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Linear Analysis of the Responses of Simple Cells in the Cat Visual Cortex

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Summary. Spatial response profiles to stationary and moving stimuli and spatial frequency tuning curves to drifting sinusoidal gratings were recorded from a series of cells in the simple family. The spatial response profiles were recorded both to stationary flashing bars and sinusoidal gratings as well as to light and dark bars and edges and gratings moving at the optimal velocity. On the assumption that cells in the simple family operate linearly, spatial response profiles recorded experimentally were compared with those predicted by inverse Fourier transformation of the spatial frequency tuning curves. Conversely, the spatial frequency tuning curves recorded experimentally were compared with those predicted from the response profiles to moving and stationary stimuli. As a result of these comparisons, it is clear that moving stimuli provide a more accurate estimate of the spatial organization of the receptive field than do stationary stimuli. Cells with the higher optimal spatial frequencies tended to have narrower bandwidths. The simple cell with the narrowest bandwidth (0.94 octave) had five, and possibly six, subregions in the spatial response profile to moving light and dark bars, the largest number of subregions we encountered.

Key words: Striate cortex – Simple cells – Linear analysis – Spatial response profiles – Spatial frequency tuning

Introduction

In the previous paper (Kulikowski et al. 1981a) we examined the responses of cortical cells to narrow stationary and moving bars or lines that were both brighter and darker than the background and studied the relationship between these responses and those to moving light and dark edges. The main aim of the present paper is to examine the relationship between the simple cell's responses to lines and edges and its spatial frequency selectivity. To this end we studied the responses of simple cells to stationary and to drifting sinusoidal gratings and prepared spatial frequency sensitivity and responsivity tuning curves. Then, on the assumption that the cell performs linear spatial summation, we compared the inverse Fourier transform of each cell's spatial frequency tuning curve with the cell's response profiles to moving lines and edges.

Following Hubel and Wiesel (1962), the responses of simple cells to moving lines and edges have been extensively studied (Pettigrew et al. 1968; Bishop et al. 1971; cf., Stone et al. 1979 for review) and more recently, and largely independently, there has also developed a considerable literature on the responses of simple cells to drifting gratings (Campbell et al. 1969; Cooper and Robson 1979; Maffei and Fiorentini 1973; cf., Maffei 1978 for review). De Valois et al. (1979), in particular, have come to regard simple cells as spatial frequency filters, responding to the two-dimensional Fourier components of patterns, rather than as bar or edge detectors. The application of spatial frequency (Fourier) methods to simple cell responses implies linear spatial summation over the cell's receptive field. Hence, provided the cell is operating within its linear range, the responses to moving lines and edges and to drifting gratings are mathematically equivalent. The responses to lines by cells with symmetrical and antisymmetrical receptive fields represent the respective cosine and sine components of the inverse Fourier transform of the spatial frequency tuning curve (Kulikowski and King-Smith 1973), whereas the responses to edges are integrals of the responses

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to lines. Despite this possible equivalence, there has, as yet, been relatively little attempt to integrate the two experimental approaches. The only detailed comparisons that have so far been attempted in the literature (Movshon et al. 1978a; Andrews and Pollen 1979) have been made using responses obtained by different methods of stimulus presentation, the spatial frequency tuning curves being determined with drifting gratings and the spatial response profiles with stationary stimuli. We avoided this inconsistency by using moving stimuli in both cases although, if time allowed, we also recorded the spatial pattern of the responses to a stationary flashing bar. Our comparison is probably more relevant to the operating conditions of simple cells in the normal animal. In general simple cells respond better to moving than to stationary stimuli and spatial response profiles to moving stimuli can be obtained much more quickly and reliably than to stationary flashing stimuli.

A preliminary account of some aspects of the present paper have been published elsewhere (Kulikowski and Bishop 1981a). The results obtained in the previous (Kulikowski et al. 1981a) and in the present paper form the basis for the development of a detailed theory of the spatial position and spatial frequency relations in the receptive fields of simple cells (Kulikowski et al. 1981b).

Methods

The cells examined in this report form part of the series described in the preceding paper (Kulikowski et al. 1981a) and details of our general methods are given in that paper. Cats were prepared under halothane/N_2O anaesthesia and subsequently paralyzed. Single cell recordings were carried out in area 17 and the 17/18 border region using glass-insulated tungsten microelectrodes under N_2O/O_2 anaesthesia.

Spatial Frequency Tuning Curves

Contrast sensitivity and responsivity tuning curves were obtained from the cortical cells using sinusoidal gratings drifting at a constant temporal frequency. The initial exploratory procedures for each cell, aimed at determining both the range and the optimum of the spatial and the temporal frequencies of the drifting grating, were carried out by listening to the spike responses over the loudspeaker. The responses from simple cells were clearly modulated by the passage of the grating bars over their receptive fields. Once an approximate estimate had been made of the optimal temporal frequency (drift rate in spatial cycles per second) for the optimal spatial frequency, this drift rate was held constant and only spatial frequency was varied systematically. Each grating drifted at a constant temporal frequency two, or sometimes three, spatial cycles forward and then backward, thereby preventing adaptation to a direction of movement. The grating spatial frequency could be varied continuously between 0.25 and 10 c/deg, although, in practice, it was varied in 0.05 log unit steps (1/6 octave). Two kinds of spatial frequency tuning curves were determined.

Contrast Sensitivity Curves

For a given spatial frequency, the grating contrast was reduced to the threshold value at which no modulated discharge could be heard (Enroth-Cugell and Robson 1966). The reciprocal of the minimum contrast threshold was taken as the maximum contrast sensitivity and subsequently normalized to one. The search for this optimum was first carried out by varying spatial frequency continuously and only then was a range of spatial frequencies chosen in convenient steps to determine the tuning curve (Movshon et al. 1978b). Special attention was paid to the range around the expected optimal spatial frequency both to determine the bandwidth and to check whether or not the cell had a tuning curve with multiple maxima.

Responsivity Curves

Once the contrast sensitivity curve had been determined, the grating contrast was held constant, usually at 0.2, and average response histograms were recorded over the same range of spatial frequencies. If it was found that, at the optimal spatial frequency the response was saturated, the whole sequence was repeated at a lower contrast (usually 0.1). In keeping with other authors (e.g. Tolhurst and Movshon 1975), the responses were usually plotted against a fixed time during which the grating drifted two cycles irrespective of its spatial frequency. The alternative method is to plot the responses as a function of the distance covered by two cycles of the grating. In this case the responses are averaged over fewer bins for the finer gratings since two cycles of a fine grating cover a smaller distance than two cycles of a coarse grating. In either case the mean amplitude of the responses to the various spatial frequencies can be readily determined since the responses of simple cells have shapes resembling half-wave rectified sinusoids (Movshon et al. 1978b; Andrews and Pollen 1979).

Bandwidth of Tuning Curves

For each tuning curve two estimates of the bandwidth were made, both based upon the upper (f_u) and lower ($f\ell$) spatial frequencies either for half-sensitivity or for half response amplitude. One estimate of the bandwidth (B_{oct}) was given by the ratio of the upper and lower spatial frequencies expressed in octaves (i.e. decimal log unit/0.3). The other estimate (B_{df}), introduced by Thompson and Tolhurst (1979), gave the bandwidth as the difference between the frequencies divided by the optimal spatial frequency $[(f_u-f\ell)/f_o]$.

Results

The linearity of spatial summation by simple cells was tested by two methods devised by Enroth-Cugell and Robson (1966). One test involves the nature of the cells' responses to drifting sinusoidal gratings and the other concerns the presence or absence in the receptive fields of a null position at which the introduction or removal of a grating pattern yields no significant response. The recording time available was rarely

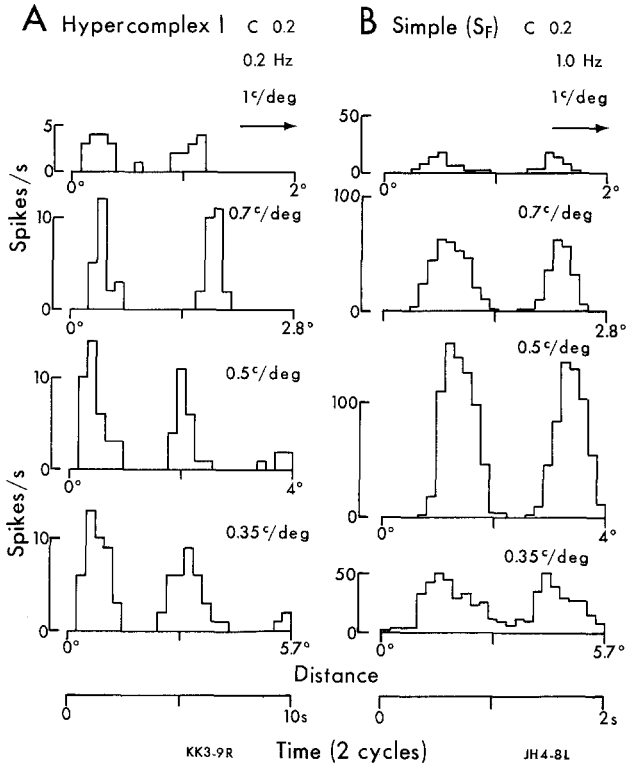

Fig. 1A, B. Averaged response histograms to sinusoidal gratings of four spatial frequencies drifting at constant rates in the preferred direction. Note a relatively broad spatial frequency tuning in (**A**) hypercomplex I cell (located in area 17, lamina III near the border with lamina IV), and narrower in (**B**) fast simple cell (located on the border of areas 17–18, lamina VI)

long enough for us to obtain all the detailed quantitative data we needed. Of the 37 cells in the simple family to give a reasonably adequate range of quantitative data, only 20 cells (including 6 fast simple cells) were systematically tested for the linearity of their spatial summation.

Responses to Drifting and Stationary Flashing Sinusoidal Gratings

To drifting sinusoidal gratings simple cells give a response that is modulated in synchrony with the passage of the bars of the grating across their receptive fields and the response continues to be modulated at the highest spatial frequencies to which the cell responds (Movshon et al. 1978a; Andrews and Pollen 1979). The cells respond over only approximately half of each cycle remaining silent during the remaining portion of the cycle (Fig. 1). To a stationary flashing sinusoidal grating placed at different phase positions across their receptive fields the cells respond with a complete sinusoidal profile, the ON responses forming one half-period and the OFF responses the other half-period (Fig. 2, Aa and Ba). Since the response profiles of typical simple cells to sinusoidal gratings have already been extensively examined (Movshon et al. 1978a; Andrews and Pollen 1979) it will only be necessary to illustrate two relatively extreme examples of the degree of linear summation to be found among cells in the simple family. The hypercomplex I cell in Figs. 1A and 2A is a linearly responding cell in the simple family whereas the other (Figs. 1B, 2B and 4B), a fast simple cell (cf. Kulikowski et al. 1981a), shows clear evidence of a non-linear component in its responses. In their more general properties hypercomplex I cells and fast simple cells also represent extreme examples of cells in the simple family. Hypercomplex I cells differ from typical simple cells in being end-stopped, responding well to short bars and poorly or not at all if the bar is lengthened. For further details regarding fast simple see Kulikowski et al. (1981a).

The linearly-responding hypercomplex I cell in Fig. 1A had a rather broad spatial frequency tuning curve ($B_{df} = 1.35$; $B_{oct} = 1.8$). To gratings drifting at a constant temporal frequency of 0.2 c/s, the cell's responses remained unchanged for spatial frequencies between 0.35 and 0.7 c/deg. Although the fast simple cell (S_F: Fig. 2A) responded about 10 times more vigorously than the hypercomplex I cell and continued to respond to quite high stimulus velocities, above 20°/s, its responses to gratings drifting at a constant temporal frequency (1 c/s) seem to be essentially the same as those of the other cell. There is, however, a characteristic difference. Whereas each of the hypercomplex I cell's responses to a bar of the grating begins and ends abruptly, with a clear non-responding zone between responses, each of the responses of the fast simple cell has a much more gradual onset and offset. This slight tendency in the direction of an unmodulated response is clearly evident at the lowest spatial frequency in Fig. 1B (0.35 c/deg) where there is no silent period between adjacent responses. The cell had no spontaneous activity so that this rounding-off effect was not due to the presence of a maintained discharge. In all probability the fast simple cell had a threshold high enough to mask the appearance of most of the unmodulated component that was present in the response.

A much clearer distinction between the degree of linearity displayed by the two cells in Fig. 1 is revealed by their responses to a stationary flashing grating in Fig. 2. With the grating in different phase locations the responses of the hypercomplex I cell have the typical sinusoidal profile, each being separated from its neighbour by a null position. By contrast the fast simple cell does not have a null

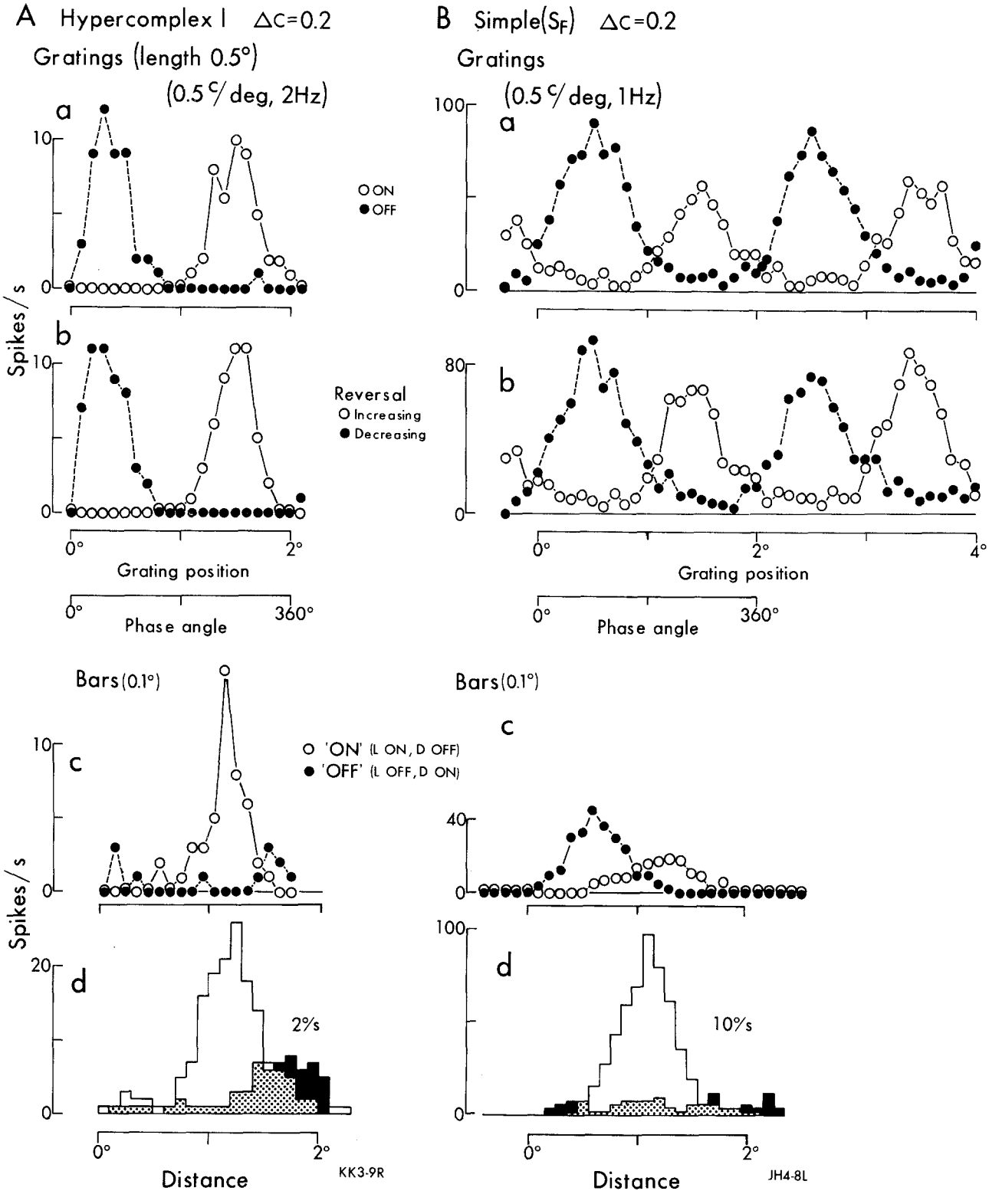

Fig. 2A, B. Average response histograms for the two cells in Fig. 1, obtained by presenting a 0.5 c/deg grating either on and off (a) or reversed in contrast (b), at the same change in contrast ($\Delta C = 0.2$). Each point represents the averaged response of the transient component as a function of position (phase) of the grating. For comparison, similar histograms are shown for stationary flashing bars (c); note that the light on – dark off and light off – dark on responses were averaged to increase accuracy. The bottom graphs (d) are response histograms to moving bars

position. The ON and the OFF response profiles (open and filled circles) overlap significantly and there is no phase location of the grating at which the cell fails to respond. It is worth noting that these observations are the same for the same change in contrast whether the change is achieved by turning the grating on and off (a) or by using contrast reversal (b). Thus the tests for a null position clearly classifies the hypercomplex I cell as linear and the other as non-linear.

For comparison, Fig. 2 also shows the responses of the above two cells to stationary flashing bars (c) and to moving bars (d). For both cells there is a considerable degree of overlap between the regions responding to either the light or the dark bars and the responses of this fast simple cell to the moving bars would not have been anticipated on the basis of the response profiles to the stationary flashing bars. Further evidence of a strong degree of non-linearity in the responses of this cell will be discussed below in relation to Fig. 4.

Of the 14 ordinary simple and hypercomplex I cells, 12 were tested by the null-point method, 7 by their responses to drifting sinusoidal gratings and 5 by both procedures. Of the 5 cells tested by both procedures, four showed both a null-point to a stationary flashing grating (Fig. 2A) and the characteristic half-wave rectified type of response to a drifting sinusoidal grating as in Fig. 1A. The remaining cell did not have a null-point and had the rounded-off type of response to a drifting grating as in Fig. 1B. Nine of the 12 ordinary simple-type cells revealed a null-point when tested with a stationary flashing grating and 6 of the 7 cells tested with a drifting grating had responses like those in Fig. 1A. Our tests showed no obvious differences between simple and hypercomplex I cells in respect to the linearity of their spatial summation.

All six fast simple cells tested with a stationary flashing grating failed to show a null-point and three of the 6 reacted to a drifting sinusoidal grating with the rounded-off type of response as in Fig. 1B. However, none of the fast simple cells showed the non-modulated type of response to fine gratings that is characteristic of Y-cells in the retina and lateral geniculate nucleus (Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976).

The above analysis indicates that the majority of the cells we classified as simple and hypercomplex I types had spatial summation that was approximately linear, the remaining cells showing varying degrees of non-linearity. Nevertheless we felt justified in classifying the latter cells in the simple family not only because of their general response properties but also because they reacted to gratings in a manner that was approximately predictable from their receptive field arrangement thereby providing an easily interpreted, if non-linearly coded, output signal. It is worth noting that whereas the null test accentuates the non-linear properties of cells, the responses of simple cells to moving bars and edges tends to emphasize their linear properties. Thus the presence of some non-linear components in the responses of simple cells does not affect the basic regularity of their response profiles to moving bars and edges. Furthermore the departure from full spatial summation by fast simple cells can be reduced by decreasing either the contrast (below 0.1) or the velocity (below 5°/s) of the moving bar and edge stimuli.

Comparison of Responses to Bars and Edges with Spatial Frequency Tuning

To the extent that simple cells exhibit linear summation of their responses, the spatial pattern of these responses should be reconstructed by inverse Fourier transformation of the respective spatial frequency-responsivity tuning curves. Brief reference to some of the problems associated with these reconstructions is needed at this stage to provide the basis for a description of our results (cf. Movshon et al. 1978a; Andrews and Pollen 1979). Our reconstructions have generally been based on contrast sensitivity tuning curves since they are easier to record than responsivity curves. However, we found that the two kinds of spatial frequency tuning curves are not much different (see below). Although we used constant temporal frequency tuning curves for our Fourier transformations rather than constant angular velocity curves (cf. Andrews and Pollen 1979), these two procedures should give identical results (Tolhurst and Movshon 1975; Movshon et al. 1978b).

Fourier transformation requires a knowledge of the phase of the response at each spatial frequency. Unfortunately, phase information was lost in our procedures for determining both the contrast sensitivity and responsivity tuning curves. In general therefore, we assumed that the receptive fields were either perfectly symmetrical or perfectly antisymmetrical. Not infrequently, however, the spatial response profiles of our simple cells were not ideally symmetrical and antisymmetrical and a better fit between reconstructed and recorded profiles was achieved, not by ideal cosine and sine transforms, but by assuming a small constant spatial phase shift. Mathematically this may be expressed as a spatial phase shift from a cosinusoidal inverse Fourier transform towards a sinusoidal transform. For any given tuning curve, the cosine and sine inverse transforms

can be computed. Subsequently, the dominant profile can be corrected by adding (or subtracting) the other transform, the fractional addition being the tangent of the phase angle (usually below 15°).

Spatial Response Profiles Predicted from Tuning Curves

We had available the responses to moving bars and edges from all 27 simple cells for which spatial profiles were reconstructed and, from 14 of these cells, we also recorded response profiles to a stationary flashing bar. For about 80% of the simple cells we found a reasonably good fit between the reconstructed and the recorded profiles to moving stimuli whereas in only about 50% of the cells was the fit reasonable when the comparison was with profiles in response to the stationary stimulus. The best agreement we obtained was in the case of four cells that had an unusually high level of spontaneous activity, three of these cells (A, B and C) being illustrated in Fig. 3. In each case the cell is responding to optimally-oriented bars and edges moving at the optimal velocity over the receptive field, the upper histogram in each pair being for the preferred direction and the lower for the opposite direction. Spatial response profiles (continuous lines), reconstructed by inverse Fourier transformation of the respective contrast sensitivity tuning curves (Ac, Bd, and Cd), are compared with the corresponding recorded profiles by aligning them immediately above the respective responses to the bars and edges. In addition, for two of the cells, we also recorded spatial profiles (Ba and Ca) to a stationary flashing bar.

Cell A (Fig. 3) had a receptive field that was almost ideally antisymmetrical (see Kulikowski et al. 1981a). This cell's optimal spatial frequency (1 c/deg) and the bandwidth (B_{df} = 0.84, B_{oct} = 1.3) of its tuning curve (Ac) were close to the mean values for all the cells in the simple family (see Table 1) and the reconstructed spatial profiles for both the moving bars (Aa) and edges (Ab) closely resemble the ideal antisymmetrical transforms. One of the main factors leading to nonlinearity in the responses of simple cells is their relatively high threshold indicated by the absence, or near absence, of spontaneous firing. Cell A (Fig. 3), with a spontaneous discharge of about 10 spikes/s, was one of only two cells among the 37 cells in the simple family that we examined quantitatively to have such a high level of spontaneous firing and, in keeping with this observation, the lowest thresholds (contrast below 0.01). The good fit achieved by the reconstructed profile is probably due, in large part, to the cell's low threshold. The relatively high maintained discharge also provides a direct indication of the antagonism between the subregions responding to the light (L) and dark (D) bars and edges. If, in a given subregion, a light stimulus activates the cell then a dark stimulus suppresses the cell's spontaneous activity, and vice versa for the opposite type of subregion, leading to the absence of areas in the histograms common to both responses (dotted regions). Despite the good fit described above, however, it is worth noting that the smallest subregions in both the reconstructed profiles are without counterparts in the recorded profiles (see Discussion).

The two remaining cells in Fig. 3 were recorded close to one another in layer IV along the same electrode track. They each had a very fine spatial organization with subregions subtending only 0.25°–0.3° and among the smallest we encountered. Cells B and C also had relatively high optimal spatial frequencies (1.7 and 2.0 c/deg, respectively) and narrow bandwidths (B: B_{df} = 0.64, B_{oct} = 1.0; C: B_{df} = 0.63, B_{oct} = 0.94). The striking feature about the responses of these two cells is the number of subregions present in both the reconstructed and the recorded profiles, possibly six in the recorded profile from cell C. The latter number of subregions is the most we have encountered so far and the response profile of this cell to the stationary flashing bar is also unusual in that it could be interpreted as having six subregions alternatingly ON and OFF. Cell B has a symmetrical spatial response profile whereas for cell C the profile is antisymmetrical.

Tuning Curves Predicted from Spatial Response Profiles

In Figs. 3 and 4 we have compared spatial response profiles recorded experimentally with those predicted from sensitivity (responsivity) tuning curves. Now the reverse procedure is adopted: smoothed spatial profiles to stationary flashing and moving stimuli are used to predict tuning curves in terms of their optimal spatial frequency and half-sensitivity bandwidth. Table 1 shows results obtained for the 13 simple cells for which adequate data were available.

For seven cells, the moving edge responses were integrals of the moving bar responses with sufficient accuracy as to predict virtually the same tuning curve in each case. In five of the remaining six cells, however, the edge responses predicted sharper tuning curves (narrower bandwidths) than the bar responses. This was especially clear for cells with a high threshold as evidenced by their absence of spontaneous activity.

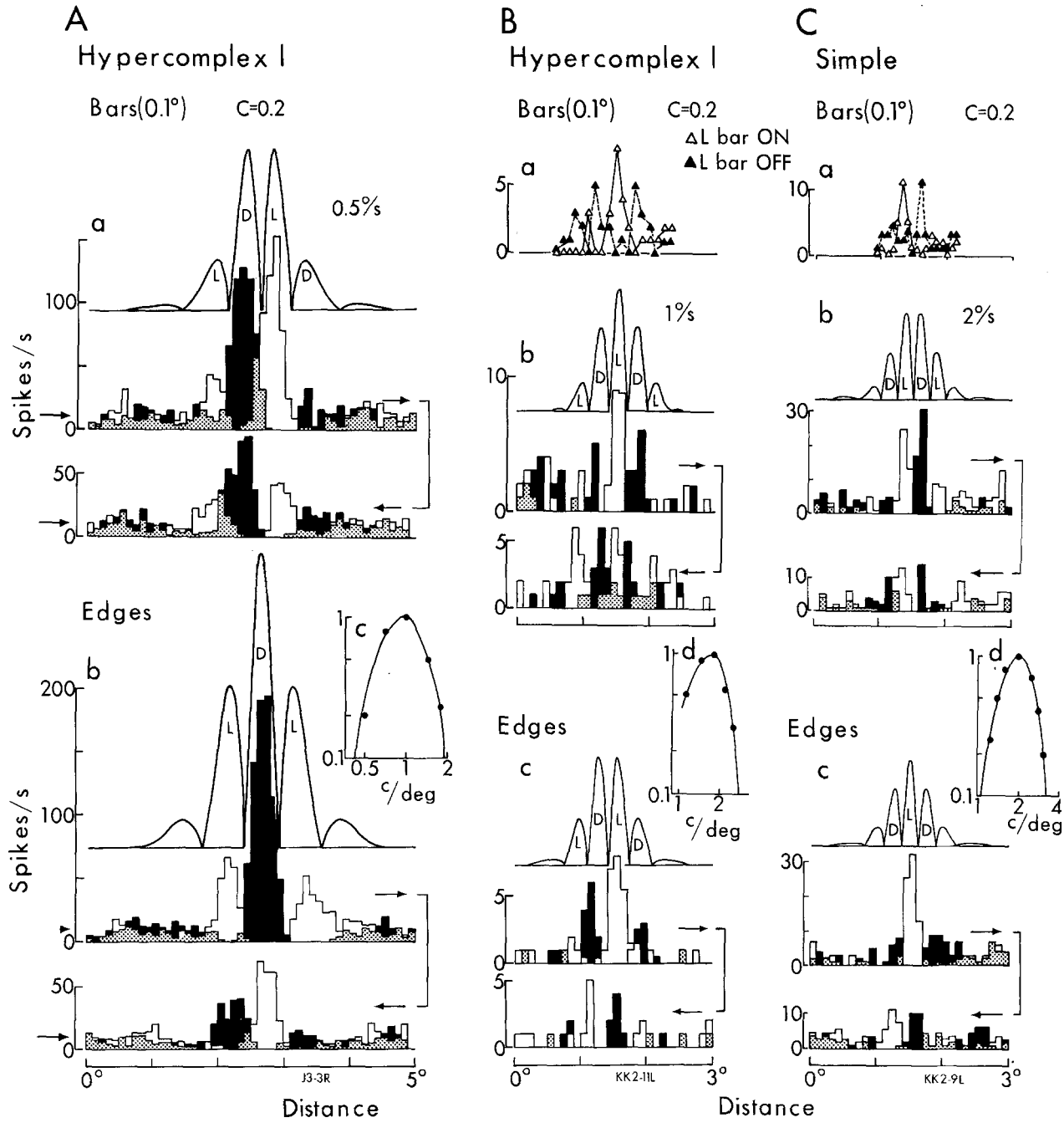

Fig. 3A–C. Spatial profiles (continuous lines) predicted by the inverse Fourier transformation of the spatial frequency sensitivity tuning curves (Ac, Bd, Cd) of three cells in the simple family compared with their averaged response histograms to moving bars (Aa, Bb, Cb) and edges (Ab, Bc, Cc). For each spatial frequency tuning curve (Ac, Bd, Cd), the maximum contrast sensitivity has been normalized to one. The responses to the light and dark bars (open and filled histograms, respectively) were recorded separately and then combined, the dotted parts of the combined histogram being common to both responses. The responses to the light and dark edges were treated similarly. The two cells (B, C), with responses to stationary flashing bars (Ba, Ca), were located in lamina 4 and had receptive fields with centres within about 1° of the visual axis. Note that all three cells were spontaneously active, but cell A had rather a high activity (10 spikes/s)

For each cell three tuning curve bandwidths were estimated on the basis of the responses to stationary flashing bars, to moving bars and to moving edges. Each of these predicted bandwidths was then compared to the bandwidth of the experimentally recorded tuning curve in terms of a ratio obtained by dividing the predicted values by the recorded value. A ratio of one would indicate perfect correspondence in each case. These individual ratios were then used to calculate mean values for each of the three kinds

Table 1. Ratio of predicted (b) and experimentally recorded (B) bandwidths of spatial frequency tuning curves. For each of 13 cells in the simple family the bandwidths of the spatial frequency tuning curves predicted on the basis of the responses to stationary flashing bars, to moving bars and to moving edges are compared with the experimentally recorded bandwidth in terms of the ratio predicted (b)/experimental (B). Units 11, 12 and 13 are atypical. Units 11 and 12 are illustrated at A and B, respectively, in Fig. 4. N = 10 refers to the first 10 units. HCI, hypercomplex I; S, simple; Fast S, fast simple

Cell No.	Cell Type	Spontaneous activity (spikes/s)	Contrast sensitivity			Stationary flashing bars		Moving bars		Moving edges		Spatial arrangement of subregions
			[a]f_o	[b]B_{oct}	[c]B_{df}	b_{oct}/B_{oct}	b_{df}/B_{df}	b_{oct}/B_{oct}	b_{df}/B_{df}	b_{oct}/B_{oct}	b_{df}/B_{df}	
1	HCI	1	2.3	1.45	0.87	1.35	1.42	1.20	1.20	1.20	1.20	Symmetrical
2	HCI	1	1.8	1.0	0.64	1.04	1.06	1.0	1.0	1.0	1.0	
3	HCI	0.2	0.77	1.47	1.04	1.10	1.23	1.06	1.08	1.06	1.08	
4	HCI	0.4	0.5	1.85	1.30	1.42	1.26	1.18	1.08	1.18	1.08	
5	S	0	1.4	1.22	0.86	1.66	1.72	1.54	1.49	1.48	1.44	
6	S	2	2.0	0.94	0.63	1.27	1.22	1.12	1.11	1.49	1.40	Antisymmetrical
7	S	0.4	0.72	1.47	0.89	0.98	1.08	1.23	1.29	1.23	1.29	
8	HCI	0.2	0.5	1.62	1.16	1.54	1.29	1.05	0.95	1.05	0.95	
9	S	0.2	0.55	1.20	0.75	1.56	1.55	1.42	1.47	1.05	1.07	
10	HCI	0.2	0.65	1.43	0.97	1.36	1.27	1.06	1.03	1.06	1.03	
11	HCI	0	1.0	1.35	0.85	1.83	2.50	1.52	1.78	1.14	1.17	Symmetrical
12	Fast S	0.3	0.52	1.36	0.98	1.94	2.45	1.95	2.28	1.34	1.24	
13	Fast S	0.2	1.0	1.40	0.93	1.05	1.07	1.21	1.15	1.03	1.02	Antisymmetrical
Mean(±SD)						1.32	1.31	1.19	1.17	1.18	1.15	
N = 10						0.23	0.20	0.17	0.19	0.18	0.17	
Mean(±SD)						1.39	1.47	1.27	1.30	1.18	1.15	
N = 13						0.31	0.48	0.27	0.38	0.17	0.15	

[a]f_o = optimal spatial frequency, [b]B_{oct} = Bandwidth in octaves, [c]B_{df} = Bandwidth $(f_u - f_\ell)/f_o$

of stimuli. It is evident that the ratios are generally largest for stationary flashing bars and that those for moving edges are only marginally smaller than those for moving bars. In other words moving stimuli predict spatial frequency tuning curves more accurately than stationary flashing bars. Since the mean ratio for moving stimuli is about 1.2, the estimate of the bandwidths they provide is probably broader than the experimentally obtained values by some 15–30%. On the basis of the above results moving stimuli provide a more accurate estimate of the spatial organization of the receptive field than do stationary stimuli. This observation is of considerable practical importance since light and dark edges are readily available stimuli and recording the responses to moving stimuli is less time-consuming and less technically demanding than to stationary flashing stimuli.

Distribution of Symmetrical and Antisymmetrical Spatial Profiles

We analyzed the pattern of the subregions in the receptive fields of 37 cells in the simple family distinguishing the symmetrical and antisymmetrical types mainly on the basis of their responses to moving light and dark bars and edges. In making these discriminations we did not find the spatial pattern of the responses to stationary flashing bars particularly helpful and the recording of these patterns was, in addition, both more time-consuming and technically demanding. In addition, it is our experience that moving stimuli frequently reveal the presence of weaker flanking subregions that would be either not in evidence or distorted if only stationary flashing stimuli were used. Spatial response profiles are relatively undistorted only when the

velocity of the stimulus is near the optimal (Kulikowski 1979). When the velocity is reduced below the optimal, symmetrical response profiles tend to become antisymmetrical and vice versa. Recordings were therefore always made at the optimal stimulus velocity as given by preliminary qualitative testing but, in addition, 11 cells were tested quantitatively over a range of stimulus velocities. Even so, response variability not infrequently made a decision difficult and we were unable to classify seven cells (18%) one way or the other. The number of cells in this category would have been higher if, for each cell, only one average response histogram had been available. Our decisions were taken only after the analysis of average response histograms to moving light and dark bars and edges and not infrequently these were repeated at least twice under slightly different conditions to make sure that optimal stimulation was achieved.

Taking into account all the above factors, we classified 16 cells as symmetrical (42%) and 15 as antisymmetrical (40%), the remainder being unclassified. Typical problem cases are shown in Fig. 4. It would have been difficult to classify cell A as symmetrical on the basis of the response profiles to either the stationary (Aa) or the moving (Ab) bar. However, other recordings made from this cell as well as the clear responses to the light and dark edges (Fig. 4Ac) qualify the cell as symmetrical.

Intervention of Nonlinearity

There is a wide spectrum in the quality of the fit between the reconstructed and the recorded spatial profiles and many factors may intervene to degrade the match (see Discussion). The good fit shown by the cells in Fig. 3 represents one end of the spectrum and the poor fit shown by the two cells in Fig. 4 illustrates the opposite end. Both contrast sensitivity (S) and responsivity (R) tuning curves were available for the two cells in Fig. 4 and the corresponding inverse Fourier transforms for the two tuning curves have been aligned above the respective responses to the bars and edges. In this figure only the responses in the preferred direction of stimulus motion are illustrated. The hypercomplex I cell in Fig. 4A was extensively studied (cf. Kulikowski et al. 1981a: Fig. 4A) but only the responses to edges and 0.25° wide bars are illustrated. The reconstructed profile has well-marked flanking regions that are, for the most part, absent from the recorded profile. On the basis of the near-equality of the responses to the light and dark edges, the spatial profile of this cell is probably of the symmetrical type but the flanking responses to the dark bar are relatively weak and, on the right hand side, almost absent.

As shown above (Fig. 2B), the fast simple cell in Fig. 4B had no null position when tested with a stationary flashing grating. The presence of nonlinearities was therefore to be expected, not only on this basis, but also because of the high threshold indicated by the complete absence of spontaneous firing. This cell also had a spatial profile of the symmetrical type, although the flanking regions in response to the dark bar are very weak in comparison to the centrally-located response to the light bar. Nevertheless there are powerful, almost equal, responses to the light and dark edges although without a sign of any additional weaker flanking subregions. Rather unexpectedly also, the profile to the stationary flashing bar (Ba) shows only two regions, with the response to negative contrast (decreasing) being slightly the stronger. Again there is almost no evidence of the multiple relatively powerful flanking subregions present in the reconstructed profiles. It is worth noting that, for both the cells, the responsivity tuning curve (R) is narrower than the sensitivity curve (S), making the flanking subregions in the corresponding reconstructions slightly more prominent and the fit poorer in comparison with the recorded profiles.

In the case of the cell in Fig. 4B, further tests failed to reveal the presence of the flanking subregions predicted on the basis of the tuning curves. A maintained discharge was produced by a conditioning technique modified from Henry, Bishop and Coombs (1969). In this modification a light bar was located in the ON subregion and flashed on and off asynchronously with respect to the moving light and dark bars.

The cells in Figs. 3 and 4 comparing the reconstructed and recorded spatial profiles are extreme examples. For most cells the fit is intermediate, being generally rather good for moving bars and edges and poorer for stationary flashing bars.

Spatial Frequency Tuning: Sensitivity Versus Responsivity

Movshon et al. (1978b) found no significant difference between the bandwidths of the spatial frequency tuning curves whether they were based on contrast sensitivity or on responsivity. We made this comparison in the case of nine cells in the simple family and found the bandwidth for responsivity slightly narrower ($B_{df} = 0.87 \pm 0.35$ SD) than for sensitivity ($B_{df} = 1.02 \pm 0.2$ SD) although the difference was not significant. In this group, seven cells had B_{df} (responsivity) less than B_{df} (sensitivity) and only two cells,

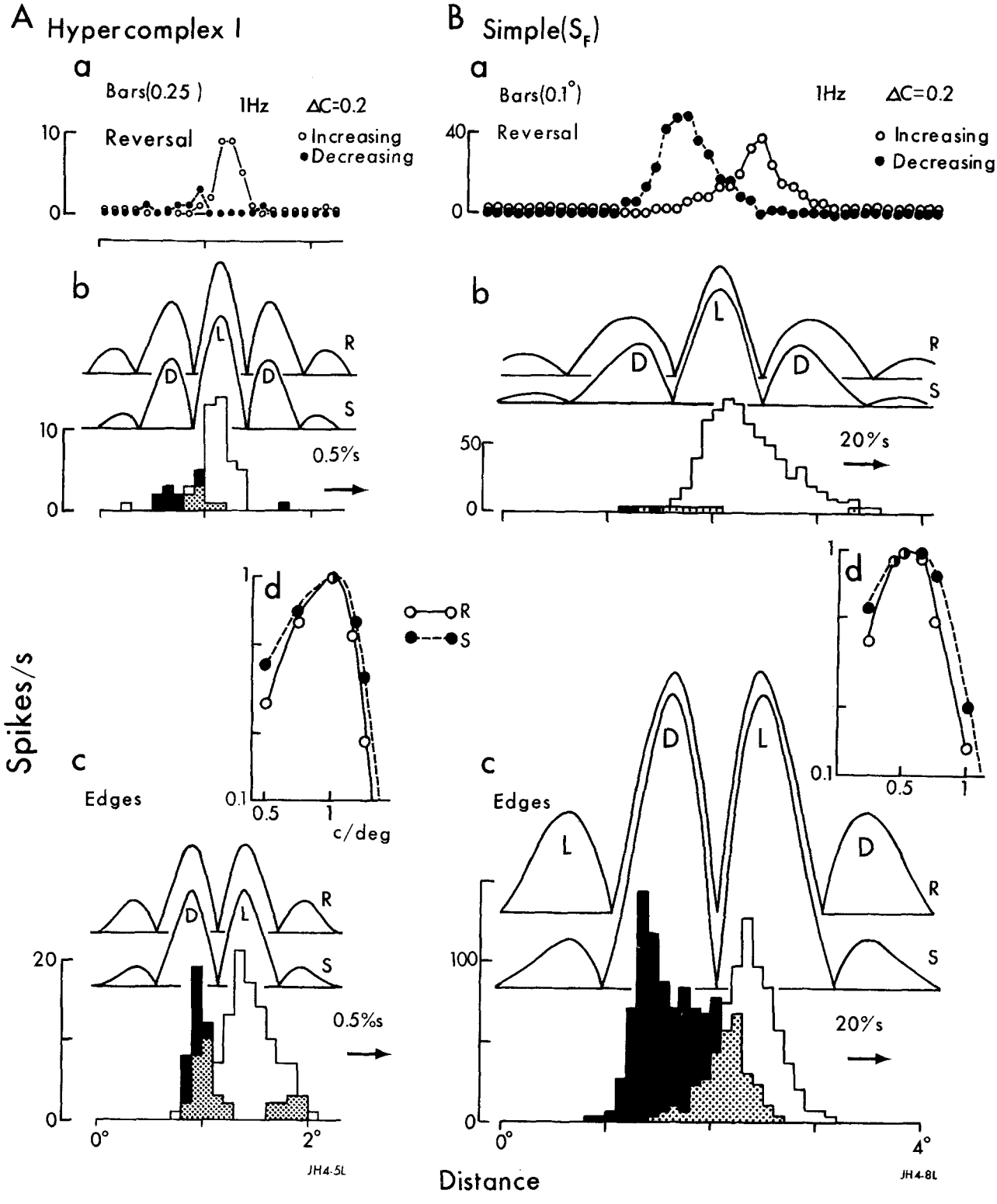

Fig. 4A, B. Examples of poor agreement between response histograms and either sensitivity (S) and responsivity (R) profiles predicted respectively from sensitivity (dashed lines in d) and responsivity (continuous lines in d) tuning curves. **A** Hypercomplex I cell (border of laminae III/IV) with a strong sustained response but with a relatively high contrast threshold, **B** fast simple cell with a sharp transient response (Lamina VI). Neither cell has any significant spontaneous activity

both broadly tuned, gave the opposite result. On principle we might expect the responsivity curves to be more sharply tuned than the sensitivity curves because the presence of a threshold would tend to eliminate the responses as the upper and lower spatial frequency limits are approached. On the other hand, the use of gratings of relatively high contrast may saturate the responses, thereby broadening the responsivity tuning curves. When these two opposite factors operate, responsivity curves may not differ much from sensitivity curves. Movshon et al. (1978b) found the two curves not significantly different. They used drifting gratings of contrast 0.5 and the responses of many cells in the simple family saturate at a contrast of 0.3–0.4 (Movshon and Tolhurst 1975).

Spatial Frequency Tuning: Bandwidth as a Function of Optimal Spatial Frequency

Figure 5 shows how bandwidth (B_{df}) varies with optimal spatial frequency (f_o). All the contrast sensitivity tuning curves used in the preparation of this figure were obtained from cells having both general properties and a spatial arrangement of subregions in their receptive fields that qualified them for inclusion in the simple family. In particular we were careful to exclude cells (e.g. B cells) that had properties intermediate between those in the simple and complex families. Of the 27 cells included in Fig. 5, 10 were simple (open and filled circles), 14 were hypercomplex I (open and filled squares) and three were fast simple (Triangles). Dots inside symbols indicate the 5 cells with receptive field centres within about 1° of the centre of the area centralis, whereas the filled symbols are for cells with receptive fields 3°–5° eccentric.

There is a clear tendency for cells with higher optimal spatial frequencies to have narrower bandwidths, the slope of the regression line fitted to all 27 data points being –0.30 ± 0.05 SD. Removing the fast simple cells from the analysis does not alter the slope. The mean optimal spatial frequency for the total population is 1.0 c/deg ± 0.54 SD (range 0.5–2.3) and the mean bandwidth B_{df} = 0.94 ± 0.17 SD (range 0.63–1.35) (B_{oct} = 1.40 ± 0.2 SD, range 0.94–1.8). The spatial profiles reconstructed from these mean values are analyzed in a subsequent paper (Kulikowski et al. 1981b). The scatter of the data points around the regression line does not indicate any systematic variation in bandwidth for any group of cells other than the variation due to different optimal spatial frequencies. For example, the three fast simple cells have a slightly wider mean

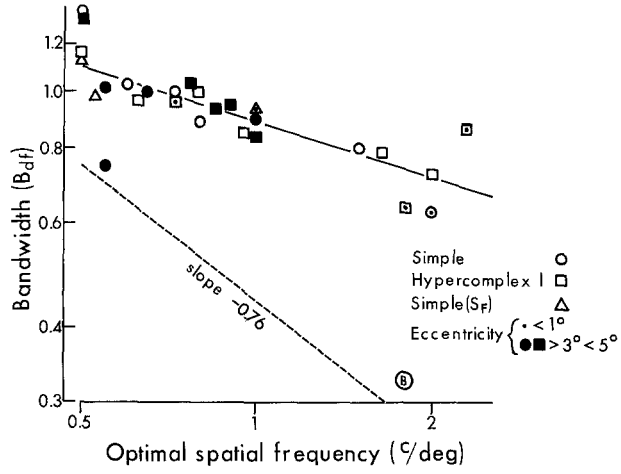

Fig. 5. Bandwidth (B_{df} = width of a tuning curve at half sensitivity divided by the optimal spatial frequency) as a function of optimal spatial frequency for various types of cells. The regression line (continuous) has a slope of –0.3; the dashed line indicates a slope of –0.76 reported by Thompson and Tolhurst (1980). Note that the encircled 'B' marks a typically narrow bandwidth of a nonlinear silent periodic cell

bandwidth (B_{df} = 1.01 ± 0.1 SD) corresponding to a mean optimal spatial frequency of 0.67 c/deg. On the other hand the hypercomplex I cells have a slightly narrower bandwidth (B_{df} = 0.92 ± 0.17 SD) in keeping with a higher optimal spatial frequency (1.14 c/deg). As a consequence, the cells in the cluster above 1.5 c/deg (mean f_o = 1.88 c/deg) had a narrow mean bandwidth (B_{df} = 0.74 ± 0.1 SD; B_{oct} = 1.15 ± 0.2 SD). The spatial response profiles of the two cells with the narrowest bandwidths (0.64 and 0.63) are illustrated in Fig. 3B and C, respectively. The two cells with the broadest tuning curves (B_{df} = 1.35; B_{oct} = 1.8) were located in the border region between laminae III and IV (cf. Thompson and Tolhurst 1980) although other cells in this region did not have particularly broad bandwidths. The cell with the low optimal spatial frequency of 0.55 c/deg and narrow bandwidth (B_{df}: sensitivity, 0.75; responsivity, 0.70) had at least four subregions in its recorded spatial profile. The data point labelled B in Fig. 5 belonged to a silent periodic cell with a bandwidth of 0.33. Silent periodic cells, which were the only cells we encountered with such a narrow bandwidth, have properties intermediate between simple and complex and display nonlinearities in their responses even with optimal stimulation (Kulikowski and Bishop 1980b).

Variations in Optimal Spatial Frequency

Figure 5 shows that cells representing the very centre of the visual field, within about 1° of the visual axis,

are tuned to both high (up to 2.3 c/deg) as well as relatively low (0.7 c/deg) spatial frequencies, the latter cells being encountered in the 17/18 border region. Thus in this restricted region of the visual cortex the optimal spatial frequencies of the cells can vary by a factor of at least 3.3. We observed such a range in three out of four penetrations, with only a twofold change over the range in the remaining penetration. While it is perhaps not surprising that variations of this degree were found near the 17/18 border (cf. Movshon et al. 1978b) we have also observed variations by a factor of two in penetrations restricted to the striate cortex. Such a range of optimal spatial frequencies can occur in cells with receptive fields at the same, or nearly the same, eccentricity in recordings along a single microelectrode penetration. There were two particular sites within the depth of the cortex at which such variations in optimal spatial frequency occurred, namely in the border region between laminae III and IV and in lamina VI. Our experiments were not designed to test for a possible columnar organization of preferences for spatial frequencies since all the electrode penetrations were along Horsley-Clarke verticals and rarely either tangential or perpendicular to the cortical surface.

Discussion

Limitations of Linear Analysis

Hubel and Wiesel (1962) clearly recognized the essential feature of simple cells by stressing that their receptive fields consist of separate subregions having spatial summation within and mutual antagonism (inhibition) between the subregions. The most rigorous test for linear spatial summation is the null-position test of Enroth-Cugell and Robson (1966) which, as Movshon et al. (1978a) have shown, is passed by the majority of cells in the simple family. Summation is, however, linear only over a certain range of stimuli reasonably close to optimal. In addition, by taking into account the absence of a null position in fast simple cells we have to recognize various degrees of linearity in cells ranging from linear simple to nonlinear fast simple. The neurons in the simple family are, in turn, to be distinguished from A-cells and silent periodic cells. The latter two types are clearly nonlinear and have only a weak linear component.

Many observations indicate limits to the linearity of the responses from simple cells

(a) The responses to bars moving broadside along the line of the optimal orientation are not predicted by linear analysis. Instead of zero responses there is suppression of both the spontaneous and the driven discharge (Bishop et al. 1973).

(b) Direction selectivity is not predicted by linear analysis. Over 60% of simple cells respond to movement opposite to the preferred direction with responses less than one third those in the preferred direction. Not only is the response from the discharge region smaller but there may also be a more general suppression of activity from a wider area.

(c) Certain stimuli, such as random visual noise (Hammond and MacKay 1977), that do not activate simple cells, may nevertheless have a suppressive effect that is not predicted on the basis of linear interaction.

(d) The temporal properties of the responses of simple cells may not be linear if the velocity of the stimulus departs significantly from the optimal. While the responses to bars and edges moving at suboptimal velocities behave in a reasonably linear manner this is not the case when the velocity is significantly above the optimal (Kulikowski 1979). On the basis of linear analysis the responses at any velocity should be a linear function of the time constants of the responses to stationary flashing bars (King-Smith 1978) but this is not observed in practice. Unfortunately, nonlinearities are induced by the sudden application of a stimulus (including presumably high stimulus velocities) so that the time constants based on the application of a stationary flashing bar provide unreliable estimates (cf. Tolhurst et al. 1980).

Significance of Linear Spatial and Spatial Frequency Characteristics

The essential linearity of simple cells and the possible organization of their receptive fields into symmetrical and antisymmetrical pairs suggest that they approximate the ideal detectors described by Gabor (1946). This possibility is developed in detail in a subsequent paper (Kulikowski et al. 1981b) but brief reference is needed here for the purposes of discussion. The spatial frequency tuning curves of cells with narrow and medium bandwidths and their response profiles closely approximate the theoretical Gabor functions (cf. Fig. 3). On the assumption that the response profiles of the receptive fields along the x axis have the mathematical form of Gabor elementary signals they can be described in terms of the product of a Gaussian envelope and cosine and sine functions

$$s(x) = e^{-x^2/2\sigma^2} \begin{Bmatrix} \cos \\ \sin \end{Bmatrix} 2\pi f_o x \qquad \ldots\ldots \quad (1)$$

These functions describe localized harmonic oscillations (antagonistic receptive field subregions) where σ is the standard deviation of the Gaussian envelope of sensitivities of all the subregions and f_o is the optimal spatial frequency. For these functions, the product of the uncertainties in signalling spatial position (Δx) and spatial frequency (Δf) has a theoretical minimum of $\Delta x \Delta f = \frac{1}{2}$. The components of this product may, however, be chosen to reduce one uncertainty only at the expense of the other. Hence the greater the precision in spatial frequency the poorer the definition in spatial position and vice versa. Gabor's theory does not specify a particular distribution of optimal spatial frequencies and tuning curve bandwidths nor does it necessarily require ideal cosine and sine spatial response profiles. These problems will now be examined.

Bandwidth Versus Spatial Frequency

From equation (1) above, the simplest formula for the bandwidth of the spatial frequency tuning curve is given by the equation $B_{df} = 0.375/f_o\sigma$ (Kulikowski et al. 1981b). On the basis of this relationship, we shall consider two extreme models for the extraction of visual information and, since these models are given detailed consideration in the subsequent paper, only a brief outline is needed here. Model (a): in this model σ is constant indicating that, irrespective of f_o, all the receptive fields at a given eccentricity have the same size. Model (b): here the bandwidth B_{df} is constant, i.e. the product $f_o\sigma$ is constant. Model (a) has attracted most attention (cf. Robson 1975) since it suggests an emphasis on the extraction of spatial frequency information at the expense of spatial localization. In Fig. 5 bandwidth (B_{df}) is plotted against optimal spatial frequency on log-log coordinates. On this plot model (a) would be represented by data points arranged along a slope of –1.0. The data in Fig. 5 do not support this model as the slope is only –0.3. To date the only other report with data that bear on this problem (Tolhurst and Thompson 1979) gives the slope as –0.76 although a more recent analysis suggests a slope of –0.44 (Tolhurst – pers. commun.). These intermediate slopes rule out model (a) as the only mechanism in operation and suggest either a genuinely intermediate system, or that models (a) and (b) operate in conjunction. While an intermediate system embodying scatter and redundancy may be the most efficient (Kulikowski et al. 1981b), joint operations of the two systems, one minimizing uncertainty with respect to spatial frequency and the other uncertainty in spatial localization may offer greater scope for processing visual information in different ways.

Bandwidth of Tuning Curves

Various investigators have compared the spatial frequency tuning curves of simple cells obtained experimentally with the Fourier transform of their static spatial response profiles. Whereas De Valois, Albrecht and Thorell (1978) and Movshon et al. (1978a) obtained reasonable agreement, Andrews and Pollen (1979) observed that the static response profiles predicted broader tuning curves than those obtained experimentally. Our data indicate that tuning curves are predicted more accurately on the basis of the response profiles to moving bars and edges than on the basis of the responses to a stationary flashing bar (Table 1). Thus, for the 27 cells in Fig. 5, the bandwidths of the tuning curves obtained experimentally with moving gratings differ little from the predictions based on the responses to moving bars and edges.

Since only simple family cells in the striate cortex are believed to operate in an essentially linear manner, our quantitative observations on the responses to moving bars and edges and the predictions in respect to tuning curves ensure that only cells in the simple family have been considered in the present investigation. This is particularly important since cells having properties intermediate between those in the simple and complex families may be deceptively similar to simple cells in respect to those aspects of their behaviour that are most easily observed. Of special interest in this regard are the silent periodic cells (or the closely related B-cells of Henry et al. 1978) that have small receptive fields and little or no spontaneous activity but whose spatial frequency tuning curves have bandwidths significantly below one octave (Kulikowski and Bishop 1981b). We have not encountered linear simple cells with bandwidths below 0.9 octave ($B_{df} = 0.6$). Linear simple cells with bandwidths as low as 0.5 octave would require a receptive field organization composed of many more than the maximum number of 5–6 significant subregions that we have observed with moving bar responses or the 4–5 with moving edge responses. Similar upper limits to the number of subregions in the receptive fields of simple family cells have also been found in two other related studies, one of 88 cells (Camarda et al., in prep.) and the other of 30 cells (Vidyasagar and Kulikowski, in prep.). To have confidence that a very narrow bandwidth has been obtained from a linear simple cell it should be demonstrated that the spatial response profile has an appropriately large number of subregions and conversely, when there are a large number of subregions, the bandwidth should be sufficiently narrow. Since receptive field descriptions

in terms of responses to bars and edges on the one hand and to gratings (tuning curves) on the other are equivalent, the claim that the latter provide better predictions of the responses to complex patterns such as checkerboards (De Valois et al. 1979) results from a misunderstanding. Simple cell responses to checkerboard patterns can be predicted without recourse to Fourier analysis (MacKay 1981).

Symmetry and Antisymmetry

If the operation of simple cells is to conform to Gabor's theory of communication (Gabor 1946) it is essential that the cells be arranged in pairs with the spatial response profile of one member of a pair in quadrature with that of the other. In the literature, consideration has so far been limited to the simplest case where the spatial profiles are either symmetrical (cosine) or antisymmetrical (sine). Using response histograms to stationary flashing bars, Movshon et al. (1978a) found the ratio of symmetrical to antisymmetrical receptive field types to be 2/3 although they recognized many fields as being intermediate in type. As our main criteria for the classification of spatial response profiles we used the responses to light and dark bars moving at optimal velocities (cf., King-Smith 1978; Kulikowski 1979) in conjunction with the responses to moving light and dark edges. When all the various factors were taken into consideration, we concluded that 43% of the simple cells in our sample had symmetrical response profiles and 41% antisymmetrical, the remainder being unclassified mainly as a result of inadequate data. Less clear groupings emerge when the responses to only one set of stimuli are considered. Among 88 cells examined in an independent study (Camarda et al., in prep.), with the analysis limited to a consideration of the responses to moving light and dark edges, 39% could be regarded as symmetrical and 36% as antisymmetrical, the remaining 25% being in an intermediate group. All the above results indicate that there is an approximately equal number of symmetrical and antisymmetrical types with a considerate scatter in between. While response profiles of intermediate type may well occur normally, they could arise as the result of non-optimal stimulus velocities since the form of the profiles is a function of stimulus velocity (Kulikowski 1979). However, if the cells in a pair have similar temporal properties their responses will each suffer the same change in spatial phase and so, by remaining in quadrature, may still fulfil the conditions of Gabor functions. In the light of the above considerations it seems that there is only a small probability of encountering pairs of cells with ideally symmetrical and antisymmetrical response profiles and sufficiently close together in the cortex to be regarded as a pair. In the present study we found only two such pairs out of a total of 37 cells.

Psychophysical Studies

In human vision, Kulikowski and King-Smith (1973) and King-Smith and Kulikowski (1973) have proposed detection mechanisms having symmetrical and antisymmetrical spatial arrangements of a medium spatial-frequency bandwidth. They called these mechanisms line and edge detectors, respectively, since they were evaluated by means of threshold detection. With linear summation at threshold, these detectors can also be represented as sampling cosine and sine components of the Fourier transform of the visual signals since both descriptions are equivalent (Kulikowski and King-Smith 1973; cf. also Shapley and Tolhurst 1973; Tolhurst 1977). From their observations, King-Smith and Kulikowski (1975) evaluated the bandwidth of a proposed mean elementary mechanism (subunit) to be about $B_{oct} = 1.47$ which is virtually the same as the mean bandwidth of the simple cells in the present study ($B_{oct} = 1.40$; cf. also Movshon et al. 1978b). The bandwidth of the proposed human mechanism was also shown to decrease slightly as a function of optimal spatial frequency, the data of King-Smith and Kulikowski (1975) giving a slope of about –0.2. This slope approximates that of –0.3 for the data in Fig. 5. However, it should be noted that different evaluations of the bandwidth of the proposed human mechanisms have been made in two other studies: Graham (1978) suggested a narrower bandwidth and Wilson (1978) a broader.

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