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LENGTH SUMMATION IN SIMPLE CELLS OF CAT STRIATE CORTEX

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Abstract—We have examined two models for the preference displayed by cortical simple cells for elongated stimuli having a particular orientation. Both assume that geniculate afferents with aligned receptive fields pool to form the receptive field of the cortical unit. The first model [Marr and Hildreth, *Proc. R. Soc. Lond. Ser. B* **200**, 269–294 (1980)], includes AND gating along the length axis so that a simple cell does not fire unless a critical number of its afferents with adjacent receptive fields are firing. The second model assumes that geniculate input is simply summed over subunits and then passed through a firing threshold. Both models account for the unresponsiveness of simple cells to spots of light, but the *AND* model predicts a discontinuous length threshold, while the *summation* model predicts that length and contrast should be interchangable in the determination of the response threshold. Experiments in which length and contrast were systematically varied support the summation model, and extend the notion of linear spatial summation to the length axis in simple cells.

Visual cortex Spatial summation

INTRODUCTION

One of the most striking differences between the receptive fields of neurons of the lateral geniculate nucleus (LGN) and those of neurons of the striate cortex is the preference for elongated bars and edges over spots of light or dark. Hubel and Wiesel (1959, 1962), in their pioneering studies of orientation selective cortical neurons, suggested that the preference displayed by simple cells might result from their receptive fields being derived from a set of LGN neurons whose own receptive fields were aligned. A simple cell would than be optimally excited only when a stimulus passed simultaneously over the receptive fields of all of its afferent geniculate neurons.

A problem for this proposal in its simplest form is that LGN neurons will respond to small spots or lines of any orientation. Thus a long bar might be an effective stimulus for a simple cell only within a narrow range of orientations, but a small spot or a line of any orientation should readily activate it. Although the orientation tuning of simple cells broadens as line length is decreased, responsiveness also decreases (Henry *et al.*, 1974; Rose, 1977; Kato *et al.*, 1978). In general, simple cells respond poorly or not at all to small spots of moderate contrast.

Marr and Hildreth (1980; Marr and Ullman, 1981; Marr, 1982) have suggested that simple cells are driven by neurons of the lateral geniculate nucleus through a combination scheme of logical conjunction, or AND gating. Their model specifies two distinct AND mechanisms, but we are concerned here with the one that acts *along the length of the receptive field*. In this model, simple cells fire only when *each* of a criterion number of LGN cells are *all* firing at some specified level; that is, only when oriented features are present in the neural image provided by afferent input from the LGN. The motivation for this idea comes from belief that simple cells are "pattern detectors" in the sense favored by trigger-feature models of neural receptive fields (e.g. Lettvin *et al.*, 1959; Barlow, 1972). As Marr and Hildreth state, "By adding nonlinear operations in the longitudinal direction, one can . . . construct an operator that *detects* oriented zero-crossing segments" (p. 209, our italics). Neural signals are not easily thought of as conveying logical states, so a literal AND operation is implausible; a comparable combination rule could, however, be implemented by a facilitatory (perhaps multiplicative) interaction among subunits. A simple cell constructed in this way would not be activated by any short stimulus, regardless of its contrast. We shall refer to this scheme as the *AND* model.

This proposal can be contrasted with what we will refer to as the *sum-to-threshold* model. In this model too, the responses of LGN neurons whose receptive fields lie along a common receptive field axis are pooled to give rise to the orientation preference of simple cells. But here geniculate input to a simple cell is simply *summed*, rather than AND gated, and is then passed through a firing threshold. In this view, a simple cell fails to respond to a short stimulus primarily because such a stimulus will activate only one or a few LGN afferents, and the response of a few subunits alone will not exceed the threshold required to activate the simple cell.

The difference between these models is most clearly seen when responses to stimuli that vary both in

length and in contrast are considered. The *sum-to-threshold* model predicts that for any choice of stimulus length, there will be a contrast below which no response is elicited. This contrast level will vary inversely with stimulus length, so that long stimuli (which activate many subunits) will have low contrast thresholds, while short stimuli (activating only a few subunits) will have higher thresholds. This implies that it should be possible to *exchange* stimulus contrast for stimulus length while maintaining some criterion response. The *AND* model, however, requires that some criterion number of geniculate afferents should be activated before the simple cell gives *any* response. Thus for stimuli shorter than a criterion length, no amount of contrast will elicit a response. Stimuli longer than the criterion, on the other hand, will all have similar contrast thresholds, because once a sufficient number of afferents is active, signals from all afferents will combine to yield responses. This implies that, over a wide range, the contrast required to elicit some criterion response should be independent of stimulus length.

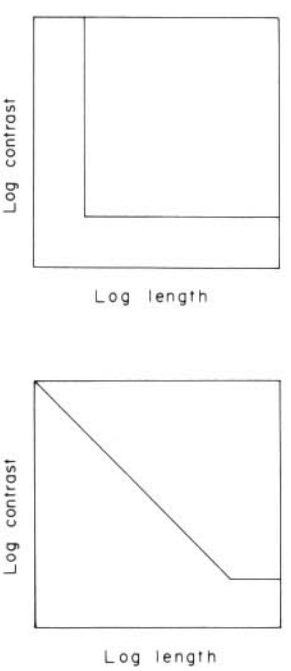

Fig. 1. Schematic predictions of the two models. In each case, the contrast–length plane is represented, and the line represents the locus of all combinations of length and contrast that should yield some small criterion "threshold" response. Top: the "AND" model. The square shape of the threshold locus reflects the prediction that there should be a constant length threshold regardless of stimulus contrast. Bottom: the "sum-to-threshold" model. The diagonal shape of the threshold locus reflects the prediction that length and contrast should be capable of exchange to yield equivalent responses. Note that when the diagonal has a slope of -1, as shown, perfect reciprocity between length and contrast obtains. The flat portion of the curve at low contrasts and large lengths corresponds to increasing the stimulus length beyond the borders of the receptive field.

Figure 1 schematically illustrates the predictions of the two models. Shown for each is a length-contrast plane, on which is drawn the predicted locus of all combinations of length and contrast yielding a criterion "threshold" response. The diagonal line predicted for the sum-to-threshold model (Fig. 1, bottom) reflects the prediction that the increase in response produced by a slight increase in length should be compensated by a slight decrease in contrast. Note that the length and contrast axes are logarithmic, and thus that if the diagonal has a slope of -1 (as shown) it implies perfect reciprocity between length and contrast. The range of lengths for which a slope of -1 describes the data can be taken as analogous to Ricco's area in classical spatial summation tests (e.g. Graham *et al.*, 1939). The square corner predicted for the AND model (Fig. 1, top) reflects the constant length threshold, regardless of contrast, that is a feature of this model.

In out test of these models, we presented simple cells with sets of stimuli that varied in both length and contrast. The results uniformly conform with the predictions of the sum-to-threshold model, and reject the AND model.

METHODS

Extracellular recordings were made from neurons in the primary visual cortex (area 17) of adult cats. Initial surgery was performed under halothane anesthesia, and consisted of venous cannulation for infusion, tracheal cannulation for artificial respiration, and bilateral section of the cervical sympathetic trunk to reduce eye movements. During recording, the animal was paralyzed with an infusion of muscle relaxant (pancuronium bromide, $0.2\,mg \cdot kg^{-1} \cdot hr^{-1}$, or gallamine triethiodide, $10\,mg \cdot kg^{-1} \cdot hr^{-1}$) in a lactated dextrose Ringer's solution ($2.7\,ml \cdot hr^{-1}$), and was artificially ventilated with a mixture of N_2O, O_2 and CO_2 (typically 49:49:2) supplemented with an infusion of sodium pentobarbital ($0.5–1.5\,mg \cdot kg^{-1} \cdot hr^{-1}$). The expired pCO_2 was maintained near 4%, rectal temperature near 37.5°C, and EEG and EKG were monitored continuously to ensure the adequacy of anesthesia and the soundness of the animal's physiological condition. Accommodation was paralyzed and the pupils dilated with topical atropine sulfate and the nictitating membranes were retracted with neosynephrine HCl, both administered as needed. The corneas were protected with zero-power contact lenses containing 4 mm clear pupils, and the eyes were refracted by direct ophthalmoscopy and corrected with external lenses to render the retinas conjugate with a screen 57 cm distant.

Tungsten-in-glass microelectrodes (Levick, 1972) were used to isolate neurons from the region of striate cortex representing the central 5° of the visual field in penetrations directed either perpendicular to the crest of the central gyrus or down the initial few mm of the medial bank of the central sulcus.

Sinusoidal gratings were generated on the face of a Hewlett-Packard 1332A display oscilloscope. The mean luminance of the oscilloscope face was held constant at 40 cd/m^2 (P31 phosphor). The equipment included facilities for electronically gating the display so as to produce gratings of arbitrary length (parallel to the orientation of the grating) and arbitrary position on the screen; regions of the screen in which gratings were not presented were fixed at the mean luminance.

Minimum response fields were first plotted on a tangent screen and cells were initially classified as simple (Hubel and Wiesel, 1962) if they exhibited nonoverlapping discharge regions to the introduction or withdrawal of bright and dark bars. This classification was later corroborated during stimulation with gratings by the criterion that gratings of optimal spatial frequency elicit a response whose modulated component at the fundamental temporal frequency of stimulation be in excess of the mean discharge level (Movshon *et al.*, 1978; De Valois *et al.*, 1982). Typically, the observed ratio of fundamental to mean response was greater than 1.5. Our observations suggest that this measure distinguishes the same simple and complex groups as the tests used by Hubel and Wiesel (1962; see also Movshon *et al.*, 1978). Before experiments involving variations in stimulus length were begun, the cell's optimal orientation, spatial frequency, drift rate, and direction of drift were determined using peri-stimulus time averaging methods.

The study of each cell involved first the identification of the center of the receptive field along the length axis. This was accomplished by means of an experiment that generated a length–position function [cf. the "bilateral length excitatory profiles" of Kato *et al.* (1978)]. The stimulus was a grating whose spatial frequency, orientation, drift rate and direction were all optimized, and which was gated so as to be limited to a small extent in the direction parallel to the grating's orientation. The length of the gratings was great enough to produce reliable responses but shorter than the overall receptive field. The grating patch was presented several times at each of several adjacent nonoverlapping positions, in pseudo-random order. Peri-stimulus time histograms were accumulated, and the data were Fourier transformed to reveal the amplitude of the modulated component at the fundamental temporal frequency of stimulation, f_1.

Next, five lengths of grating patch, all centered on the receptive field as indicated by the length–position curve, were each presented at 10 different contrasts, arranged in 3 dB steps. Lengths were chosen to span a range from the shortest patch that would give any response, to one which exceeded the extent of elicited responses in the length–position curve. Contrasts were chosen to span a range from less than the threshold contrast for the longest patch to just above threshold contrast for the shortest patch used.

RESULTS

We studied the responses of 12 simple cells from 6 cats. Figure 2 shows length and contrast data collected from one such cell. The upper plot shows a family of length–response functions, each at a different stimulus contrast; the lower plot shows a family of contrast–response functions, each at a different stimulus length. In the length–response functions, data are plotted for only several of the 10 contrasts to reduce clutter.

Consider first the length–response functions in Fig. 2(a). It is evident that the minimum length at which a response could be elicited depended on stimulus contrast, and did not have a fixed value. Thus the stimulus of highest contrast elicited a response at lengths as small as 0.25 deg, while lower contrast

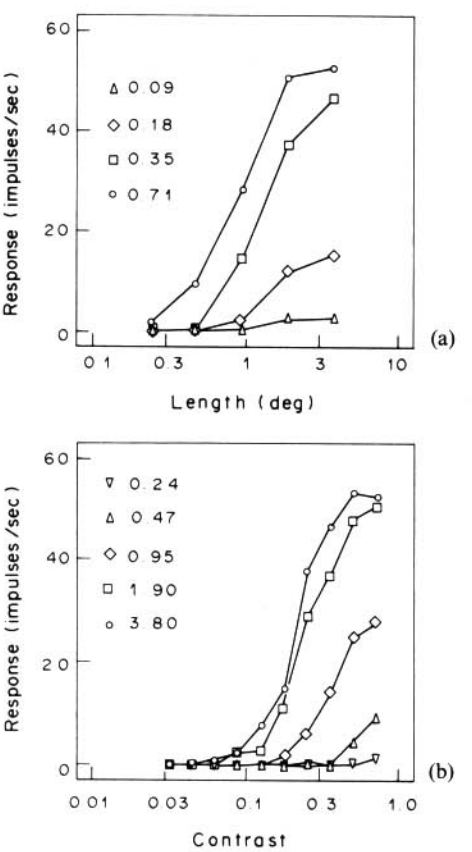

Fig. 2. (a) Length–response functions for a simple cell, measured with the range of contrasts indicated in the panel. The unit was tested with gratings with optimal values of spatial frequency: 0.93 c/deg; orientation: 32 deg clockwise from vertical; temporal frequency: 4 Hz. The ordinate scale shows the magnitude of the modulated response as given by the amplitude of the fundamental component of the Fourier transform of the actual response. The abscissa shows the length of grating patch in degrees of visual angle. This graph shows only four of the ten length–response curves collected, to reduce clutter. (b) Contrast–response functions for the same cell; the same data are plotted as in (a) but with contrast on the abscissa. The different lengths are indicated in the panel. All the data collected are shown.

stimuli required lengths as great as 2 deg. This general feature was common to all cells studied, and can also be seen in the length-response functions for two other cells shown in Figs 4(a) and 5(a).

Consider next the contrast–response functions shown in Fig. 2(b). In a manner complementary to the length–response functions, the contrast–response functions show that contrast threshold always depended on the length of the stimulus. At low contrasts, only the longest stimuli elicited a response; as contrast was increased, progressively shorter and shorter stimuli became effective. The cell of Fig. 2 responded to the two longest patches at a contrast of about 0.06, and to the next three shorter patches at contrasts of 0.18, 0.50 and 0.71, respectively. As can be seen, this general pattern is also characteristic of the two other cells illustrated, in Figs 4(b) and 5(b); it was characteristic of all the cells in our sample.

Once contrast threshold was exceeded, responses increased monotonically with contrast in all cases; the contrast–response functions for different lengths tend to be roughly parallel on the logarithmic contrast axes. Thus the contrast–response data suggest that the effect of changing stimulus length is equivalent to a multiplicative scaling of stimulus contrast (which causes a rigid horizontal translation of the response functions in these coordinates). This is consistent with the idea that each incremental piece of the receptive field stimulated as a stimulus is lengthened contributes a response which simply adds to the response of the cell.

In Fig. 3(a) we show a 3-dimensional perspective representation of the complete length– and contrast–response data we collected from the cell of Fig. 2. The unlabelled axis rising from the base-plane represents response magnitude. Slices through this surface parallel to the length or contrast axes would show individual length– or contrast–response functions, like those in Fig. 2.

Figure 3(b) shows a representation of this surface as a set of contoured iso-response levels. The lowest contour level corresponds to about one-tenth the maximum response, with higher levels spaced similarly; the tick-marks on each contour point "downhill". Comparing these contours with the hypothetical ones of Fig. 1, it is clear that they resemble the predictions of the sum-to-threshold model. The dashed line in Fig. 3(b) shows a slope of -1, which would represent perfect reciprocity between length and contrast. For a reasonably wide range of lengths and contrasts, each contour, particularly at low response levels, runs diagonally with a slope near -1. Only when length and contrast are high, at the upper right of the plot, do the contours deviate importantly from the diagonal; this is due to the fact that the longest length used extended beyond the borders of the neuron's receptive field and thus produced a less-than expected increase in response (cf. Graham *et al.*, 1939). Figures 4(c) and 5(c) show contour plots for the data sets taken from the other two cells. The

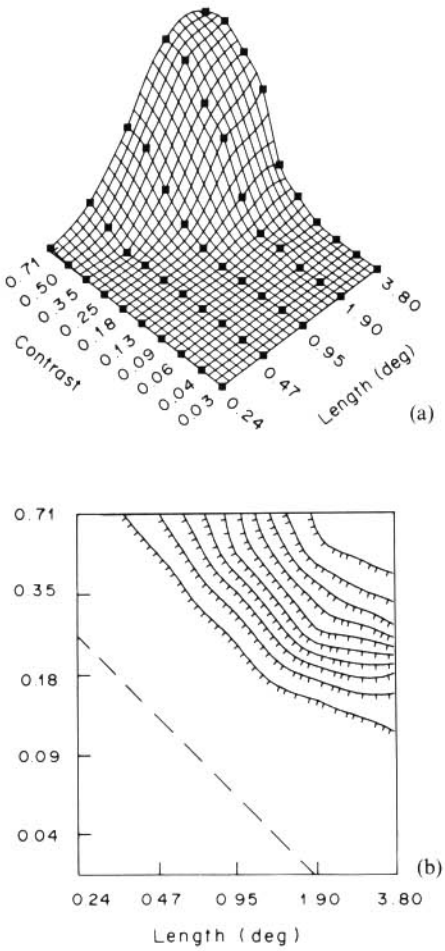

Fig. 3. (a) The data from Fig. 2 are replotted here as a three-dimensional perspective view of the contrast–length response surface. The height of the surface above the base plane represents response magnitude; the peak response amplitude was 53 impulses/sec. The smooth grid surface is a spline interpolation through the data points; actual data are indicated by filled diamonds. (b) A contour map representing the three-dimensional surface of (a). Lines show loci of constant surface height, or iso-response levels, derived from the interpolation shown in (a). The spacing of the contour lines is one-tenth the maximum firing rate. Ticks point toward lower response levels. The dashed line indicates a slope of -1, corresponding to perfect reciprocity between length and contrast.

same diagonal pattern is evident, as it was also evident in the other cells of our sample.

For many of the cells we studied, like those shown in Figs 2–3 and 5, there was a length beyond which increases did not produce a reliable change in response. Other cells showed a *decrease* in response as length increased beyond some value. The cell illustrated in Fig. 4 displays this feature to a mild degree. Apart from this end-inhibition, such cells resembled simple cells in all respects including those discussed above: within the limited range of effective test lengths available, it was possible to discern

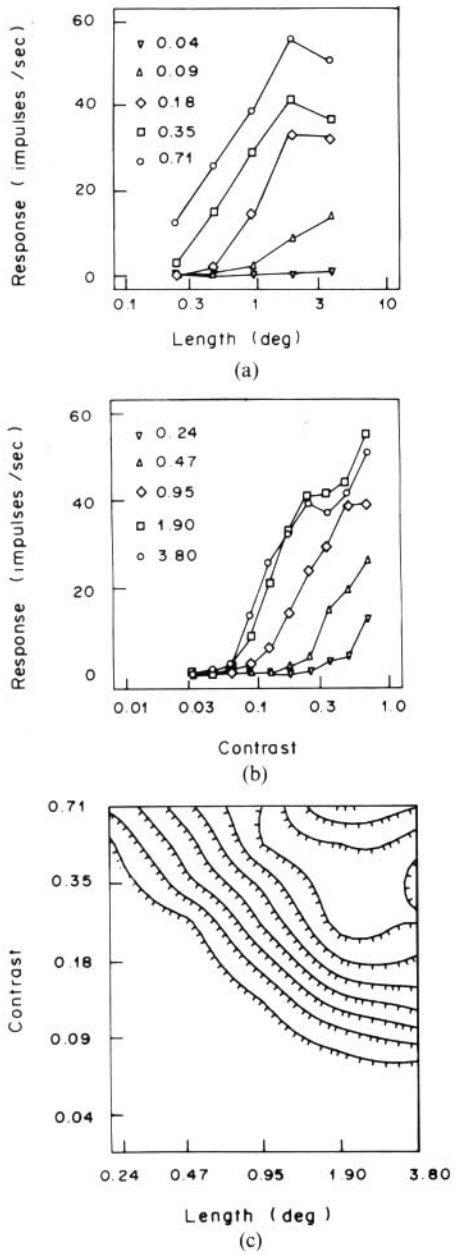

Fig. 4. (a) Length–response functions for another simple cell. Spatial frequency: 0.4 c/deg; orientation: 11 deg; temporal frequency: 4 Hz. Otherwise as for Fig. 2(a). (b) Contrast–response functions for same cell as in (a), plotted as in Fig. 2(b). (c) Contour map representation of the contrast–length response surface. Maximum firing rate of 55 impulses/sec; contour spacing approximately one-tenth this value. Otherwise as in Fig. 3(b).

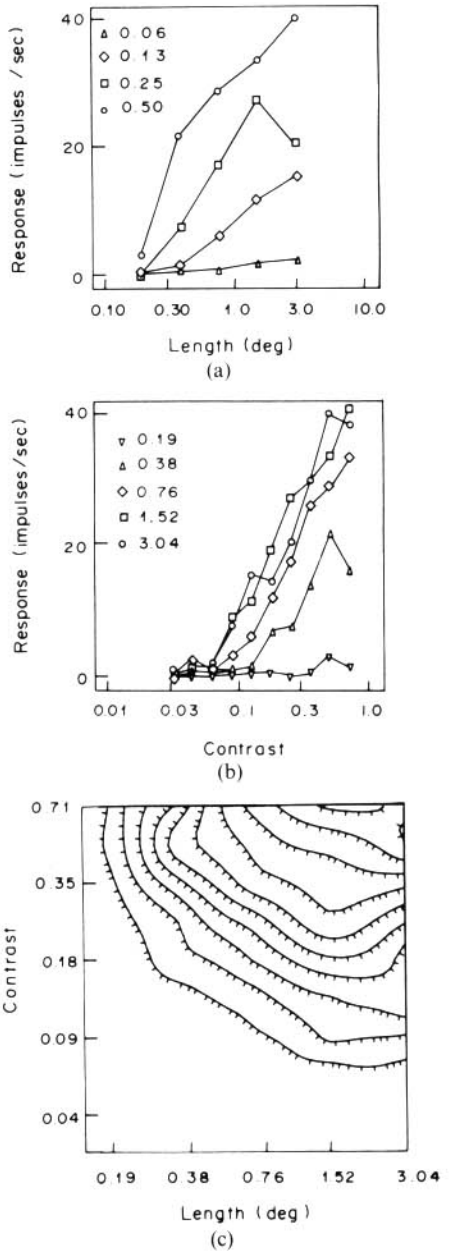

Fig. 5. (a) Length–response functions for another simple cell. Spatial frequency: 1.6 c/deg; orientation: 160 deg; temporal frequency: 4 Hz. Otherwise as for Fig. 2(a). (b) Contrast–response functions for same cell as in (a). Otherwise as for Fig. 2(b). (c) Contour map representation of contrast–length response surface. Maximum firing rate of 41 impulses/sec; contour spacing approximately one-tenth this value. Otherwise as in Fig. 3(b).

length–contrast exchanges of the sort shown in Fig. 2. These cells are presumably the "simple-type hypercomplex" cells of Dreher (1972). Our data, along with those of others (Kato *et al.*, 1978; Henry *et al.*, 1978), reveal no difference—other than end-inhibition itself—in receptive field organization between these cells and "conventional" simple cells lacking end-inhibition.

DISCUSSION

Evaluation of the models

Our data show two clear results. First, length and contrast can be exchanged over large ranges of both variables, in a manner consistent with the sum-to-threshold model. Second, we failed to observe a fixed threshold for either length or contrast, as the AND

model predicts. Most cells responded reliably—if weakly—to stimuli as little as one-tenth their optimal length, given sufficient contrast. Conversely, most cells responded reliably to rather low contrasts if the stimulus was made long enough.

Previously reported features of simple cell responses have indicated that the AND model is inadequate. Several workers have shown that the response of simple cells increases smoothly and gradually with stimulus length (e.g. Gilbert, 1977; Kato *et al.*, 1978; Henry *et al.*, 1978). While suggestive, this finding does not by itself refute the AND model, which does not specify what result is to be expected when the criterion length is exceeded. In addition, Henry *et al.* (1978) measured the responses of simple cells to high-contrast lines of different lengths, and concluded that these cells summed responses linearly along their length; this summation was said to be followed by a threshold nonlinearity. These data also do not rule out the AND model, since they were obtained with stimuli of uniformly high contrast. Their conclusions, however, are fully consonant with our own, and with those reached by Movshon *et al.* (1978) in their examination of spatial summation across the width of the receptive fields of simple cells.

In our experiments, we manipulated both length and contrast over large ranges. Our demonstration that there is, in fact, no demonstrable "criterion length" in simple cells, at *any* contrast, appears to dispose of the AND model. Moreover, our observation of linear length-contrast exchange confirms the prediction of the sum-to-threshold model.

Marr and Ullman (1981) considered the AND mechanism as a specific component of the mechanism of the directional selectivity seen in many simple cells. We observed no difference in the pattern of results that depended on the directional selectivity of a cell. For example, the three neurons of Figs 2–5 varied in their directionality from nearly bidirectional (the cell of Fig. 5) to almost completely directional (the cell of Fig. 4). We also saw no effect on the pattern of the results of variations in the distribution of excitatory and inhibitory receptive field regions, or in the precision of a cell's orientation or spatial frequency selectivity. Though our sample in this study was relatively small, the uniform behavior of all neurons tested encourages us to conclude that it is characteristic of cells of the simple type.

Aspects of the sum-to-threshold model

The nonlinearity in the sum-to-threshold model is probably a simple consequence of the low or absent maintained discharge typical of simple cells, and reflects the fact that some amount of excitatory input is necessary to overcome the hyperpolarization of the cell membrane that this implies. This resting hyperpolarization typically has a value equivalent to −10 "impulses/sec"—that is, stimuli that produce incremental responses of about 10 impulses/sec are required to elicit a discharge in the absence of other excitation (see Movshon *et al.*, 1978). The threshold nonlinearity has the effect of causing simple cells to be rather insensitive to small spots of light or short stimulus lengths. The ineffectiveness of small stimuli is further insured by other factors, including response saturation at earlier levels in the visual pathway, and light scatter, both of which would be significant at the high contrasts needed to excite cortical neurons with small stimuli.

It seems likely that pooling along the length of the simple receptive field is performed in a weighted fashion, with centrally located afferent rececptive fields given most weight, and more peripheral ones accorded less. This would account for the roughly Gaussian position–response curves we and others regularly observe (Henry *et al.*, 1978).

Finally, it should be noted that the regular pattern of length–contrast exchange seen in the data of Fig. 2 militates against the notion that simple cells detect "trigger features" in the visual environment (or a neurally filtered version thereof; Barlow, 1972; Marr, 1982). Each length–contrast contour line in the plots of Figs 3(b), 4(c) and 5(c) indicates the set of length–contrast combinations that yield the identical response. For a moderate response level, this set includes small stimuli of high contrast, long stimuli of low contrast, and numerous intermediate combinations. None of these different stimuli (only the longer members of which contain extended contours) could be distinguished by consulting the output of a particular simple cell.

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