Does image movement have a special nature for neurons in the cat's striate cortex?

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The question of whether a moving image is especially effective for stimulating visual neurons was studied in the striate cortex of the cat. Receptive fields (RFs) of simple and complex neurons were stimulated with optimally oriented bright and dark bars that either moved smoothly or were presented statically at an array of positions across the RF. A linear prediction of responses to the smooth movement was calculated by superposition of the responses to stationary presentation of these bar stimuli. A comparison between responses to actual movement and their prediction showed that the relative effectiveness of a moving stimulus decreases with speed. Effects of "conditioning" stimuli and nitrous oxide anesthesia were also studied. Both simple and complex units exhibited on average slightly lower than predicted responses for both bright and dark bars, even when they moved in the preferred direction of the unit. Movement in the opposite direction usually elicited even lower response levels, suggesting nonlinear suppression. These results imply that a moving image has no special efficacy for visual neurons but rather that it has a special propensity to elicit suppression when it moves in the nonpreferred (null) direction of a neuron.

Key words: image movement, receptive field, neural response, visual cortex, stationary bar presentation, linearity, directional selectivity, cat

Image movement has been considered by many investigators to have special efficacy for stimulating neurons, especially in the visual cortex of the cat. Such efficacy implies that responses in these neurons to moving images should exceed predictions based on other known receptive field (RF) properties. We have been studying the feline visual cortex to determine whether either simple or complex units might exhibit special sensitivity to moving images and whether differences in the way they process information about image movement might correlate with expected differences in other RF properties. For example, complex units have brief and supposedly weak responses to stationary presentations of (static) bar stimuli, and yet they respond briskly to bars moving at relatively high speeds. Simple units, on the other hand, give sustained responses to static bar presentations and respond poorly at stimulus speeds greater than about 20 deg/sec. These temporal differences suggest that in simple units, responses to movement might be highly predictable from stationary properties whereas in complex units, movement may have a special significance in terms of its potency for driving these neurons.
responses to static and moving stimuli. Our approach differs from those of others mainly in that we have constructed linear predictions for moving stimuli (bright and dark bars) using actual responses to isolated static presentations of the same stimuli obtained at close spacing across the RF. We then compared these movement predictions with responses to real movement, not only in terms of shape of the response as a function of position in the RF but also in terms of absolute firing rate. Such a comparison of firing rates requires that at the time of the experiment measurements of responses to both static and moving stimuli be interleaved with each other to cover the same time period; otherwise, drifts in eye position and fluctuations in excitability may differentially affect the two measures.

Data gathered in this way afford a direct test of the efficacy of moving stimuli and also illustrate unpredictable consequences of image movement such as directional selectivity. The expected result was that complex units, and perhaps simple units also, might exhibit higher than predicted peak firing rates for bars moving in the preferred direction, thus suggesting a specially effective nature of movement. Instead we found that in most simple units, and in even more complex ones, responses to movement fell short of predictions based on static responses. Some of these results have been reported briefly elsewhere.  

Methods

We recorded three or four times from adult cats that had been prepared at least 1 week previously for long-term investigation. At that time we mounted a rectangular brass tube onto the frontal bone for painless head support in stereotaxic coordinates. A stainless steel chamber was also mounted over the occipital cortex and sealed with Silastic elastomer (Dow Corning).

Prior to each recording session brief anesthesia was induced by 20 to 30 mg/kg intravenous sodium thiopental. Standard techniques, including reversible intubation and paralysis with 8.4 mg/kg/hr intravenous gallamine triethiodide (Flaxedil; Davis & Geck, Div. American Cyanamid Co., Princeton, N. J.), were used to stabilize the cat and maintain respiratory CO2 and body temperature within normal range. The electrocardiogram and in some experiments the electroencephalogram were continuously monitored to assess the state of the animal. The striate cortex was exposed via trephine, and after removal of dura the microelectrode guide tube was placed visually, and the chamber was sealed with agar and a dome of wax.

Contact lenses were used to protect corneas, and accommodation onto a tangent screen at 115 cm (2 cm/deg subtense) was adjusted with trial-case lenses and a retinoscope. Optic discs were plotted through dilated pupils, either with an optical system that brightly illuminated the retinal region around the optic disc or later with a fiber optic approach.

During a few early experiments we used a 70:30 mixture of N2O/O2 while we recorded units. In preliminary comparisons between ventilation with N2O/O2 and room air we noticed characteristic changes in spontaneous firing rate and variability of responses that seemed to reduce the distinctiveness of responses (reported elsewhere). Because of this reduction in the signal-to-noise ratio we suspended general use of N2O during unit recording, but we have presented here a comparison of results with and without N2O.

After the last experiment the animal was sacrificed, and the brain was fixed in place. Location of penetrations in (striate) area 17 was ascertained by a combination of cortical topology, following the sequence of RF positions in maps of Tusa et al. and histology aided by 20 μAmp × 20 sec electrolytic lesions. In 12 animals 40 μm cresyl violet-stained sections were used to reconstruct electrode tracks and corroborate other findings. Units in these animals constituted 74% of the sample considered here.

Unit search procedure and visual stimuli. We began to search for orientation selective units in upper cortical layers while projecting a 35 by 40 deg oscillating and slowly rotating 0.33 cycle/deg square-wave grating onto the tangent screen. The large size of this pattern precluded our finding units with significant peripheral field suppression, but it is unlikely that exclusion of such "hypercomplex" units has altered our population statistics materially, because of recent demonstrations that this suppression occurs independently of other RF properties.
After finding a unit, we occluded the less effective eye and hand plotted on the tangent screen the minimum response field. We then centered upon it the optical axes of four computer-controlled projectors, the selection of which was designed to determine quantitative RF classification and predictability of information from moving images. Bright portions of images had a luminance of 5.4 to 6.8 cd/m², and dark portions had a uniform luminance of 1.7 to 1.1 cd/m², providing a contrast ratio of 0.5 to 0.8 log units. The lower contrast values were used in an attempt to avoid saturation-type nonlinearities in comparisons of movement responses with linear predictions.

Positions, durations, and sequence of visual stimuli were controlled by a specially modified LINC-8 computer. We began machine-plotting by obtaining a quantitative estimate of the preferred direction and orientation of a unit. The computer rotated an oscillating 0.33 cycle/deg square-wave grating to sample directions of broadside motion until we obtained a function covering a full 360 deg in 5.6 deg steps. We set the direction and orthogonal orientation for all subsequent stimuli using the peak of this function.

Edges and bright bars were presented at the preferred orientation by two separate projectors with shutters and with mirror galvanometers that always moved the stimuli broadside across the RF. Dark bars were presented by a third (two-dimensional) projector that, in addition to the X-axis mirror galvanometer that controlled broadside position, used a Y-axis mirror galvanometer to rapidly introduce and withdraw endwise a dark bar that was limited on one end. The homogeneity of the surrounding luminance was carefully adjusted to avoid transition artifact as the bar and surround were moved 15 deg at 5500 deg/sec (central 12 deg in 2.2 msec).

The fourth projector was a computer-gated film-strip projector that could project low-contrast, 0.5 cycle/deg square-wave gratings always adjusted to drift in the preferred direction. This "conditioning" stimulus was used to increase asynchronously the neural background firing rate by 1 to 15 Hz for better assessment of units with strong inhibitory response phases.

To obtain a quantitative basis for classifying RFs, we selected a size of RF region to be stimulated and used the computer to present an interleaved and repeating sequence of stimuli consisting of (1) a bar moving at two effective velocities having a ratio of 4 and chosen from the five already presented and (2) static presentations of the same bar at 29 closely spaced RF positions and at two durations designed to match the speeds used: (position increment)/ (duration) = speed. In later experiments we interleaved presentations of a bar moving at the same average speeds but in stepwise or "jerky" fashion, using the same RF position increments and durations as above.

Data recording. Microelectrodes of tungsten in glass were used throughout. We measured impedances in the cortex at between 15 and 35 megOhms, using current injection at 60 Hz. After amplification with a field-effect input differential amplifier, unit responses were displayed on an oscilloscope and, when necessary, were separated from one another on-line with an amplitude window-discriminator. Voltage-level crossings were converted into standard pulses which the computer used to produce and display on-line peristimulus time (PST) histograms of growing response patterns.

Results

We studied cortical areas 17 and 18 of 15 adult cats in 41 separate experiments. Attention here will be restricted to (striate) area
Fig. 1. Responses to moving and stationary bars in a simple and a complex striate unit. A to C, Simple unit 276-2. A, Responses to optimally oriented bright bar moving smoothly rightward (upper bars) and leftward (lower bars; note arrowheads) at 0.73 deg/sec through 12 deg (x). Numbers at left are firing rate (r) calibrations in impulses per second (Hz) away from central zero line (upper and lower scales always equal). Short lines above and below are photocell markers which indicate width and position of bright bar with respect to the RF. Large RF is associated with large retinal eccentricity (6.7 deg). B, Hand-plotted minimum response field as appeared on tangent screen. Scale of vertical distance (y), horizontal position (x), and scale of horizontal distance correspond to those of horizontal axis in histogram above. Arrows indicate preferred direction (always adjusted to the right in this paper). Broken bar shows width of stimulus. C, Three-dimensional response surface ("plane") showing responses to stationary bar presentations at 29 RF positions separated by 0.375 deg. Horizontal axis represents time (t) during stimulus cycle (heavy bar corresponds to stimulus-on period: 512 msec), vertical axis represents average firing rate (r) in Hz, and slanting axis represents space (x) in 29 discrete steps. Bent arrows connecting with A and B show spatial correspondence. Horizontal arrow indicates photocell position. Vertical and horizontal lines at bottom indicate responsivity and time calibrations. Lowest histogram represents stimulus-free period: spontaneous rate, 2.3 Hz. D to F, Complex unit 254-3. D, Responses to a smoothly moving bright bar as in A. Speed was 1.46 deg/sec through 6 deg. RF was within 2 deg of the area centralis. Other conventions as in A. E, Hand-plotted minimum response field as in B. F, Static responses as in C. Stimulus on, 512 msec; position increment, 0.188 deg; spontaneous rate, 7.5 Hz.

17, although preliminary results indicate no significant differences in conclusions for area 18. The present results are drawn from 190 simple and complex striate units (see Methods for criteria) identified in 34 experiments involving area 17.

We limited detailed analysis to a smaller group of 69 units about which we had sufficient information to classify as simple or complex, and to compare responses to moving and static stimuli. Units in the larger group were eliminated mainly because of in-
Fig. 2. Construction of a linear prediction for smooth movement of simple striate unit 257-5, by superposition of stationary responses. A, Static responses exhibiting weak bright-off excitatory, strong bright-on excitatory, and very weak bright-off excitatory responses. Stimulus on, 512 msec; position increment, 0.125 deg; spontaneous rate, 7.2 Hz. For other conventions see Fig. 1. B, Responses at three consecutive positions have been placed in a staggered temporal relationship that represents responses to sampled (stepwise) smooth movement at a velocity = (position increment)/(stimulus duration). Vertical (rate) scale has been expanded to agree with that of C and D below. When these are added vertically (note arrows) it is necessary to subtract the extra spontaneous activity that results from doubly represented temporal overlap in adjacent responses. C, Partial superposition that corresponds to the central portion of D before being corrected for the bin width in D and E. The bent arrows between C and D indicate compression of number of bins and correspondence of position. D, Complete linear superposition for both directions of travel (see arrowheads) for the bright bar used in A. Stimulus marker (dark horizontal line) corresponds to the three positions at which the bar illuminated the photocell. The zero ordinate has been separated from the center to accommodate negative firing rates produced by subtracting spontaneous rate. E, Responses to actual smooth movement of the same bright bar at the simulated velocity (0.24 deg/sec) through 4 deg. Effectiveness ratios (see text): preferred direction, 0.76; null direction, 0.56.

Complete data or poor overall signal-to-noise ratio. Only three units failed because of poorer responses to static than to moving stimuli, and another two failed because of poorer responses to moving stimuli. We find, in general, that if one records PST histograms of responses to static stimuli, such responses, although sometimes very brief, are almost always as reliable as those to moving stimuli.

We compared statistically responses to moving and statically presented stimuli having a variety of characteristics, to assess under what conditions smooth image movement might have unpredictable consequences in simple and complex units: bright- vs. dark-bar stimuli, movement in preferred vs. non-preferred, or "null," direction, with vs. without a conditioning stimulus, with vs. without N₂O, and over a wide range of speeds. A description of the measured RF properties and of our movement prediction precedes those comparisons.
Responses to moving and stationary bars. Fig. 1 illustrates typical results from striate experiments in which moving and static presentations of optimally oriented bright bars were interleaved, on the left for a simple unit and on the right for a complex unit. Hand-plotted minimum response fields in B and E illustrate the shape of the RF and the relative width of bright bars used in quantitative tests. A and D show responses to the bars as they moved back and forth across the RFs, upward-pointing bins for rightward motion (note arrowheads) and downward-pointing bins for leftward motion (conventions of refs. 5 and 7 but rotated clockwise 90 deg). The reversal in direction of time affords a direct up-down comparison between the location of responses in space for the two directions of motion. The centered dark lines above and below histograms are photocell markers that are stored during the experiment as one bit of each data bin (see also ref. 4). In Fig. 1 they indicate width of the bright bars and correspondence of position.

The complex unit on the right (D) showed a rather uneven response to movement of a bright bar in either direction, with a slight preference for rightward motion. The simple unit on the left (A) exhibited clearly bimodal responses, especially for the preferred, rightward direction. The RF structure underlying such bimodal responses to a moving bar is not evident from results of this sort of test alone. Bimodality could result from two strong bright-on excitatory regions equidistant from the photocell position, but there are other possibilities.

Such uncertainties are usually resolved by three-dimensional plots of responses to a spatial sequence of static presentations of the same bright bars, as shown in Fig. 1, C and F. These plots, called "response planes" by Stevens and Gerstein, give a relatively complete characterization of the static RF properties of a unit. They are also a form of spatial impulse function or, in this case, line-weighting function in that they are measured with a long, relatively thin bar. The three-dimensional response surface (we shall use the term plane to comply with previous terminology) is constructed of 29 individual PST histograms of responses to these bars, presented at evenly spaced RF positions along a spatial axis directed into the plane of the figure. The horizontal axis denotes time within each stimulus cycle (dark bar indicates stimulus duration). The vertical axis denotes average firing rate (note calibration at bottom in spikes/sec). The bent arrows indicate spatial correspondence between the three different plots, the middle arrow denoting the photocell position.

The response plane shown in C indicates that the bimodal response to rightward bright-bar motion (A) for this simple unit resulted from a strong bright-on excitatory region to the left of the photocell and a bright-off excitatory region nearly centered on the photocell. Therefore the righthand peak in A was chiefly dependent on bright-off excitation elicited by the trailing edge of the bar leaving the region near the photocell rather than the suggested possible bright-on excitation when the bar moved into the region to the right of the photocell. This unit thus fits the description of Hubel and Wiesel as a simple neuron with only two antagonistic adjacent regions; or, considering the weak bright-on excitatory region to the right, possibly with a bright-off excitatory region surrounded by bright-on excitatory flanks of very uneven strength.

Responses of the complex unit shown in F agree with the Hubel-Wiesel description of complex units in that the unit exhibited both bright-on and bright-off excitatory responses across most of its RF. Although such responses could not result from a process that was linear with respect to intensity (because responses to stimulus onset and removal were not of opposite sign), it remains an open question whether an accurate prediction of responses to smooth movement could be produced from these static responses.

Construction of a linear prediction for movement. We wanted to construct a prediction of responses to bar movement that would take into account the measured properties at each of 29 RF positions alone (as in Fig. 1, C and F) but would exclude nonlinear interactions between RF regions that might occur...
Fig. 3. Comparison between responses to smooth movement and their linear predictions in simple striate unit 278-5. A, Static responses exhibiting bright-off excitatory responses to the left of bright-on excitatory responses. Stimulus on, 128 msec; position increment, 0.188 deg; spontaneous rate, 0.0 Hz. Other conventions as in Fig. 1, C. B, Responses to actual smooth movement of the same bright bar at 1.46 deg/sec through 6 deg. Other conventions as in Fig. 1, A. C, Linear prediction of smooth movement response for same bright bar as above. Note similarity to smooth movement responses in B for position, shape, and amplitude of response to rightward movement. Effectiveness ratios: preferred, 1.12; null, 0.39. Other conventions as in Fig. 2, D.

during actual movement. Our first guiding principle was that the prediction should accurately represent the average speed of smooth movement, requiring static data with shorter durations at each position for higher speeds (position increment divided by bar duration equaled speed). Because of the limited number of positions measured, we were limited to predicting responses to stepwise or jerky movement. Such a prediction represents responses to smooth movement in the same sense that a movie portrays movement. At durations and position increments less than a critical value for each neuron, responses to the two stimuli should be indistinguishable.

Fig. 2 illustrates for a simple striate unit how individual responses (B) to static bright-bar stimuli at the central three positions of a response plane (A) were added sequentially, so that the response to the removal of the bar from one position coincided in time with the response to the onset of the bar at the next position (mimicking jerky movement). Be-
cause responses during the stimulus-off period were added vertically (note arrows in B) to those from the following stimulus-on period, the extra spontaneous firing activity during the doubly represented period of overlap had to be subtracted. Spontaneous rate was independently assessed from the lowest histogram of A, measured during a stimulus-free period.

The resulting summation, shown in C, represents the linear prediction for jerky bar movement from left to right across the central three positions of the region covered by histograms of A. The prediction excludes nonlinear effects because it includes data only from single position tests rather than from actual jerky movement.

Since bar width was roughly optimized by hand for each unit, the bar width sometimes exceeded the distance between successive static presentations, which reduced the independence of adjacent histograms in planes like A. Photocell stimulus markers (not shown in B) were carried through the calculation and in this case show that the width of the bright bar equaled the distance of three position increments, the photocell being centered on the position with an arrow in A. This spatial overlap did not affect the validity of the linear prediction for movement, however, because of a second guiding principle that each point in the RF should experience the same increased total duration of illumination (constant energy), whether by contiguous multiple short flashes as in the prediction of C and D or by a single long period when the wide bar moved smoothly across as in E.

Fig. 2, D, shows results of sequential addition for both directions of movement across the complete RF. Bent arrows between C and D indicate the corresponding regions of the partial and complete superpositions, respectively. Note that data of C are compressed into a smaller number of bins in D to compare with those in E and that only the upper bins of D correspond to the left-right direction illustrated in C. Subtraction of overly represented spontaneous activity often allowed negative (inhibitory) response predictions, although negative regions were never very significant. To account for these brief fluctuations around zero, the zero rate ordinate (clear line through data) was offset from the baseline in D and E.

For comparison with the prediction of D the responses to actual bar movement at the mimicked velocity are shown in E, with the same time and responsivity scales. The temporal compression between A and B and between C and D always created bin durations in D that were identical to those in E, allowing the closest possible qualitative and quantitative comparison between the response to smooth movement and its prediction. For the preferred direction (upper bins) both shape and absolute magnitude of the response functions were similar, with the exception of periodic peaks in D that were associated with the initial transient component of responses to static stimuli. It is evident that the temporal and/or spatial stimulus increments of this jerky movement prediction were not small enough to exactly represent smooth movement. The overall similarity in response, however, indicates that in the preferred direction of this simple unit, responses to smooth movement of a bright bar were relatively well predicted from a linear superposition of static presentations, even though the spatial resolution of the prediction was rather coarse. For the null direction of E, however, the firing rate was considerably lower and differently distributed than the prediction in D, further supporting previous proposals\textsuperscript{5-24} that directional selectivity depends heavily on nonlinear suppression generated for bar movement in the null direction. We use the term suppression here rather than inhibition because this nonlinear effect can occur in the absence of postsynaptic inhibition in the neuron being measured (see Discussion, Emerson and Gerstein\textsuperscript{5}).

**Linearity assessments in simple units.** We constructed predictions of responses to movement for a total of 47 simple units, including that of Fig. 2. Comparisons of predictions with responses to movement in three more examples of simple units are illustrated below.

**Bright bars.** The first example, shown in
Fig. 4. Comparison of responses to smooth and jerky movement with their linear prediction in simple striate unit 311-4. A, Static responses exhibiting bright-off excitatory, bright-on excitatory, and bright-off excitatory responses. Stimulus on, 32 msec; position increment, 0.25 deg; background rate increased by asynchronous drifting ("conditioning") grating, 8.1 Hz. Other conventions as in Fig. 1, C. B, Responses to smooth movement of the same bar at 7.81 deg/sec through 8 deg. Other conventions as in Fig. 1, A. C, Responses to jerky movement of the same bright bar with the same stimulus duration and position increment as used in A and in the superposition below in D. The average velocity is the same as for smooth movement in B. This test represents a more direct comparison with the superposition in D than smooth movement. It differs from D in that the stimulus remained on the tangent screen rather than turning off between presentations to allow recovery as in A and D. D, Linear prediction of responses to jerky (and smooth) movement of the same bright bar as above. Smooth/predicted effectiveness ratios: preferred, 0.47; null, 0.18. Other conventions as in Fig. 2, D.
Fig. 3, is a simple unit that exhibited one strong bright-off excitatory region to the left of a single strong bright-on excitatory region (see A). Smooth movement of the same bright bar at 1.46 deg/sec elicited rather asymmetric (directionally selective) responses, showing in B a preference for rightward motion. This sort of static RF asymmetry is very common in simple units (see Fig. 1 of Emerson and Gerstein) and was used by Hubel and Wiesel to explain stronger responses to stimuli moving in the preferred direction on the basis of "... the synergistic effects of leaving an inhibitory area and simultaneously entering an excitatory one..." Indeed, the linear prediction (C) shows that although the same number of impulses was expected for movement in either direction, the order of response components produced an expected higher maximum rate for rightward motion; and in this case there is reasonable agreement with rate of responses to smooth rightward motion shown in B. The prediction shown in C also illustrates that nonlinear suppression during smooth leftward motion completely eliminated the expected lefthand bright-off excitatory response but did not affect the righthand bright-on excitatory response. (For a discussion of spatial and temporal properties of this nonlinear mechanism see Emerson and Gerstein). Fig. 4 illustrates results of a similar comparison for a simple unit that had a central bright-on excitatory region flanked on either side by bright-off excitatory regions (A). In this case we used a rightward-drifting low-contrast (0.07 log unit peak-trough) "conditioning" grating to increase the average background firing rate by about 8 impulses/sec for better assessment of inhibitory response phases (see Methods). Responses to smooth movement of a bright bar at 7.81 deg/sec, shown in B, demonstrate a unimodal response for either direction of motion and, on either side of the main response, show depressions in firing rate that extend somewhat below the artificially increased background firing rate of 8 Hz. Such inhibitory regions, often called "sidebands," are considered by Sherman et al. to be diagnostic for simple units. These inhibitory regions are associated with the bright-off excitatory flanking regions in A. Inhibition in this case was probably caused by onset of the bright stimulus, suggesting the possibility that rebound from inhibition may be the cause of excitation when turning off a static stimulus. Weak bright-on inhibition in response planes of Figs. 1, C, 2, A, and 4, A, appears as a flatter region preceding bright-off excitatory responses.

In this experiment we also moved the bar through the RF in a stepwise or jerky fashion at the same average velocity as in B but with the same position increments as in A. The similarity, both qualitatively and quantitatively, between responses to this sequence shown in C and responses of B indicates that this unit did not distinguish readily between jerky and smooth movement at this speed. Although the linear prediction shown in D, as mentioned above, was strictly a prediction of responses to jerky movement shown in C, similarity between B and C made the prediction also a good test of linearity in B. The shape of the prediction agreed approximately with responses to smooth movement in the preferred direction. As in previous examples, however, movement in the null direction elicited response levels far lower than predicted. This unit shared the property with many others that responses to movement in the preferred direction also fell short of predicted levels by a factor of about 2 (note vertical scale difference). Such a discrepancy cannot be explained adequately by unrepresented inhibition in static responses (i.e., neurons cannot fire at negative rates), since in many units the conditioning guaranteed a nonzero response rate for all regions of the response plane.

Dark bars. A final example of a simple unit is given in Fig. 5 to show that analysis with dark bars provides results comparable to that using bright bars. The response plane in A shows that this unit displayed a weak dark-off excitatory region to the left of a dark-on excitatory region, although the left off-responses were much stronger when we used longer stimulus presentations (not shown). This general trend in the data suggests that
Fig. 5. Comparison of responses to smooth and jerky movement of a dark bar with their prediction in simple striate unit 320-5. A, Static responses exhibiting weak dark-off excitatory responses to the left of dark-on excitatory responses. Stimulus on, 32 msec; position increment, 0.25 deg; conditioned background rate, 5.1 Hz. Other conventions as in Fig. 1, C. B, Responses to actual smooth movement of the same dark bar at 7.81 deg/sec through 8 deg. Note complementary stimulus marker. Other conventions as in Figs. 2, E, and 1 A. C, Responses to jerky movement at the same average velocity as above in B. Other conventions as in Fig. 4, C. D, Linear prediction of responses to jerky (and smooth) movement of the same dark bar as above. Smooth/predicted effectiveness ratios: preferred, 0.72; null, 0.16. Other conventions as in Fig. 2, D.
there was a minimum duration of presentation required to elicit off excitation (again, a possible rebound whose magnitude depends on duration of on-inhibition). This unit also was conditioned with a drifting grating (of higher luminance to compensate for higher luminance surrounding the dark bar). Responses to smooth and jerky dark bar movement at 7.81 deg/sec, shown in B and C, illustrate that this unit preferred the statically predicted rightward direction of motion and that at this velocity it responded similarly to the two modes of movement. (Note that the stimulus marker is complementary to those of other figures). As in the previous unit, responses to movement in the preferred direction agree in shape but fall short of the predicted peak firing rate shown in D. As in the unit of Fig. 5, bar presentations of longer duration elicited stronger and more widely distributed bright-off excitatory responses (not shown). Conditioning was usually not necessary in complex units because spontaneous activity was more vigorous than in simple units.

Smooth movement of the same bright bar demonstrated a preference for rightward movement as shown in B. Jerky movement of the bar as shown in C elicited responses exhibiting the same directional preference but with a clearer response to each rapid stepwise movement than shown in previous examples. This serrated appearance of responses to jerky motion was common in complex units and probably associated with highly transient responses to static stimuli. There seemed to be sufficient information in the spike train of most complex units to easily distinguish between smooth and jerky movement, whereas in simple units the distinction would be more difficult to make. Finally, the prediction in D for the preferred direction has the same general shape as in both B and C, but again with the serrated appearance of C only. As in some simple units, the predicted rate of firing in some complex units agreed well with that elicited by smooth movement; however, in many other complex units such as the unit in Fig. 6, the predicted rate of firing shown in D clearly exceeded the obtained rates in B and C.

Thus smooth and jerky motion even in the preferred direction were at a disadvantage as compared with the prediction for this complex unit. As usual, responses to movement in the opposite direction fell short of the prediction by an even larger margin, indicating that nonlinear suppression operates in directionally selective complex units as well as in simple units.

Effects of varying stimulus parameters. We varied stimulus direction, speed, and sign of contrast to assess the effects of these parameters on how well we could predict responses to movement from responses to static bar presentations. Effects of nitrous oxide and conditioning stimuli were also tested. Table I lists the ratios of actual/predicted peak firing rate for simple and complex units as they were stimulated by bars moving in both the preferred and null directions. We were able to use a single (peak) measurement for comparison because the shapes of the actual and predicted curves, at least for the preferred direction, usually agreed well (cf. Figs. 2 to 6). We obtained peak values of equivalent reliability by smoothing both actual and predicted curves with a sliding rectangular average the width of which was sometimes necessary in noisy data such as in Fig. 6, D. Equal bin duration in the two measures justified use of a subjective criterion of smoothness, and we found it
Fig. 6. Comparison of responses to smooth and jerky movement with their prediction in complex striate unit 308-5. A, Static responses exhibiting overlapping bright-on and bright-off excitatory responses. Stimulus on, 128 msec; position increment, 0.375 deg; spontaneous rate, 17.8 Hz. Other conventions as in Fig. 1. B, Responses to actual smooth movement of the same bright bar at 2.93 deg/sec through 12 deg. Other conventions as in Fig. 1, A. C, Responses to jerky movement at the same average velocity as above in B. Note initial transient responses at each stimulus displacement. Other conventions as in Fig. 4, C. D, Linear prediction of responses to jerky (and smooth) movement of the same bright bar as above. Smooth/predicted effectiveness ratios: preferred, 0.49; null, 0.26. Note that prediction also shows transient responses as in jerky movement of C.
Table I. Mean actual/predicted peak-firing-rate values and 95% confidence limits of the mean for striate units under a variety of stimulus conditions

<table>
<thead>
<tr>
<th>Direction of movement:</th>
<th>Simple (47 units)</th>
<th>Complex (22 units)</th>
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<tbody>
<tr>
<td></td>
<td>Preferred</td>
<td>Null</td>
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<tr>
<td>Speed range (deg/sec):</td>
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<tr>
<td>0.24-0.98</td>
<td>0.96 (65)</td>
<td>0.35</td>
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<td>1.46-3.91</td>
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<td>0.48-0.62</td>
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<td>5.86-15.63</td>
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<td>0.27-0.53</td>
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<tr>
<td></td>
<td>0.47-0.91</td>
<td>0.23 (5)</td>
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<td>0.11-0.35</td>
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<td>Stimulus sign:</td>
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<tr>
<td>Bright bar</td>
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<tr>
<td>Dark bar</td>
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<td>0.25-0.54</td>
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<td>Effects of conditioning:</td>
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<td>All others</td>
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<td>0.91 (88)</td>
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<td>0.80-1.02</td>
<td>0.40-0.56</td>
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<td>Effects of N₂O 70:30 N₂O/O₂</td>
<td>0.84 (17)</td>
<td>0.27</td>
</tr>
<tr>
<td>All others</td>
<td>0.48-1.20</td>
<td>0.18-0.36</td>
</tr>
<tr>
<td></td>
<td>0.93 (98)</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>0.84-1.02</td>
<td>0.44-0.55</td>
</tr>
<tr>
<td>All assessments</td>
<td>0.92 (112)</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>0.83-1.01</td>
<td>0.41-0.55</td>
</tr>
</tbody>
</table>

Number of assessments that contributed to each value is listed in parentheses.

both fast and reproducible. Values for double peaks in either direction were averaged before calculations described below.

Means, 95% confidence intervals of the mean, and the number of assessments that contributed to each value are given in Table I. Measurements with bright and dark bars and at different speeds were treated as independent assessments even when made on the same units. Effects of conditioning and N₂O were averaged with other results for each unit before means were assessed, except where these two effects were being examined separately. Low values in this table indicate poor performance (low effectiveness) for moving stimuli as compared with the prediction. In general, ratios greater than 1 were not found. Therefore these data rejected the hypothesis that movement is especially effective compared with predictions based on simply summing static responses. The average relative efficacy of stimulus movement varied between a fraction and 1, depending on the cell type and experimental conditions.

We calculated small-sample 95% confidence limits for mean values of each sample in Table I (using t values). These 95% confidence limits give an estimate of the range within which the true means lie for each sample. Unfortunately, because of unequal numbers of assessments across conditions, multiple assessments in some units, and incomplete data in some units, it was not possible to apply usual inferential statistics to evaluate differences among the many conditions. Therefore, to evaluate the reliability of effects, we considered the calculated 95% confidence intervals, the number of assessments, and the consistency of trends in the face of variation in other parameters.

Stimulus speed was divided into three ranges on the basis of the stimulus duration...
used for calculating the movement prediction (512, 128, and 32 msec in order of increasing speed). The exact speed within each group in Table I corresponded to the size of position increment used (0.125 to 0.5 deg). Table I illustrates a consistent trend toward decreasing effectiveness of a moving bar as its speed increased.

No reliable difference appeared between the effectiveness ratios for bright and dark bars. Similarly, conditioning gratings made no appreciable difference, although each of the four effectiveness ratios was slightly higher under conditioning. Nitrous oxide elicited a convincing difference only for the null direction of simple units, although all four effectiveness ratios were somewhat lower under N₂O.

Simple vs. complex for both directions. For the null direction the means and distribution of values within the samples of simple and complex units were so similar as to suggest similar mechanisms for suppressing responses to movement in the null direction. For the preferred direction, however, simple units consistently showed higher mean effectiveness ratios than did complex units under the same conditions. The effect of stimulus speed on this difference will be considered below.

The most robust differences occurred between opposite directions of motion for either simple or complex units. Under almost every condition the difference between mean values was large compared with the 95% confidence intervals.

Discussion

We have compared responses of striate neurons to moving bars with a prediction constructed from the responses of the unit to static presentations of the same bar measured over the same period. Because our prediction is a linear convolution (Fig. 2), such a comparison amounts to a test of cortical unit linearity under the condition of image motion, assuming that smooth movement can be well represented by jerky movement (Figs. 4 to 6).

Movement in the preferred direction. For the preferred direction of image movement the average simple unit and also the average complex unit approached linearity by exhibiting an actual/predicted effectiveness ratio relatively near 1 (Table I). Presumably, what Movshon et al.¹⁰ call “spatial” nonlinearities in complex units were already present in the static responses used for our movement predictions. In the case of simple units the value 1 lies within the 95% confidence interval for eight of nine conditions, suggesting essential linearity for simple units. This result for movement in the preferred direction corroborates the good qualitative agreement obtained between static spatial organization and Fourier predictions of that organization drawn from results of sinusoidal analysis.⁶ ⁹ Tests of spatial summation by others also have demonstrated essential linearity when bars or edges of increasing length were used.²⁵⁻²⁶ Simple units, once their thresholds were exceeded, and complex units exhibited relatively linear length summation until they saturated from excess flux.

Because of the proximity to 1 of many mean values for the preferred direction and the range of values under each condition (S.D. 0.48 for all simple units; 0.34 for all complex units), it is necessary to consider why some individual units exhibit effectiveness ratios above 1 and others exhibit ratios considerably below 1. Values greater than 1 suggest the possibility that some units, including a higher proportion of simple than complex ones, may be exhibiting nonlinear facilitation for movement in the preferred direction. The presumed especially effective nature of a moving stimulus depends upon such nonlinear facilitation, and yet Emerson and Gerstein⁵ and others²⁴ have shown that it occurs only rarely, if at all, in simple units. Whether the minority of units exhibiting effectiveness greater than 1 also exhibit spatially specific nonlinear facilitation⁵ remains to be tested.

In the case of complex units, Movshon et al.¹⁰ have demonstrated nonlinear facilitation for certain spatiotemporal stimulus pairs, suggesting facilitation for movement in the preferred direction. And yet mean effectiveness values for the preferred direction (third column, Table I) fell below those of simple units, suggesting that complex units may re-
spond even more weakly to image movement than simple units do. This result is surprising because complex units are reputed to be especially sensitive to motion. This discrepancy can be explained partly by an unequal distribution of stimulus speeds used for our two populations. That is, a 22% increase in mean stimulus excursion (complex units have larger RFs for the same eccentricity) along with decreases in traverse time increased the mean speed we used for complex units by 51% over that used for simple units. Because of the tendency, especially for complex units, to decrease their effectiveness ratio with increases in speed, the values for complex units would have been higher if tested at the same velocity as for simple units. Because of the tendency, especially for complex units, to decrease their effectiveness ratio with increases in speed, the values for complex units would have been higher if tested at the same velocity as for simple units. Table I shows an average decrease in effectiveness ratio of 0.121 for each doubling of speed in the preferred direction. We used this approximation to obtain a corrected value of 0.94 for the preferred direction in all complex units as compared with 0.92 for all simple units. This increase in mean would bring the value for the preferred direction of complex units just within the lower 95% confidence limit for that of simple units but still not greater than the effectiveness ratio for simple units.

The occurrence of effectiveness ratios less than 1 in a majority of both simple and complex units suggests the possibility of a specific form of suppression that is dependent on spatiotemporal properties particular to motion. Such suppression would lead to the opposite of what is normally implied by the special nature of motion, since a moving stimulus would be less effective rather than more effective. Although such a motion-dependent suppression is possible, we believe that low effectiveness ratios for the preferred direction of cortical units depend on a purely temporal difference between moving and flashing stimuli that lowers responses to moving stimuli. Specifically, a slowly moving stimulus resides in sensitive RF regions long enough to cause a change in the state of adaptation, which appears as a decrease in responsivity of the unit. During static testing, on the other hand, the adaptive state can recover between stimulus presentations, causing an increase in the prediction and a resulting decrease in the effectiveness ratio (see also Discussion of Emerson and Gerstein). Vautin and Berkley have demonstrated such an adaptive effect of moving bar or grating stimuli on subsequent responses of simple and complex units. They found a reduction in responses that depends on firing rate of the cortical unit involved and, for moving bars, has a time constant between 2 and 9 sec. This time constant seems appropriate to explain low effectiveness ratios for stimulus speeds below about 2 deg/sec. The effect is nonlinear because it represents a decrease in a multiplicative or gain factor.

A different mechanism is suggested for the reliable decrease in effectiveness ratios seen at higher stimulus speeds. Since the duration of static presentation necessary to match the mimicked velocity decreases as the speed increases, the prediction becomes increasingly dominated by strong initial transient responses (note appearance of Fig. 2, D). The effectiveness ratio decreases accordingly. If these cortical neurons were behaving linearly, then in the prediction the initial transient excitation at one position would be canceled by opposite and nearly equal inhibition occurring simultaneously when the stimulus turned off at the previous position. To register this inhibition faithfully, however, requires a spontaneous rate at least as great as the depth of the inhibition, since neurons cannot have negative firing rates. The low spontaneous rates of cortical neurons, especially in simple units, lead to nonlinearities that contribute to the described decreases in the effectiveness ratio at high speeds. This underrepresentation of inhibition is known as a threshold or rectification nonlinearity and applies to all neurons operating near threshold.

Our use of a conditioning grating was designed to minimize threshold nonlinearities by increasing the average background activity sufficiently to avoid unregistered inhibition. The small increase in effectiveness shown in Table I for conditioned responses is an indication that threshold nonlinearities in unconditioned units may have lowered effectiveness ratios, but only to a small extent. However, even in conditioned units it may
be unreasonable to expect a conditioning stimulus to compensate exactly for these deficiencies by linearly adding a constant excitatory influence. Stone and Fabian12 showed that as peripherally as in retinal ganglion cells the interaction between inhibitory and excitatory stimuli produced lower than expected response levels. Thus uncorrectable threshold nonlinearities may have an influence.

In addition, a moving conditioning stimulus may adapt the cell in the preferred direction of motion, the direction in which we always moved the conditioning grating. Two isolated examples that were only weakly directionally actually reversed their preferred direction under conditioning. Frost28 has shown a strong effect of this same kind in the tectum of pigeons. Such directional effects severely limit the utility of drifting gratings as conditioning stimuli for studying motion.

**N2O.** We have attempted to use N2O for light anesthesia during single unit experiments. However, in this laboratory16 N2O seems to reduce response specificity. The present study shows that N2O may also cause a consistent, but perhaps not reliable, reduction in the effectiveness of moving stimuli as compared with their linear prediction. The highest S.D. (0.70) for all samples occurred in simple units for the preferred direction, supporting our impression that N2O decreases response reliability.16

**Motion in the null direction.** Although the effectiveness ratio for movement in the preferred direction often fell somewhat below 1, every sample mean in Table I calculated for the null direction fell well below this linearly predicted value. Such a deficit strongly supports the conclusion that bar movement in the null direction elicits strong nonlinear suppression of responses below the level predicted by the linear superposition.5, 24

A ratio of effectiveness values for the preferred/null direction (Table I) is closely related to the preferred/null peak firing rates one could measure directly for the two directions. Each measure usually designates the same preferred direction. However, the effectiveness value represents the raw peak firing rate divided by the value expected linearly on the basis of static asymmetries. Therefore the ratio of effectiveness values gives an accurate indication of the dependence of directional selectivity on purely nonlinear mechanisms as opposed to "directional asymmetry," which may include dependence on linear mechanisms.5 Although effects from asymmetries that are dependent on linear mechanisms will reverse their preferred direction with a change from a bright to a dark bar, the directional ratio of effectiveness values bears no direct relationship to stimulus contrast, and as with directional selectivity, it can remain unaltered through such a change. For discussions of directional selectivity and sign of stimulus contrast see refs. 5 and 29.

In the present experiment both bright and dark bars elicted directionally selective responses that depended heavily on nonlinear mechanisms. The average directional effectiveness ratio for simple units was 1.92 and for complex units was 1.58. Individual units showed much larger than mean values in this total population, which was selected independently of its directional properties. In addition, many simple units exhibited even higher raw values of directional asymmetry because of spatial RF asymmetries that enhanced raw directional performance. Complex units, on the other hand, usually lack such spatial asymmetries and are therefore dependent mainly on nonlinear mechanisms. However, even without the aid of linear mechanisms, simple units exhibited stronger directional selectivity, suggesting that they depend even more on nonlinear mechanisms of directional selectivity than do complex units.

In general, the stimulus condition that involved the largest discrepancy from linearity was a bar moving in the null direction of a simple or complex RF. Thus the special nature of a moving stimulus lies not so much in its special efficacy in driving cortical units as in its power to elicit nonlinear suppression of responses when it is moving in the null direction for a visual neuron.

**Note added in proof.** We now recognize two distinct subgroups in the complex family of RFs,20 one relatively sustained in response to
static bars and the other transient. The group of 10 sustained units, when separated from the total group of 22 "complex" units shown in Table I, exhibits a mean effectiveness ratio of 0.92 for bar movement in the preferred direction at an average speed of 1.14 deg/sec. This effectiveness value is identical to that shown in Table I for simple (sustained) units at a similar average speed (1.45 deg/sec), and it indicates that the lower effectiveness values of typical complex (transient) units are correlated with their transient temporal properties rather than with their mixed on-off intensive properties.

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REFERENCES


