point, it is reasonable to question why a lower-order area such as V2 should have any need of kinetic boundary information extracted at some higher cortical level. One plausible explanation that is particularly attractive, considering that the luminance boundaries usually match the KE boundary in KE-selective V2 neurons, is that these cells may help disambiguate object edges that are partially obscured by surface markings and sharpen KE information by merging it with the abundant positional information concerning luminance edges that is available at this level. The merging of several cues (Leventhal et al. 1998) might explain why kinetic boundaries appear to look distinct despite being potentially derived from coarse, motion-processing RFs. Psychophysical studies confirm that the spatial properties of kinetic boundaries, such as vernier sensitivity, are as precise as those for luminance-defined boundaries (Regan 1989; Regan and Hamstra 1992) and that boundaries can be more precisely localized when multiple cues can be utilized (Rivest and Cavanagh 1996). On the other hand, more mundane, computational functions of the KE feedback to V2, such as holding the multiple attributes of a single retinal locus in register with one another, are also conceivable. Whatever the exact function of the KE orientation selectivity of V2 neurons may ultimately be, the presence of this and other higher-order contour selectivities, such as that for illusory contours (von der Heydt and Peterhans 1989), makes V2 unique among early visual areas.

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