

SPATIAL SELECTIVITY OF CONTRAST ADAPTATION: MODELS AND DATA

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(Received May 1980; in revised form 8 August 1983)

Abstract—Contrast threshold elevation was measured in human observers at a single spatial frequency (4 or 8 c/deg) after adaptation to gratings at different contrasts and spatial frequencies. When plotted against adapting contrast, the threshold elevation functions for different adapting frequencies were neither straight nor parallel, which poses difficulties for the "equivalent contrast transformation". The different functions appear to form a single family, differing by a scaling factor that depends on spatial frequency but is independent of contrast. This is similar to expressing the aftereffect as a proportion of its peak value. A multiple channel, "fatigue" model of adaptation is shown to be consistent with the results, provided the channel shape is appropriate and channels overlap considerably in the frequency domain. Channel bandwidth is estimated at 1.4 octaves, similar to that of cortical cells.

Adaptation Contrast sensitivity Spatial frequency Gratings Psychophysics

INTRODUCTION

The aspect of contrast adaptation studied in the greatest depth has been the reduction of contrast sensitivity—threshold elevation—that follows exposure to a supra-threshold grating. Threshold is raised only for test gratings of a similar spatial frequency (Blakemore and Campbell, 1969) and orientation (Blakemore and Nachmias, 1971). Hence the aftereffect has been taken to imply the existence of a system of multiple channels, each tuned to a particular range of spatial frequencies and orientations, operating to analyze the retinal image. Much effort has been devoted to measurement of the orientation and spatial frequency selectivities of threshold elevation and their dependence on other variables such as luminance, direction and velocity of movement, bar width, polarity, phase and so on (Graham, 1972; Sullivan *et al.*, 1972; Tolhurst, 1973; Sharpe and Tolhurst, 1973a, 1973b; Tolhurst *et al.*, 1973; De Valois, 1977a; Nagshineh and Ruddock, 1977; Jones and Tulunay-Keesey, 1980).

The question therefore arises as to how the tuning curves of aftereffects should be expressed and compared. The question is not trivial, because there are several different ways in which threshold elevation may be scaled, for example as a contrast threshold difference, or as a contrast ratio (R), or as $\log(R)$ or $\log(R - 1)$. The last two have been the most widely used. In addition there are several ways of expressing the selectivity or bandwidth of the effect once a scale has been chosen. Blakemore and Nachmias (1971) proposed an elegant solution to this problem by expressing the magnitude of quite different after-

effects (threshold elevation and the spatial frequency shift) on a common scale. Their method—the "equivalent contrast transformation" (ECT)—has been described in detail by Blakemore and Nachmias (1971) and by Movshon and Blakemore (1973).

The ECT method relies on the empirical finding that the magnitude of aftereffects tends to decrease (a) as the adapting pattern's orientation or spatial frequency deviates from that of the test pattern, and (b) as the adapting contrast decreases. Hence the effect of variations in the adapting pattern can be expressed in terms of an equivalent variation in adapting contrast. The selectivity of an aftereffect is then represented by the decline of equivalent contrast plotted as a function of adapting orientation or spatial frequency. Bandwidth (half-width at half-height) can be defined as that change in adapting orientation or frequency which is equivalent to a reduction in adapting contrast by a factor of two. ECT eliminates the units in which the aftereffect was originally measured, and so allows different aftereffects to be compared on a common scale. Blakemore and Nachmias (1971) found that threshold elevation and the spatial frequency shift had very similar orientation bandwidths of about 7 deg. Movshon and Blakemore (1973) found that the orientation bandwidth of threshold elevation given by ECT was constant across different adapting spatial frequencies, even though the raw data appeared to show sharper tuning at higher spatial frequencies. Thus the ECT method of expressing the tuning of adaptation effects has had success in unifying and simplifying large bodies of data (see also Georgeson and Sullivan, 1975; Sharpe and Tolhurst, 1973a, b; Blakemore *et al.*, 1973). However, the known empirical relations lead one to predict that the selectivity given by ECT should not be invariant with

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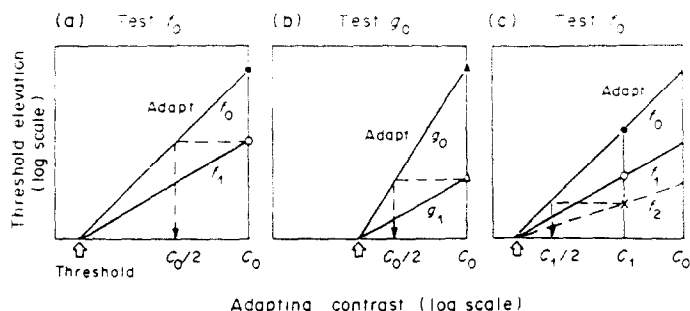


Fig. 1. Schematic illustration of the equivalent contrast transformation. See Introduction for details.

adapting contrast, and that channel bandwidth should appear to increase at lower adapting contrasts (see below).

Our purpose in this paper is twofold: (a) to measure threshold elevation as a function of adapting spatial frequency and contrast, in search of an alternative simplifying description of threshold elevation data which may be invariant with adapting contrast and (b) to explore the properties of a general model of adaptation in order to relate our empirical measures to possible underlying mechanisms selective for spatial frequency.

The working of ECT is illustrated schematically in Fig. 1. This figure makes the simplifying but empirically supported assumption that threshold elevation is a linear function of adapting contrast (in log-log co-ordinates) and extrapolates to zero near the threshold (open arrows in Fig. 1.) for the adapting pattern (Blakemore and Campbell, 1969; Movshon and Blakemore, 1973; Dealy and Tolhurst, 1974). Adapting to a fixed contrast c_0 produces elevation values [symbols in Fig. 1(a,b)] that depend on adapting frequency. Hence when testing at f_0 [Fig. 1(a)] there exists some adapting frequency (f_1) for which threshold elevation (open circle) has an equivalent contrast $c_0/2$. The frequency range $f_1:f_0$ would define the bandwidth of adaptation. In a second condition [Fig. 1(b)] testing at frequency g_0 , the elevation produced by g_1 (where $g_1/g_0 = f_1/f_0$) may be much less (open triangle) but if the g_0 function is also steeper, the equivalent contrasts of f_1 (re f_0) and g_1 (re g_0) may be identical and then the ECT bandwidth in the two cases will be the same, even though the data initially appeared to show different tuning.

In Fig. 1(c) we consider a lower adapting contrast, c_1 . Adapting frequency f_1 does not have an equivalent contrast of $c_1/2$ and compared with Fig. 1(a) the bandwidth increases to some new value given by $f_2:f_0$. It is evident from Fig. 1(c) that if the threshold elevation functions for f_0 , f_1 and f_2 have different slopes, then ECT bandwidth will vary with adapting contrast; only if the functions were parallel would the bandwidth estimate be the same for all adapting contrasts. The data of Blakemore and Nachmias (1971, Fig. 7) are rather too scattered to allow a firm decision on this point. On the other hand the results of Dealy and Tolhurst (1974) clearly favour the

change-of-slope interpretation, but they used only two test frequencies and so it is not possible to estimate bandwidths from their data. Therefore, to obtain clearer information on spatial frequency bandwidth as a function of adapting contrast and to test further the descriptive power of ECT, we performed two experiments, each measuring contrast threshold at a single test spatial frequency after adaptation to a wide range of spatial frequencies and contrasts.

After this paper was submitted, we learned of very similar experiments conducted independently by Swift and Smith (1982). Their results are at odds with those of Dealy and Tolhurst (and our own) and do not support the change of slope discussed above. This important discrepancy will be discussed in detail below.

METHODS

Vertical sine-wave gratings were displayed on an oscilloscope (Telequipment D83, yellow-green phosphor P31) and were viewed binocularly from a distance of 114.6 cm at which the circular display subtended 4 deg, with a constant mean luminance of 16 cd/m² against a very dim background. Adapting and test gratings were temporally modulated sinusoidally (counterphase) at 1 Hz to minimize after-images of the adapting grating. Contrast thresholds for test gratings of 4 c/deg (Experiment 1) and 8 c/deg (Experiment 2) were measured by the method of adjustment under various adapting conditions. Each experimental session had a standard format. The observer adapted for 2 min to a blank screen (zero contrast) and then switched into an adapt (10 sec)-test (3 sec) cycle during which he set the test contrast to threshold. He set first the threshold for the adapting spatial frequency to be used in that session, and then the unadapted threshold at the test frequency itself. Each threshold was determined by 4 or 5 successive readings and plotted points are the averages of two separate sessions. The observer then adapted for 2 min to the lowest adapting contrast, made 4 or 5 test settings with the usual adapt-test cycle, increased the adapting contrast by a factor of two (0.3 log units), adapted for a further 2 min and carried on in this way until all 9 levels of adapting

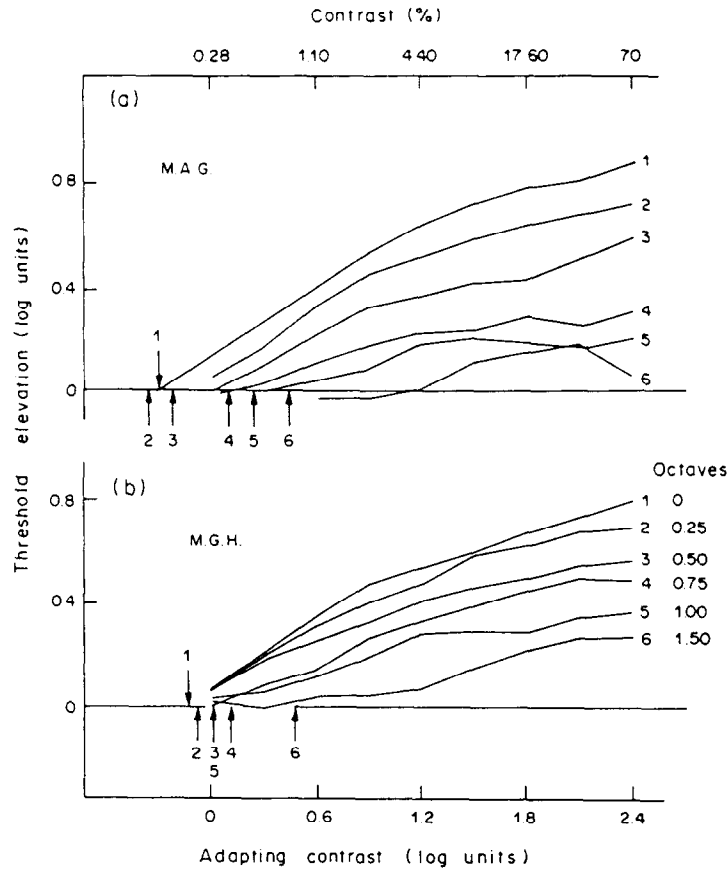


Fig. 2. Experiment 1. Threshold elevation as a function of adapting contrast for six different adapting frequencies, 0–1.5 octaves above the test frequency (4 c/deg). Arrows indicate the contrast thresholds for the adapting patterns. (a) Subject M.A.G. (b) Subject M.G.H. Adapting contrast is shown on the upper abscissa in percent and on the lower abscissa in log units re the lowest value used (0.28%). The same convention for log adapting contrast is used in Figs 3–6.

contrast from 0.28 to 70% had been presented. Thus adapting contrasts were given in a strictly ascending order rather than randomly, to avoid the need for long de-adapting periods after every few trials. This cumulative procedure is common to many of the earlier studies cited above. We examine later its possible influence on the results. Different adapting spatial frequencies were presented in random order in separate sessions, allowing sufficient time for recovery from adaptation to occur between sessions. The two authors served as subjects in the experiments.

RESULTS

Experiment 1: test at 4 c/deg

In this first experiment we adapted to 6 spatial frequencies at or higher than the test frequency (4 c/deg) over a range 0–1.5 octaves. The unadapted threshold was averaged across all 12 sessions and the results are shown in Fig. 2 as threshold elevations in log units relative to this overall baseline. For clarity, symbols have been omitted from the Figure and the data points have been joined by straight line segments with no smoothing or curve fitting. Each curve has been numbered and corresponding contrast thresh-

olds for each adapting frequency are represented by arrows on the abscissa.

For both subjects the results had three main features: (1) the curves showed negative curvature, tending towards saturation at higher adapting contrasts, (2) the slope of the curves decreased with increasing adapting frequency, (3) the curve for each adapting frequency appeared to begin at approximately its own threshold value. Thus it could be that for each subject all the curves had the same form, differing only by a horizontal shift and a vertical scaling factor. This possibility is analyzed quantitatively below.

Figure 3 shows two further ways of presenting the results: as untransformed threshold elevation curves (a) and as ECT curves (b) where equivalent contrast is plotted in log units relative to the fixed adapting contrast (which is shown in log units attached to each curve, with the same convention as the abscissae of Fig. 2). The main point here is that at low contrast the range of effective adapting frequencies if anything decreased [Fig. 3(a)] but the bandwidth given by ECT increased markedly [Fig. 3(b)]. Bandwidths were determined conventionally by the point at which equivalent contrast had fallen by a factor of two

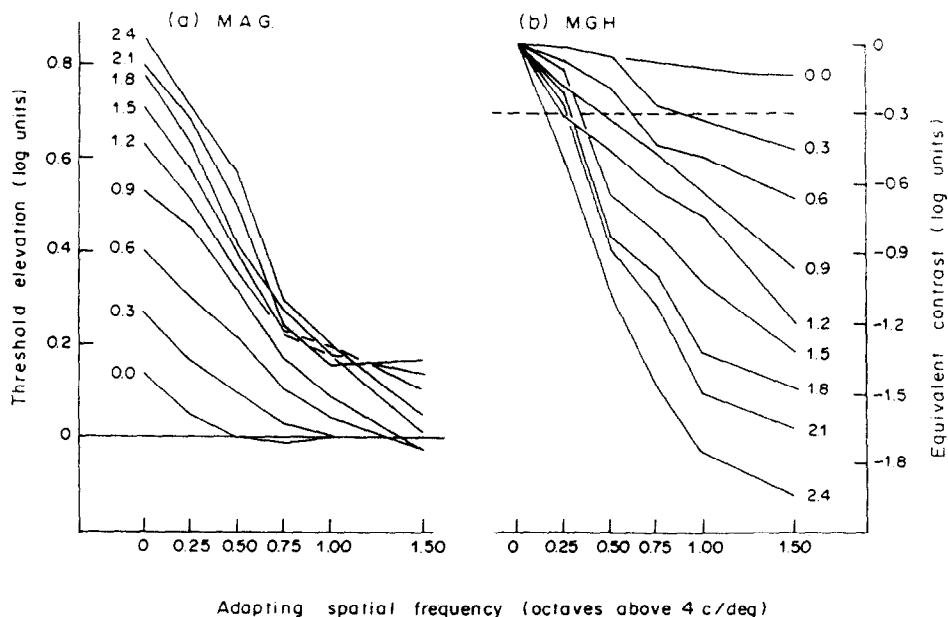


Fig. 3. Data of Fig. 2 re-plotted as functions of adapting spatial frequency with log adapting contrast (see legend to Fig. 2) as parameter. (a) Subject M.A.G. (b) Data for M.G.H. expressed as equivalent contrast (log units) and normalized to the point (0,0) by vertical translation of the curves.

[dashed line in Fig. 3(b)], and for both subjects bandwidths given by the ECT procedure (Fig. 4, triangles) were about 4 times wider at low contrast (0.5–1%) than at high contrast (35–70%). Thus although the experimental data of Fig. 2 depart from the idealized scheme of Fig. 1(a,c) in several respects,

the essential prediction that ECT bandwidth would increase at low contrast was confirmed.

Experiment 2: test at 8 c/deg

To obtain complete tuning curves, rather than half curves, we repeated the experiment, but tested at

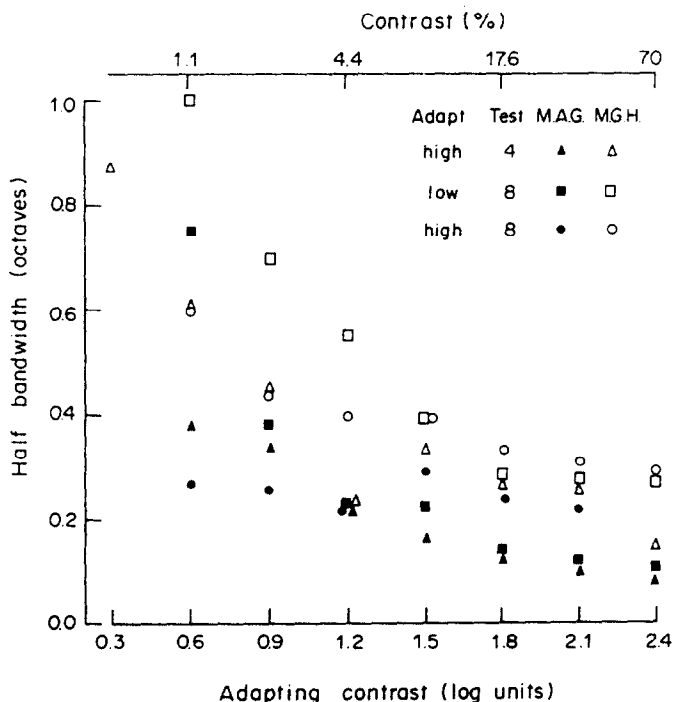


Fig. 4. Summary of equivalent contrast results. Each point is the half-bandwidth at half-height derived from the ECT curves as shown in Fig. 3(b). Points are plotted separately for the high and low frequency portions of the curves (Experiment 2, 8 c/deg) and for Experiment 1 (4 c/deg) in which only higher frequencies were studied.

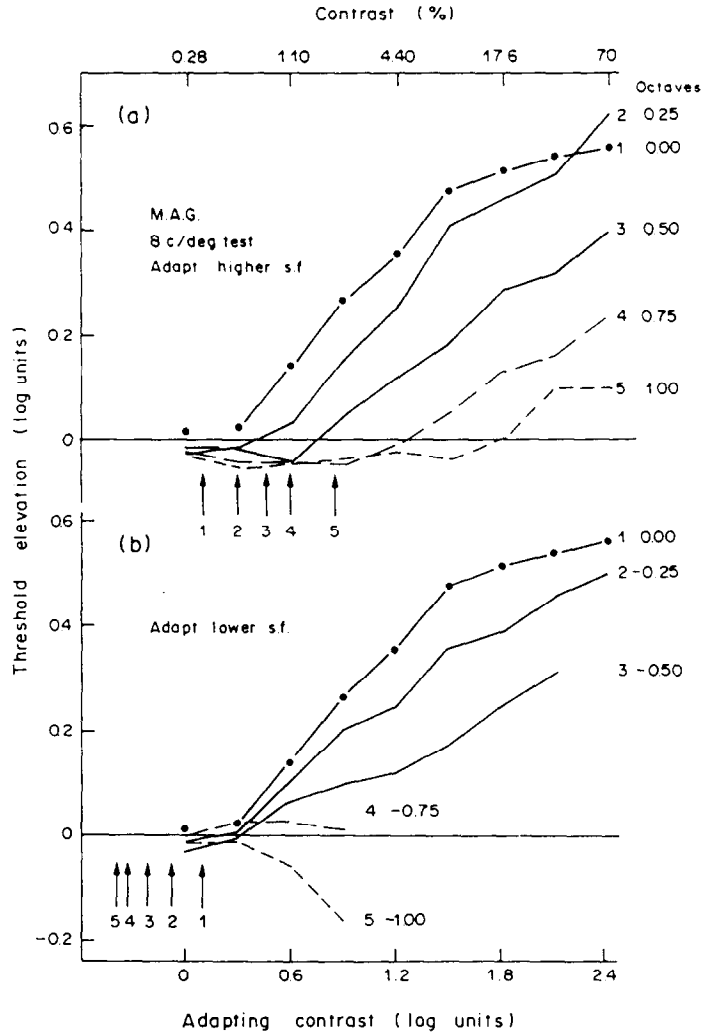


Fig. 5. Threshold elevations at 8 c/deg after adapting to spatial frequencies 0-1 octaves (a) above or (b) below the test spatial frequency. Arrows indicate contrast thresholds for each adapting pattern. All gratings modulated at 1 Hz as in Experiment 1. Subject M.A.G.

8 c/deg and adapted to frequencies in the range ± 1 octave. The results are presented in Figs 5 and 6 with the same conventions as Fig. 2. Some data points are absent from these graphs because in some conditions, particularly the lower spatial frequency, higher adapting contrasts, the subjects could not reliably distinguish the test grating from the "hallucinations" or illusory gratings produced as an aftereffect of adaptation (Georgeson 1976, 1980; Tolhurst and Barfield, 1978). Reports of threshold facilitation after adaptation (De Valois, 1977b) should therefore be treated with caution when the adjustment method is used. Nevertheless, the data are sufficiently complete to draw some firm conclusions.

The overall pattern of results was similar to that of Experiment 1. With ECT, the bandwidth estimates increased as adapting contrast decreased. The two sets of results are compared in Fig. 4. When the data were expressed as threshold elevation versus adapting contrast (Figs 5 and 6) (a) the functions had the same form but were curvilinear not straight, (b) the slope

decreased as the adapting frequency deviated from the test frequency and (c) the functions appeared to be displaced laterally by an amount related to the contrast threshold for the adapting pattern. This description of the data is evaluated below.

Do threshold elevation curves form a single family?

Threshold elevation data (in log units) for each adapting frequency were entered into a regression analysis against the data for which the adapting frequency equalled the test frequency. If the two subsets of data (e.g. curves 4 and 1 in Fig. 2) have the same form then the correlation between them should be high. The slope of the regression line would then reflect the differences in vertical scaling of the functions. If in addition the functions are laterally displaced [point (c) above] then the y -intercept of the regression line should be closer to zero when this displacement is taken into account. Thus the regression was performed both with and without a horizontal shift of the data determined by the thresh-

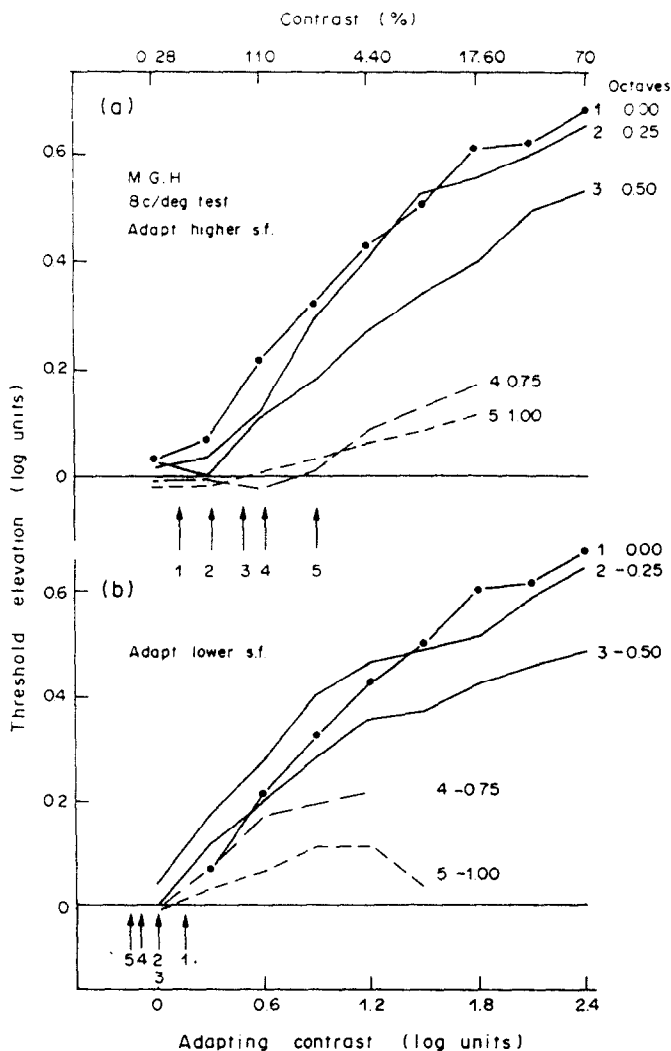


Fig. 6. As Fig. 5, for subject M.G.H.

old measurements (arrows in Figs 2, 5 and 6). When a shift was introduced in one set of data, corresponding values in the other set (curve 1) were obtained by linear interpolation. Adapting contrasts that lay below threshold were omitted from the analysis.

For both subjects and both experiments there was a total of 26 pairs of regression lines (with and without a threshold shift). The correlations were generally high (Table 1) but with occasional low values where the number of points in the sample was small. At 4 c/deg, 8/10 correlations with a threshold shift were higher than 0.95 and 7/10 cases showed a y -intercept closer to zero with a threshold shift than without it. At 8 c/deg, omitting 4 cases with $n < 5$, the corresponding figures were 9/12 correlations greater than 0.95 and 10/12 improvements of intercept. Overall, omitting the 4 cases with $n < 5$, the average correlation coefficient was 0.923 without a threshold shift and 0.949 with a shift. This increase was not statistically significant ($t = 1.68$, d.f. = 21, $P > 0.10$ two-tailed). On the other hand, the mean absolute value of the y -intercept decreased from 0.096 log

units to 0.045 log units and this improvement was highly significant ($t = 3.79$, d.f. = 21, $P < 0.002$ two-tailed). Thus with the high correlations and small intercepts shown in Table 1, the data at a given test frequency (Figs 2, 5 and 6) can to a good approximation be described as a single family of curves, differing by a horizontal shift and a vertical scaling factor.

DISCUSSION

Empirical issues

With hindsight, the complications caused by the lateral shift (a function of the contrast threshold for the adapting frequency) could have been avoided by adapting to just one spatial frequency and testing at several, rather than the other way around. Blakemore and Campbell (1969) and others have used the "test-at-many" procedure, but it has been conventional in studies using ECT to "adapt-at-many". It now seems to us that testing-at-many is not only quicker and easier, but also theoretically more tractable, because

Table 1. Regression analysis

Adaptation frequency (octaves)	Slope	Intercept	<i>r</i>	<i>n</i>	Subject	Test frequency
0.25	0.95	-0.09	0.997	8	M.A.G.	4 c deg
	0.88	0.03	0.995	9	M.G.H.	
0.50	0.68	-0.05	0.991	9	M.A.G.	
	0.64	0.09	0.995	8	M.G.H.	
0.75	0.34	0.03	0.960	8	M.A.G.	
	0.68	0.01	0.991	8	M.G.H.	
1.00	0.26	0.02	0.903	8	M.A.G.	
	0.50	-0.01	0.987	8	M.G.H.	
1.50	0.25	-0.05	0.784	7	M.A.G.	
	0.44	-0.03	0.945	7	M.G.H.	
-1.00	0.16	0.00	0.617	6	M.G.H.	8 c deg
-0.75	0.54	-0.02	0.976	5	M.G.H.	
-0.50	0.52	-0.03	0.948	7	M.A.G.*	
	0.66	0.03	0.994	7	M.G.H.	
-0.25	0.85	-0.02	0.990	8	M.A.G.*	
	0.75	0.10	0.982	7	M.G.H.	
+0.25	1.09	-0.03	0.992	8	M.A.G.	
	0.99	0.02	0.989	7	M.G.H.	
+0.50	0.79	-0.06	0.992	7	M.A.G.	
	0.75	0.05	0.996	7	M.G.H.	
+0.75	0.53	-0.08	0.970	7	M.A.G.	
+1.00	0.31	-0.06	0.895	6	M.A.G.	

The table shows regression and correlation of log threshold elevations, at each adapting frequency, against those obtained at 0 octaves. A "threshold shift" (see text) was included in all but 2 cases (marked*) where the fit was clearly better without it. At 8 c/deg, 4 cases with $n < 5$ were omitted from the table.

it should generate a family of curves all radiating from a common threshold point (Dealy and Tolhurst, 1974; cf. Fig. 1). According to the analysis presented above, the curves differ by a scale factor which depends on spatial frequency but not on adapting contrast. It may be this scale factor, rather than ECT, that most simply describes the spatial frequency selectivity of contrast adaptation.

To summarize our results Fig. 7 (solid circles and triangles) shows the scaling factor (slopes in Table 1) as a function of relative spatial frequency. The outcome should be equivalent to expressing log threshold elevation as a proportion of the peak elevation, after compensation for the threshold shift. These

proportions are, by implication, invariant with adapting contrast.

When previous studies of the spatial selectivity of adaptation were summarized in the same way, a fair degree of agreement was obtained. Solid squares in Fig. 7 show the results of Blakemore and Nachmias (1971) expressed in terms of the scale factor described above. The solid diamond is the single scale factor obtainable from Dealy and Tolhurst (1974). Open symbols represent results from two studies employing the test-at-many procedure with a single adapting stimulus. Here the log elevations are expressed as proportions of the maximum value, obtained at zero octaves. The fair agreement in spatial tuning emerg-

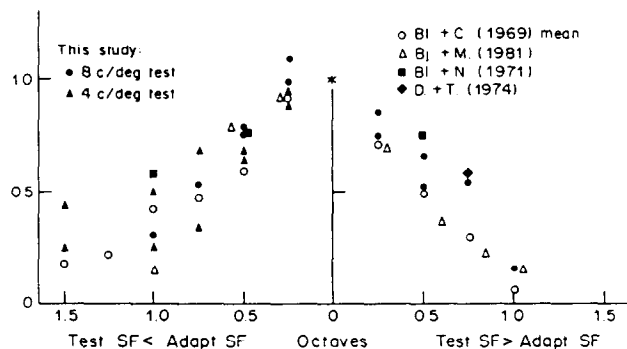


Fig. 7. Spatial frequency dependence of threshold elevation expressed as a proportion. Solid circles and triangles: show the scaling factor (slopes in Table 1) as a function of adapting frequency for the 2 observers at 2 test frequencies. Solid squares: scaling factors derived from data of Blakemore and Nachmias (1971) who tested at 4 frequencies after adapting to a range of contrasts at 8.4 c/deg. Diamond: scaling factor from Dealy and Tolhurst (1974) who tested at 2 frequencies after adapting to a range of contrasts at 4 c/deg. Open symbols represent data obtained after adapting at a single spatial frequency and contrast. Log threshold elevations as a function of test frequency are here expressed as a proportion of the peak elevation. Data were re-calculated from Blakemore and Campbell (1969) [open circles: results averaged over 4 separate adapting frequencies, 3.5, 5, 7.1 and 10 c/deg] and Bjorklund and Magnussen (1981) [open triangles, adapting frequency 6 c/deg]. There is a fairly good agreement across studies when a proportional measure is used.

Table 2. Conditions used in three adaptation studies

	Swift and Smith (1982) Experiment 1, 2	The present study	Dealy and Tolhurst (1974)
Threshold method	Adjustment, 2AFC	Adjustment	Adjustment
No. of subjects	1, 2	2	1
Viewing	Binocular?	Binocular	Binocular
Background	Dark	Dark	?
Field size (deg)	8 × 6	4	6.2 × 4.5
Luminance (cd/m ²)	32, 65	16	150
Temporal frequency (Hz)	0	1	0
Order of adapting contrasts	Increasing	Increasing	Increasing
Recovery between adapting contrasts	2 min	No	No
Test duration (sec)	<5, 2	3	10
Adaptation duration (sec)	60, 75	120	180
"Top-up" (sec)	20, 15	10	20

ing from these various studies encourages the view that the proportional/scale factor measure of threshold elevation is a useful and robust description of the data.

It is worth noting that where ECT was useful in extracting a constant orientation bandwidth across a wide range of adapting and test conditions (Blakemore and Nachmias, 1971; Blakemore *et al.* 1973), the invariance would also have been made apparent by plotting each tuning curve as a proportion of its own maximum. It is also interesting that the interocular transfer of threshold elevation is invariant with adapting contrast when expressed as a proportion of the monocular effect (Bjorklund and Magnussen, 1981).

Resolution of conflicting results: temporal factors?

Swift and Smith (1982) performed extensive experiments very similar to ours, but obtained a pattern of results quite different from those shown in Figs 2, 5 and 6. When test and adapting frequencies were unequal, Swift and Smith found that threshold elevation did not begin until the contrast of the adapting grating was considerably above its own threshold, but thereafter the functions for different adapting frequencies were nearly parallel, with slopes of about 0.4 (Experiment 1, method of adjustment) or 0.3 (Experiment 2, forced-choice method). Our threshold elevation curves begin very close to the threshold for the adapting pattern, but have slopes that depend on relative spatial frequency, and tend to saturate at higher adapting contrasts. These findings (Figs 2, 5 and 6) confirm and extend those of Dealy and Tolhurst (1974). There are of course differences between all three sets of studies in stimulus conditions and procedure, summarized in Table 2, but it seems to be the temporal conditions of the adapting procedure that distinguish Swift and Smith's study from the other two. In their Experiment 1, which is the most comparable one, they adapted initially at each contrast for only 1 min and allowed a 2 min break before increasing the level of adapting contrast. The other two studies adapted for 2 and 3 mins, with no recovery period between contrast levels. These differences in procedure would be unimportant only if adaptation were always maximal after a 1 min

period. Blakemore and Campbell (1969, Fig. 3) used a 15 c/deg adapting grating and found no increase in threshold elevation beyond 40 sec adaptation time. However, recent extensive experiments by Bjorklund and Magnussen (1981), Rose and Lowe (1982) and Rose and Evans (1983) show that this is not a general result, and that adaptation grows slowly over the course of many minutes. Recovery from adaptation also depends on the duration of inspection. We suspect therefore that Swift and Smith's results may underestimate the magnitude of threshold elevation because they adapted for relatively brief periods. Accumulation of adaptation over time would occur quite slowly in their experimental sessions because of the 2 min recovery periods given between contrast levels. The underestimation could thus have been greater at the lower adapting contrasts, presented earlier in the session. The high threshold for the onset of adaptation at neighbouring spatial frequencies could therefore be the result of temporal factors in adaptation interacting with its spatial selectivity. If this is correct, the narrow spatial tuning curves derived by Swift and Smith would also be a result of these temporal influences.

Are our own data influenced by temporal effects? Figure 8 shows control data collected one week after Experiment 1, under the same conditions, except that the adapting contrast was held constant from one 2 min adapting period to the next. Four threshold settings were made (with the usual adapt-test cycles) after each period of continuous adaptation. It is clear that thresholds continued to rise after the first 2 min period, particularly at the higher adapting contrasts. However, the data from the cumulative procedure of Experiment 1 (large open symbols) seem to reflect the maximum threshold elevation obtainable at each adapting contrast. We therefore conclude that our results are not seriously influenced by temporal factors, while those of Swift and Smith (1982) may well be.

Theoretical issues: a general model of threshold elevation

What is the relation between the empirical tuning curves derived from adaptation (Fig. 7) and the tuning of channels in human vision? We can draw no

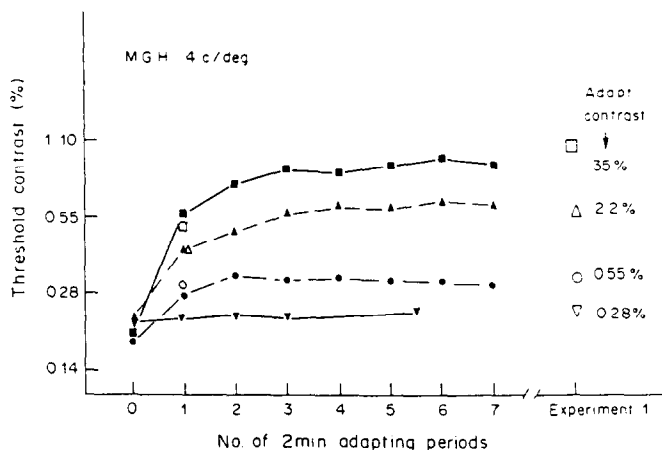


Fig. 8. The influence of adapting duration on contrast thresholds. Subject M.G.H. adapted and tested repeatedly at 4 c/deg. Comparison with this subject's data from Experiment 1 (large open symbols) suggests that the cumulative procedure of Experiments 1 and 2 did measure the maximum elevation obtainable at each adapting contrast. Small open symbols show results from single adapting periods.

conclusions without a theoretical model which makes explicit assumptions about the processes of contrast detection and the nature of contrast adaptation. For example, a widely held view is the fatigue assumption: that mechanisms in the visual system are adapted (desensitized) as a function of their own responding. An alternative view, persuasively argued by Dealy and Tolhurst (1974), is that adaptation may be a result of prolonged inhibition driven by excited channels. If a channel were inhibited by some units other than itself, then it could be adapted even when inactive. Adaptation would reflect the tuning of inhibitory interactions between channels, as well their individual excitatory tuning. Clearly, the interpretation of adaptation experiments depends greatly on which of these assumptions, fatigue or inhibition, is favoured. We have explored the properties of a fatigue model and find that with a few plausible assumptions, particularly those concerning the shape of the channel's tuning curve, results of the form shown above are quite well predicted.

Assumptions of the fatigue model

(1) *Linear channels.* There exists a set of spatial-frequency tuned, linear filters spaced D octaves apart on a logarithmic frequency axis. The sensitivity curve of the i th channel is given by

$$S_i(f) = \exp \left[- \left(\frac{|f - f_i|}{K} \right)^Q \right]$$

where f is spatial frequency in octaves, f_i is the centre frequency of the channel, K is the spread of the channel in octaves, and Q is a parameter that controls the shape of the tuning curve independently of its spread. If $\log S_i$ is plotted against f , the tuning curve is easy to envisage: when $Q = 1$ its shape is triangular with a sharp peak at f_i ; when $Q = 2$ its shape is parabolic; when $Q = 3$ its shape is slightly more flat-topped and steep-sided than a parabola (see insets in Fig. 9).

(2) *Response pooling.* The output of the i th channel to test frequency f_o is given by: $r_i = c \cdot g_i \cdot S_i(f_o)$, where c is test contrast, S_i is sensitivity as above, and g_i is a gain factor that represents each channel's state of adaptation. The observer's contrast sensitivity is determined by the response R pooled across channels

$$R = \left[\sum_i r_i^n \right]^{1/n}.$$

This non-linear pooling formula has been widely used with $n = 3$ or 4 to represent the effects of probability summation on thresholds in a multiple channel model (e.g. Wilson and Bergen, 1979; Watson, 1982). The value $n = 3.5$ was used in all the examples illustrated. Threshold is reached when R reaches a fixed critical value. With other factors held constant, R is proportional to c . It follows that threshold elevation—the ratio of adapted to unadapted thresholds—is given by computing the ratio of R (unadapted) to R (adapted) when c is arbitrarily set to 1.

(3) *Adaptation rule.* The gain factor g_i is determined by each channel's responsiveness to the adapting stimulus. Let the adapting frequency be f_1 , with contrast c_1 . If the unadapted response $[c_1 \cdot S_i(f_1)]$ exceeds a certain value $[c_0]$, then

$$g_i = [c_1 \cdot S_i(f_1) / c_0]^{-m}$$

otherwise $g_i = 1$. This expression for g_i represents the idea that if a channel's response is below a certain threshold value no fatigue occurs, while if it is above that value the output gain decreases, such that $\log g_i$ is a linear function of $\log c_1$, with slope $-m$. It turns out that when adapting and test frequencies are equal [$f_1 = f_o$] the slope of the predicted threshold elevation vs adapting contrast [EvC] function also has slope m . A survey of 12 studies in the literature gave empirical values ranging from 0.15 to 0.60. The 3 studies considered in detail here (Table 2) agreed quite well, with values of 0.30–0.45. The value $m = 0.4$ was used

throughout. The threshold for adaptation, c_0 , was given a value of 0.25.

The above assumptions are an elaboration of those outlined, but apparently not implemented, by Swift and Smith (1982).

(4) *Contrast saturation*. An optional feature of the calculations was to include a compressive non-linearity before the channel stage. Adapting contrast, c_1 , was transformed to a new value, $c_2 = A \cdot c_1 / (A + c_1)$, where A is the semi-saturation constant. For contrasts much less than A , c_2 is effectively c_1 unchanged, so any saturation was assumed not to affect the form of the threshold calculations. For $c_1 = A$, $c_2 = A/2$ and for $c_1 > A$, c_2 tends to the value A . Such a compression of input contrast was motivated by the curvature in our own data and by the results of Albrecht and Hamilton (1982) who found that saturation of spatial-frequency tuned cells in cat and monkey cortex occurred as a function of input contrast, not response rate, when the cells were tested with different spatial frequencies.

(5) *Contrast sensitivity function (CSF)*. For both our observers, log contrast sensitivity declined linearly with spatial frequency over the range 4–16 c/deg with a slope of 0.10 log units per c/deg. Thus a second optional feature of the model was to attenuate the adapting contrast by this rule, to represent variations in the observer's sensitivity to the adapting spatial frequency.

Assumptions 4 and 5 were not included except where noted below. At present, spatial pooling of responses and effects of retinal inhomogeneity have been omitted from the model (but see Williams *et al.*, 1982). The omission may not be too serious, because eccentricities in the experiment did not exceed ± 2 deg. If the changes in gain (g_i) were nearly homogeneous over this range, then the threshold improvement due to spatial pooling could be the same before and after adaptation, leaving the threshold elevation ratio unaffected.

Behaviour of the model

The main aim of this modelling exercise was to determine the form of the predicted threshold elevation vs contrast (EvC) functions when different assumptions are made about the system of channels. The spread K was held constant at 0.8 octaves and initially a fairly dense spacing of channels, at $D = 0.1$ octave intervals, was assumed.

Variation of channel shape produces marked changes in the form of the EvC functions. When channel shape is triangular [$Q = 1$, Fig. 9(a)], the functions for different adapting frequencies are parallel, with lateral displacements given approximately by the channel sensitivity curve. However, with a "domed" channel shape [$Q = 3$, Fig. 9(b)] the main effect of variation in adapting frequency is to vary the slope of the functions, with very little displacement and only slight upward curvature in the lower functions.

To see why this occurs, we must consider the relative responses of different channels to the test frequency f_0 , both before and after adaptation to f_1 . Before adaptation the channel centred at f_0 is the most sensitive and responds most; after adaptation that is not necessarily so. A channel centred at f_i , away from f_0 and more remote from f_1 , is inherently less sensitive to f_0 but may also be even less adapted than the f_0 channel. Hence the channel at f_i may be more responsive to f_0 than is the f_0 channel itself. For such a shift in the peak response to occur, one can show that as f_i departs from f_0 the reduction in the f_i channel's log sensitivity to f_0 must be less than the reduction in its sensitivity to f_1 multiplied by the adaptation exponent, m . A tuning curve with a fairly flat top and steep sides satisfies this requirement, because a channel suitably adjacent to f_0 is still quite sensitive to the test frequency but very insensitive to the adapting frequency. A triangular channel does not satisfy the above requirement when $m < 1$ and hence no peak shift occurs. The f_0 channel dominates the pooled response R and the EvC curves all grow at the same rate (m), their displacement with f_1 reflecting the f_0 channel's decreasing sensitivity to f_1 .

Examining the pattern of responses across individual channels for the cases illustrated in Fig. 9(a,b), when $Q = 3$ we found a progressive shift in the peak response as adapting contrast increased, but there was no peak shift when $Q = 1$, confirming the interpretation given above. When peak shifts occur, the pooled response R (as well as the peak value itself) is effectively spared from part of the adapting effect and so threshold elevation grows at a rate less than m [Fig. 9(b)].

It is particularly interesting that in the case of $Q = 3$ [Fig. 9(b)] a change of slope alone is sufficient to characterize the effect of varying the adapting frequency. Moreover, the proportional scaling factor extracted from these model results is very closely related to the tuning curve of an individual channel, as shown in Fig. 10.

What happens if channels are not densely overlapping in the frequency domain? When there was very little overlap [$D = 1.2$, Fig. 9(c)] or none at all, the behaviour was the same as a single-channel model. Then whatever the channel shape, all EvC functions have slope m and their displacement with f_1 exactly equals the test (f_0) channel's decreasing sensitivity to f_1 . This is the model considered by Swift and Smith (1982), because they assumed that only the f_0 channel would contribute to detection. The parallel functions reported by Swift and Smith (1982) are evidently not incompatible with a multiple-channel fatigue model [Fig. 9(a,c)], but our results and those of Dealy and Tolhurst (1974) favour the form shown in Fig. 9(b). Changes in channel shape or channel spacing are sufficient to produce both forms of prediction.

If the channel overlap is moderate, equal to half the spread K [$D = 0.4$, Fig. 9(d)], the EvC curves are

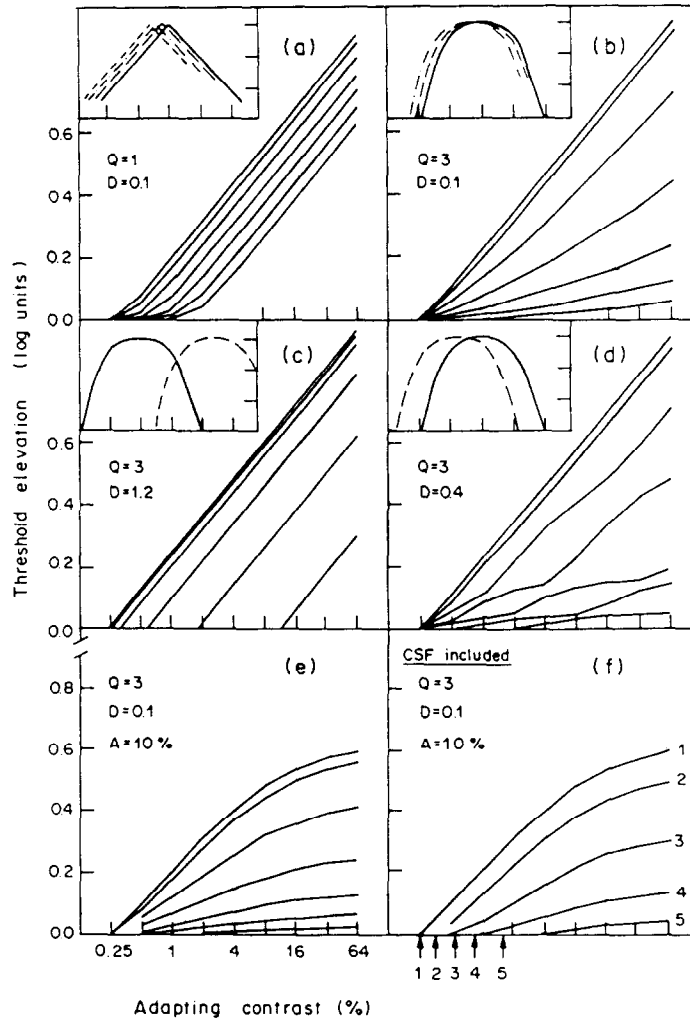


Fig. 9. Predictions from the model described in the text. Each panel shows the predicted threshold elevation at a constant test frequency, as a function of adapting contrast. The parameter is adapting spatial frequency: the highest curve in each case represents 0 octaves (adapt = test frequency); successively lower curves represent increases of adapting frequency in 0.25 octave steps. Insets (a-d) show the assumed sensitivity curves and spacing of channels in the model. Inset scale divisions: abscissa, 0.5 octaves; ordinate, 0.25 log units. The variable Q controls channel shape; the variable D is the spacing in octaves. In (e) and (f) the insets would be as in (b). In (f), the arrows show relative thresholds for the adapting frequencies, assuming that curve 1 represents 8 c/deg. See Discussion for details. Panel (f) includes all 5 features of the model: selective channels, response pooling, contrast adaptation ("fatigue"), input contrast saturation, and variations in contrast sensitivity for the adapting stimulus. The predicted elevations should be compared with those of Figs 2, 5(a) and 6(a).

rather bumpier but the change of slope is clear enough, and the scaling factors extracted are very similar to the case of dense overlap (see Fig. 10, triangles).

When input saturation is introduced [Fig. 9(e)] families of curves similar to our experimental ones are obtained. The scaling factor representing frequency selectivity is virtually unchanged (Fig. 10, crosses). This is not surprising, since the compression of input contrast amounts only to a non-linear re-scaling of the high contrast part of the abscissa: Fig. 9(e) is a horizontally stretched version of Fig. 9(b). When a parabolic channel shape is assumed ($Q = 2$; Gaussian on a linear ordinate), a rather similar family

is generated, but here the similarity between scaling factor and channel tuning is not quite so close (not illustrated). Thus the channel shape parameter Q is not absolutely critical in modelling the form of our results.

Finally, when the overall contrast sensitivity factor is introduced (assumption 5), model and data are remarkably similar in form: compare Fig. 9(f) with Figs 2, 5(a), 6(a). Again this is not surprising, because assumption 5 merely shifts the curves of Fig. 9(e) laterally by the amount indicated by the arrows. The key aspect of the model results is the variation in slope and convergence to a common threshold point illustrated in Fig. 9(b).

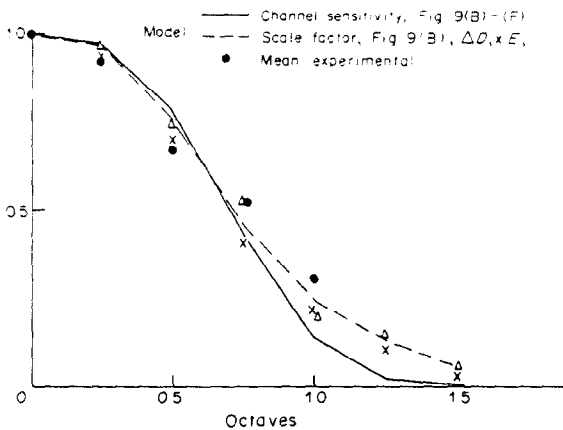


Fig. 10. Solid line: relative sensitivity of channels in the model ($Q = 3$, $K = 0.8$) on a linear ordinate. Dashed line: scaling factor derived from regression analysis on Fig. 9(b), performed as for the experimental data (Table 1), except that no threshold shift was introduced because all channels were assumed to have the same sensitivity (no CSF factor). Triangles and crosses: scaling factors derived from Figs 9(d), 9(e). Solid circles: experimental scaling factors from Table 1, averaged across test frequencies, subjects and sign of adapting frequency.

SUMMARY AND CONCLUSIONS

The spatial selectivity of threshold elevation is not invariant with adapting contrast when the aftereffect is expressed in terms of equivalent contrast [Figs 3(b), 4]. However, a frequency-dependent scaling factor was extracted from the data which expressed the selectivity of the aftereffect independently of adapting contrast (Table 1 and Fig. 7). This raised the possibility that the selectivity of spatial frequency channels could also be derived from the data. With certain assumptions about channel shape and spacing, a fatigue model is consistent with the form of our results and thus provides an alternative to the inhibition model of Dealy and Tolhurst (1974). The underlying channel sensitivity curve required to model the form of our results has almost the same shape as the predicted scaling factor plotted against spatial frequency (Fig. 10). Thus on this model the average experimental scaling factor (solid symbols in Fig. 10) is close to the relative sensitivity of an individual channel. A channel whose bandwidth at half-height is 1.4 octaves predicts the results quite well. Psychophysical studies of spatial frequency masking by filtered noise have also led to a channel whose shape on logarithmic axes is symmetrical with a flat-top and steep sides, with a bandwidth of 1.5 octaves (Pelli, 1981; but see also Henning *et al.*, 1981).

It is perhaps encouraging that the median bandwidth of a large sample of cortical simple cells in the monkey was also 1.4 octaves (De Valois *et al.*, 1982) and that, even in the subset restricted to the fovea, peak frequencies were densely distributed over a range of 5 octaves, implying the considerable overlap in the frequency domain that our model requires.

Similarly, Movshon *et al.* (1978) and Kulikowski and Bishop (1981) found the mean bandwidth of simple cells in the cat to be 1.4 octaves, with a domed, steep-sided channel shape, rather like the one we have suggested. Cortical cells (but not LGN cells) exhibit strong contrast adaptation in the form of a change in contrast gain (Ohzawa *et al.*, 1982). The main assumptions of the model are therefore physiologically realistic, as well as being consistent with the psychophysical data.

Acknowledgements—This work was supported by S.E.R.C. Grant No. GR/B/14401. We thank R. A. Smith and D. J. Tolhurst for correspondence and N. Graham for advice, encouragement and an invaluable preview of part of her forthcoming book.

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