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Spatial Frequency Analysis in Early Visual Processing [and Discussion]

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Spatial frequency analysis in early visual processing

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The existence of multiple channels, or multiple receptive field sizes, in the visual system does not commit us to any particular theory of spatial encoding in vision. However, distortions of apparent spatial frequency and width in a wide variety of conditions favour the idea that each channel carries a width- or frequency-related code or 'label' rather than a 'local sign' or positional label. When distortions of spatial frequency occur without prior adaptation (e.g. at low contrast or low luminance) they are associated with lowered sensitivity, and may be due to a mismatch between the perceptual labels and the actual tuning of the channels. A low-level representation of retinal space could be constructed from the spatial information encoded by the channels, rather than being projected intact from the retina.

1. The visual representation of retinal space

(a) *Channels, features and neural images*

When stripped down to its essentials, the multiple spatial frequency channel model of visual analysis – amply reviewed in the previous paper by Campbell – appears to be claiming remarkably little: that for a given retinal location and orientation there exist several visual receptive fields of different sizes (figure 1*a*). Such an assertion seems harmless enough, and hardly calculated to split the world forever into Professor Barlow's two camps: the 'frequency freaks', who were for it, and the 'feature creatures', who were against it. Let us therefore dig a little deeper, to see where real disagreement arises.

Assuming linearity, the simple centre-surround receptive field (r.f.) must act as a bandpass spatial filter. Small r.fs respond to high spatial frequencies, large ones to low frequencies, and so on. This is the message from very many studies in neurophysiology and psychophysics. If the topographic projection of the retina onto the cortex were perfectly orderly, then one could literally think of the pattern of cell responses as being a filtered neural image of the stimulus. Restricting the problem to one dimension, that image would be the convolution of the input waveform with the r.f. profile.

Figure 1 (*b*) shows the profiles for four channels computed in response to a single bar of medium width. Small units respond with a characteristic Mach band (peak and trough) pattern at each edge, while the larger units respond with a single peak in the centre of the bar.

In a second example (figure 1*c*) we see the response to a group of four bars. The smaller units clearly resolve individual bars, while the larger units appear to treat the pattern much as though it were a solid bar.

None of this is the least bit unexpected or controversial, but I have found these computations very instructive in thinking about the problems that the system has to face in interpreting its input. Ironically, the multiple-channel model as stated so far is consistent with almost any theory of spatial representation in what Marr (1976) has called 'early visual processing.'

Emphasis on the spatial profiles of figure 1 could lead to either the traditional image-based, isomorphic projection theories, in which one might include the work of Von Bekesy, Ratliff and Cornsweet, or to more sophisticated feature-map ideas, the most important of which is surely the work of Marr (1976). Marr rightly attacks earlier naïve notions of feature detection, in so far as they assumed a one-to-one correspondence between the firing of a single unit and the detection of a visual feature. Receptive fields are sensitive to a range of stimuli, and therefore 'feature detection' is itself a problem in pattern recognition.

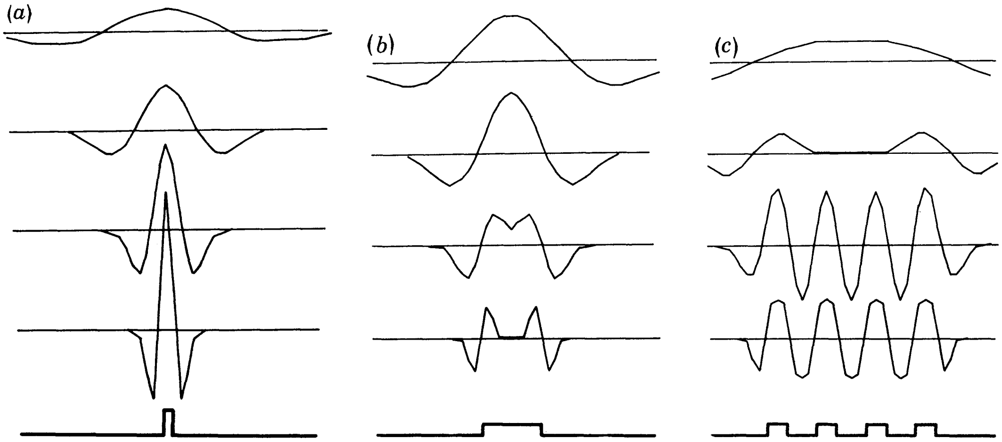

Figure 1. Four response profiles ('neural images') computed by convolving four sizes of receptive field weighting function with the stimulus waveform (lowest trace). (*a*) When the input is a narrow pulse, the responses simply illustrate the four weighting functions used. Each is a triple Gaussian function (Macleod & Rosenfeld 1974) and each differs from the next by a factor of two in height and width. (*b*) Responses to an elongated pulse which represents a solid light bar. (*c*) Responses to a cluster of four bars.

(*b*) '*Local signs*' *and Fourier spectra*

Marr's (1976) program analyses the spatial distribution of peaks, troughs and zero crossings in the response profiles to parse or segment the input into a set of visual primitives – EDGE, LINE, SHADING EDGE, etc., each of which is tagged with a list of attributes – orientation, contrast, fuzziness and position. The primal sketch model, of which this is the first stage, is important because it is, as far as I know, the only coherent attempt to solve this theoretical problem in a general way. However, it appears to share with earlier ideas a reliance on the exact preservation of spatial coordinates as a means of determining spatial relations. For example, in a coordinate-based approach, the width of a bar or the separation of two parallel lines could be given by finding the location of each line or edge and then calculating the difference between the two coordinate values. For at least the last two centuries it has been taken as more or less self-evident that the spatial projection of the retina on to the cortex served to set up a spatial coördinate map of this kind (see Boring 1942, p. 78ff). In the nineteenth century each retinal point had its 'local sign', and in Marr's system each feature ('symbolic assertion') has its positional label.

We can begin to see why the introduction of Fourier ideas had such a shock effect. They appeared to be denying this whole tradition, and replacing the spatial representation of space with its dual: the Fourier transform, in which spatial layout is not represented in an explicit way. Now this never was, or never should have been, the case, since none of the evidence for 'channels' has ever implied that they were anything other than relatively local analysers: receptive fields. The novelty lies in the idea that the pattern of responses across r.f. sizes, rather than across space, might be of primary importance in the encoding of spatial features and spatial relations. Such a pattern could be a neural approximation to the discrete (i.e. spatially limited) Fourier transform.

In short, then, merely discovering the existence of multiple r.f. sizes does not reveal their perceptual roles in representing the visual array. The entire collection of r.f. responses constitutes a data base which could be operated on in a number of ways, and neither single-unit studies nor psychophysical detection experiments give much information about such perceptual operations, since neither approach actually investigates the way that things look.

(*c*) *Distortions of perceived spatial frequency*

Only one well known phenomenon gives direct support to the frequency-based coding hypothesis. It is Blakemore & Sutton's (1969) after-effect: the spatial frequency shift. Inspection of one spatial frequency makes higher test frequencies seem even higher, lower ones even lower. The result is easily explained as a shift in the balance of frequency channel activity, but is difficult to account for on the spatial coordinate view. There is no reason why altering the sensitivities of the various filters by adaptation should alter the spacing of peaks and troughs in the output profile.

However, the processes of adaptation are not fully understood and there is evidence that Blakemore & Sutton's frequency shift is more complicated than we previously thought (Heeley 1979). Therefore, I have been attempting to devise experiments that can reasonably distinguish between the spatial and the frequency approaches without using adaptation. The subject of the rest of this paper is a class of size and frequency shifts that occur without adaptation, but which also support the frequency coding model. It turns out that a wide range of stimulus manipulations produce variations in apparent width or spatial frequency, and that all the effects conform to a general rule.

2. NATURAL VARIATIONS OF PERCEIVED SIZE

(*a*) *A possible code for bar width*

To begin with, I chose to look at single bars, because they are simple in the space domain but complex in the frequency domain. The aim was to make apparent width vary in a way predictable from the frequency viewpoint, but not from the spatial one.

On the Fourier view, the width of a bar could be given not by the positions of its edges, but by a computation on the 'neural spectrum' – the distribution of responses across channels. As a concrete example, one effective rule for extracting width is to take a weighted sum of the responses across different sizes of r.f. *centred on the bar*. Thus a possible width index is

$$W = \sum W_i R_i / \sum R_i,$$

summed across field sizes $i = 1$ to $i = n$, where R_i is response magnitude and W_i is equal to field size. Even with only four channels, W is found to vary monotonically with stimulus width over quite a wide range. In a linear model, dividing by the sum of all R_i makes the index W independent of stimulus strength. The values W_i represent the idea that each r.f. has a size- or frequency-specific label – a 'specific nerve energy' in older terminology – but the final result is a combination of weighted evidence from all r.fs. In fact, here it is the average of the active r.f. sizes, weighted by the amount of their activity.

If now we take a single light bar and add a thin dark bar to its centre, we convert it into a pair of parallel light lines of the same total width. This modification alters the pattern of channel responses, and hence also alters the index W. If the index is taken at the centre of the pattern as before, and only positive responses are included, then an apparent increase in width of about 40% is predicted. This occurs because responses go negative for small r.fs, but not for large ones. On the other hand, the theory based on location of peaks or edges would predict little or no change in width.

In several experiments similar to those described below I have found that pulse pairs or triplets, or fragments of grating (say 3 or 4 cycles), do look considerably wider than a solid bar of the same physical width, by around 20–40%. However, there is an obvious difficulty with the assumption that the system applies the same rule for extraction of width to patterns that are so clearly different. The evidence in favour of this particular rule is so far only preliminary. Spatial theories might counter with the older idea of 'contour repulsion' to explain the twin-line experiment, but as a matter of fact neither these computations nor the direct alignment experiment of Rentschler *et al.* (1975) give any support for the existence of contour repulsion.

(*b*) *Perceived bar width as a function of contrast*

A second approach, which overcomes the difficulties just described, is to keep the pattern constant throughout, and to vary its contrast. As contrast decreases, the response of relatively high frequency channels should drop below threshold first because they are the less sensitive ones. At low contrasts a bar would be represented only in the lower frequency units, and so should look both wider and more blurred. Subjects fixated midway between two vertical bars on an oscilloscope screen. The left-hand bar varied in contrast from trial to trial, and the subject's task was to adjust the width of the right-hand bar (whose contrast was fixed) to appear to match that of the left.

For all subjects and all bar widths (1.5–24′) the bars looked 1–2′ narrower at the lower contrasts, or equivalently they looked wider at higher contrasts (figure 2). In percentage terms the effects were greatest at the narrower test widths (1.5′, 3′, 6′), and these differences of 30% or more were perceptually very striking. One immediately thinks of scattered light, or Helmholtz's idea that light regions 'irradiate' into their darker surrounds. This cannot be the explanation, however, because the same result held for dark bars, using two different procedures for blocking and ordering the trials, to control for various possible procedural artefacts. The narrowing effect persisted right down to the threshold of visibility.

(*c*) *Perceived spatial frequency as a function of contrast*

Although these results were something of a blow to the hypothesis outlined above, the story took on a new turn with the next experiment: even sinusoidal gratings look finer at low contrast. This result cannot be explained by any of the ideas discussed so far, but along with the bar results it implies an underlying process of some generality. The experiment was similar to that described above, except that the single test and comparison lines were replaced by sinusoidal gratings. To minimize adaptation, the patterns were presented for only 0.5 s every 3.5 s. The subject made the spatial frequency-matching adjustment over a number of presentations until he was satisfied with the match. The results for four subjects are shown in figure 3 for four different spatial frequencies of test grating. Different frequencies were obtained by varying the viewing distance – a procedure deliberately chosen because it kept the number of cycles constant, but varied the target area in a way suitable for each spatial frequency being tested.

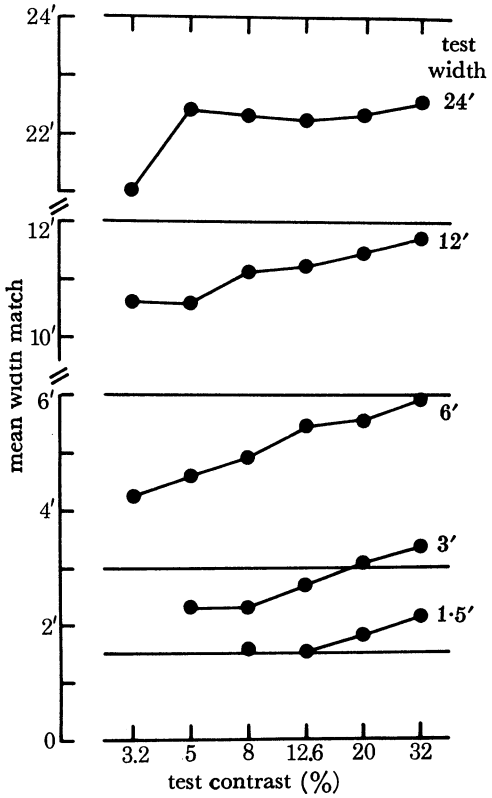

Figure 2. Mean results from five subjects who adjusted the width of a comparison bar to match the width of a test bar whose contrast and width are indicated in the figure. Both bars were light increments presented for 1 s every 3 s on a steady luminous background. The bars were vertical and each was ½° from the fixation point.

The result is surprising but unambiguous: for all subjects and all spatial frequencies, apparent frequency increased linearly as the logarithm of the contrast decreased. The mean shift was very large (30–40 %) at low contrasts, but it is clear from figure 3 that the phenomenon occurs progressively over the whole range of contrasts used, and is not something that arises only when the target is nearly invisible.

The slope of the curves may be steeper for the high frequencies, but unfortunately only two or three contrast levels were visible at 20 cycles/deg, so that any increase in slope must be taken as a tentative result.

It is remarkable that, when the effect is large, not only do the bars seem thinner and more closely packed, but there also appear to be more of them. The difference in appearance between low and high contrast gratings is illustrated in figure 4.

The message to be drawn, I suppose, is that before the frequency-based theory can be tested on bars or other objects with complex spectra, one must know how their individual components would behave. Before attempting an explanation let us consider a few more cases.

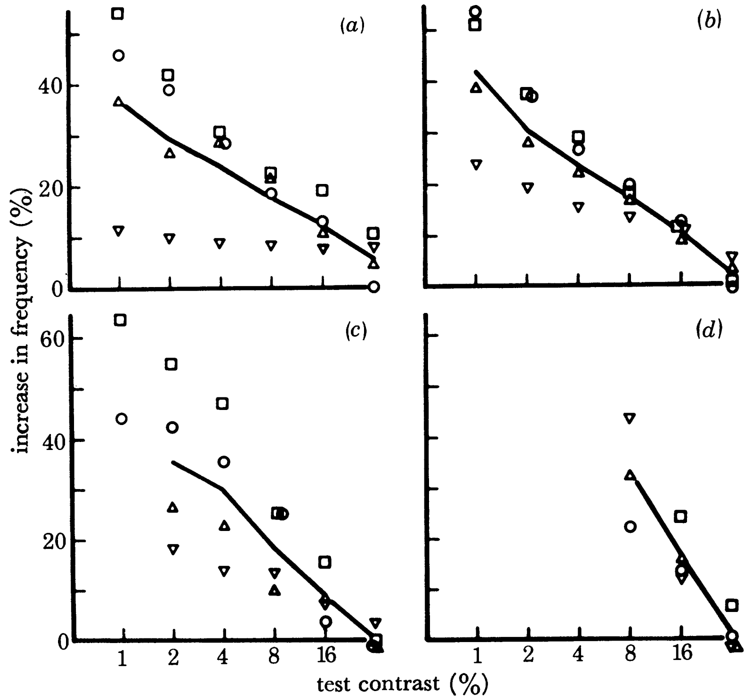

FIGURE 3. Spatial frequency matching experiment. Symbols show data from individual subjects, while solid lines indicate group mean values. Test spatial frequency was (*a*) 2.5, (*b*) 5.0, (*c*) 10.0, (*d*) 20.0 cycles/deg.

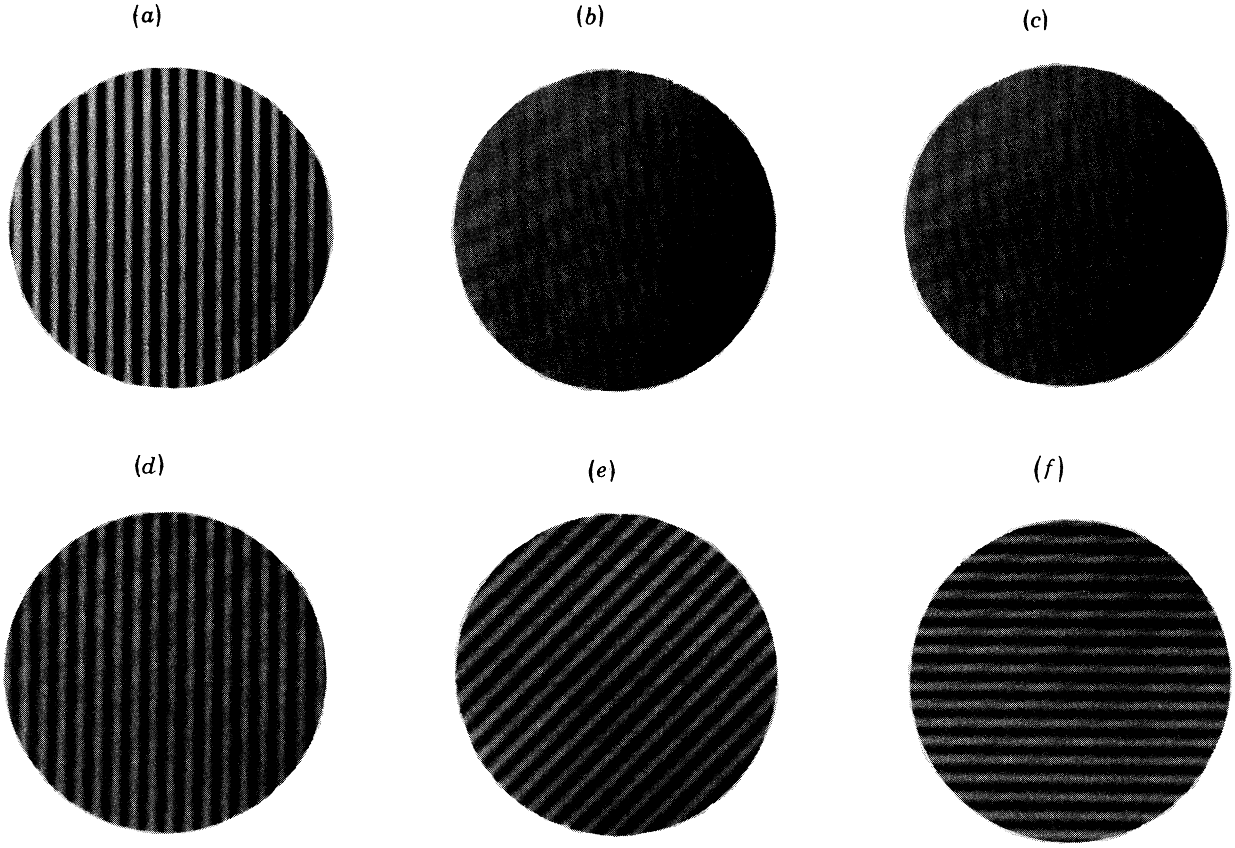

FIGURE 4. Sinusoidal gratings allow the reader to verify for himself the effects reported. All six gratings have the same spatial frequency. Comparison of (*a*) with (*b*) should reveal that at low contrast, gratings appear finer than at high. The effect may be enhanced by viewing from several metres away, and by fixating midway between (*a*) and (*b*). Alternate fixation of (*b*) and (*c*) demonstrates that a peripheral target appears finer than a foveal one. Alternate fixation of (*a*) and (*b*) illustrates the interaction between contrast and eccentricity (see text). (*d*), (*e*) and (*f*) demonstrate the effects of orientation. Most observers should see (*e*) as finer than (*d*) or (*f*). Viewing from a distance should again enhance the perceived differences.

(*d*) *Spatial frequency and retinal eccentricity*

William James (1890, p. 140) noted that objects viewed peripherally looked smaller than those viewed foveally (see also Newsome 1972). It turns out that the apparent spatial frequency of gratings behaves in a similar fashion. Figure 5 illustrates a frequency-matching experiment similar to that of figure 3, except that there were three conditions of fixation. When the observer fixated midway between the gratings (solid symbols), apparent frequency increased at low contrast, although with the subjects used the effect was smaller than in figure 3. When fixation was on the right-hand (comparison) grating (open symbols with dot), the test grating, now seen 5° peripherally, seemed to be of an even higher frequency by an extra 10–20%. Correspondingly, a peripheral comparison grating had a higher apparent frequency than a foveal test grating, and so had to be set to a lower frequency for apparent equality (open symbols). Interestingly, the interaction between contrast and fixation position was highly significant: the effect of contrast on apparent frequency was much greater peripherally than foveally. This may explain why the powerful effect of contrast has not previously been reported. Most visual experiments are conducted with foveal viewing, where the influence of contrast is least.

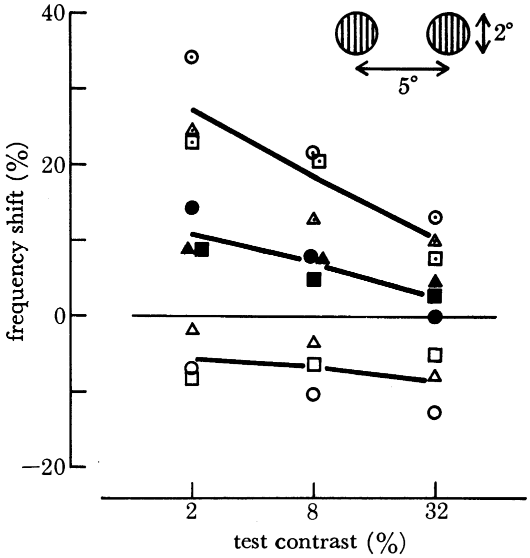

FIGURE 5. Spatial frequency matching as a function of contrast and eccentricity. Symbols show data from three individual subjects; solid lines join group means. Test spatial frequency, 5 cycles/deg. For details see text.

3. EXPLANATORY SCHEME FOR THESE EFFECTS

(*a*) *Functional similarity in effects of luminance and contrast*

Reduction of mean luminance is a third manipulation that produces an increase of apparent fineness, akin to that produced by reduction of contrast or increase in eccentricity. William James (1890, p. 142) remarked on this phenomenon too, and Virsu (1974) verified it experimentally for gratings and single targets such as letters or spots. Virsu's explanation was that at lower luminances the optimal stimulus size for a receptive field increases, or, equivalently, that the optimal spatial frequency is lower (figure 6). This latter result has recently been established for cat cortical cells by Bisti *et al.* (1977). Virsu's explanation may sound paradoxical, for at low luminance spatial frequencies seem higher, not lower. However, if the significance of a cell's output – its size 'label' – remains unchanged even though its response properties have shifted, then the perceptual result follows. To put it simply, imagine a cell tuned to 5 cycles/deg in bright conditions. If its optimum frequency shifts to 4 cycles/deg in dim conditions, while its label remains at 5, then of course a 4 cycles/deg input is reported as 5 cycles/deg, i.e. higher than it should be. Virsu (1974) found the shift to be greater at high spatial frequencies than low, and the physiological results of Bisti *et al.* fit well with this.

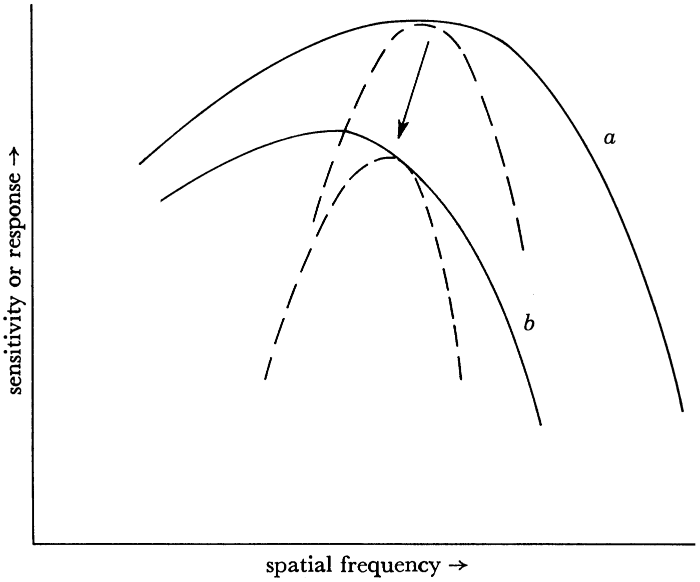

FIGURE 6. Solid curves show schematically the visual system's overall sensitivity in two conditions, (*a*) and (*b*). Broken curves represent the hypothetical shift in spatial frequency tuning of a single channel. Condition (*a*) could be: foveal viewing, high mean luminance, high contrast, vertical orientation or sustained presentation. Condition (*b*) would correspondingly be: peripheral viewing, low luminance, low contrast, oblique orientation or brief presentation.

Therefore I suggest a similar explanation for the effect of contrast, namely that the optimal spatial frequency for cortical cells increases steadily with contrast, while the spatial significance of their outputs is invariant. This is a serious matter, for it implies that the response characteristic of individual channels is nonlinear over the whole contrast range, and this conclusion makes the modelling of visual responses much more intractable, but I have so far been unable to come up with a viable alternative. One might opt, for example, for a threshold nonlinearity where, as contrast decreased, the number of active units would also decrease. However, since high spatial frequency channels are less sensitive than low ones, we would have to expect high frequency units to fall below threshold sooner, just as the higher harmonics of a square-wave grating become invisible at low contrast while the fundamental is still visible (Campbell & Robson 1968). In that case the distribution of responses should shift to lower frequency channels and patterns should look coarser at low contrasts, which is just the opposite of the truth.

Physiologically, the question of response tuning as a function of contrast has not been directly investigated, but in a sample of cat cortical cells Movshon *et al.* (1978) found that the few cells tuned to high spatial frequencies did exhibit an upward shift in their optimum frequency when the contrast was high. This result is consistent with the explanation offered above.

(*b*) *A general rule*

To add to the growing list of variables, it has also been found (Tynan & Sekuler 1974; Kulikowski 1975) that gratings look finer with brief presentations (e.g. 20 ms) than with longer ones (e.g. 200 ms). It therefore appears that from this whole set of results we can infer a very general rule: *when retinal spatial frequency is held constant, any other manipulation that takes the stimulus closer to threshold also increases its apparent spatial frequency.*

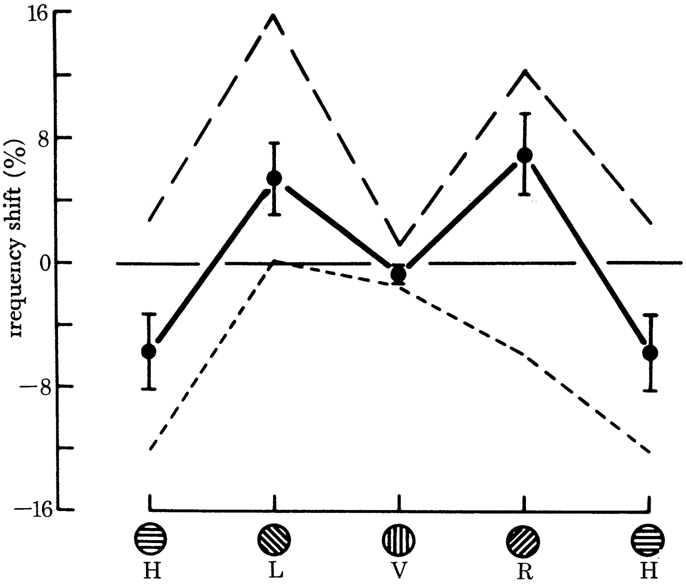

FIGURE 7. Spatial frequency matching as a function of test orientation. Test frequency, 16 cycles/deg; contrast, 12 %; foveal successive viewing of test and comparison gratings for 0.5 s each, with 0.5 s delay. Solid symbols and lines show means (± 1 s.e.) of six subjects. Broken lines illustrate two subjects; see text.

(*c*) *Effects of grating orientation*

In normal observers, sensitivity for high-frequency oblique gratings is lower than for horizontal (H) or vertical (V) ones (Campbell *et al.* 1966). From the rule given above, we can predict that obliques should also look finer than H or V. Figure 7 shows the results from an experimental test of this prediction.

Subjects adjusted the spatial frequency of a vertical grating to appear to match that of a test grating presented at any one of four orientations: H, V, left oblique or right oblique. Solid symbols show the mean results from six subjects. Oblique gratings did indeed look finer than V, but unexpectedly H was apparently coarser than V on average. The mean results, however, cannot be taken at face value, since we are dealing with a heterogeneous group of subjects. Data from individual subjects are illustrated by the two extreme cases (figure 7, broken lines). A subject with normal vision (upper curve) shows no H–V asymmetry, but a powerful oblique effect as predicted. At the other extreme, an optically corrected, astigmatic subject (the author) shows just the reverse. Fortunately this result supports the rule rather than contradicting it, for this subject is less sensitive to V than to H (Georgeson & Sullivan 1975, figure 9) and for him V looks finer than H as expected from the rule. A closer investigation of these relations is in progress.

One could imagine that the results described here on the effects of luminance, tilt, eccentricity and duration were all consequences of lowered apparent contrast, showing itself in different guises. This is, however, most unlikely because Georgeson & Sullivan (1975) found that, despite their lesser sensitivity, dim, oblique or eccentric gratings did not normally appear to have lower contrast. Instead 'contrast constancy' prevailed. The frequency shifts are therefore associated with changes in sensitivity rather than apparent contrast. In the case of brief presentations, however, apparent contrast may well play an important role, since it is known that apparent contrast decreases at short durations (Kitterle & Corwin 1979).

4. Conclusions

(a) *Mismatch between the tuning of channels and their perceptual signs*

In summary, my hypothesis is this: in conditions where the visual system as a whole suffers an attenuation of contrast sensitivity (which in fact occurs particularly at high spatial frequencies), the individual channels undergo a corresponding transformation (figure 6) which mimics that of the overall system, and leads to changes in apparent size and spatial frequency. The perceptual changes occur because each channel carries an invariant perceptual 'sign' or meaning that does not alter when the spatial selectivity of the channel shifts. If the hypothesis is correct, it becomes interesting to ask why the system is unable to compensate for these changes. Why does 'spatial frequency constancy' not exist in conditions where contrast constancy does? It is tempting to suppose that the process underlying the frequency shifts is closely related to that of contrast constancy, for in peripheral vision and at higher spatial frequencies compensation for loss of sensitivity needs to be more powerful, and it is in these conditions that the influence of contrast on perceived spatial frequency is greatest (figures 3 and 5).

(b) *Retinal coordinates: constructed or projected?*

The phenomena discussed in this paper are inconsistent with the 'neural image' concept implied by the convolution profiles of figure 1. For even if the channel tuning did vary in the way proposed (figure 6), the periodicity in the response profile would not alter (compare the bottom two traces in figure 1*c*). A strong conclusion would be that such a neural image does not exist at all. On the other hand, if it does exist, it is unlikely that spatial relations are represented metrically in it. If a coordinate map is used as an early visual representation, then it might be constructed from the locally encoded picture fragments rather than transmitted intact from the retina. It would be rather like putting together a jigsaw by finding out what is on each piece, and which pieces match up, rather than by knowing *a priori* where each piece should go. In addition, we know that the retinotopic mapping in the cortex does not hold locally, for within the Hubel & Wiesel (1974) hypercolumn there is a random scatter of r.f. locations over a limited region of retina. Of course, neurons could be jumbled anatomically while being well ordered functionally, but in view of the psychophysical evidence I prefer the conjecture that the retinotopic mapping presents at best a rough indication of location and that the detailed construction of visual space is carried out by quite different coding principles.

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Discussion

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1. Both Dr Campbell and Dr Georgeson cite the 'frequency shift effect', observed with linear gratings, as evidence for spatial frequency analysis by the human visual system, but there are at least two published studies (de Valois 1977; Burton *et al.* 1977) that show that adaptation effects involving the light bars of the gratings are independent of the dark bar width, and vice versa. Such independence appears to be directly contrary to the concept of spatial frequency analysis by the visual system.

2. In his experiments Dr Georgeson has measured the apparent bar widths of linear, sine-wave gratings presented at different contrast and mean illumination levels. His discussion implied that the spatial characteristics of the gratings are defined entirely by the light distribution in the retinal images. Yet, even if scattered light effects can be neglected, any nonlinearity involved in signal transmission along the visual pathways will distort the sine-wave grating profile causing the apparent bar width to depend on grating contrast and mean illumination level (Maudarbocus & Ruddock 1973).

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M. A. GEORGESON.

1. As I emphasized in my talk, there are two distinct issues: (*a*) what are the response properties of units in the visual system, and (*b*) what perceptual message do they convey? With respect to (*a*), the work cited supports earlier conceptions of the multiple-channel model, with additional emphasis on the subpopulations of on- and off-centre neurons. I see no contradiction here. On the other hand, if Dr Ruddock is saying that the evidence supports the idea that local width, and *not* spatial periodicity, is the message conveyed by the system, then I agree that this is an important contribution to the literature, and I am glad that he has brought his paper to my attention. Previous work could be interpreted in either way. It should be remembered, though, that after adaptation to gratings, threshold elevation is selective for test spatial frequency but not for the width of single test bars (Sullivan *et al.* 1972). Again, this is not a contradiction, but is to be understood in terms of the low sensitivity of high frequency channels (or, if you insist, small r.fs!).

2. In my experiments, subjects adjusted the *spatial frequency* (s.f.) of a comparison grating. It is not obvious to me that apparent variations in the *duty cycle* of the test grating, however caused, would lead the subject to alter his s.f. setting, nor why he should choose to increase the frequency (to match, say, light bar width) rather than decrease it (to match, in this case, dark bar width). Subjects report, and my impression is, that overall differences in texture density are observed. Moreover at 20 cycles/deg, any variation in duty cycle caused by harmonic distortion must surely be negligible, since the harmonics that define it (40 cycles/deg or more) would be invisible, especially at the low contrasts used (not more than 32 %). Yet at 20 cycles/deg the effect of contrast on apparent s.f. is very powerful (figure 3). Harmonic distortion therefore cannot be the explanation. Bar-width encoding remains viable, however, provided that shifts in all the local width signals are integrated to produce a perceptually finer texture.

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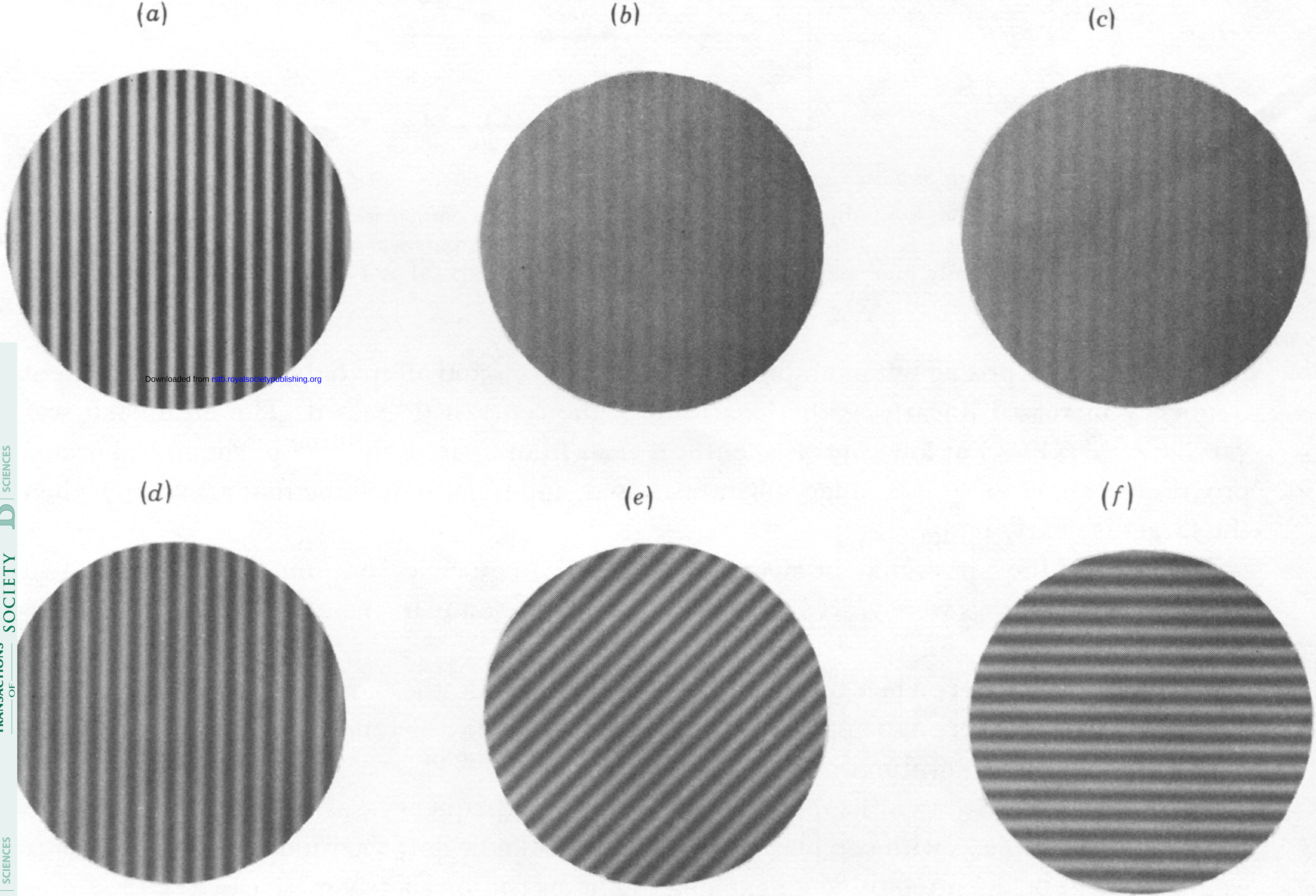

FIGURE 4. Sinusoidal gratings allow the reader to verify for himself the effects reported. All six gratings have the same spatial frequency. Comparison of (*a*) with (*b*) should reveal that at low contrast, gratings appear finer than at high. The effect may be enhanced by viewing from several metres away, and by fixating midway between (*a*) and (*b*). Alternate fixation of (*b*) and (*c*) demonstrates that a peripheral target appears finer than a foveal one. Alternate fixation of (*a*) and (*b*) illustrates the interaction between contrast and eccentricity (see text). (*d*), (*e*) and (*f*) demonstrate the effects of orientation. Most observers should see (*e*) as finer than (*d*) or (*f*). Viewing from a distance should again enhance the perceived differences.