Spatial Frequency Adaptation: Threshold Elevation and Perceived Contrast

ROBERT J. SNOWDEN,*† STEPHEN T. HAMMETT*‡

We have measured the spread of contrast adaptation across the dimension of spatial frequency. Threshold elevation was tightly tuned to the adapting spatial frequency but became much broader as test contrast was increased. This means that, for a given test frequency, there are some frequencies which do not raise threshold but do result in a loss of perceived contrast. The contrast dependence, retinal specificity and interocular transfer of adaptation effects elicited from same- and remote-frequency adaptation were compared. While we were able to show some distinct differences between threshold and suprathreshold tests, we were unable to demonstrate any reliable differences in the retinal specificity and interocular transfer between same- and remote-frequency adaptation. Copyright © 1996 Elsevier Science Ltd.

Adaptation   Perceived contrast   Interocular transfer   Retinal specificity

INTRODUCTION

The notion of "channels" in psychophysical research is now firmly rooted and has had considerable success in explaining a variety of results from masking, adaptation, summation and discrimination experiments, as well as other paradigms (for reviews see Braddick, 1978; Graham, 1989). Amongst the postulated channels are those tuned for spatial frequency—the rate at which a pattern repeats itself. This variety of techniques has culminated in a general consensus that spatial frequency channels have a bandwidth of around one to two octaves depending upon spatial frequency (channels at lower spatial frequencies have greater bandwidths; Stromeyer & Julesz, 1972; Wilson et al., 1983; Georgeson & Harris, 1984).

Perhaps the most compelling evidence for the existence of spatial frequency channels is the report of spatial frequency specific threshold elevation following adaptation (Blakemore & Campbell, 1969). After staring at a high contrast grating of a particular spatial frequency, more contrast was required to be able to detect a grating of the same spatial frequency than before this adaptation, whereas the detectability of a quite different spatial frequency was unaffected. This report was quickly followed by the finding that if a high contrast grating is viewed for some time, it gradually fades in contrast

(Blakemore et al., 1971). The two findings can then be brought together—when a high contrast grating is viewed, activity in some spatial frequency channel is generated which decreases over time. This, in turn, results in both a loss of perceived contrast and in threshold elevation. Indeed this type of idea can be applied to any notion of channels, such as those for orientation or direction of motion etc. One clear idea from this model is that the channels are fixed filters with a specific width along the filtering dimension. Hence measurements of this width should be the same for all techniques employed (given certain assumptions). Blakemore et al. (1973) measured both the orientation tuning and the spatial frequency tuning of the perceived loss of contrast at several different contrasts, and compared these estimates to others using threshold elevation (Blakemore & Campbell, 1969; Movshon & Blakemore, 1973). They found that filter widths from both threshold and suprathreshold measurements were in good agreement, hence supporting the model outlined above. Recently, however, we (Snowden & Hammett, 1992) had cause to measure orientation bandwidths at both threshold and suprathreshold levels (i.e., loss of perceived contrast) and found radically differing functions. While our threshold elevation measurements were in good agreement with previous threshold measurements, we found that orientation tuning reduced as the contrast of the test grating increased. At high test contrasts we still found some loss of perceived contrast, but this was approximately equal across all test orientations (similar results have followed; Li & Aslin, 1992; Ross, 1992; Aslin & Li, 1993). There appears, therefore, to be a dissociation between threshold and suprathreshold phenomena—the threshold for detecting a horizontal

*School of Psychology, University of Wales College of Cardiff, Cardiff CF1 3YG, U.K.
†To whom all correspondence should be addressed [Tel +44 1222 874000, ext. 4937; Fax +44 1222 874858; Email snowden@cardiff.ac.uk].
‡Present address: Laboratoire de Psychologie Expérimentalle, Université Réné Descartes, 75006 Paris, France.

grating, after adapting to a vertical grating, is unaffected but the same grating appears faded in contrast when presented at suprathreshold levels. The simple link between threshold measures and suprathreshold measures outlined above is clearly violated by this finding and we must think of other explanations, or a more elaborated version of the above theory.

Given the difference between the orientation tuning at threshold level and at suprathreshold level, it is natural for us to ask if the tuning of other channels also varies as a function of the test contrast. The first part of this paper describes some measurements of spatial frequency tuning of contrast adaptation at threshold and suprathreshold levels. We then go on to examine the retinal specificity of the adaptation effects at both threshold and suprathreshold levels, and the interocular transfer of these effects.

METHODS

Stimuli

All stimuli were sinusoidal in luminance in both space and time (counterphase flicker). The stimuli were produced on VSG 2.2 or 2.1 graphics boards (Cambridge Research Systems) and displayed on either a MAC RGB monitor for experiments 1–3 or a Joyce oscilloscope for experiments 4 and 5. The output of the grating generator was gamma-corrected by an internal look-up table. The screen was refreshed at 60 Hz (MAC) or 100 Hz (Joyce). The mean luminance of all stimuli was 96 cd/m^2 (MAC) and 150 cd/m^2 (Joyce) and normally was viewed binocularly from a distance of 57 cm. In experiment 4 we needed to view monocularly so as to assess interocular transfer. Details of these procedures are presented along with that experiment. The test stimuli had a diameter of 4 cm (4 deg) and were centred 4 cm (4 deg) to the left and right of the fixation marker. The adapting stimulus had a diameter of 6 cm (6 deg) and was centred 4 deg to the right of the fixation marker. The rest of the screen (20 × 15 cm) was unpatterned and at the mean luminance. The starting phase of all stimuli on all trials was randomly generated and all stimuli were counterphase modulated at a rate of 2 Hz to avoid the generation of conventional afterimages.

Test stimuli were presented for brief intervals of notional duration 900 msec (940 msec Joyce). The pattern was at full contrast for 500 msec (520 msec Joyce) and was ramped linearly on and off over a period of 200 msec (210 msec Joyce). Each interval was signalled by a tone.

Procedures

The experiments measured the perceived contrast of the test patterns and the threshold contrast for detection of the patterns. Two test patterns were shown in a spatial-interval binary-choice paradigm. To measure perceived contrast, we used a contrast matching technique. A standard contrast was presented in the left window whilst the right window contained a test contrast. Subjects pressed a button to indicate in which window they

perceived the pattern to have a higher contrast (note that all judgements were between patterns which were identical in spatial frequency and temporal frequency). No feedback was given. The staircase procedure (see below) changed the test contrast so that over a series of trials it tended to appear similar to the standard contrast.

For threshold measurements the standard contrast was merely set to 0% and the subject gave a yes/no decision as to whether the test contrast was visible (i.e., was it perceptually greater than 0% contrast?). All other conditions were identical.

To measure the effects of adaptation the following regime was employed. After a short period adapting to the mean luminance, there was an initial adaptation period of 120 sec. Subjects then went into a readapt-test sequence. The adapting pattern was presented for 10 sec, the screen was then blank (at mean luminance) for 250 msec and the test stimulus was presented for 940 msec. Immediately after the subject's response the adaptation pattern reappeared for the next readapt-test sequence. On any block of trials, a single adapting pattern was used. On every experiment one of these adapting contrasts was 0%. This served as a baseline from which all adaptation effects were assessed. This is particularly important as we have recorded some visual field asymmetries in perceived contrast for several of our observers.

For each standard contrast the contrast of the test pattern was controlled by a PEST procedure (Taylor & Creelman, 1967). Each staircase ran for 32 trials and was set to converge at 75% correct for the threshold measurements and at 50% for the match measurements. Pilot estimates informed our initial starting level for each condition, and the computer then started each staircase from this level ± 10%. The initial step size of the staircase was 10% of the starting level.

In any block of trials a number of conditions were interleaved (typically several test spatial frequencies, or test contrasts). Psychometric functions were then plotted and fitted by probit analysis. Each measurement was repeated three times. Elevation levels were calculated by taking the mean of the three ratios of adapted to unadapted measurements. Estimates of error were taken by the standard error of the mean of these three ratios.

Subjects

A number of subjects were used throughout the course of these experiments. Two of them were non-naive experienced observers with much practice on the particular tasks of these experiments (the authors RS and SH). All the others were naive volunteers with varying amounts of psychophysical experience who were paid for their services. No subject reported any visual defect or wore any form of optical correction in their normal lives.

EXPERIMENT 1. SPATIAL FREQUENCY TUNING OF CONTRAST ADAPTATION

Measurements of threshold contrast and measurements of matching contrast to standards of 4 and 32% were

(a) Threshold

(b)

Matching
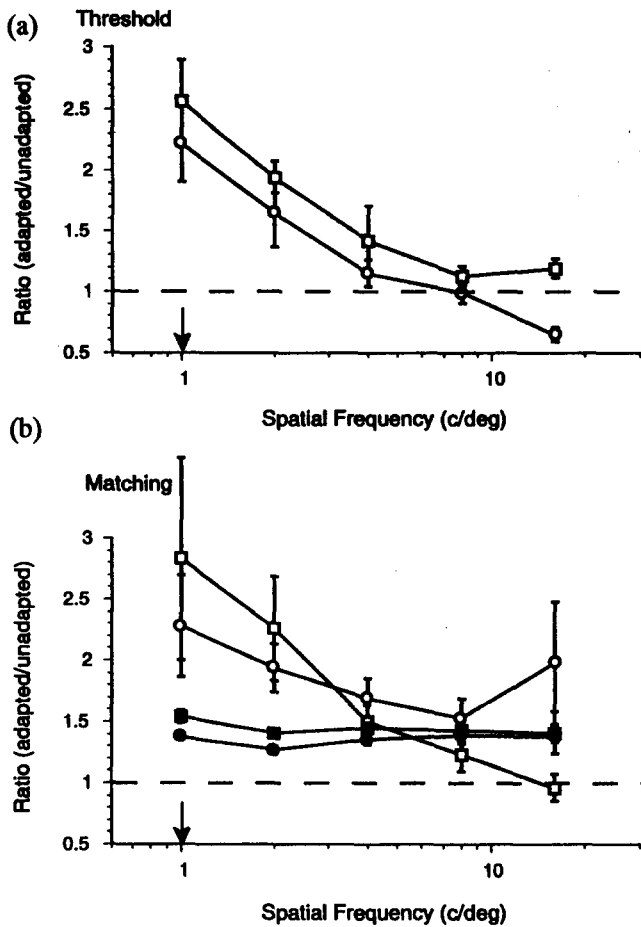

Spatial Frequency (c/deg)

FIGURE 1. The ratio of adapted to unadapted thresholds or matches is plotted as a function of test spatial frequency. The adapting spatial frequency was 1 c/deg (indicated by bold arrow). Results are shown for two subjects, squares for RS and circles for SH. Error bars represent ±1 SEM. (a) The results from the measurement of contrast thresholds. (b) The results from the measurement of contrast matches with open symbols for matches at 4% and solid symbols for matches at 32%.

(a) Threshold

(b)
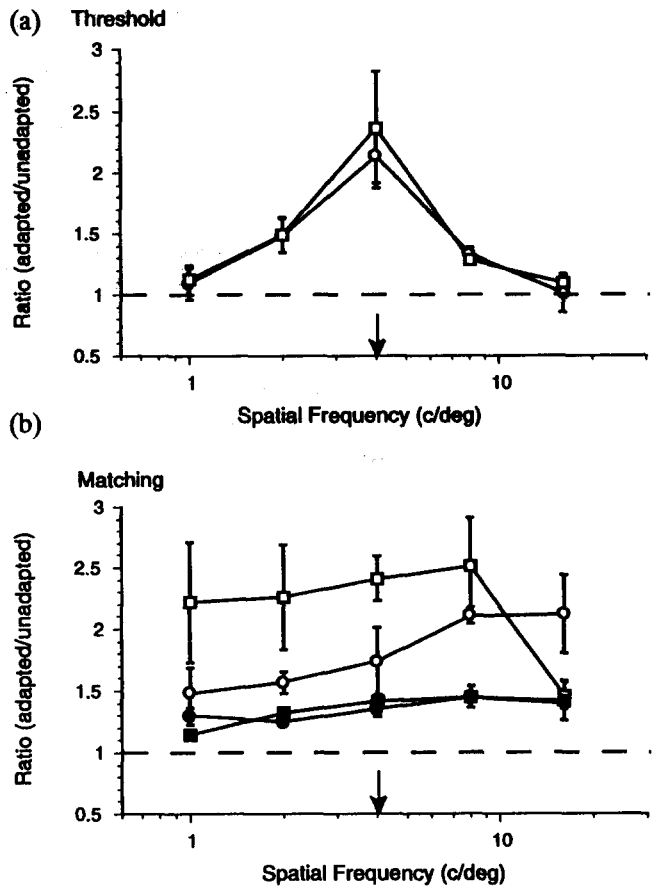
Matching

Spatial Frequency (c/deg)

FIGURE 2. The ratio of adapted to unadapted thresholds or matches is plotted as a function of test spatial frequency. The adapting spatial frequency was 4 c/deg. Other conditions as in Fig. 1.

taken. We used the strategy of adapting to one and testing at many, rather than vice versa, so that the problems trying to equate different adapting patterns for sensitivity, perceived contrast or "adapting power" did not come into play (Blakemore *et al.*, 1973; Snowden, 1991, 1994). For the results displayed in Fig. 1, the adapting pattern had a spatial frequency of 1 c/deg (indicated by bold arrow on the abscissa). Three measurements were taken for the adaptation contrast of 0% (we refer to this as the unadapted condition) and three for the adaptation contrast of 64% (referred to as the adapted condition) and the mean ratio of these three measurements is plotted against the test spatial frequency. The error bars represent ±1 standard error of these means. Figure 1(a) depicts the results for merely detecting the presence of the test pattern (threshold sensitivity). In line with a large number of previous studies (e.g. Blakemore & Campbell, 1969; Georgeson & Harris, 1984) we find that the maximum threshold elevation is found at the adapting spatial frequency (in this case 1 c/deg) and falls off to be near zero by 2 log units higher (4 c/deg). Figure 1(b) depicts

the results from the matching experiments. The open symbols refer to the condition of matching to a standard of 4%. As with the threshold results, maximal elevation occurs at the adapting spatial frequency and this falls off as the difference between test and adapt spatial frequency increases. However, the rate of fall is now somewhat less steep. There is still a significant elevation in match contrast for both subjects at both two and three octaves away and one of the observers still has a significant effect four octaves away. For the match to a standard of 32% (solid symbols), there appears to be no obvious peak in the function. Instead there is an approximately 50% increase in match contrast needed at all of the test spatial frequencies we tested.

The results when adapting to 4 c/deg are depicted in Fig. 2. Again the threshold results [Fig. 2(a)] are in line with previous measurements of threshold elevations after adaptation. The matching functions [Fig. 2(b)] are not the same as this threshold function. Matching to 4% produces a function which is far less peaked than threshold elevation (for example, testing at 1 or 16 c/deg produced no threshold elevation but almost doubled the required match contrast). Matching to 32% produced functions which look essentially flat.

The results when adapting to 16 c/deg are depicted in Fig. 3. Once more the threshold results [Fig. 3(a)] show

(a)

Threshold

5.49±0.48

(b)

Spatial Frequency (c/deg)

Matching

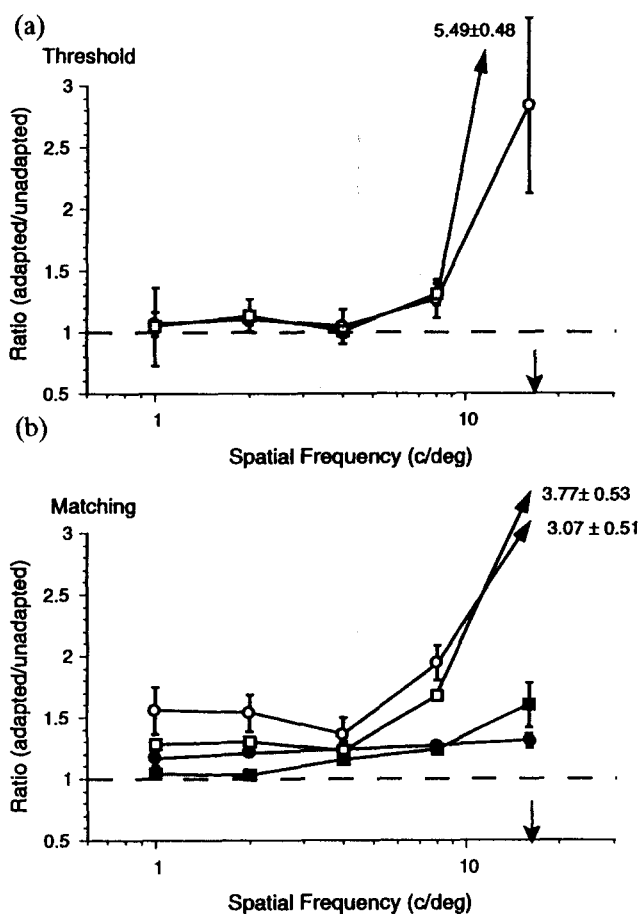3.77± 0.53

3.07 ± 0.51

Spatial Frequency (c/deg)

FIGURE 3. The ratio of adapted to unadapted thresholds or matches is plotted as a function of test spatial frequency. The adapting spatial frequency was 16 c/deg. Other conditions as in Fig. 1.

tight tuning around the adaptation spatial frequency with elevation down to less than 1/4 of its maximal strength by one octave difference. The slightly tighter tuning at higher frequencies is in line with previous estimates using different techniques (Wilson *et al.*, 1983). Matching to 4% produces a function which still peaks strongly at the adaptation frequency but gives some elevation, even when testing four octaves away. Matching to 32% produced functions which are flatter than the 4% matches. For both subjects the effect gradually reduces as the difference between test and adapting frequency increases. One subject showed no effect three or four octaves away, while the other still showed a small but significant effect.

The results from these experiments can be fairly simply summarized—for threshold elevation maximal elevation takes place at the adapting frequency and the bandwidth of the adaptation is fairly narrow (between one and two octaves). Match elevation shows a somewhat similar function at low match contrasts but with a much broader bandwidth, and at higher match contrasts there is little or no tuning for spatial frequency. The effects of cross-spatial frequency adaptation can, hopefully, be seen in the simple demonstration provided in Fig. 4. When fixating the central box the two gratings on either side

should appear to have similar contrast (for some viewers this will not be the case—in the course of our studies we have found a number of people with marked visual field asymmetries in perceived contrast; see also Georgeson, 1987). Now stare at the upper fixation box for about a minute, moving your eyes around the box so as to avoid the build-up of conventional after-images. When your view returns to the lower fixation box, the grating on the right should appear to be reduced in contrast. Note that the spatial frequencies of the test and adapting pattern differ by about 2.5 octaves. This pattern of results is reminiscent of the pattern of results we reported in our previous study of orientation tuning (Snowden & Hammett, 1992) i.e., tight tuning near threshold which broadens with increasing test contrast until the function is essentially flat. It is, therefore, tempting to suggest that a similar process may occur in both the domains of orientation and spatial frequency processing.

EXPERIMENT 2. REMOTE VS SAME SPATIAL FREQUENCY ADAPTATION: ROLE OF TEST CONTRAST

The results of experiment 1 clearly point to the role of test contrast in determining the spatial frequency tuning of contrast adaptation. In order to quantify this effect further, we decided to sample the test contrast domain more thoroughly, by comparing conditions where the adaptation and test pattern have the same spatial frequency and when they have very different spatial frequencies. We chose the test frequency to be 10 c/deg and then adapted to either 1 or to 10 c/deg. Note that under these conditions we expect to get a strong threshold elevation when adapting to 10 c/deg, but no threshold elevation when adapting to 1 c/deg (see Figs 1 and 3). This was confirmed in a pilot study (data not shown).

The results are shown in Fig. 5. For adapting and testing at the same spatial frequency we get the greatest amount of match elevation at the lowest contrasts, and this declines as the test contrast increases. This result is entirely in line with a previous investigation of this issue (Georgeson, 1985). Georgeson suggests that this pattern of results is consistent with a subtractive process by which adaptation serves to remove a set amount of contrast from the neural image (let us say 4%). Any pattern of contrast 4% or less then becomes invisible (threshold is elevated) and, for example, patterns of 8% now look only 4% and hence the ratio of adapted to unadapted contrast is high (in this case 2.0). At higher contrasts the effect is much less marked when plotted as a ratio. If the test contrast is 64% then it will appear to be 60% and our ratio will be only 1.07. This subtractive model appears a good first approximation to the same-spatial frequency adaptation. The remote-spatial frequency adaptation appears to follow a different function to the same-spatial frequency adaptation. Though the effect is small, the function seems essentially flat as a function of test contrast. This pattern of results is not easily accommodated by a subtractive model. Instead we need a model of adaptation that reduces perceived
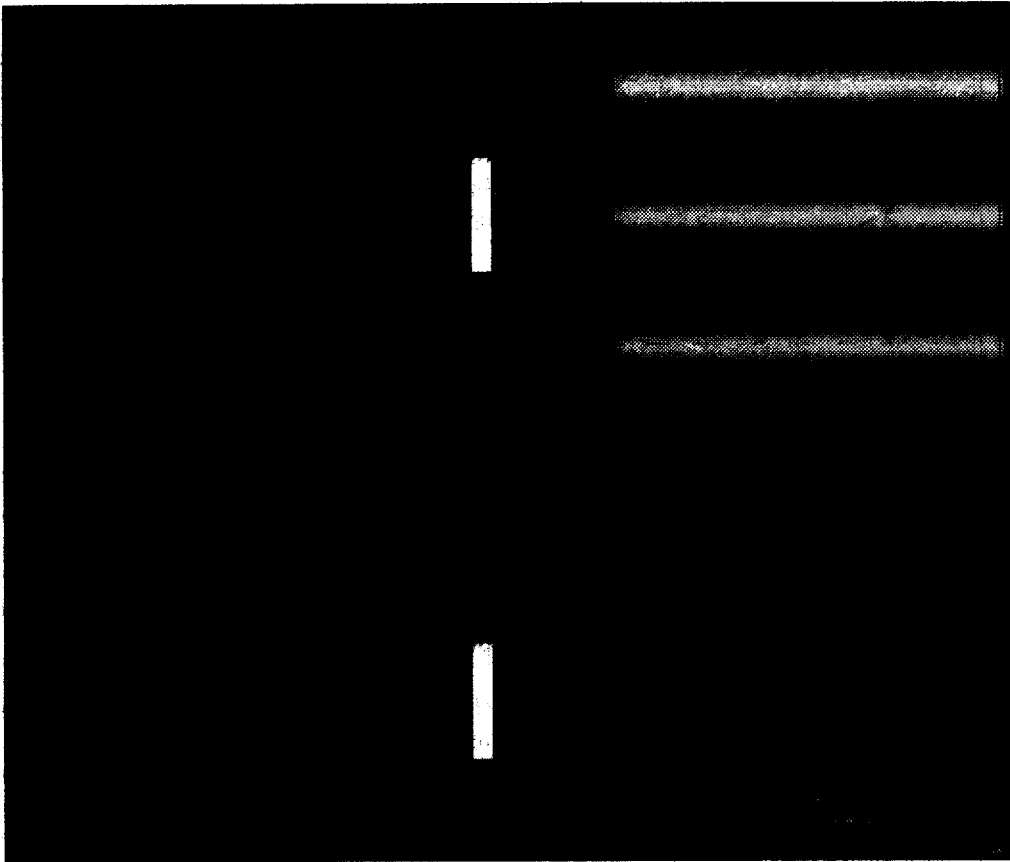
FIGURE 4. A demonstration of the loss of perceived contrast following adaptation to remote spatial frequencies. When initially fixating the lower rectangle, the two grating patterns either side should appear to have equal contrast (though many people appear to have some asymmetry). Now fixate the upper rectangle for 1–2 min letting your eyes move around the box, so as to avoid the build-up of conventional after-images. Upon returning your gaze to the lower rectangle, the grating on the right should appear somewhat faded.

contrast by a constant fraction—a multiplicative or divisive effect.*

A similar pattern of results to those produced in this experiment was found in our investigation of same- or remote-orientation adaptation (Snowden & Hammett, 1992). So once again this suggests that the processes involved in mediating same- and remote-spatial frequency adaptation may be the same as those involved in same- and remote-orientation adaptation effects. Snowden & Hammett (1992) also noted that there were some conditions (at high test contrasts) where subjects seemed to get a greater adaptation effect from the remote condition than from the same condition. The same small trend appears to occur in the present data also with a tendency for a greater adaptation from the 1 c/deg grating than from the 10 c/deg at the two highest test contrasts. The interpretation of this result is complicated by several factors. One interpretation is that the subtractive and divisive effects are mediated by separate processes, and

which is most effective depends upon certain stimulus characteristics. Alternatively, both effects are manifestations of the same processes under different conditions (e.g. Ross, 1992). At first, this second model cannot account for how the remote-spatial frequency effect could be the greatest. However, if one takes into account the idea that stimuli of equal contrast but two different spatial frequencies can have different effective adaptation contrasts (see Snowden, 1994), then this cross-over may be simply due to differences in effective adaptation contrast. To explain the earlier results we would need to postulate some difference in the effective adaptation contrasts of vertical and horizontal gratings.

EXPERIMENT 3. RETINAL SPECIFICITY OF ADAPTATION

So far we have demonstrated considerable differences in adaptation spatial frequency and orientation specificity as the contrast of the test grating is increased. We decided, therefore, to examine other well documented aspects of contrast adaptation which have so far only being examined using threshold elevation as a measure of the adaptation effects. In this experiment we examine the retinal specificity of these effects, and in the next

*By this, we mean the operation appears as a divisive effect. This does not necessarily imply that the processes that lead to this effect must themselves be divisive in nature. For instance, strong hyperpolarization of a cell or thresholds can serve to introduce nonlinearities that mimic a divisive process (see Amthor & Grzywacz, 1991).
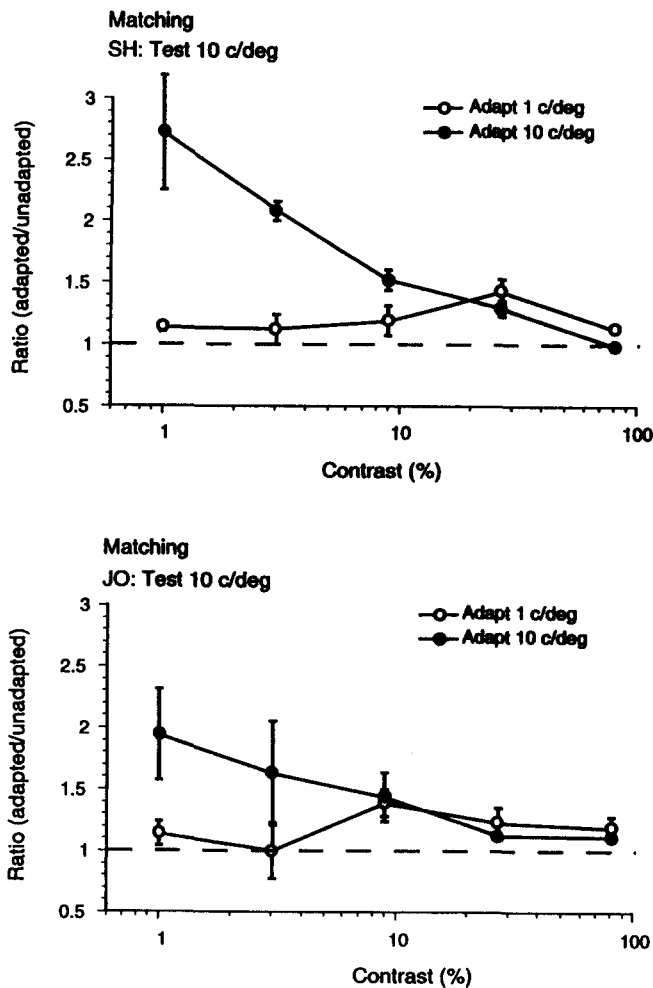
FIGURE 5. The ratio of adapted to unadapted matches is plotted as a function of the contrast of the test pattern. All test patterns had a spatial frequency of 10 c/deg, whereas the adapting patterns could have a spatial frequency of 10 c/deg (solid symbols) or 1 c/deg (open symbols). Upper panel for subject SH and lower panel for subject JO.

(experiment 4) we examine the interocular transfer of these effects.

Several studies have shown that the effects of threshold elevation from contrast adaptation are confined to the area of adaptation, with a small enhancement of thresholds from gratings which are somewhat displaced from the area of testing (Ejima & Takahashi, 1984, 1985). However, there appear to be little data on whether suprathreshold stimuli behave in a similar manner. The issue is given further impetus by findings from experiments on simultaneous contrast perception. Recent reports (Chubb et al., 1989; Cannon & Fullenkamp, 1991, 1993) have shown that a peripheral stimulus can alter the perceived contrast of a central stimulus, while an earlier report suggests that a similar configuration does not elevate thresholds (Klein et al., 1974). It is possible to explain this particular difference between threshold and suprathreshold vision by suggesting that only the central portion of the test pattern governs threshold, whilst the whole of the test pattern may be involved in suprathreshold vision (Tolhurst & Thompson, 1975; Snowden, 1995). The similar pattern of results we have obtained

using our remote-spatial frequency condition (namely no threshold elevation but a loss of suprathreshold contrast) suggested to us that we may be seeing manifestations of a similar process. We have, therefore, examined the effects of adapting to a stimulus which surrounds the test pattern, but does not infringe upon it, for both same- and remote-spatial frequency adaptation.

In order to allow for a large surround pattern which did not infringe upon the site of the test pattern, the size of the test patterns was reduced to a circle of 1 deg diameter. The adapting stimuli was an annulus that had an outer radius of 6 deg and an inner radius of 1 deg (see upper left portion of Fig. 6). We took measurements of threshold, and matches to gratings of 3 and 27% after adapting to either 0% contrast annulus (baseline) or 64%. In addition, for purposes of comparison, we repeated all these measurements with an adapting stimulus where the central portion had not been removed (we shall refer to this as the "normal" adapting pattern—see upper right portion of Fig. 6).

The results of adapting to the annulus stimulus are shown on the left of Fig. 6. Several aspects of these results seem worth noting. Firstly, considering thresholds, we see there is no increase in threshold when the surround has quite different spatial frequency than the centre. When they share the same spatial frequency there appears to be a very small but consistent increase in threshold. A similar very small increase in thresholds when the site of adaptation abuts the test site has been previously reported (Ejima & Takahashi, 1984, 1985). This increase may be due to some small spread of adaptation from the adapting site, or due to small variations in fixation which mean that some of the inner edges of the annulus occasionally infringe onto the site of the test pattern. The matching conditions produced results which varied quite considerably from subject to subject; it is, therefore, hard to draw many firm conclusions from the data. There appears to be an elevation in match contrast—all points fall above the baseline matches (i.e., when the annulus had 0% contrast). It also seems that for both same- and remote-spatial frequency adaptation, the match elevations are greater than the threshold elevation.

The results for the normal adaptation pattern are shown on the right of Fig. 6. We should expect the results to be predictable from experiment 2 (and previous results e.g. Georgeson, 1985; Snowden & Hammett, 1992). For the same-spatial frequency adaptation we expect the greatest effect at threshold and the effect to lessen with increasing test contrast. While this is the case overall, and clearly shown in the data from two of our subjects, the third (SB) seems to show a surprisingly small amount of threshold elevation. We offer no explanation for this. The remote-spatial frequency adaptation shows the predicted results—no threshold elevation and a fairly similar amount of elevation for matching at both 3 and 27%.

We would like to briefly compare the results from the annulus and normal adaptation conditions, particularly for the remote-spatial frequency adaptation. Firstly, it is
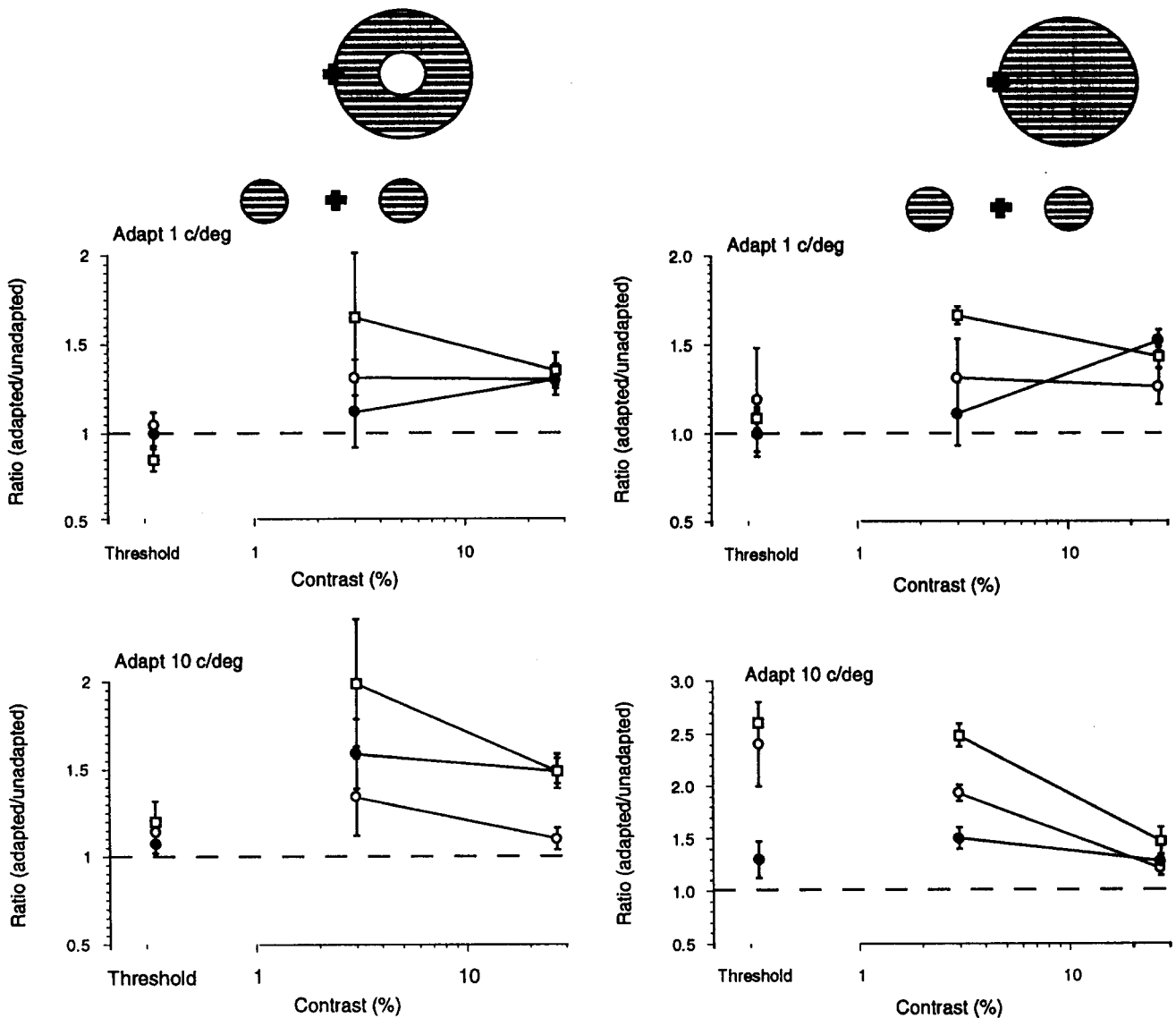
FIGURE 6. The ratio of adapted to unadapted matches is plotted as a function of the contrast of the test pattern. All test patterns had a spatial frequency of 10 c/deg, whereas the adapting patterns could have a spatial frequency of 1 c/deg (upper panels) or 10 c/deg (lower panels). The left panels depict the results when the adapting pattern was an annulus, so that no part of it impinged upon the test site, whereas the right panels depict the results when the centre of the annulus was also filled by a grating (the "normal stimulus"). These stimuli are represented at the top of each panel. Results from three observers are plotted: squares = JO, open circles = SH and solid circles = SB.

noticeable that while there appears to be considerable inter-subject variability, there is intra-subject consistency. Subject SB shows little effect at 3% and a strong effect at 27%, subject JO shows a very strong effect at 3% which reduced at 27%, whereas subject SH shows about the same effect at both contrasts. We do not know where this inter-subject variability arises from. It may well be connected to the considerable inter-subject variability that has been reported by Cannon & Fullenkamp (1993) for contrast matching with simultaneous surrounds (as opposed to the successive effects reported here). Cannon & Fullenkamp (1993) suggest that there may be two processes which are activated by surround contrasts, one inhibitory and one facilitatory. The strength of each process varies with stimulus conditions and the weightings may vary from person to person. Secondly, the size

of the matching elevations is very similar for the annulus condition and the normal condition.

To summarize the results of this experiment: (1) it appears that the remote-spatial frequency adaptation effect persists even when the site of adaptation does not infringe upon the test pattern; (2) while same-spatial frequency adaptation seems reasonably well confined to the site of adaptation when assessed by threshold elevation, it appears less confined when assessed at suprathreshold levels.

EXPERIMENT 4. INTEROCULAR TRANSFER OF EFFECTS

It is well documented that many contrast adaptation effects persist to some degree when the eye of testing is different to the eye of adaptation (for reviews see

Moulden, 1980; Blake *et al.*, 1981). The effects are most well documented for the case of threshold elevation (Bjørklund & Magnussen, 1981) and seem to depend upon intact binocular mechanisms, as observers who show deficits in binocular processing also show no, or reduced, transfer of interocular adaptation (Movshon *et al.*, 1972). The effects are normally assessed in terms of how strong the effect is when adapting in the same eye as when testing vs when adapting in the opposite eye to that tested, such that the interocular transfer is defined as: (elevation in opposite eye/elevation in same eye).

Thus, if the effect is equally strong in the same and opposite eyes we have 100% transfer, while if there is no effect in the opposite eye there is 0% transfer. We shall use the same conventions here. The transfer of threshold elevation for patterns of the same spatial frequency is typically in the order of 66% for normal observers (Movshon *et al.*, 1972; Bjørklund & Magnussen, 1981). Unfortunately there appear to be no reports of the size of the transfer of contrast matching elevations. Previous notions that contrast match elevations are merely on a continuum from threshold elevations would suggest that this figure be unaltered.

Methods

In order to perform this experiment we had to change our experimental equipment. We tried, however, to retain conditions as similar as possible to the previous experiments. Alternate frames were displayed to the subject through two light valves (LV050AC, Display-Tech Inc.), one over each eye. The valves were synchronized to the start of each frame and operated so that when one was open the other was shut. Hence all even frames were presented to the right eye and odd frames to the left eye. By this system we were able to present different stimuli to each eye when we so desired. The Joyce scope was updated at a rate of 100 Hz, hence each eye was updated at 50 Hz. At this rate there is no perceptible flicker.* Two further advantages of this set-up are that the subjects appeared quite unable to tell into which eye the patterns were being presented, and that we were able to present a field of mean luminance to the other eye instead of a dark field which occurs with normal shutters or patching the eye. The valves reduced the retinal illumination by approximately 0.5 log units when open. All subjects were screened to ensure the presence of stereo vision by the Titmus stereo test and had a stereo acuity of at least 50 sec arc.

We had three variables to manipulate: (1) test contrast (threshold elevation vs match elevation-test contrast was 27%); (2) specificity of adaptation (adapt and test at same vs different spatial frequency); and (3) eye of adaptation (test and adapt in same vs different eye). For simplicity we always presented a test pattern of 6 c/deg to the left

TABLE 1. Interocular transfer of adaptation

| Pattern | Elevation (ratio) | | | |
| | Same | | Different | |
Eye	Same	Different	Same	Different
Threshold				
RS	2.60**	1.83**		
SH	2.14**	1.62**		
MB	1.76**	1.47**		
Match				
RS	1.33**	1.15*	1.53**	1.10
SH	1.36**	1.02	1.48**	1.06
MB	1.82**	1.55**	1.41**	1.26**

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.

Interocular transfer (%)

$$= \frac{(\log C_a - \log C_u)_{\text{different eye}}}{(\log C_a - \log C_u)_{\text{same eye}}} * 100$$

| | | Interocular transfer (%) | |
		Same	Different
Threshold	RS	63	
	SH	64	
	MB	69	
Match	RS	51	22
	SH	5	14
	MB	73	68

eye and altered the adapting pattern accordingly (left eye or right eye, spatial frequency of 6 or 1 c/deg). All other conditions were as in previous experiments.

Results

The results are presented in Table 1. The upper part of the table gives the threshold elevation ratio (threshold adapted/threshold unadapted) and an indication of whether the elevation was significant. The lower part gives the calculated interocular transfer (IOT). Several points can be made. In considering threshold elevations when adapting and test patterns are of the same spatial frequency,† we can see that even though the amount of adaptation varies quite markedly from subject to subject, the IOT appears similar at around 66%, and in very good agreement with previous measurements (Movshon *et al.*, 1972; Bjørklund & Magnussen, 1981). Secondly, there is significant threshold elevation for the match contrasts in the same eye for all subjects. In the interocular case, only one subject had a strong adaptation effect, another a weak one and one had no effect. For the remote-spatial frequency case all subjects once again gave significant match elevations (in two cases greater than the same-frequency adaptation). In the interocular condition once again only one subject gave a significant interocular

---

*We originally set up this experiment on the MAC monitor running at 60 Hz (therefore, each eye updated at 30 Hz). This produced strong and nauseous flickering and hence we opted to change to a faster monitor.

†We did not measure threshold elevations for patterns of different spatial frequency as all our previous measurements have shown no threshold elevation—hence consideration of possible interocular transfer is meaningless.

TABLE 2. Binocular summation

Contrast thresholds (%)			
	Left	Right	Binocular
RS	2.28 ± 0.21	2.89 ± 0.20	1.79 ± 0.13
SH	1.89 ± 0.10	1.81 ± 0.16	1.07 ± 0.10
MB	2.91 ± 0.39	2.31 ± 0.10	1.89 ± 0.25
Summation index = C_{bin}/C_{mon}			
	Left	Right	Average
RS	1.27	1.61	1.41
SH	1.77	1.70	1.73
MB	1.54	1.22	1.38

effect (noticeably the same subject who gave a strong interocular effect for same-frequency adaptation). In considering the calculated IOT one has to be careful* when considering small values. The value has quite dramatic inter-subject variability for both same- and remote-frequency adaptation. For one subject (SH) there appears to be little interocular transfer of the match elevations despite a normal threshold IOT. For another (MB) the match IOT appears similar in size to the threshold IOT. For yet another (RS), the match elevation IOT is similar in size to the threshold IOT, but appears much reduced for the remote-spatial frequency adaptation.

Clearly there is wide inter-subject variability in these measurements. One possible source could be due to eye dominance and/or the amount of "binocularity" of the subject. While all subjects had good stereo acuity, this may not guarantee equal contrast sensitivity in each eye, or good binocular summation (Lema & Blake, 1977). We therefore measured threshold sensitivity for each observer's eyes individually (monocular thresholds) and together (binocular threshold) in a supplementary experiment.

EXPERIMENT 4. (SUPPLEMENT): BINOCULAR SUMMATION

These measurements employed a two temporal-alternate forced-choice procedure, but all other stimulus parameters and timings were as in the main experiment. Test spatial frequency was always 6 c/deg.

The results are shown in Table 2. Threshold contrast is given in the upper part and a summation index in the lower part. All observers showed evidence of intact binocular summation—indeed these estimates appear somewhat larger than previous estimates (Campbell & Green, 1965; Lema & Blake, 1977). It is noticeable that while observer SH has about equal sensitivity in each of his eyes, observer RS was significantly more sensitive in his left eye, whilst observer MB was significantly more sensitive in his right eye.

These results do not really provide a basis for

---

*For example, let us consider the case where the same eye produces an insignificant ratio of 1.01 and so does the opposite eye. Would we then want to claim 100% transfer!?

explaining the pattern of results in the main experiment. While the greater IOT shown by observer MB might be somewhat explicable by the fact that the different eye condition involved adapting his dominant eye (one gets greater transfer from dominant to non-dominant eye than vice versa; Movshon et al., 1972), and the poorer IOT of RS due to the opposite dominance, the fact that both showed normal threshold elevation transfer is not.

Discussion

The results of experiment 4 are difficult to interpret due to quite different patterns of results being produced by each observer. A few tentative statements though may be made. Firstly, for the two most experienced observers (and the authors!) there appear to be significant effects for the matching task for the same eye but these became insignificant (or nearly so) for the interocular case. This occurred for both same and remote-frequency adaptation. A similar lack of interocular transfer in a matching task has been reported (Aslin & Li, 1993). However, a third (and naive) subject produced significant effects in all conditions. Secondly, the remote-frequency adaptation results once again appear to mirror the same-frequency adaptation result.

EXPERIMENT 5. ORIENTATION TUNING OF REMOTE-SPATIAL FREQUENCY EFFECT

We have so far suggested that the remote-spatial frequency adaptation effect we have described in this paper is similar in nature to the remote-orientation effect we described in an earlier report (Snowden & Hammett, 1992). In that report we described how the orientation tuning of contrast adaptation was narrowly tuned for threshold elevation effects, but then broadened to be essentially flat at high contrasts. We suggested that the results might reflect two separate processes, one subtractive and one divisive. The subtractive process dominates at low contrasts, whereas at higher contrast one begins to see a greater reflection of the divisive process. By postulating that the subtractive effect is narrowly tuned for orientation, whereas the divisive effect is isotropic, the pattern of results can be explained. One prediction of this theory is that if we isolate the "divisive" component, it would be isotropic at whatever contrast we tested. However, in the previous experiment, we only used adapting and test gratings of the same spatial frequency. Hence we could never be sure of how much of the tuning for orientation we observed was due to the subtractive process. The present finding that there is still some contrast matching elevation for adapting, and testing with spatial frequencies many octaves apart may allow us to titrate out the pure "divisive" process. Our prediction is that there should be no orientation tuning of the remote-spatial frequency adaptation effect, even at low test contrasts.

Our experimental set-up is as described in our previous report of remote-orientation adaptation (Snowden & Hammett, 1992). Our only difference is that we now either adapted to 1 c/deg and tested at 10 c/deg, or vice
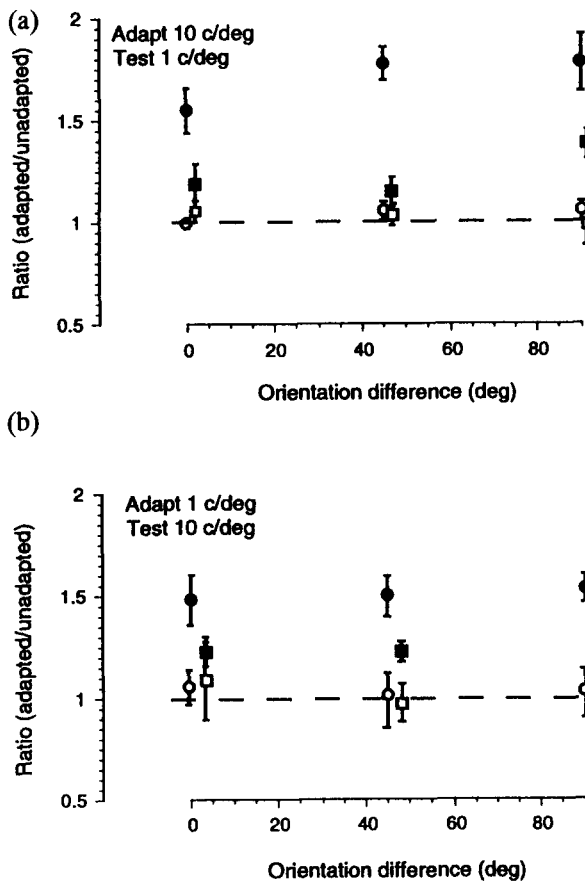
(a)

(b)

FIGURE 7. The ratio of adapted to unadapted matches and thresholds is plotted as a function of the orientation difference between the adapting and test pattern. In (a) the test patterns had a spatial frequency of 1 c/deg whereas the adapting patterns had a spatial frequency of 10 c/deg. In (b) the spatial frequencies are reversed. Threshold measurements are represented by open symbols, whereas matches are represented by solid symbols. Results from two observers are plotted: squares = SH, circles = RS.

FIGURE 8. This depicts the same conditions as Fig. 7(a) but for eight naive observers.

versa. We chose these particular spatial frequencies as they are well beyond the range of classical adaptation experiments (see Figs 1–3). Our test patterns were always vertical and we had adaptation conditions that were different in angle by 0, 45 or 90 deg. We examined a low match contrast condition (4%) for any threshold elevation effects.

The results are shown in Fig. 7. Figure 7(a) depicts the results when we adapted to a grating of 10 c/deg and tested at 1 c/deg. Thresholds (open symbols) were unaffected by adaptation at all orientations, as expected. Matches were elevated by adaptation at all orientations, though there is a considerable difference in the size of this effect for the two observers. The effects of orientation on the effect appear negligible, if there is any effect it seems that greater elevation occurs for orthogonal gratings than parallel gratings. Figure 7(b) depicts the results obtained when adapting to 1 c/deg and testing at 10 c/deg. Once again thresholds were not significantly elevated at any orientation, while matches were significantly elevated at each orientation.

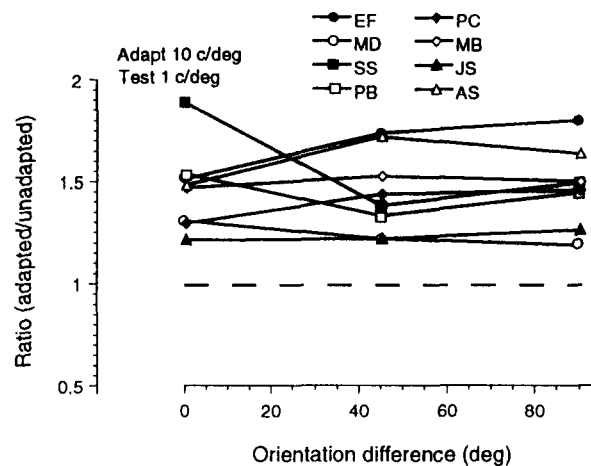The issue of whether elevation can be greater when

adapting to remote orientations is of some importance, as many current models could not account for adaptation being greater under these conditions. From Fig. 7 it is most noticeable that there is a considerable inter-subject difference in the size of the effect, and that there is a small tendency for elevation to be greater for the remote orientation. We therefore ran a number of naive subjects through the "adapt 10 test 1" regime to get some indication of inter-subject differences and whether the finding of greater remote adaptation is reliable. The results from eight observers are shown in Fig. 8. Large inter-subject differences are apparent in both the size of the adaptation effect and in its orientation tuning. Some observers show greater adaptation to remote orientations (EF, PC, AS), others appear essentially similar (MB, JS) and others greater adaptation for the same orientation (MD, SS, PB). The reasons for these large inter-subject differences is unclear. Similar large differences in the effects of surround patterns on perceived contrast have been reported (Cannon & Fullenkamp, 1993). We suggest, therefore, that there is no strong evidence for greater adaptation from remote orientations than from same orientations.

GENERAL DISCUSSION

The major findings of the present study are:

1. Spatial frequency tuning of contrast adaptation is tightly tuned near threshold but broadens when measured at successively higher test contrasts.
2. When test and adapting patterns have the same spatial frequency, the loss of perceived contrast is well described by a subtractive effect; when they are radically different it can described (to a first approximation) by a divisive (multiplicative) effect.
3. The remote-frequency adaptation effect can be elicited by stimuli that do not impinge upon the test site. However, this is also true for same-frequency adaptation at suprathreshold levels, though the threshold elevation effect is confined to the site of adaptation.

4. There is some (though weak) evidence that the IOT of suprathreshold effects may be smaller than the threshold effects.

5. The remote-spatial frequency effect appears to show little or no tuning for orientation.

Relationship to previous studies

Our finding that thresholds for contrast perception are elevated after contrast adaptation, and that they are confined to spatial frequencies similar to the adapting pattern, has been reported many times. The bandwidth of our threshold elevation is in good agreement with previous reports (e.g. Georgeson & Harris, 1984) including the finding that the function appears somewhat more tightly tuned at higher spatial frequencies (Wilson et al., 1983). Surprisingly, there is only one previous report of the spatial frequency tuning of the loss of perceived contrast after adaptation. Blakemore et al. (1973) report the loss of perceived contrast for a single spatial frequency after adapting to a number of different spatial frequencies. They report that the tuning is essentially similar at all test contrasts and similar to the estimates obtained by measuring threshold elevation in an earlier study (Blakemore & Campbell, 1969). Clearly this result is very different from that reported here. A similar discrepancy exists between Blakemore's group's estimates of orientation tuning at suprathreshold levels and more recent studies (Li & Aslin, 1992; Ross, 1992; Snowden & Hammett, 1992; Aslin & Li, 1993). The reasons for the discrepancy are far from clear. There are (at least) two possibilities. As mentioned above, the Blakemore study employed the "adapt many, test one" technique. With this technique, as Blakemore and colleagues point out, a problem arises in equating the contrast of the adapting patterns. Should one use the same physical contrast, same multiples of threshold, or same perceived contrast (or something else)? Given that the relationship between adapting contrast and threshold elevation is not the same at each spatial frequency (Snowden, 1994) this could well distort the function as adapting contrast is varied. We think the approach of "adapt one, test many" neatly side-steps some of these problems. Secondly, in the study of Blakemore and colleagues, subjects attempted to quickly adjust the contrast of a test grating so as to match a standard grating. The time course for this adjustment must be in the order of seconds (Blakemore and colleagues' estimate is 1–2 sec). It could be that the small elevation effect from the remote spatial frequencies could be lost in such a time.

Possible explanations of the remote effects

There appear to be a number of possible explanations of the present pattern of results. Here we outline three possibilities.

One possibility is that there exists two mechanisms to adaptation—one whose effects appear as a subtractive process and is quite well tuned in the domains of orientation and spatial frequency, and another process which is divisive (multiplicative) and appears to have little tuning with respect to orientation and spatial frequency. Both subtractive and multiplicative adaptation processes have been suggested to occur in the domain of light adaptation (e.g. Hayhoe et al., 1987) which may have their counterparts in the domain of contrast adaptation. One may ask if our studies provide any evidence for the existence of two separate processes. We attempted to look for evidence for two separate processes by examining whether there were different characteristics associated with similar and remote adaptation. However, we found little evidence to support such a notion. Whilst we have found considerable differences between threshold effects and suprathreshold effects (in terms of retinal specificity and interocular transfer) when we directly compared suprathreshold effects (contrast matching) produced by remote or same-spatial frequency adaptation, they appeared similar, even to the extent that the individual differences were constant across the two conditions. As such, the notion of two separate processes receives little support from these studies.

Secondly, a single process model has been proposed (Ross & Speed, 1991; Ross et al., 1993) which involves adaptation repositioning and reshaping the contrast–response function. As the model currently stands it cannot explain how one can have no threshold elevation but a loss of suprathreshold contrast (unless one allows for some change in the tuning of the underlying filters as a function of contrast). However, closely related models may well prove successful. For example, in considering the response of area MT neurones to changes in dot density in the cell's preferred direction of motion in the presence of other motions, Snowden et al. (1991) show that both subtraction models and division models do not explain the data. However, a model which incorporates a division-like process occurring before subsequent saturation was quite successful [see their Fig. 13(c)]. Such a model has some formal equivalence to the Ross & Speed (1991) model, as both involve contrast compression. One major prediction of this result would be that the effect from remote orientations or frequencies should never exceed the effect produced by similar ones. In both indirect and direct tests, Ross and Speed (personal communication) show the remote effect never exceeds the similar one. There are some occasions in the present data (see Figs 5, 7 and 8), and in our previous study, where we seem to show that the remote effect can be greater. In this study we have shown considerable inter-subject variability in many of our tests and, as both earlier studies used only a small number of observers, some of the variance may be due to this. Secondly, and possibly related to the previous point, Ross and Speed (personal communication) have shown that small changes in criterion (such as only judging the dark bars) can alter the results. As such, the case for remote adaptation ever outstripping similar adaptation is as yet not proven.

A third possibility is that there is only one process, which relies on the differences in task between threshold detection and contrast matching (see Hammett et al., 1994). Let us say that the adapting pattern desensitizes

filters tuned to the appropriate dimension. In considering thresholds, we presume that threshold would be reached when any filter is stimulated to a great enough degree. Threshold elevation is, therefore, reasonably well confined to the filters that were affected by adaptation. In determining perceived contrast it is possible that the activity of more than one filter along this dimension is taken into account. As physical contrast grows it is well known that cells of the striate cortex (and many other regions) begin to saturate (Albrecht & Hamilton, 1982) whilst perceived contrast still grows steadily (Cannon, 1985; Georgeson, 1991). This could occur because neurones slightly away from the optimal spatial frequency/orientation are not yet saturated and their response can be taken into account in some way.* Thus in our case of adaptation, as test contrast grows we will be recruiting the response of filters tuned to quite different spatial frequencies, and hence the tuning function of the spread of adaptation will be broader at higher contrasts.

Each of these models is still highly speculative, and these models are far from exclusive. More refined tests will hopefully begin to decide upon their relative merits.

Physiological findings

It has been known for some time that the response of individual neurones (at least those in the striate cortex) is susceptible to the effects of adaptation (Maffei et al., 1973; Movshon & Lennie, 1979; Ohzawa et al., 1982; Bonds, 1991). The major effect seems to be to reposition the contrast response function. These experiments have generally employed test patterns of similar spatial characteristics as the adapting pattern. None have employed patterns of very different spatial characteristics.

Experiments that have involved presenting two patterns simultaneously have employed patterns of very different spatial characteristics. Morrone et al. (1982) show that a cell's (in cat striate cortex) response to its optimal stimulus can be reduced by the addition of a second stimulus (of orthogonal orientation), even though the cell does not respond to this second stimulus if presented in isolation. More recently, DeAngelis et al. (1992) have extended this finding to show a similar reduction in response when a grating of non-optimal spatial frequency is superimposed upon one of optimal spatial frequency. Two other findings are also relevant to the current psychophysical tests. DeAngelis et al. (1992) also measured the orientation tuning of this "remote-spatial frequency" suppression and show that it is little or none (i.e., the suppressive effect was equally strong at each orientation). This finding is similar to that of the current experiment 5, showing no orientation tuning of the cross-spatial frequency adaptation effect. Secondly, they measured the region over which the suppression could be elicited and showed that it was no bigger than the excitatory receptive field. This seems somewhat

different to the results from the current experiment 3. However, one can note that the size of the loss of contrast was similar for the annulus and normal conditions (Fig. 6, top panels) suggesting that while the surround can have an effect it was not enhanced by also having the centre filled. Likewise, one could imagine the centre alone giving an effect which is not further enhanced by the surround (as DeAngelis et al. describe). It would be interesting to see if a surround, alone, could affect the cell's response to the centre pattern (some such effects have been previously described; Blakemore & Tobin, 1972).

What is the point of these interactions? A popular notion is that these interactions serve to normalize the response of each cell to some measure of activity within a local cortical area or contrast within the image (Bonds, 1991; DeAngelis et al., 1992; Heeger, 1992). For example, Heeger's model summates the activity of all cells within a local area, irrespective of their orientation and spatial frequency tuning, and uses this as a factor to normalize the activity of the same cells. This model, therefore, has some interesting parallels with the current psychophysical data, in that it involves a division-like process with little or no tuning for orientation and spatial frequency. Other models of contrast-gain mechanisms also exist which place the site of contrast-gain before the filtering operations (Albrecht & Geisler, 1991). This also suggests the process would show a lack of orientation tuning and rather poor spatial frequency tuning, which is similar to the results presented here and previously. Our attempt to gain some insight into the site of the remote-spatial frequency effect (by looking to see if it occurred before or after binocular combination) unfortunately proved rather ambiguous and so we are unable to provide any help in distinguishing between these models (see also Aslin & Li, 1993).

The physiological data then provide a rich seam of information and interest. However, we currently have no clear model of how the response of individual cells (particularly since all the above data were obtained from cat striate cortex) is transformed into a perception of contrast. It is also worth noting that there are other interactions between stimuli which have not been covered in this brief review (e.g. Nelson, 1991a, b).

In conclusion, we have demonstrated that the loss of perceived contrast produced by contrast adaptation can have characteristics which are different from those produced by measurements of threshold elevation. More and more findings are showing that the visual system shows complex interactions between stimulus elements under suprathreshold conditions. Understanding and modelling these interactions will clearly be an important challenge for vision scientists for some years to come.

REFERENCES

Albrecht, D. G. & Geisler, W. S. (1991). Motion selectivity and the contrast response function of simple cells in the visual cortex. *Visual Neuroscience, 7*, 531–546.
Albrecht, D. G. & Hamilton, D. B. (1982). Striate cortex of monkey and cat: contrast response function. *Journal of Neurophysiology, 48*, 217–237.

---

*Unfortunately the physiological evidence speaks against this idea. Albrecht & Hamilton (1982) show that cells saturate at a specific contrast rather than a specific response level.

Amthor, F. R. & Grzywacz, N. M. (1991). The nonlinearity of the inhibition underlying retinal directional selectivity. *Visual Neuroscience, 6,* 197–206.

Aslin, R. N. & Li, A. (1993). Multiple mechanisms of contrast adaptation. *Investigative Ophthalmology and Visual Science Supplement, 34,* 1362.

Bjørklund, R. A. & Magnussen, S. (1981). A study of interocular transfer of spatial adaptation. *Perception, 10,* 511–518.

Blake, R., Overton, R. & Lema-Stern, S. (1981). Interocular transfer of visual aftereffects. *Journal of Experimental Psychology; Human Perception and Performance, 7,* 367–381.

Blakemore, C. & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology (London), 203,* 237–260.

Blakemore, C., Muncey, J. P. J. & Ridley, R. M. (1971). Perceptual fading of a stabilized cortical image. *Nature, 233,* 204–205.

Blakemore, C., Muncey, J. P. J. & Ridley, R. M. (1973). Stimulus specificity in the human visual system. *Vision Research, 13,* 1915–1931.

Blakemore, C. & Tobin, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Experimental Brain Research, 15,* 439–440.

Bonds, A. B. (1991). Temporal dynamics of contrast gain in single cells of the cat striate cortex. *Visual Neuroscience, 6,* 239–255.

Braddick, O. (1978). Channels in vision: Basic aspects. In Held, R. (Ed.), *The handbook of sensory physiology,* (Series Ed.). New York: Springer.

Campbell, F. W. & Green, D. G. (1965). Monocular versus binocular visual acuity. *Nature, 208,* 191–192.

Cannon, M. W. (1985). Perceived contrast in the fovea and periphery. *Journal of the Optical Society of America A2,* 1760–1768.

Cannon, M. W. & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast: Inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Research, 31,* 1985–1998.

Cannon, M. W. & Fullenkamp, S. C. (1993). Spatial interactions in apparent contrast: Individual differences in enhancement and suppression effects. *Vision Research, 33,* 1685–1695.

Chubb, C., Sperling, G. & Solomon, J. A. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences, USA, 86,* 9631–9635.

DeAngelis, G. C., Robson, J. G., Ohzawa, I. & Freeman, R. D. (1992). Organization of suppression in receptive fields of neurons in cat visual cortex. *Journal of Neurophysiology, 68,* 144–163.

Ejima, Y. & Takahashi, S. (1984). Facilitory and inhibitory after-effect of spatially localized grating adaptation. *Vision Research, 24,* 979–985.

Ejima, Y. & Takahashi, S. (1985). Effect of localized grating adaptation as a function of separation along the length axis between test and adaptation areas. *Vision Research, 25,* 1701–1708.

Georgeson, M. (1991). Over the limit: Encoding contrast above threshold in human vision. In Kulikowski, J. J. (Ed.), Vision and visual dysfunction, 5, Cronly-Dillon, J. R. (Series Ed.). London: Macmillan Press.

Georgeson, M. A. (1985). The effect of spatial adaptation on perceived contrast. *Spatial Vision, 1,* 103–112.

Georgeson, M. A. (1987). Temporal properties of spatial contrast vision. *Vision Research, 27,* 765–780.

Georgeson, M. A. & Harris, M. J. (1984). Spatial selectivity of contrast adaptation: Models and data. *Vision Research, 24,* 729–741.

Graham, N. V. S. (1989). *Visual pattern analysers.* Oxford: Oxford University Press.

Hammett, S. T., Snowden, R. J. & Smith, A. T. (1994). Perceived contrast as a function of adaptation duration. *Vision Research, 34,* 31–40.

Hayhoe, M. M., Benimoff, N. I. & Hood, D. C. (1987). The time-course of multiplicative and subtractive adaptation process. *Vision Research, 27,* 1981–1996.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience, 9,* 181–197.

Klein, S. A., Stromeyer, C. F. & Ganz, L. (1974). The simultaneous spatial frequency shift: A dissociation between the detection and perception of gratings. *Vision Research, 14,* 1421–1432.

Lema, S. A. & Blake, R. (1977). Binocular summation in normal and stereoblind humans. *Vision Research, 17,* 691–695.

Li, A. & Aslin, R. N. (1992). Contrast adaptation and perceptual 'filling in' at specific retinal locations. *Investigative Ophthalmology and Visual Science Supplement, 33,* 1256.

Maffei, L., Fiorentini, A. & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science, 182,* 1036–1038.

Morrone, M. C., Burr, D. C. & Maffei, L. (1982). Functional implications of cross-orientation inhibition of cortical cells. I. Neurophysiological evidence. *Proceedings of the Royal Society of London B, 216,* 335–354.

Moulden, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosophical Transactions of the Royal Society of London B, 290,* 39–55.

Movshon, J. A. & Blakemore, C. (1973). Orientation specificity and spatial selectivity in human vision. *Perception, 2,* 53–60.

Movshon, J. A., Chambers, B. E. & Blakemore, C. (1972). Interocular transfer in normal humans and those that lack stereopsis. *Perception, 1,* 483–490.

Movshon, J. A. & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurons. *Nature, 278,* 850–852.

Nelson, S. B. (1991a). Temporal interactions in the cat visual system. I. Orientation selective suppression in the visual cortex. *Journal of Neuroscience, 11,* 344–356.

Nelson, S. B. (1991b). Temporal interactions in the cat visual system. II. Suppressive and facilitatory effects in the lateral geniculate nucleus. *Journal of Neuroscience, 11,* 357–368.

Ohzawa, I., Sclar, G. & Freeman, R. D. (1982). Contrast gain control in the cat visual cortex. *Nature, 298,* 266–268.

Ross, J. (1992). How adaptation and masking alter contrast gain perception. *Perception, 21,* Supplement 2, 60.

Ross, J. & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London B, 246,* 61–69.

Ross, J. R., Speed, H. D. & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Research, 33,* 2051–2056.

Snowden, R. J. (1991). Measurement of visual channels by contrast adaptation. *Proceedings of the Royal Society of London B, 246,* 53–59.

Snowden, R. J. (1994). Adaptability of the visual system is inversely related to its sensitivity. *Journal of the Optical Society of America A, 11,* 25–32.

Snowden, R. J. (1995). The effect of contrast surrounds on contrast centres: Merely normal masking? *Investigative Ophthalmology and Visual Science Supplement, 36,* 438.

Snowden, R. J. & Hammett, S. T. (1992). Subtractive and divisive adaptation in the human visual system. *Nature, 355,* 248–250.

Snowden, R. J., Treue, S., Erickson, R. E. & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience, 11,* 2768–2785.

Stromeyer, C. F. & Julesz, B. (1972). Spatial-frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society of America, 62,* 1221–1232.

Taylor, M. M. & Creelman, C. D. (1967). PEST: Efficient estimates on probability functions. *Journal of the Acoustical Society of America, 41,* 782–787.

Tolhurst, D. J. & Thompson, P. G. (1975). Orientation illusions and aftereffects: Inhibition between channels. *Vision Research, 15,* 969–972.

Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research, 23,* 873–882.