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Effect of spatial waveform on apparent spatial frequency

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Abstract

We examined the effect of spatial waveform on the perceived spatial frequency of a grating target. The luminance profile of 0.5 *c*/° sinusoidal gratings was modified by either compressive or expansive power functions, and was presented alternately with a true sinusoidal grating. Subjects matched the apparent spatial frequency of the two gratings using a method of adjustment. Both compressive and expansive power functions lowered the perceived spatial frequency of the grating, irrespective of the stimulus contrast. Rectified sine wave gratings were also found to reduce apparent spatial frequency. The magnitude of the spatial frequency shifts with spatial waveform diminished with successive matches, which may represent a change in matching strategy employed by observers. Calculations and a further experiment suggest that judgements of spatial frequency may in part be determined by the separation between edges in a grating. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Apparent spatial frequency; Spatial waveform; Contrast transducer; Size discrimination

1. Introduction

The perceived spatial frequency of grating stimuli can be altered by a number of experimental conditions. Dark adaptation produces an apparent increase in spatial frequency (Virsu, 1974), as does brief presentation time (Georgeson, 1985; Kulikowski, 1975; Tynan & Sekuler, 1974), decreased stimulus contrast (Georgeson, 1985) and peripheral viewing (Harris & Wink, 2000; Marran & Davis, 1990). Many of these shifts have been attributed to changes in the tuning characteristics of spatial-frequency tuned channels (Tynan & Sekuler, 1974; Virsu, 1974), or to alterations in the relative activation of sustained and transient channels (Kulikowski, 1975; Tolhurst, 1975; Tyler, 1974). Adaptation to a grating also shifts the apparent spatial frequency of subsequently presented gratings of a similar spatial frequency (Blakemore, Nachmias, & Sutton, 1970; Blakemore & Sutton, 1969), with the shift being away from the spatial frequency of the adapting grating.

Rapid counterphase flicker of low spatial frequency gratings can produce an increase in perceived spatial frequency (Kelly, 1966). This increase has often been referred to as "frequency doubling" because the perceived spatial frequency often appears to be twice as high as the actual spatial frequency presented. Such doubling has been attributed to a rectifying non-linearity in the visual system (Tyler, 1974), although other work suggests that both rectification and compression are involved (Kelly, 1981). Despite its name, however, the apparent spatial frequency of the stimulus is not always exactly double the true spatial frequency (Demirel, Vingrys, Anderson, & Johnson, 1999; Parker, 1981, 1983; Richards & Felton, 1973) but may be greater or less than double, depending on the spatial and temporal characteristics of the stimulus, the viewing eccentricity and the adaptation state of the observer. It has been suggested that fractional shifts in apparent periodicity and true spatial frequency doubling may represent distinct effects (Parker, 1983; Virsu, Nyman, & Lehtiö, 1974).

The apparent spatial waveform of a frequency doubled stimulus is not sinusoidal, but has narrow nodes and wide antinodes (Tyler, 1974). It is not known what effect, if any, this change in the spatial waveform has on perceived spatial frequency. Given this altered spatial waveform, along with the existence of fractional shifts in periodicity reported for a frequency doubled stimulus, we determined the influence of alterations to the spatial

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waveform of a sinusoidal grating on the perceived spatial frequency of the grating.

2. General methods

2.1. Apparatus and procedure

Stimuli were presented on a calibrated video monitor system (VSG 2/4 graphics card, Cambridge Research Systems Ltd., Kent, UK, and Sony™ CPD-G500 colour monitor, frame rate 100 Hz) which subtended 22° × 17° (W × H) at the 1 m viewing distance, and had a mean luminance of 46 cd/m^2. Ambient room illumination was dim.

For all stimuli, contrast linearly increased over 400 ms, remained at the specified contrast for 1000 ms, and then linearly decreased to zero over 400 ms. The minimum time between the offset of one stimulus and the onset of another was 200 ms. Gratings were presented across the visible extent of the monitor, with fixation maintained via a dark, central fixation point. Spatial phase was randomly varied for each presentation.

Contrast thresholds were measured using a two-alternative forced-choice paradigm and a ZEST procedure (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994) of 30 trials, which converged at the 88% correct level.

2.2. Subjects

Five subjects with normal corrected visual acuities participated in the experiments. Subjects viewed the monitor monocularly with their preferred eyes and natural pupils. All five subjects were vision scientists who were experienced psychophysical observers and were familiar with the concept of spatial frequency, although four of the five observers were naïve to the purpose of the study. The study complied with the tenets of the Declaration of Helsinki and was approved by the Legacy Health Systems Institutional Review Board, with all subjects giving informed consent prior to participation.

3. Experiment 1: effect of waveform compression and expansion

3.1. Aims and methods

We determined whether alterations in spatial waveform could alter the perceived spatial frequency of a grating. The relative luminance profile of a 0.5 c/° sine wave grating was altered by a transducer function, such that:

$$L_{\text{relative}} = \left(\frac{\sin(2\pi s x) + 1}{2}\right)^p, \quad (1)$$

where s is the spatial frequency, x is the angular position in space, and p is the transducer exponent. The effect of the transducer function can be seen in Fig. 1, where increasing values of p produces thinner bright peaks in the waveform. When p is equal to unity, the waveform is sinusoidal. The absolute luminance of the grating patterns used is the experiments was given by the following equation:

$$L = B + BC(2L_{\text{relative}} - 1), \quad (2)$$

where B is the background luminance (46 cd/m^2) and C is the contrast. Contrast was defined as Michelson contrast, i.e.:

$$C = (L_{\max} - L_{\min})/(L_{\max} + L_{\min}), \quad (3)$$

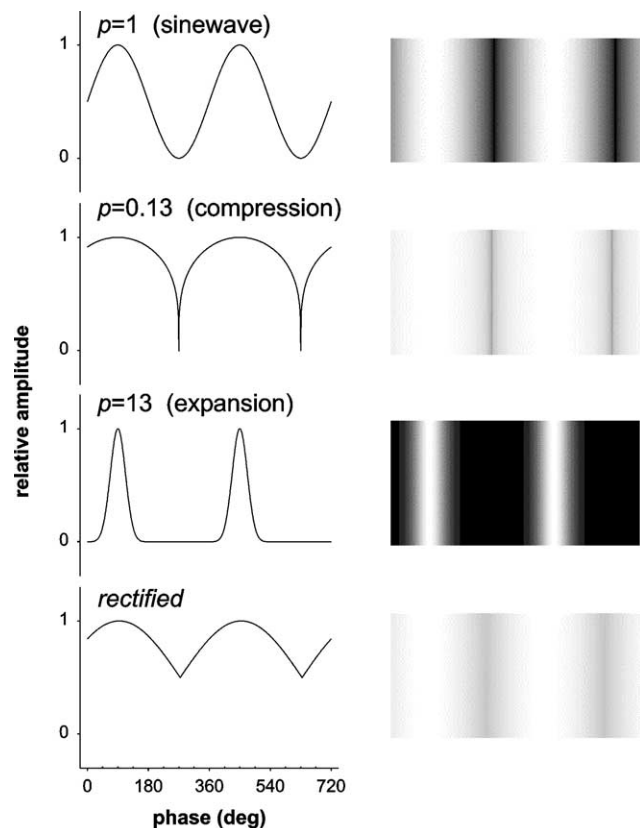

Fig. 1. Luminance profiles of various grating stimuli. Values for p give the exponent of the luminance transducer used to produce the gratings (see Eq. (1)), whereas the lowest waveform is produced by rectification of a sine wave. The schematics on the right hand side of the figure give the approximate appearance of each grating. They are presented for illustrative purposes, and are not intended to represent a quantitatively accurate rendition of the stimuli.

where L_{max} and L_{min} are the maximum and minimum luminances in the waveform, respectively. A rectified 0.25 *c*/° sine wave was also investigated (Fig. 1, lowest function), giving a spatial frequency of 0.5 *c*/°.

The perceived spatial frequency of the distorted gratings was determined using a matching task. The distorted grating was presented first, followed by a sine wave grating, after which the subject altered the spatial frequency of the sine wave grating up or down by 0.0125 log units. Subject repeated this procedure until they reported that the best match had been made. No specific instructions were given as to what strategy should be used in performing the spatial frequency match. The initial sine wave grating was randomly assigned a spatial frequency up to ±10 steps from 0.5 *c*/°. The distorted grating was oriented at 45° and the sine wave grating at 135°, to minimise the possibility of directly matching bar or after-image locations.

All sinusoidal waveforms and gratings altered by the transducer given in Eq. (1) had a contrast of 0.20. Rectified gratings had a peak luminance equivalent to that of the sinusoidal gratings (i.e. 55.2 cd/m^2), and a trough luminance equivalent to the background luminance of 46 cd/m^2.

3.2. Results

The results are plotted in Fig. 2, with matching results shown as a percentage shift from the true spatial frequency. Matches made when p is unity (i.e. a sine wave grating) are close to veridical, indicating that all subjects could accurately perform the matching task. As p departs from unity, the apparent spatial frequency of the distorted grating decreases. In addition, rectified sine wave gratings (filled circles) also demonstrate a reduction in the perceived spatial frequency. The maximum shift differs for various observers, ranging from approximately 5% for subject AJA to 20% for subject BF.

To examine the significance of these shifts, a repeated measures ANOVA on ranks was performed for each subject's results at $p = 0.13$, 1 and 360 (i.e. the extremities of the functions in Fig. 2), as well as for the rectified waveform. Either four (CAJ, BF, FAE, EV) or five (AJA) repeated measures were performed for each of these waveforms. A Dunnett's post-hoc test was used to compare each group to the $p = 1$ condition. For all subjects except EV, the shifts in apparent spatial frequency were significant ($p < 0.05$). Subject EV failed to show a significant effect even after six repeated

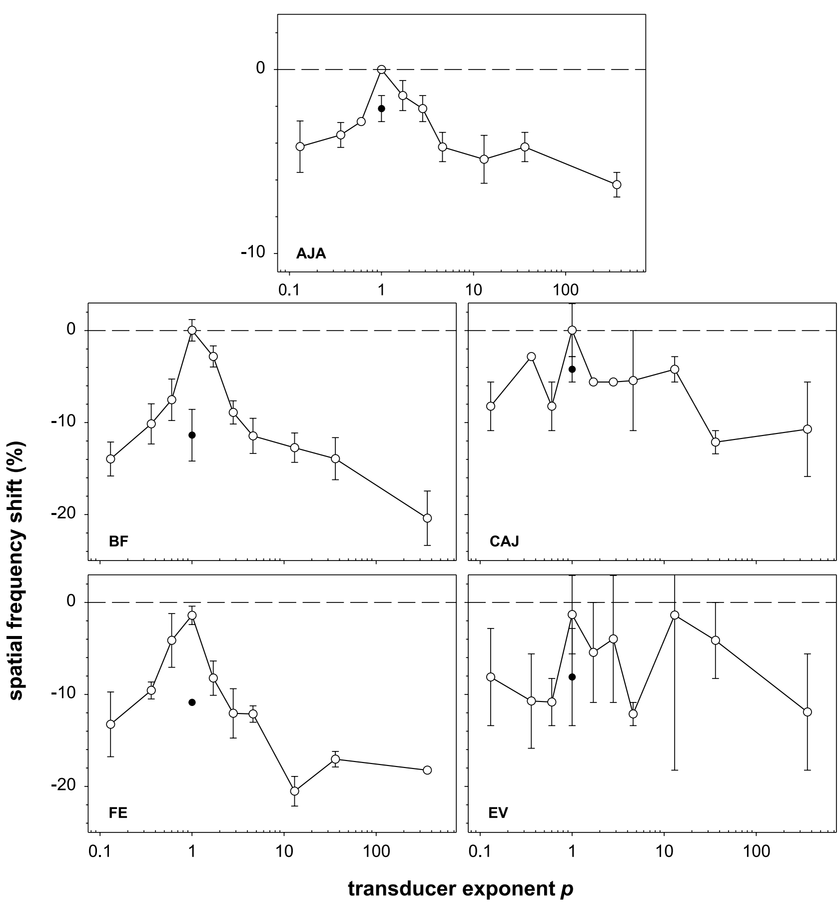

Fig. 2. Transducer exponent p versus shift in apparent spatial frequency. Data points with filled symbols were obtained using rectified sine wave gratings. Data points represent the average (±SEM) of two matching attempts.

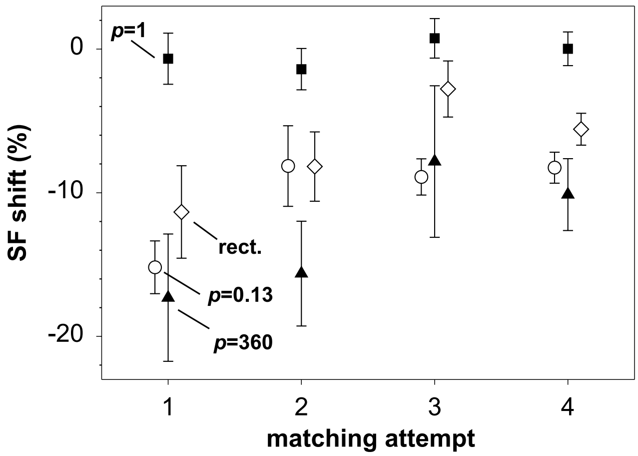

Fig. 3. Effect of serial matching attempts on apparent spatial frequency shift. Data points give the average of four observers, ±SEM. For clarity, some points have been horizontally displaced.

measures, although all average matches for the nine distorted matches are less than for an undistorted match; the probability of such an occurrence purely by chance is less than 0.01.

During the experiment, it appeared that the magnitude of the shift in apparent spatial frequency decreased with subsequent matching attempts. Fig. 3 presents a quantitative account of this effect, in which the average spatial frequency shift for various waveforms is plotted as a function of the match number. Subject AJA's data was excluded from this analysis, as he had prior experience in performing the matching task described in this experiment.

For matching sine wave gratings (filled squares), there is little effect of repeated matching on either the accuracy or variability of matches, suggesting that all subjects showed no systematic shifts in performing the matching task per se (paired *t*-test, match number 1 versus 4, $p = 0.80$). The average results for the non-sinusoidal gratings, however, show a reduction in apparent spatial frequency shift when subsequent matching attempts are made (paired *t*-test, match number 1 versus 4, $p < 0.01$). Despite this reduction, the matches from all three non-sinusoidal waveforms are still significantly different ($p < 0.05$) from a sinusoidal match upon the fourth matching attempt (repeated measures ANOVA on ranks, Dunnett's post-hoc test).

4. Experiment 2: effects of luminance and contrast

4.1. Aims and methods

It is unlikely that the distorted waveforms in Experiment 1 are all equally visible at a given contrast. As such, we wished to determine what effect p had on the contrast sensitivity to a grating. In addition, we wished to determine the robustness of the spatial frequency shifts found in Experiment 1 to alterations in contrast.

Contrast sensitivity was determined using a two-alternative forced-choice procedure of grating orientation (45° or 135°). Sensitivity was based on the geometric mean of two trials from each of four observers.

The spatial frequency matching task was identical to that described in Experiment 1, except that the contrast of the distorted grating was varied. Owing to the high contrasts used, spatial waveforms were scaled to eliminate any changes in average luminance from the background level. The following contrast metric was used:

$$\text{contrast} = (L_{\text{max}} - L_{\text{ave}})/L_{\text{ave}} \quad \text{for } p \leqslant 1, \tag{4}$$

$$\text{contrast} = (L_{\text{min}} - L_{\text{ave}})/L_{\text{ave}} \quad \text{for } p > 1, \tag{5}$$

where L_{ave} is the mean luminance of the grating. The absolute luminance of the grating was given by the following equation:

$$L = a + bL_{\text{relative}}, \tag{6}$$

where a and b are constants chosen to give the required contrast (Eqs. (4) and (5)) whilst having the mean luminance of the grating, L_{ave}, equal the background luminance, B.

4.2. Results

Contrast sensitivity decreased as p departed from unity (Fig. 4), and so it may be that the reduced detectability of the distorted gratings results in a shift in apparent spatial frequency. Fig. 5 shows that increasing stimulus contrast has little effect on the perceived spatial frequency, however. Most importantly, the use of high contrasts fails to negate or reverse the spatial frequency shifts seen in Experiment 1, indicating that stimulus contrast does not play an important role in this perceived spatial frequency shift.

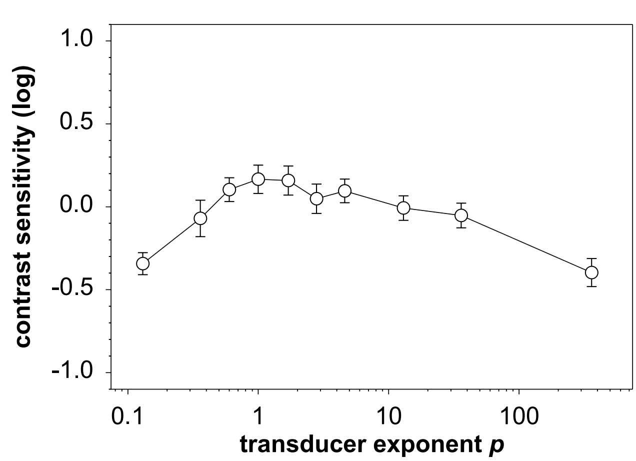

Fig. 4. Contrast sensitivity as a function of the contrast transducer exponent, p. Data points give the average of four observers, ±SEM.

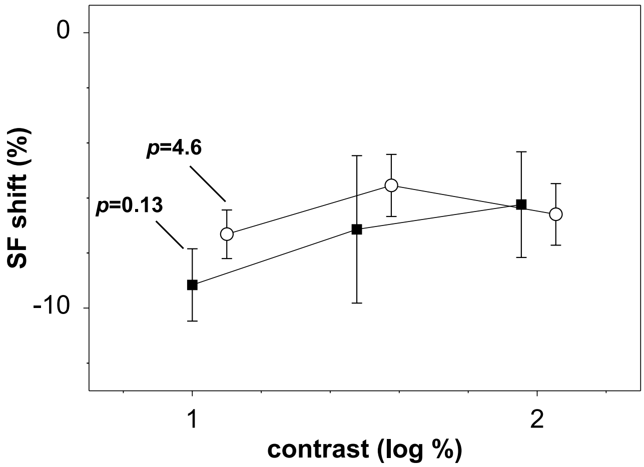

Fig. 5. Effect of contrast on apparent spatial frequency shift. Data points give the average of five observers, ±SEM. For clarity, the data for the $p = 4.6$ curve (◯) have been displaced to the right by 0.1 log units.

5. Experiment 3: effect of criterion on periodicity

5.1. Aims and methods

Both compressive and expansive alterations of a waveform resulted in a shift in apparent periodicity in Experiment 1. However, it is unclear what criterion the subjects used to determine spatial frequency. For sinusoidal stimuli, spatial frequency matching can be successfully performed by equating the distance between the centre of successive dark or light bars in the stimulus (*bar separation matching*). Matching may be equally successful if the width of either the light or dark bars are matched (*bar width matching*). This experiment was designed to examine these two criteria for matching. Three subjects were investigated (AJA, BF and FE), based on their reliable matching performance in Experiment 1.

A matching experiment similar to that described in Experiment 1 was performed, except that subjects were asked to use bar width as their criterion. For $p \leqslant 1$, subjects were asked to match the width of the light bars in both the distorted grating and the sinusoidal grating, whereas for values of $p > 1$, subjects were asked to match the width of the dark bars in the distorted grating to the light bars in the sinusoidal grating. In this way, subjects matched the width of the widest bars in each grating. Given a consistent criterion for the location of the edge separating light and dark bars, this strategy is equivalent to determining the separation between the closest edges of two successive narrow bars. Subjects were asked also to match the widths of the light and dark bars in two sinusoidal gratings. All stimuli had contrasts of 0.20, as defined in Experiment 2, and produced no shift in average luminance.

In addition, subjects were asked to perform the same matching task outlined above, except using the distance between the centres of bars as a criterion. For $p = 0.13$ and 1, subjects matched the distance between the dark bars in both the distorted grating and the sinusoidal grating, whereas for $p = 360$, subjects matched the distance between the light bars in the distorted grating to the distance between the dark bars in the sinusoidal grating. In the way, subjects were always matching the distance between the centre of the bars that appeared the narrowest.

5.2. Results

The left-hand panel of Fig. 6 gives the results of the matching task based on bar width, expressed as a shift in spatial frequency. The form of the results are similar to those of Experiment 1 (Fig. 2), wherein the spatial frequency shifts more rapidly as exponents decrease from unity than when exponents increase from unity. The

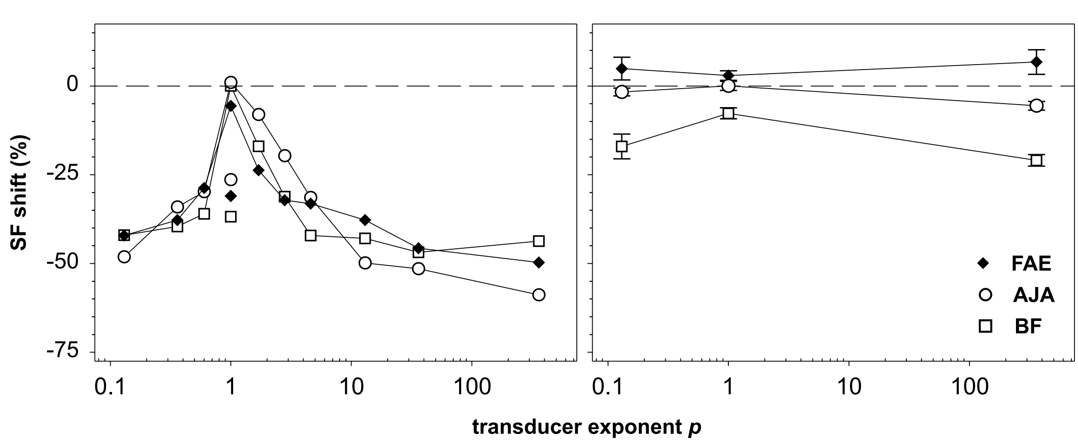

Fig. 6. Effect of matching criterion on spatial frequency shift. Left panel: matching the width of the widest bar in each grating. As in Fig. 2, unconnected points at $p = 1$ are for the rectified grating condition. The average SEM was 3.3. Right panel: average of five matches (±SEM) of the separation between the centre of the narrowest bars in each grating.

magnitude of the spatial frequency shift, however, is greater than in Experiment 1 and is more homogeneous between observers. The spatial frequency shift tended to be slightly larger for the maximum expansive exponent ($p = 360$) than for the maximum compressive exponent ($p = 0.13$), similar to that found in Experiment 1 (Fig. 2).

When subjects were asked to judge the distance between the centre of the narrowest bars (Fig. 6, right panel), spatial frequency shifts were substantially smaller than when judgements were based on bar width (left panel). For subject BF, significant differences between the sinusoidal matches ($p = 1$) and the distorted gratings ($p = 0.13$ and 360) were still evident (repeated measures ANOVA ($p < 0.001$), Dunnett's post-hoc test). Significant variation was not found for subjects AJA and FAE after five matches ($p = 0.06$ and 0.6, respectively).

When subjects were asked to match the width of the white bars to the width of the dark bars in two sinusoidal gratings, white bars were judged to be 1.26 times (SEM 0.05) wider.

6. Discussion

Our results demonstrate that altering the spatial waveform of a grating can lead to alterations in its apparent spatial frequency. Both compressive and expansive alterations resulted in a spatial frequency percept that was less than veridical, and our results cannot be explained by alterations in the visibility of the grating or by changes in average luminance.

It is not clear that our results can be explained using existing models of apparent spatial frequency shifts. Alterations in perceived spatial frequency have been attributed to shifts in the peak sensitivity of spatial-frequency tuned channels (Tynan & Sekuler, 1974; Virsu, 1974). If higher centres presume the frequency tuning of these channels to be constant, a shift in peak sensitivity will be interpreted as a change in the spatial frequency of the stimulus. Both dark adaptation (Virsu, 1974) and rapid presentation (Tynan & Sekuler, 1974) decrease surround inhibition in receptive fields, shifting spatial frequency tuning to lower frequencies. A decrease in apparent spatial frequency could theoretically result from an increase in surround inhibition, although it is not readily apparent how the stimuli used in this study could produce such changes.

Alterations in the balance between sustained and transient channels has also been suggested to cause shifts in spatial frequency (Kulikowski, 1975; Tolhurst, 1975; Tyler, 1974), wherein increasing activation of transient channels increases the perceived spatial frequency. It could be argued that increased high spatial frequency harmonics in the distorted stimulus favours the stimulation of sustained channels, thereby lowering the perceived spatial frequency. However, it has been found that the presence of a higher spatial frequency harmonic acts to increase the apparent spatial frequency of a low spatial frequency grating stimulus (Maddess & Kulikowski, 1999). This finding is opposite to that outlined in our paper, and may be due to the fact that only a second harmonic was added to distort the sinusoidal waveform (Maddess & Kulikowski, 1999). In addition, the matching paradigm used by Maddess and Kulikowski (vertically oriented gratings, viewed concurrently) was different to ours (orthogonally oriented gratings, viewed consecutively), which raises the possibility that different matching criteria were used by the observers in each study. The influence of matching criteria is discussed below.

Experiment 3 demonstrated that the criterion used for matching gratings has a large effect on apparent spatial frequency. When the width of the widest bars are matched, shifts in spatial frequency of a similar pattern to those seen in Experiment 1 are found, albeit of a larger magnitude. To make these width judgements, subjects must determine the "edge" separating the light and dark bars. Computational models of spatial vision often presume that edges occur at zero-crossing points in the second derivative of the waveform (Marr & Hildreth, 1980; Watt & Morgan, 1983), and such modelling provides good predictions of the locations of edges in one-dimensional non-sinusoidal gratings (Georgeson & Freeman, 1997). We determined the location of the second derivative zero-crossing points in our distorted gratings, and thereby calculated the width of the widest bars for each value of p. The results shown in Fig. 7 (dashed line), where the widest bar width is represented as a shift in spatial frequency relative to $p = 1$. The shape of this function is similar to the average results found in Experiment 3 (circles), although the model predicts that the exponent $p = 360$ produces slightly less

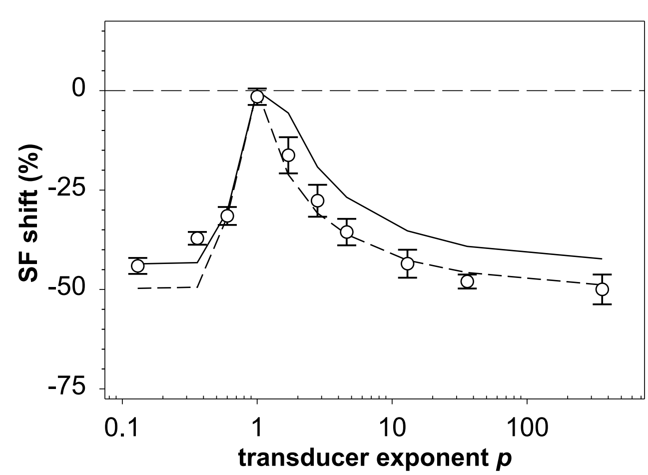

Fig. 7. Spatial frequency shift predictions based on zero-crossings in the second derivative of the spatial waveform, assuming either a linear (- - -) or non-linear (—) luminance transduction. Circles show the average (±SEM) of the data from Fig. 6 (left panel).

shift than $p = 0.13$, contrary to our experimental results. In addition, the model overestimates the spatial frequency shift when p is small. The model, however, fails to account for the non-linear transduction of luminance within the visual system. Therefore, a compressive luminance transducer function was applied to each waveform before determining the second derivative, with the transducer being identical to the Naka–Rushton function used by Georgeson and Freeman (1997) (i.e. $n = 1$). A normalised semi-saturation luminance constant $S = 1$ was used, as this adequately predicted the ratio of light to dark bar widths in a sinusoid, as determined in Experiment 3 (experimentally determined ratio = 1.26, model prediction = 1.28). The results are shown by the solid line in Fig. 7. Predictions of the spatial frequency shifts when $p < 1$ are improved, however the new model now underestimates the shifts when $p > 1$. The new model also fails to capture the larger spatial frequency shifts seen for $p = 360$ than for $p = 0.13$. It is possible that a more accurate model could be created by incorporating the effects of linear spatial filtering as outlined by Georgeson and Freeman (1997), although the improvements in fit obtained by these authors are small when compared to the effects of luminance transduction non-linearities. Such changes are likely to be smaller than the inter-observer differences in Fig. 6, making further optimisation of the second-derivative model difficult to justify. It must be remembered that although second-derivative models can accurately account for edge location judgements (Georgeson & Freeman, 1997), it does not necessarily follow that such models should accurately account for judgements of the separation between adjacent edges. Despite this potential limitation, the model does provide a reasonable prediction of the form and magnitude of the spatial frequency shifts observed.

When matching is based on a judgement of the distance between the centre of the thinnest bars in the grating, spatial frequency shifts are markedly reduced or eliminated (Fig. 7, right panel). Using the same computation model outlined above, the location of bars may be predicted from the position of peaks or troughs in the second derivative of the waveform (Georgeson & Freeman, 1997), which corresponds to the luminance peaks and troughs in our stimuli. Therefore, the model predicts no spatial frequency shifts when judgements are made using bar locations. Despite this, values of p less than or greater than unity still resulted in significant reductions in spatial frequency for subject BF ($p < 0.001$), and approached significance in subject AJA ($p = 0.06$). Reducing the width of the bars in grating stimuli may perturb local size mechanisms in a similar way to that found in the Delboeuf illusion (Jaeger & Lorden, 1980; Oyama, 1977), thereby resulting in a relative overestimation of bar separation even if bars position itself is accurately predicted. Such an effect may be symmetrical for both compressive and expansive contrast transducers, as both produce thin bars (whether light or dark) that provide the most spatially defined indicator of bar position, and presumably the most salient stimulus to size detectors. The salience of these thin contrast bars can be seen in Fig. 1, where it is easy to imagine that the compressed grating ($p = 0.13$) is shifted by 180° relative to the expanded pattern ($p = 0.13$), despite both having identical phases. As an alternative explanation, it may be that some subjects cannot fully discount the widely discrepant information regarding bar separation provided by the width of the intervening wide bar (Fig. 6, left panel).

We found that the magnitude of the spatial frequency underestimation in Experiment 1 decreased on successive matching attempts (Fig. 3). Our finding that this effect occurs in distorted waveforms and not sinusoids (Fig. 3) is superficially similar to the learning effects described by Fiorentini and Berardi (1981) for distorted, but not sinusoidal, gratings. These authors, however, found a general increase in discrimination performance with training, and so this cannot explain the systematic change found in our study. It is more likely that our effect represents a change in the strategy employed by the observer. Early matching attempts may be more heavily influenced by the width of the widest bar in the grating stimulus, which is equivalent to judging the separation between adjacent edges of the most spatially defined bars. Spatial frequency shifts may then reduce if the subject attempts to concentrate more on the separation between the centres of the bars in the grating, which more faithfully encodes spatial frequency (Fig. 7, right panel). It is possible, however, that other strategies exist to encode spatial frequency that do not depend on local judgements of bar width or bar separation. Nyman and Rovamo (1980) found judgements of single period widths could be altered when a grating was flickered, whereas judgements over distances of three times the period remained veridical under stationary and flickering conditions. Their results suggest that periodicity judgements over a broader spatial extent may be more robust to those derived from local information, and that it may be possible to make an assessment of overall periodicity. Similarly, spatial frequency percepts derived from the peak sensitivity of spatial-frequency tuned channels (Tynan & Sekuler, 1974; Virsu, 1974) may be more robust to local changes in spatial information. It is unlikely that investigations employing purely sinusoidal gratings will be able to elucidate the matching strategies of observers, as accurate matches can be made using any one of a number of different strategies (e.g. bar width matching, bar separation matching, judgements of overall periodicity). The use of non-sinusoidal grating stimuli may provide a useful tool for the further investigation of spatial frequency matching strategies.

It is possible that the shifts in apparent spatial frequency outlined in this paper are manifest in investigations of the frequency doubling phenomenon. The spatial waveform of the frequency doubling stimulus has been reported to be similar to a rectified sine wave (Tyler, 1974), and we found a rectified sine wave grating produced a significant reduction in apparent spatial frequency. Although increases in apparent periodicity are typically interpreted in terms of mechanisms that increase apparent periodicity, there is no reason why the periodicity shift cannot be the net result of effects that both increase and decrease periodicity. As such, fractional periodicity shifts below doubling could result from the actions of a true frequency doubling mechanism and a mechanism that reduces apparent periodicity (such as outlined in this paper). It has been suggested that fractional shifts arise from separate mechanisms to those producing the true frequency doubling effect (Parker, 1983). While it has been reported that adaptation, eccentricity and temporal frequency can cause shifts in the perceived spatial frequency of a grating (Georgeson, 1985; Harris & Wink, 2000; Kulikowski, 1975; Marran & Davis, 1990; Tynan & Sekuler, 1974; Virsu, 1974), the results of our present investigation show that spatial waveform can also affect perceived spatial frequency. Our study suggests that the results of spatial frequency matches between gratings whose waveforms are not identical must be interpreted with caution, as large criteria-dependant effects can occur.

References

Blakemore, C., Nachmias, J., & Sutton, P. (1970). The perceived spatial frequency shift: evidence for frequency-selective neurones in the human brain. *Journal of Physiology*, *210*, 727–750.

Blakemore, C., & Sutton, P. (1969). Size adaptation: a new aftereffect. *Science*, *166*, 245–247.

Demirel, S., Vingrys, A. J., Anderson, A., & Johnson, C. A. (1999). Spatiotemporal properties of the frequency doubling effect. *Investigative Ophthalmology and Visual Science*, *40*, S42.

Fiorentini, A., & Berardi, N. (1981). Learning in grating waveform discrimination: specificity for orientation and spatial frequency. *Vision Research*, *21*, 1149–1158.

Georgeson, M. A. (1985). Apparent spatial frequency and contrast of gratings: separate effects of contrast and duration. *Vision Research*, *25*, 1721–1727.

Georgeson, M. A., & Freeman, T. C. A. (1997). Perceived location of bars and edges in one-dimensional images: computational models of human vision. *Vision Research*, *37*, 127–142.

Harris, J. P., & Wink, B. (2000). Invariance of the perceived spatial frequency shift of peripherally viewed gratings with manipulations of contrast, duration, and luminance. *Vision Research*, *40*, 931–941.

Jaeger, T., & Lorden, R. (1980). Delboeuf illusions: contour or size dectector interactions? *Perceptual and Motor Skills*, *50*, 376–378.

Kelly, D. H. (1966). Frequency doubling in visual responses. *Journal of the Optical Society of America*, *56*, 1628–1633.

Kelly, D. H. (1981). Nonlinear visual responses to flickering sinusoidal gratings. *Journal of the Optical Society of America*, *71*, 1051–1055.

King-Smith, P. E., Grigsby, S. S., Vingrys, A. J., Benes, S. C., & Supowit, A. (1994). Efficient and unbiased modifications of the QUEST threshold method: theory, simulations, experimental evaluation and practical implementation. *Vision Research*, *34*, 885–912.

Kulikowski, J. J. (1975). Apparent fineness of briefly presented gratings: balance between movement and pattern channels. *Vision Research*, *15*, 673–680.

Maddess, T., & Kulikowski, J. J. (1999). Apparent fineness of stationary compound gratings. *Vision Research*, *39*, 3404–3416.

Marr, D., & Hildreth, E. (1980). Theory of edge detection. *Procedings of the Royal Society London B*, *207*, 187–217.

Marran, L., & Davis, E. T. (1990). The effects of temporal modulation and spatial location on the perceived spatial frequency of visual patterns. *Perception and Psychophysics*, *47*, 449–456.

Nyman, G., & Rovamo, J. (1980). Perceived spatial frequency of flickering gratings: a local spatial distortion. *Perception*, *9*, 403–409.

Oyama, T. (1977). Feature analysers, optical illusions, and figural aftereffects. *Perception*, *6*, 401–406.

Parker, A. (1981). Shifts in perceived periodicity induced by temporal modulation and their influence on the spatial frequency tuning of two aftereffects. *Vision Research*, *21*, 1739–1747.

Parker, A. (1983). The effects of temporal modulation on the perceived spatial structure of sine-wave gratings. *Perception*, *12*, 663–682.

Richards, W., & Felton, T. B. (1973). Spatial frequency doubling: retinal or central? *Vision Research*, *13*, 2129–2137.

Tolhurst, D. J. (1975). Illusory shifts in spatial frequency caused by temporal modulation. *Perception*, *4*, 331–335.

Tyler, C. W. (1974). Observations on spatial-frequency doubling. *Perception*, *3*, 81–86.

Tynan, P., & Sekuler, R. (1974). Perceived spatial frequency varies with stimulus duration. *Journal of the Optical Society of America*, *64*, 1251–1255.

Virsu, J. (1974). Dark adaptation shifts apparent spatial frequency. *Vision Research*, *14*, 433–435.

Virsu, V., Nyman, G., & Lehtiö, P. K. (1974). Diphasic and polyphasic temporal modulations multiply apparent spatial frequency. *Perception*, *3*, 323–336.

Watt, R. J., & Morgan, M. J. (1983). The recognition and representation of edge blur: evidence for spatial primitives in human vision. *Vision Research*, *12*, 1465–1477.