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Invariance of the perceived spatial frequency shift of peripherally viewed gratings with manipulations of contrast, duration, and luminance

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Abstract

Gratings appear of higher spatial frequency when they are viewed peripherally rather than foveally. To test the hypothesis that this effect is an artefact of particular laboratory conditions, we manipulated the contrast, luminance and presentation duration, manipulations which have also been shown to increase the apparent spatial frequency of foveally presented gratings. It has been argued that such shifts reflect an attempt to increase sensitivity by changing the receptive field properties of spatially tuned visual channels, while keeping their size labels constant. If so, and peripheral channels are not otherwise mislabelled, it should be possible to find conditions under which the apparent spatial frequency of peripherally viewed gratings matches that of foveal gratings of the same spatial frequency. In this study, manipulations of contrast, luminance, and duration had no effect on the size of the perceived spatial frequency shift in peripheral vision. Thus the putative inappropriate size labelling of peripheral visual channels is constant over a wide range of stimulus values. We speculate that this apparent constant error may result from a mechanism which normally compensates for another factor such as blur, which may otherwise lead to an overestimation of size.

Keywords: Peripheral vision; Spatial frequency; Contrast

1. Introduction

As early as 1890 William James noted that

> An object appears smaller on the lateral portions of the retina than it does on the fovea, as may be easily verified by holding the two forefingers parallel and a couple of inches apart, and transferring the gaze of one eye from one to the other. Then the finger not directly looked at will appear to shrink, and this whatever be the direction of the fingers.

Unfortunately, not all the studies published since that time have supported this description of the apparent size of peripherally viewed targets. Although many studies agree with James's original observation that peripheral stimuli appear smaller (Zigler, Cook, Miller & Wemple, 1930; Collier, 1931; Grindley, 1931; Newsome, 1972; Drum, 1977; Schneider, Ehrlich, Stein, Flaum & Mangel, 1978; Georgeson, 1980; Bedell & Johnson, 1984; Davis, Yager & Jones, 1987), some suggest that peripheral targets appear larger (Stevens, 1908; von Helmholtz, 1910; Gelb & Wilson, 1983; Bedell & Johnson, 1984; Thibos & Walsh, 1985). Two factors which seem important determinants of apparent size in the periphery are the nature of the target (whether periodic or not), and its luminance compared with the background. Whereas aperiodic stimuli may appear larger or smaller, depending upon luminance (Bedell & Johnson, 1984), gratings consistently appear of a higher spatial frequency when viewed peripherally (Georgeson, 1980; Davis et al., 1987). The present study is concerned with this shift in the perceived spatial

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frequency of peripherally viewed gratings, and what it reveals about size coding in human vision.

Eccentric viewing is only one of the stimulus manipulations which produces an increase in apparent spatial frequency. The shift can be produced by reducing luminance (Virsu, 1974), contrast (Georgeson, 1980), or presentation duration (Tynan & Sekuler, 1974), or by changing the grating orientation from horizontal or vertical to oblique (Georgeson, 1980). These effects can all be described by the general rule that any manipulation which takes a grating closer to its contrast threshold also increases its perceived spatial frequency (Georgeson, 1980).

Virsu (1974) explained the spatial frequency shift at reduced luminance by postulating a 'labelled line' model of spatial frequency coding. That is, each spatial frequency channel (perhaps a ganglion cell receptive field, or rather its cortical representation) has a spatial frequency label attached to it. When luminance is lowered, the strength of surround inhibition is reduced, so that the receptive field becomes more sensitive to lower spatial frequencies. However, because the channel's label is invariant, these spatial frequencies are perceived as higher at low luminance than they appear to be at high luminance. If it is assumed that inhibition is also decreased as duration and contrast are reduced, this idea can account for the effects of these manipulations also. The costs of this arrangement are systematic distortions of perceived size in certain conditions, and the apparent benefits an increase in sensitivity without the need to correct the 'meaning' of each labelled line. It has been suggested that the increase in perceived spatial frequency as a function of eccentricity (as well as the parameters mentioned above) can also be accounted for by a multiple spatial frequency channels model. This assumes that the receptive field size of a class of channels increases with eccentricity, but the size label associated with those channels does not change (Davis et al., 1987), or changes at a slower rate than the receptive field size.

There is an apparent problem in applying the labelled line model to peripheral vision. To induce shifts of apparent size by manipulating other parameters, one needs to produce temporarily adverse conditions, such as low luminance. However, the relationship between central and peripheral vision is constant, and it is not obvious why the apparently permanent misallocation of size labels to (say) peripheral receptive fields should occur. One possibility is that these shifts in apparent size with eccentric viewing do not occur in normal vision outside the laboratory, but are artefacts produced by the particular stimulus conditions chosen by previous investigators. Georgeson (1985) asked whether the increase in apparent spatial frequency produced by shortening stimulus duration was a primary effect of stimulus duration or a secondary effect of reduced apparent contrast at short durations. We took a similar approach to the effect of eccentric viewing, manipulating the contrast, luminance, and presentation duration of peripherally viewed gratings, and measuring their apparent spatial frequency.

2. Experiment 1. The apparent spatial frequency of peripherally viewed gratings

2.1. Introduction

This experiment examined the spatial frequency shift which occurs with eccentric viewing in a more systematic way than in previous studies. Davis et al. (1987), who used several spatial frequencies, did not investigate the effect of contrast, whilst Georgeson (1980), only reports the results for a 5 c/deg grating. A wider range of both contrasts and spatial frequencies than have previously been used were examined in this study. Sixteen combinations of four contrasts (8, 16, 32 and 64% Michelson contrast) and four spatial frequencies (0.5, 1, 2, and 4 c/deg), were studied. The size of the grating patch always remained 2.5° in diameter, and consequently the number of cycles visible varied with spatial frequency.

2.2. Method

2.2.1. Apparatus

Stimuli were generated by a Cambridge Research Systems (CRS) Visual Stimulus Generator (VSG 2.1) in an IBM compatible 486 (66 MHz) PC, and displayed on a Tektronix 608 oscilloscope, at a frame rate of 100 Hz. The linearity of the display luminance was checked with a Minolta CS-100 photometer. The oscilloscope screen subtended 12.2° wide × 9.8° high. The mean luminance of the display was 26 cd/m^2. The immediate surround of the display (35° wide × 45° high) was side-illuminated green card, roughly matched to the oscilloscope for colour and luminance. Viewing distance was 57 cm. Head position was held constant by a chin-rest. Subjects looked at the screen through a pair of welder's goggles with the left eye occluded and no lens in front of the right eye. They signalled their responses to the computer via a CRS response box (CB1).

2.2.2. Stimuli

Stimuli were two 2.5° circular patches of sinusoidal grating, whose centres were separated horizontally by 9°. The display was viewed monocularly with the right eye and subjects were instructed to fixate the right hand grating throughout the experiments. The peripherally viewed grating was therefore always at 9° eccentricity on the temporal retina of the right eye.

One potential problem with eccentrically viewed gratings is that of spatial aliasing as spatial frequency is increased and the gratings start to be undersampled. The highest spatial frequency used in our studies was 4 c/deg. Recently, Wang, Bradley and Thibos (1997) reported that the Nyquist limit at an eccentricity of 20° (a factor of two larger than used in our studies) was about 4 c/deg. We noticed no sign of aliasing of the peripheral gratings, using their criteria (misperception of orientation, loss of spatial coherence). These considerations suggest that all our stimuli were above the Nyquist limit for the eccentricity used.

2.2.3. Procedure

Presentation of the stimuli was controlled by the computer. The temporal envelope was a cosine ramp, so that contrast rose from 0 to its maximum at the start of each presentation over the first 250 ms (and fell again to 0 over the last 250 ms). The total stimulus duration was 1 s. The foveal and the peripheral stimuli were presented simultaneously, immediately after a short tone. The computer then waited indefinitely for a response. Subjects were required to decide whether the foveal or peripheral grating appeared to have the finer stripes. They were instructed to base this decision on the appearance of both light and dark bars and to report it by pressing one of two switches. They were instructed to guess if the gratings appeared the same. After each response, the next pair of gratings was presented with an inter-presentation interval of approximately 2 s. The spatial frequency of the foveal grating was fixed on each presentation whilst that of the peripheral grating was adjusted according to an interleaved double staircase procedure. On each presentation, the computer randomly selected one of the two staircases. The initial spatial frequency of one staircase was one octave higher than that of the foveal grating, and the other one octave lower. If the subject indicated that the peripheral grating had the higher spatial frequency then its spatial frequency for the next presentation on that staircase was reduced, and vice versa if spatial frequency were judged to be lower. The computer recorded the spatial frequency of the peripheral grating whenever the subject's judgement about the apparent spatial frequency of the peripheral grating was the opposite of that on the previous trial. In other words, spatial frequency was recorded if, on the previous trial, the foveal grating had the higher (lower) apparent spatial frequency, whereas on the present trial the peripheral grating had the higher (lower) apparent spatial frequency. After four such reversals of judgement, the step size of the staircase was reduced from an initial value of 0.12 to 0.03 log units, and a further six reversals were then recorded. The means of the final six reversals only, for each staircase, were combined to calculate the mean spatial frequency of the peripheral grating at reversal for each condition. The procedure therefore provides an estimate of the point of subjective equality of spatial frequency (or, with suitable changes, any other parameter) of the two gratings.

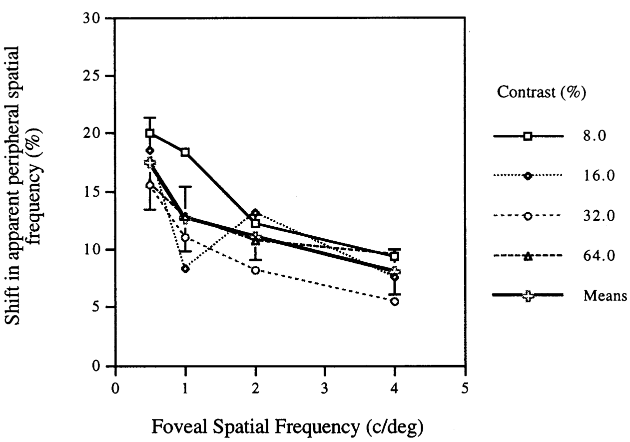

Fig. 1. Increase in apparent spatial frequency of a peripherally viewed grating compared with that of a foveally viewed grating, as a function of foveal spatial frequency. Data are shown separately for four different contrasts (8, 16, 32 and 64%) and for the mean of all four contrasts (vertical bars represent standard errors). The circular patches of vertical grating subtended a retinal angle of 2.5°, and the peripheral grating was presented on the horizontal meridian at an eccentricity of 9°. Data are means from four subjects, estimated from the last six reversal points of each of two interleaved staircases. See text for more details.

2.2.4. Subjects

The same four subjects, with normal or corrected-to-normal visual acuity, took part in the first three experiments. Two of them were the authors, and the other two were naive to the phenomena under investigation.

2.3. Results

For ease of comparison, the results were converted to a percentage shift (Percentage shift in apparent peripheral spatial frequency = ((foveal spatial frequency − matched peripheral spatial frequency)/foveal spatial frequency) × 100). Positive values therefore indicate a reduction in apparent stripe width or size, in other words an increase in the apparent spatial frequency of the peripherally viewed grating. As can be seen in Fig. 1 the peripheral grating consistently appeared to be of a higher spatial frequency than the foveal one.

The mean increase across all contrasts and spatial frequencies was 12.27%, and an independent samples t-test shows that this is significantly greater than 0 ($t(63) = -8.63$, $P < 0.01$). Further t-tests confirm that the shifts are significantly different from 0 at all spatial frequencies, when collapsed across contrast ($P < 0.01$ in all cases). A repeated measures ANOVA showed no main effect of contrast or spatial frequency. There does appear to be a trend for the effect to be smaller in

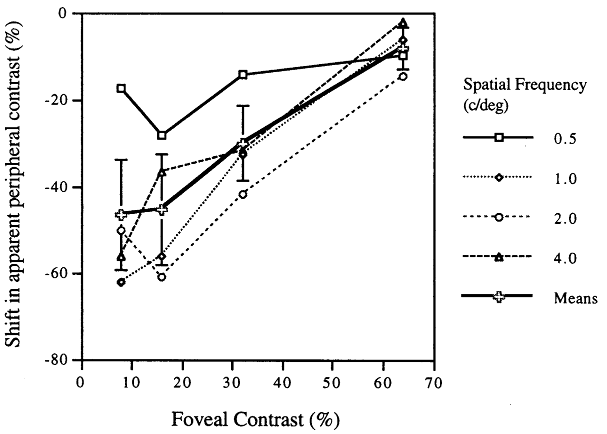

Fig. 2. Reduction in apparent contrast of a peripherally viewed grating compared with that of a foveally viewed grating, as a function of foveal contrast. Data are shown separately for four different spatial frequencies (0.5, 1, 2 and 4 c/deg) and for the mean of all four spatial frequencies. Other details as in Fig. 1.

percentage terms as spatial frequency increases, but this was not confirmed by a contrast test comparing the shifts at 0.5 and 4.0 c/deg. There was a difference of about a factor of two in the size of the shift at these spatial frequencies. The largest shifts at each spatial frequency occurred at the lower contrasts (8 or, sometimes, 16%)

2.4. Discussion

These results confirm the spatial frequency shift of peripherally viewed gratings, for a wider range of contrasts and spatial frequencies than in previous studies. They show that there is no difference in the effect as contrast changes, at least as long as the physical contrast of the two gratings is the same. However, there is a trend in the data which shows that the effect is smaller in percentage terms, as the spatial frequency of the foveal stimulus increases. Nevertheless, the flattening of the curve with increasing spatial frequency suggests that the effect would not disappear at higher spatial frequencies.

3. Experiment 2. The apparent contrast of peripherally viewed gratings of the same spatial frequency

3.1. Introduction

Peripheral viewing may reduce the physical contrast of a grating due to optical aberration, and the reduction in contrast may lead to a shift in the perceived spatial frequency (Georgeson, 1980; Gelb & Wilson, 1983; Davis, Kramer & Yager, 1986). It has been argued that this cannot be the reason for the shift because suprathreshold there is little or no attenuation of apparent contrast (e.g. Georgeson, 1980). Nevertheless it seemed important to measure the apparent contrast of the peripherally viewed gratings to ensure that it was not a factor in our conditions.

3.2. Method

The method was identical to that of Experiment 1, except that spatial frequency (which was the same for both gratings) was held constant, and the contrast of the peripheral grating varied on each presentation, according to a randomly interleaved double staircase procedure. One staircase started with a peripheral contrast 0.5 log units higher than foveal contrast, the other with a peripheral contrast 0.5 log units lower. On each presentation, subjects judged which of the two gratings appeared to have the higher contrast. Four subjects, experienced in the required judgements, took part in the experiment. Two were the authors.

3.3. Results

The results are presented in Fig. 2. The shift in apparent contrast has been converted to a percentage (Percentage shift in apparent peripheral contrast = ((foveal contrast − matched peripheral contrast)/foveal contrast) × 100)). It appears that there are substantial reductions in apparent peripheral contrast, when viewing the gratings used in Experiment 1 in our conditions. These reductions can be as large as 50% for lower contrasts and higher spatial frequencies.

4. Experiment 3. The apparent spatial frequency of peripherally viewed gratings with compensation for reduced apparent contrast

4.1. Introduction

It is clear that perceived contrast is lower for the peripheral gratings, and that this effect increases as the standard contrast is reduced. It is also possible that, even were ‘contrast constancy’ to operate (so that peripheral and foveal contrasts appeared the same) the spatial frequency shift could be caused by a reduction in the contrast of the peripheral retinal image, produced by optical aberrations. On this argument, activity in say retinal ganglion cells would govern apparent spatial frequency, but apparent contrast would be determined by separate compensatory processes in the cortex. In any case, the possibility that the spatial frequency shift is due to reduced contrast, produced by peripheral viewing, rather than peripheral viewing itself, has not been conclusively ruled out. To test this idea, Experiment 1 was re-run, but with overcompensation for the reduced apparent contrast of the peripheral gratings.

4.2. Method

The method was identical to that of Experiment 1 except for the contrast of the peripheral gratings. The contrasts of the peripheral gratings were chosen so as to overcompensate for the lower apparent contrast of the peripheral gratings. This was done using the peripheral contrast matching data (Fig. 2). The contrasts of the foveal gratings remained at 8, 16, 32 and 64% as before, but those of the peripheral gratings were now 15, 25, 48 and 75%, respectively. (From Fig. 2 it can be seen that on average a grating with 8% contrast appeared approximately 50% lower in contrast. The contrast of the peripheral grating would therefore be about 12% when it matches the perceived contrast of the foveal grating. A grating with 15% contrast therefore overcompensates.) Subjects were again asked to judge whether the foveal or the peripheral stripes appeared narrower.

4.3. Results

The mean percentage increase in apparent peripheral spatial frequency across all contrasts and spatial frequencies is 11.45%. t-tests confirm that this shift is significant at all 4 spatial frequencies when collapsed across contrast (at the $P < 0.05$ level, or better). The similarity to the results from Experiment 1 may be seen by comparing the results for this experiment (Fig. 3) with those of Fig. 1. The effect of spatial frequency (though it follows a similar trend in both experiments) appears to be stronger in the present experiment. However a repeated measures ANOVA shows no effect of spatial frequency or contrast. In order to examine the effect of overcompensation, the data from Experiments 1 and 3 were entered into a three-way repeated measures ANOVA. This analysis showed no significant effects, confirming that overcompensation for the reduced apparent contrast of a peripherally viewed grating has no effect on its apparent spatial frequency.

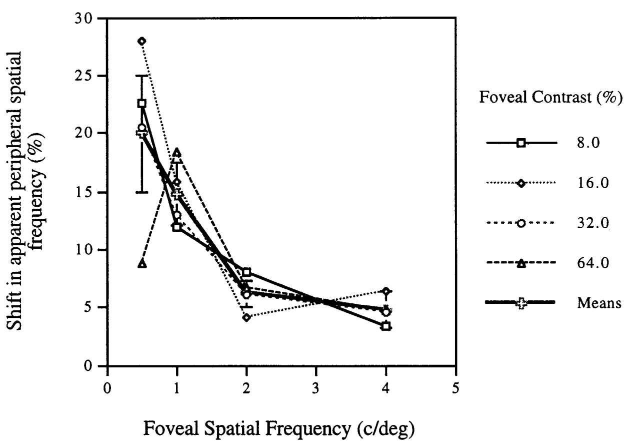

Fig. 3. Increase in apparent spatial frequency of a peripherally viewed grating compared with that of a foveally viewed grating, with compensation for reduced apparent contrast, as a function of spatial frequency. The physical contrast of the peripheral grating was increased in order to match the apparent contrast of the peripheral and foveal gratings. Other details as in Fig. 1.

4.4. Discussion

These results provide strong evidence that the perceived increase in spatial frequency associated with peripheral viewing of gratings is not a consequence of the optical or neural attenuation of peripheral contrast. If the changes in perceived spatial frequency in the periphery were caused by changes in apparent contrast, then the resulting shifts in perceived spatial frequency should either be eliminated or even go in the opposite direction. Clearly neither is the case. Moreover, although shifts in apparent contrast are smallest for the lowest spatial frequency (0.5 c/deg — see Fig. 2), the shifts in apparent spatial frequency are largest for this spatial frequency — see Figs. 1 and 3. These considerations strongly suggest that the effect is a direct result of peripheral viewing. These two experiments show that, whether the physical or the perceived contrast of the foveal and the peripheral grating are equated, there is no change in the magnitude of the peripheral spatial frequency shift.

5. Experiment 4. The effect of high luminance on the apparent spatial frequency of peripherally viewed gratings

5.1. Introduction

It has been proposed that normal dark adaptation leads to a change in the centre-surround organisation of retinal ganglion cell receptive fields (Barlow, Fitzhugh & Kuffler, 1957). On the labelled channel hypothesis, it is precisely such changes, in the absence of changes to the size labels associated with a channel, which lead to apparent shifts in spatial frequency. It may be that for the relatively low luminances chosen in this and other studies peripheral receptive field surrounds are starting to have less influence on the receptive field characteristics (e.g. this study 26 cd/m^2; Davis et al., 1987, 9 cd/m^2). Daylight in contrast can reach 800–1000 cd/m^2. Consequently it might be argued that a much higher luminance is required to provide optimal viewing conditions and to eliminate the shift in apparent peripheral spatial frequency. Experiment 4 modifies the apparatus and procedure to allow substantially higher luminances to be investigated.

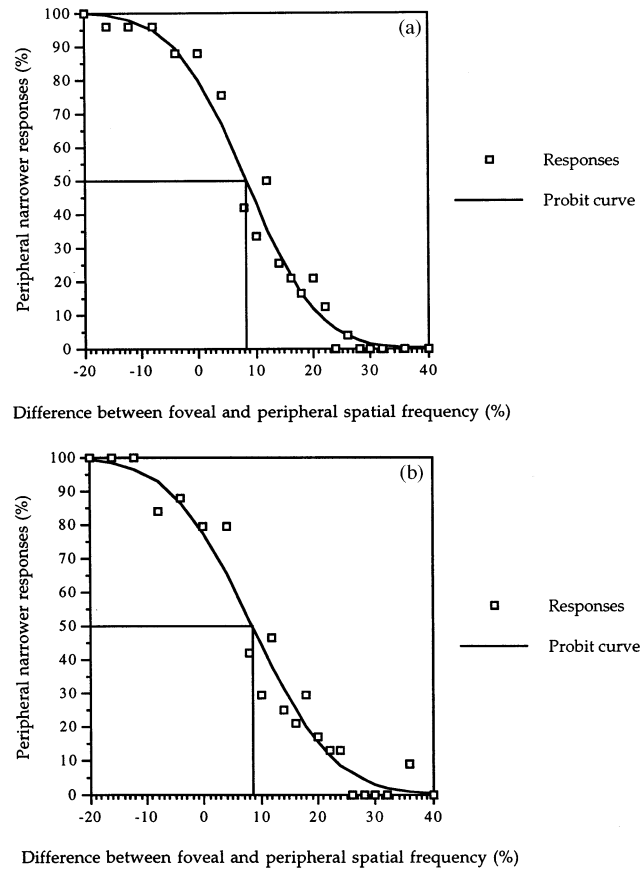

Fig. 4. Increase in apparent spatial frequency of a peripherally viewed grating compared with that of a foveally viewed grating under low and high luminance conditions. The psychometric function is plotted for the mean data from six subjects. The presentation duration in both conditions is 1000 ms. The point of subjective equality is indicated. (a) Luminance 15 cd/m^2, (b) luminance 680 cd/m^2. The two rectangular patches of square wave grating were separated by 9°, and 2.5 cycles were always visible. The spatial frequency of the foveal grating was fixed at 0.95 c/deg and the contrast of both gratings was 40%.

5.2. Method

5.2.1. Apparatus and stimuli

Stimuli were produced by generating square wave gratings with a graphics program, printing them onto overhead transparency sheets, and then mounting these as slides. When projected, the centres of the foveal and peripheral stimuli were separated by 9°, as in previous experiments with the oscilloscope display. The spatial frequency of the foveal grating remained fixed at 0.95 c/deg throughout and covered 2.4° horizontally and vertically. The light bars were in fact transparent, so the luminance of the immediate surround and the light bars was identical. Consequently, increasing the spatial frequency by less than half a cycle would not increase the number of visible cycles if the edge of the grating patch was a light bar. It was therefore decided to keep the number of cycles in the peripheral (variable) grating constant at 2.5 cycles. Thus the area covered by the peripheral grating varied with its spatial frequency. Only one spatial frequency (0.95 c/deg) and one contrast (40%) were used in this experiment. A method of constant stimuli was used in which the spatial frequency of the peripheral grating varied from presentation to presentation. There were 22 steps of peripheral spatial frequency, ranging from 20% (0.76 c/deg) lower to 40% (1.33 c/deg) higher than the foveal frequency. The step size was 2% in the expected region of the shift (based on earlier experiments) and 4% further from this region. The slides were projected on a white screen by a Kodak Carousel automatic projector, and the screen was further illuminated with an overhead projector. Viewing distance was 2 m, with the subject seated behind the projectors to avoid shadows.

Two luminance conditions were created by placing neutral density filters over the lens on the slide projector and the overhead projector. The mean luminance of the gratings was 15 cd/m^2 in the low luminance condition (comparable to that of the oscilloscope), and 680 cd/m^2 in the high luminance condition. In both conditions, the contrast remained at 40%. The presentation duration was 1000 ms and was controlled by a timed shutter.

5.2.2. Procedure

Presentation of the stimuli was manually controlled by the experimenter. The slides were presented first in one random order and then in the reverse order. Thus each test slide was presented twice to each subject. Subjects responded verbally by indicating whether the narrowest stripes appeared on the left or the right (viewing was again monocular with the right eye and subjects were instructed to fixate the right hand stimulus). Six subjects, with normal or corrected-to-normal visual acuity, carried out the experiment, four of which participated in the first three experiments. Apart from the two authors, all were naive to the purpose of the experiment. The percentage of times each subject reported that the narrowest stripes were on the right was then calculated for each slide.

5.3. Results

Psychometric functions were fitted to the group data using probit analysis. These are shown in Fig. 4a and b. Each graph shows the percentage of 'peripheral narrower' responses for each peripheral grating. The x-axis shows the difference in spatial frequency of the peripheral grating, relative to the foveal. Positive values indicate a lower spatial frequency, i.e. wider stripes. The 50% point has been marked on the y-axis. This represents the point of subjective equality of the two gratings, where 50% of the time subjects thought the peripheral grating was narrower, and 50% of the time they thought the foveal stripes were narrower. In other words, this is the best estimate of the point at which both gratings appeared to have the same spatial frequency. All of the graphs show that the peripheral grating appears to be of the same spatial frequency as the foveal one when the spatial frequency of the peripheral grating is lower. Hence the peripheral grating must appear to be of a higher spatial frequency, as was found in the earlier experiments. The mean shift for the low luminance condition was 8.25%, whilst the shift for the high luminance condition was 8.5%. Increasing the luminance has clearly not eliminated, or even reduced the size of, the shift.

5.4. Discussion

Despite the investigation of a considerable range of luminances in Experiment 4, which took the viewing conditions into the region of normal daylight, the spatial frequency shift with peripheral viewing remained roughly constant. In a previous study (Wink & Harris, 2000), we compared the peripheral spatial frequency shift at two luminances, one 26 cd/m^2, as used in Experiments 1–3 reported here. The other was the reduced luminance produced by viewing the display through a 1.5 log unit neutral density filter. As in the present experiment, the mean peripheral spatial frequency shift was similar (for the range of contrasts and spatial frequencies used in the present study) with and without the filter. Taken together, these two experiments suggest that the effect is not some artefact of the particular luminances used in earlier studies.

It is interesting to consider the size of the shift for the high contrast 0.95 c/deg square-wave gratings in this experiment (about 8%), compared with those found for the 1 c/deg sine-wave gratings in Experiments 1 (about 13%) and 3 (about 15%). Since the shift reduces for higher spatial frequencies (Figs. 1 and 3), it may be that the presence of higher harmonics in the square-wave somehow reduces the size of the shift produced by the fundamental frequency. This hypothesis could be tested in experiments in which the presence and contrast of higher harmonics was systematically varied.

6. Experiment 5. The effect of presentation duration on the apparent spatial frequency of peripherally viewed gratings

6.1. Introduction

There are a number of anatomical and physiological differences between central and peripheral vision, including the distribution of magno and parvocellular pathways (Perry, Oehler & Cowey, 1984). Since the properties of these two systems differ, it seems possible that the conditions used to examine apparent peripheral spatial frequency favour the fovea. One difference that has clearly been identified between the magno and parvo channels is their response to stimuli of differing presentation duration (Derrington & Lennie, 1984). If there are relatively more M-cells in the periphery, then the relative sensitivity of the fovea and periphery may be affected by presentation duration, such that the periphery becomes more sensitive as duration is decreased. If experimental conditions in previous studies particularly favoured the fovea, substantial changes in presentation duration should change the size of the shift. The following experiment investigates this possibility by reducing the presentation to 20 ms to ensure that the stimuli stimulate the magnocellular (transient) channels preferentially.

6.2. Method

The apparatus, stimuli and procedure were identical to those used in Experiment 4, except for the durations of presentation, which were now 150, 100, 50 and 20 ms. The luminance remained at 680 cd/m^2 throughout. Six subjects, with normal or corrected-to-normal visual acuity took part. All subjects were naive to the purpose of the experiment, and none had taken part in the previous experiments.

6.3. Results

The data for one subject were excluded as she failed to report that the foveal stimulus appeared narrower on any of the trials. The data from the other subjects are plotted in Fig. 5a–d. Psychometric functions were again fitted to the data using probit analysis. The point of subjective equality has been drawn in on each graph, and indicates the percentage shift in apparent peripheral spatial frequency of the peripherally viewed grating (150 ms = 6%, 100 ms = 11%, 50 ms = 10%, 20 ms = 12%). It is also worth noting that the slope of the psychometric functions generally gets shallower as the presentation duration gets shorter (150 ms = −3.76, 100 ms = −5.14, 50 ms = −3.06, 20 ms = −2.38), indicating that spatial frequency discrimination gets worse at short presentation durations. The slopes of the straight section of the psychometric functions were analysed and were all shown to be significantly different from each other (150 ms versus 100 ms: $t = 33.8$, $df = 12$, $P < 0.03$; 100 ms versus 50 ms: $t = -33.7$, $df = 10$, $P < 0.03$; 50 ms versus 20 ms: $t = -122.2$, $df = 14$, $P < 0.03$, after corrections for family-wise error).

6.4. Discussion

The size of the spatial frequency shift between 100 and 20 ms presentation duration remains at about 10%.

There is a suggestion in the data that the shift may be reducing at 150 ms presentation duration. However, in a further experiment, similar to Experiment 4 but not reported in detail here, we again found shifts of about 10% at durations of 150 and 1000 ms. We therefore conclude that in these conditions the size of the shift remains the same for a wide range of presentation durations. Brief presentations such as those used in this experiment are known to differentially affect the magno and parvocellular pathways. It therefore seems reasonable to conclude that the shift cannot be explained in terms of a differential distribution of magno and parvo cells across the retina.

7. General discussion

7.1. Summary of results

This series of experiments makes it clear that the increase in apparent spatial frequency associated with viewing a grating peripherally is a robust effect, which cannot be eliminated by the manipulation of a range of stimulus parameters or viewing conditions. It therefore seems that there is indeed a permanent mislabelling of peripheral channels involved in size coding. As noted in Section 1, it is understandable that reductions in contrast, luminance or presentation duration, which produce a temporary sacrifice of the accuracy of channel labelling in order to improve sensitivity, should lead to such shifts, but the notion of permanently incorrect labels, for no obvious gain, is more difficult to accept. Here we consider which explanations for the effect are more plausible in the light of our results. We discuss explanations (we think, less plausible) based on contrast coding, on channel labelling based on local properties of the retina, on properties of transient and sustained channels, and on properties of recently postulated size detectors. We then consider explanations (we think, more plausible) based on a two stage model incorporating labelled channels, and on the notion of a compensatory mechanism.

7.2. Contrast-related effects

The results provide clear evidence that the spatial frequency shift is not produced by reduced apparent

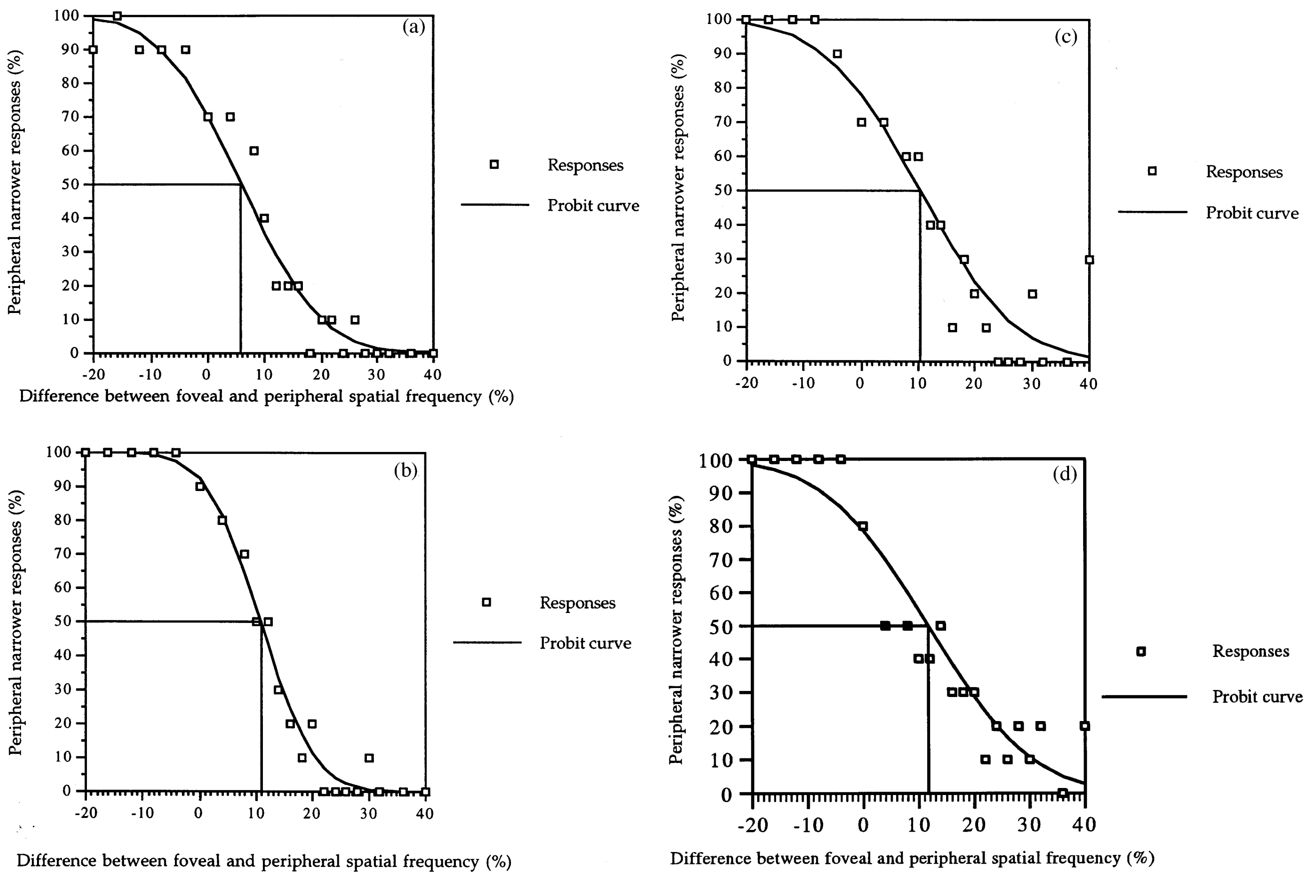

Fig. 5. The effect of presentation duration on the increase in apparent spatial frequency of a peripheral grating compared with a foveally viewed grating. Luminance in all conditions 680 cd/m^2. The psychometric function is plotted for the mean data from six subjects. (a) 150 ms (b) 100 ms (c) 50 ms (d) 20 ms. Other details as in Fig. 4.

contrast, and is an independent consequence of peripheral viewing. The complete absence of any effect of contrast is in fact rather surprising. Although it would not necessarily be expected that the effect was produced entirely by reduced apparent contrast, we might have expected some additional increase in apparent spatial frequency as contrast is reduced, since this effect has been observed at the fovea. It seems unlikely that this lack of effect arises because the stimuli are well above threshold, because the visual system does not achieve full contrast constancy in our conditions (see Fig. 2). It may be that contrast simply does not affect spatial frequency in the periphery in the same way that it has been shown to affect centrally viewed gratings. This raises the possibility that none of the manipulations normally associated with increased apparent spatial frequency at the fovea cause such a shift at eccentric locations, and warrants further investigation.

7.3. 'Compromise labelling' of receptive fields at different eccentricities

Peripheral receptive fields have to deal with inputs over a much larger dynamic range of intensities than foveal receptive fields, since they receive rod as well as cone input, and so may change their centre/surround activity ratio by a greater amount. If their spatial label was chosen to reflect receptive field spatial organisation, not when the visual system was fully light-adapted, but at some fixed proportion of the difference between the maximum light- and the maximum dark-adapted state, then peripheral labels would have systematic differences compared with those of the fovea. This idea seems unlikely, given that we found no effects of reducing and increasing mean luminance from the range typically used in studies of this type. However, it could be further tested in an experiment comparing perceived spatial frequency at two extra-foveal regions of different eccentricities, since receptive fields there would receive both rod and cone input.

7.4. Pattern and motion channels

Kulikowski (1975, 1991) has invoked pattern and motion detection mechanisms in an attempt to explain the spatial frequency shift, and dismisses the labelled channel hypothesis. He suggests that the occasionally observed phenomenon of spatial frequency doubling is produced by the motion system, which squares its inputs. Smaller (fractional) shifts, such as those reported here, result from an interaction between the motion channel, which produces doubling, and the pattern channel which signals the correct spatial frequency. He has demonstrated that fractional shifts can be produced following adaptation of either the motion or pattern channels. However this does not conclusively demonstrate that this is the cause of the shifts that we have observed. We found no evidence of doubling of apparent spatial frequency in any of our experiments, even with briefly presented stimuli which presumably favour motion (transient) channels.

Parker (1981, 1983) is also critical of Kulikowski's (1975) suggestion, and points out that the conditions required to produce doubling are very specific, and include phase reversing rather than drifting stimuli, presentation in central vision, high contrast and low spatial frequency. These are quite different to the conditions which lead to fractional shifts, and differ greatly from the stimuli used in this study. In particular, doubling seems to require central viewing. Parker has therefore concluded that these phenomena are unrelated, although he agrees with Kulikowski in acknowledging the involvement of motion mechanisms in the doubling effect.

7.5. Size detectors

A recent theory of size perception has been developed by Stuart, Bossomaier and Johnson (1993), who introduce the notion of size detectors with two input zones, analogous to motion detectors. The receptive field of a size detecting unit has two input regions a set distance apart, and the responses of the two regions are multiplied. They argue that size perception is carried out by parallel mechanisms, and that this therefore places great computational constraints on size judgement. They claim that their model can account for the Weberian behaviour of size judgement, when neither spatial frequency models nor spatial localisation models (Levi, Klein & Yap, 1988) are able to. However, it is unable to account for the apparent size judgements observed in the present experiments. Whilst it predicts a change in accuracy as viewing becomes eccentric, it does not obviously predict a consistent increase in apparent spatial frequency. Such mechanisms may be involved in size perception, but without extra postulates cannot account for the observed effects of peripheral viewing.

7.6. Labelled channels revisited

Either the visual system does not attempt to compensate for its own apparently consistent overestimation of spatial frequency under particular conditions, or it fails to do so very effectively. Georgeson and Sullivan (1975) have demonstrated that such compensation does take place in the contrast domain. The apparent lack of compensation is puzzling because Parker (1981) has shown that veridical spatial information is available to the visual system even when the apparent spatial frequency is different, since after adaptation to a temporally modulated grating contrast threshold elevation is highest at the physical not at the apparent spatial frequency. To account for this finding Parker (1981, 1983) has followed Klein, Stromeyer and Ganz (1974) and Heeley (1979) in suggesting a two-stage model. The lower stage consists of a set of filters or channels whose spatial frequency tuning is unaltered by changes of mean luminance, temporal modulation, etc. Klein et al. (1974) refer to a set of *analysers* at this stage which have spatially opponent receptive fields and feed into a detection pooling mechanism. When activity in these analysers reaches their threshold a grating is detected by the subject. The analysers have a second output to a set of *integrators*, which have a broader spatial frequency response than that of the individual analysers, since each integrator receives input from a range of analysers. A measure of central tendency is then extracted from the response distribution of the integrators and results in the perception of spatial frequency. It is this distribution of labour between mechanisms of detection (analysers) and perception (integrators) which allows both veridical adaptation and illusory perception.

This is one way to explain the existence of apparently unused veridical information, and explains the dissociation between changes in contrast threshold and shifts in apparent spatial frequency, but it still leaves a number of problems. Firstly, as Parker himself points out, there is no direct evidence to support such a hierarchical model, rather than independent processing. Secondly, in the present context, such a notion seems to ignore physiological evidence for changes in the receptive field properties of retinal ganglion cells, for example, which are presumably at the lower stage. Thirdly, the issue now becomes the nature of the process which extracts information from the first stage channels. Why do the integrators make errors in extraction, and why is there no compensation for this error? Within the limits of spatial sampling, it should be possible to recover lost information, as seems to happen with contrast. According to Parker, there are two possible answers. Either the human visual system does not care about these distortions, or the shifts in spatial frequency are a consequence of some other process which itself is advantageous to the visual system. If the visual system does not care, this would perhaps lead to large errors, but it is unlikely that it would result in such a consistent unidirectional under- or over-estimate of size. If the effect is a consequence of some other advantageous process, it is not clear what this might be, although Parker suggests that pattern discrimination may be enhanced at the expense of absolute size or texture density judgements, for example. This kind of suggestion has also been put forward to explain why visual aftereffects should occur, even though they lead to non-veridical judgements of absolute spatial frequency. However, there is no direct evidence to support this view in the present context.

7.7. A possible compensatory process

A further possibility is that the spatial frequency shift seen with peripheral viewing results from a compensatory mechanism, and one possible aberration for which it compensates is optical blur. The properties of the optics of the eye mean that no object is perfectly imaged onto the retina, but the distribution of the image of a point is spread or blurred. Point spread functions are narrowest in the central retina, and widen systematically with eccentricity (Jennings & Charman, 1978, 1981). According to Jennings and Charman (1978) there is little optical blur at 10° eccentricity. However, there may be increased neural blurring of more peripheral stimuli, because receptive field sizes increase with eccentricity. Although this would simply reduce the apparent contrast of higher frequency sinusoids without altering their spatial frequency (in the same way that the concept of neural blurring is used to explain the apparent reduction in contrast of sinusoidal gratings in monocular optic neuritis — Hess, 1983), it would also mean that neurones whose receptive fields extended further beyond the edges of aperiodic targets would be stimulated, and so might contribute to an increase in perceived size. Most of the studies which report an increase in apparent size in peripheral vision have used such stimuli (e.g. Bedell & Johnson, 1984). The explanation does not apply to gratings because blurring does not alter spatial frequency. Our own experiments, not reported here, confirm that aperiodic stimuli often appear larger in peripheral vision. However this depends on the contrast of the target with the background, and stimuli of low contrast may appear smaller. Thus one way to think about the present data is that the visual system uses a number of different mechanisms to estimate size, and combines these to give the best overall estimate. Perhaps the peripheral channels tend to underestimate local spatial frequency in order to compensate for image spread generally caused by blurring, which would tend to increase perceived size. Thus a tendency to global expansion would be opposed or cancelled by a tendency to local contraction. In summary then, in normal circumstances, the visual system may judge object size on the basis of a number of different cues. In unusual circumstances, when some cues are eliminated in the laboratory, it is possible to demonstrate that in isolation individual mechanisms appear to be poorly calibrated. However, this may occur because other cues which normally give an error of opposite sign have been removed. Where allcues are available under good natural viewing conditions, these mechanisms presumably work together to provide the optimal perception of size most of the time.

8. Conclusion

The apparent overestimation of spatial frequency produced by eccentric viewing is robust and cannot be removed by variations of stimulus contrast, luminance or presentation duration. It is not obvious why, apparently, size encoding channels in peripheral vision should be permanently 'mislabelled'. Possibilities not supported by our data are that the effect reflects the reduced retinal contrast of peripheral stimuli, that the (invariant) size labels of receptive fields are set to be accurate at some constant point in the dynamic range of the receptive field, and this dynamic range is larger for peripheral channels which receive input from rods as well as cones, and that previous studies have favoured sustained rather than transient channels. We speculate that peripheral spatial frequency channels are mislabelled to provide local compensation for the global expansion produced by blurring in the periphery.

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