



PERGAMON

Vision Research 39 (1999) 3404–3416

VISION
Researchwww.elsevier.com/locate/visres

Apparent fineness of stationary compound gratings

T. Maddess^{a,*}, J.J. Kulikowski^b^a Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, Canberra, ACT 0200, Australia^b Visual Sciences Laboratory (Optometry), U.M.I.S.T., PO Box 88, Manchester M60 1QD, UK

Received 4 June 1998; received in revised form 18 January 1999

Abstract

Patterns consisting of the sum of a sinusoidal grating and its second spatial harmonic have an apparent spatial fineness, or periodicity, that is about halfway between the two component spatial frequencies. There are also phase dependent modulations of the apparent fineness about the mean fineness shift. Covariance between individuals' phase dependent fineness shifts indicates the presence of four spatial phase channels. The apparent fineness effects, and the putative phase channels, may both be a product of a local, linear, analysis of spatial frequency content. Illusory second harmonics, as generated in the spatial frequency doubling illusion, also change apparent fineness. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Apparent spatial frequency; Spatial frequency shift; Frequency doubling; Spatial phase channels; Illusion

1. Introduction

The spatial frequency shift is an effect in which a previously presented adapting grating causes the apparent fineness of a subsequently presented test grating to appear shifted towards that of the adapting grating (Blakemore & Sutton, 1969; Blakemore, Nachmias & Sutton, 1970; Heeley, 1979). This interplay between frequencies provided strong evidence for spatial frequency channels in human vision. Simultaneous spatial frequency shifts have also been reported in which the test grating is presented within an enclosed region and the inducing grating is presented in a surround (MacKay, 1973; Klein, Stromeyer & Ganz, 1974). The present study demonstrates that shifts in apparent fineness are also observed in compound gratings that are the sum of two similar frequencies, in particular the sum of a grating and its second spatial harmonic.

The effect is topical given renewed interest in the spatial frequency doubling illusion (FD illusion) which is the basis for a new and highly effective diagnostic device for glaucoma (Maddess, 1991; Maddess &

Henry, 1992; Johnson & Samuels, 1997). The FD effect is observed when low spatial frequency gratings are either presented briefly (Kulikowski, 1975) or have their contrast modulated at high temporal frequencies, and the effect is due to a rectifying nonlinearity (Tyler, 1974; Kelly, 1981). The relationship to the current work comes from the fact that linear response components are present even when the FD illusion is vivid. For example Kelly (1981) and Kulikowski (1975) both showed that the 2H component could be substantially nulled with a static counterphase pattern leaving a strong F component visible. Hence the situation is similar to our basic finding except that the 2H component is illusory. As might be expected from this several reports have been made showing that under suboptimal conditions for producing FD the visual percept is of a pattern with intermediate textural fineness between the input grating and its second harmonic (Tynan & Sekuler, 1974; Virsu, Nyman & Lehtio, 1974; Kulikowski, 1975; Thompson & Murphy, 1978; Nyman & Rovamo, 1980; Parker, 1981; Georgeson, 1985). The present study indicates that at least some of this effect is due to the fact that under these conditions both the fundamental and the second harmonic are present and that broadly tuned spatial frequency channels lead to a percept having an intermediate apparent fineness.

* Corresponding author. Tel.: +61-2-62494099; fax: +61-2-62493808.

E-mail address: ted.maddess@anu.edu.au (T. Maddess)

2. Methods

Grating patterns were displayed on a Barco CCID 7551 monitor at a pixel resolution of 512×420 , a refresh rate of 102 Hz, and a mean luminance of 45 cd/m^2 (colour temperature 6500K). Monitor linearity was confirmed by nonlinear systems identification methods (James, Maddess, Rouhan, Bedford & Snowball, 1995; Maddess, Bedford, James & Rose, 1997). The ambient illumination was that provided by the monitor in an otherwise darkened room. Fig. 1 illustrates the spatial layout of the stimuli, the heights and widths of the stimulus regions being correctly illustrated by the axes labels. In most experiments the centrally presented grating consisted of the sum of two sinusoidal gratings: a low spatial frequency (F) and its spatial second harmonic ($2H$). The upper comparison sinusoidal grating had spatial frequency F , whereas the sinusoidal grating presented below the centrally presented compound grating had its spatial frequency set to twice F , (i.e. $2H$). In most experiments spatial phase of the $2H$ component of the central grating was the randomised experimental variable. The six small figures at the top of Fig. 2 illustrate the definition and appearance of the phase relations. The 0° phase condition for all grating components corresponded to cosine phase with respect to the monitor centre. Unless otherwise stated the comparison gratings and the F component of the compound grating were presented at 0° phase. For the compound gratings the contrast of F and the higher frequency component were both equal to 0.5. In the

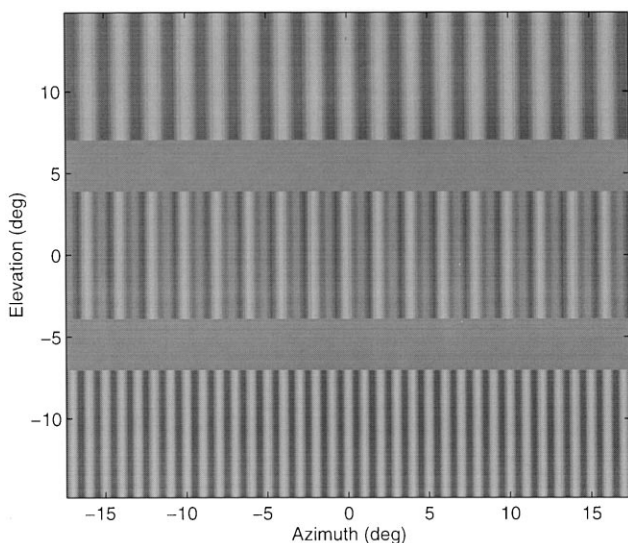


Fig. 1. When two sinusoidal gratings, one the second harmonic of the other (upper and lower gratings), are summed (middle compound grating) subjects report that the compound grating has an apparent fineness intermediate between that of the component parts. This effect is observed for a wide range of spatial frequencies, contrasts and relative phases.

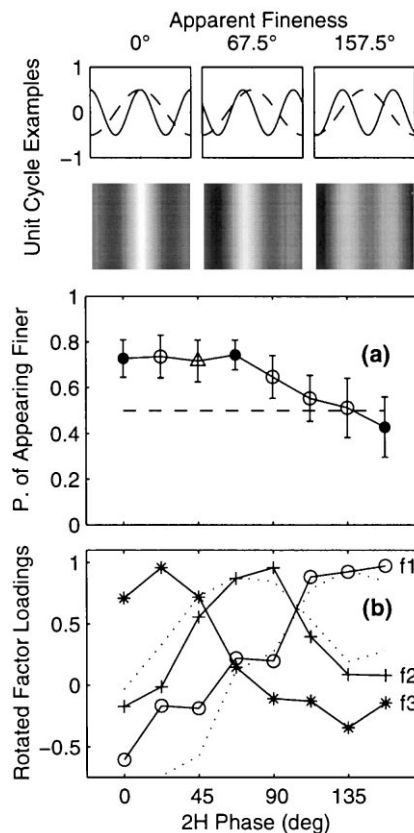


Fig. 2. (Top) The first row illustrates the brightness profiles of the summed Fundamental grating (F) and $2H$ gratings displaced to phases 0, 67.5 and 157.5° with respect to the c.r.t. centre (0°). Fig. 9 illustrates the summed profile for the 67.5° case. The second row shows the appearance of each repeated cycle of the resultant compound gratings. (a) Probability of the compound grating appearing more like the $2H$ component for nine subjects. The triangle (third from left) is the case shown in Fig. 1, while the open circles are the cases shown above. The horizontal dashed line indicates 50% probability (i.e. intermediate apparent fineness). Error bars are S.E.. (b) Rotated factor loadings for the data from the nine subjects indicate that their phase sensitivities covary in a way strongly suggesting three phase channels over the range 0 – 157.5° .

experiments of Fig. 3 the $2H$ component had half the contrast of F .

In a few experiments the third harmonic was also summed into the compound grating and in this case the contrast of the 3 components was in the ratio 1, 1/2, 1/3 as in the Fourier series for a sawtooth-wave (Tolstov, 1962). Subjects viewed the gratings monocularly having their heads secured with the aid of a chin rest at distances ranging from 0.3 to 4.8 m, thus varying the fundamental spatial frequency from 0.25 to 4 c/deg.

Subjects were instructed to 'compare the apparent textural fineness of the vertical striations' of the compound grating contained within the central stripe, with the textural fineness of the gratings above and below the line (Fig. 1). Subjects were instructed not to count the stripes, or make vernier-like matches, but rather to report whether the fineness of the central pattern was

closer in appearance to the lower ($2H$) or the upper (F) pattern in a two alternate forced choice (2AFC) paradigm. Nine subjects with normal or corrected-to-normal vision were tested, seven being naive as to the purpose of the experiments. All subjects gave informed written consent under protocol M881 of the Human Ethics Experimentation Committee of the ANU.

At the onset of each trial the monitor contained a blank field at the mean luminance. Within each presentation the contrast of the gratings was increased from 0 to the test contrast and then back down to 0. This temporal windowing function was a Blackman function: $\text{Blackman}(t) = 0.42 - 0.5 \times \cos(2\pi(t - t_0)/\tau) + 0.08 \times \cos(4\pi(t - t_0)/\tau)$, where the total duration (τ) was 2 s unless otherwise stated. In some trials the contrast of the centrally presented compound gratings was windowed with a briefer, temporally scaled version, of the window but where the maximum contrast of the test pattern was obtained at the centre of the presentation time of the upper and lower comparison gratings. In this case the windows total duration (τ) was set to one of eight ($1/2$ octave) durations between 31.3 and 500 ms. In these trials only the F grating was presented: the brief presentation being designed to produce an *illusory* spatial second harmonic of variable contrast.

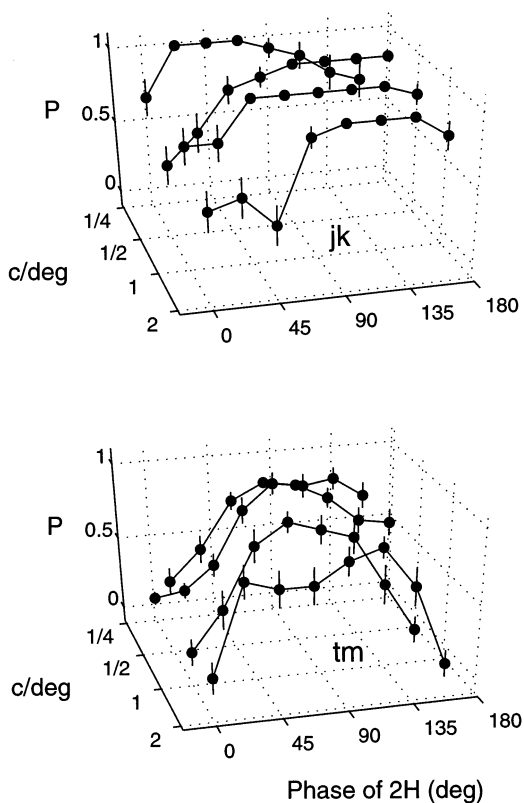


Fig. 3. Experiment of Fig. 2a repeated at four different F spatial frequencies of 0.25, 0.5, 1.0 and 2.0 c/deg, for two subjects. Note that while there is some shift in the curves the shift is not correlated with spatial frequency. Error bars are S.E., $n = 12$ for each curve.

We used a method of adjustment (MOA) procedure to measure the magnitude of the shift in apparent fineness. Subjects adjusted the spatial frequency of reference gratings to match the apparent textural fineness of the compound gratings. Subjects made a minimum of six matches for each of 16 phase combinations. The spatial layout was like previous experiments (Fig. 1) except that a pair of reference gratings replaced the upper and lower comparison sinusoidal gratings. The F component of the centrally presented compound grating was set to 1 c/deg. The spatial frequency of the reference gratings could be rapidly adjusted in 128 equal steps between 0.667 and 3 c/deg, the two reference gratings always having the same spatial frequency. The reference gratings maintained cosine phase with respect to the c.r.t. centre. The temporal onset and offset of the gratings was smooth (a half Blackman window with $\tau = 0.5$ s) but subjects were allowed to take as much time as they liked to make their adjustments. Subjects were encouraged to rapidly ramp the frequency of the reference gratings up and down until they felt they were near a match, and then to make fine adjustments. Experiments with $F + 1.5F$ were also conducted.

Factor analysis (Johnson & Wichern, 1992; Tabachnick & Fidell, 1996) was performed using SPSS. All other analyses were conducted with code written in Matlab. The regression analysis presented consisted of fitting a number of models to the modulation of the observed apparent fineness with $2H$ or $1.5F$ phase. The models could contain up to three components: a mean effect and modulations at one or two cycles per 360° of phase or both. The fact that we have fundamental and second harmonics both in our stimuli and in the measured psychometric functions could lead to confusion, therefore we develop a separate nomenclature here for the modulations of the psychometric functions. We will henceforth refer to the mean effect as M and the possible modulations of the psychometric functions at one or two cycles per 360° as the P and $2P$ terms or components. The regression analysis thus consisted of fitting a hierarchy of models the most complex being referred to as $M + P + 2P$ and the simplest M , $M + P$ and $M + 2P$ also being considered. The models were then compared with F -tests find to the most parsimonious model that fit a given psychometric function.

3. Results

3.1. Compound gratings with real $2H$

The stimulus layout for our experiments is illustrated by Fig. 1. Eight compound gratings were presented, having a fundamental spatial frequency of 1 c/deg, and a $2H$ component having a phase selected at random

from eight 22.5° steps ranging from 0 to 157.5° . The mean result (Fig. 2a), for a minimum of 12 repeats in nine subjects, indicates that subjects found the compound grating to have an apparent spatial frequency more like that of the $2H$ component. Subjects reported that the compound gratings had a periodicity between F and $2H$, which is the apparent fineness. When the subjects were presented with a copy of Fig. 1 they all reported that apparent fineness of the central grating was intermediate between that of the upper and lower patterns.

A factor analysis on the nine psychometric functions that were averaged to obtain Fig. 1 examined whether or not subjects responses to some phases covary in a manner that might suggest separate phase dependent mechanisms or *channels*. The method essentially examines the correlation matrix to identify those phases producing correlated responses. The analysis revealed three large eigenvalues (i.e. principal components) of 4.19, 2.35, 0.86 (based on standardised variables). These eigenvalues can be equated to correlation coefficients by dividing by the number of tested phases, thus the first factor accounted for $4.19/8 = 52.4\%$ of the total variation, the three factors together accounting for 92.5%. The rotated factor loadings (Fig. 2b) can be thought of as regression coefficients between the principal components of covariation and the tested phases (Johnson & Wichern, 1992; Tabachnick & Fidell, 1996). The structure revealed by the analysis is a simple one of three overlapping channels. The validity of the component associated with the eigenvalue of 0.86 is questionable (a value of 1 is often considered to be about the lower bound of factors which should be considered), however, the remaining five eigenvalues were small (together accounting for only 7.5% of the total variation), and forcing the construction of factor loadings with only two factors did not significantly change the shape of the first two functions (Fig. 2b, cf. solid and dotted curves). Moreover, other diagnostics for the three factor case (e.g. sphericity, sampling adequacy, anti-image correlation matrix) indicate that the data are factorizable and that therefore the three component model is well founded (Johnson & Wichern, 1992; Tabachnick & Fidell, 1996). The most to least significant factors, for both the two and three factor models, are shown labelled f_1 to f_3 , respectively, in Fig. 2b.

A broader range of spatial phases, frequencies and contrasts was also explored with TM and JK. In separate randomised blocks of trials (12 repeats for each condition) cases were examined where the F component was variously 0.25, 0.5, 1.0, or 2.0 c/deg (Fig. 3). The responses of JK resemble those of the other subjects whose data is illustrated in Fig. 2a. TM's response functions were more consistently sinusoidal in appearance.

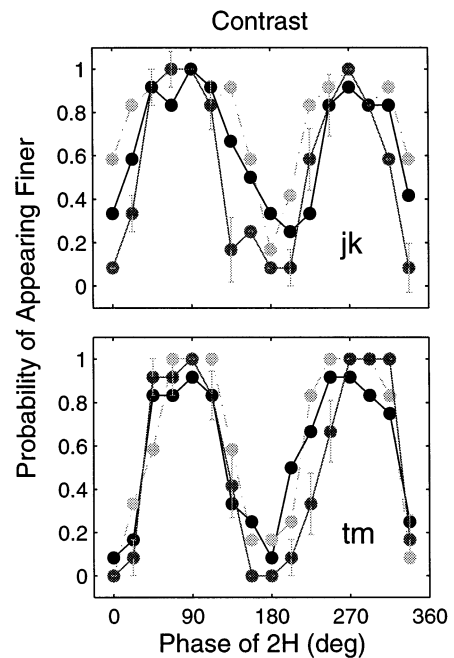


Fig. 4. Effect of contrast and broader range of spatial phases. Two subjects were tested with contrasts of the F set to 0.1 (light grey), 0.2 (mid grey) and 0.4, and $2H$ half the contrast of F . The two comparison gratings had contrasts equal to that of F . With the broader range of phases and more $2H$ phases presented the subject's responses became more phase dependent. Responses were more biased to the $2H$ end at the lower contrasts. Error bars are S.E. and are shown for the contrast 0.2 data set but the other S.E. were similar.

With further training response functions become more sinusoidal in shape as is shown by the results of later experiments in which grating contrast was varied (Fig. 4) for the 0.5 c/deg condition. In these experiments the range of $2H$ phases was extended, the 16 phases covering the range from 0 to 337.5° . Contrast appeared to have little effect although, particularly for JK, and also for TM, the lowest contrast patterns biased reported fineness toward the $2H$ component.

We next estimated the actual magnitude of the changes in apparent fineness by asking subjects to match the apparent fineness of compound gratings to that of sinusoidal gratings of variable spatial frequency. The experimental layout was as in Fig. 1 except that both the upper and the lower comparison gratings were identical, their spatial frequency being under the control of the subject (Section 2). Six repetitions for each of the 16 phases used in the experiments of Fig. 4 were obtained from four subjects. These subjects included TM and three of the naïve subjects used in the experiments of Fig. 2a. The resulting spatial frequency matches for each subject were regressed onto models containing a mean fineness shift and sinusoidal fineness modulation components that changed with the phase of the $2H$ grating. We examined regression models (Section 2) containing a mean apparent fineness (M) modulation at the fundamental (i.e. one cycle per 360° of $2H$

grating phase = P) and/or the second harmonic (i.e. two cycles per 360° of $2H$ grating phase = $2P$). The full model, $M + P + 2P$, containing both fineness modulation components and the mean effect, was required to fit the data of all four subjects (e.g. the mean F statistic for accepting the full model over the lesser model containing only the mean plus fundamental effects was 7.31 ($df_{2,11}$, $P < 0.01$)).

Fig. 5 shows the mean spatial frequency matches for each phase. The solid lines represent the fitted $M + P + 2P$ regression models. The mean fineness shift was to a spatial frequency of 1.58 ± 0.11 S.E. c/deg. The mean amplitudes of the phase dependant modulated components were 0.151 ± 0.05 S.E. c/deg for P , and 0.076 ± 0.027 S.E. c/deg for $2P$. The ratio of the modulated/(mean - 1) fineness shifts averaged 0.26 (range 0.09 to 0.055) for P , and 0.17 (range 0.06 to 0.35) for the $2P$ component. Overall, the average maximum modulation of the apparent fineness by grating phase was thus about 40% of the mean effect (cf. $0.43 = 0.17 + 0.26$, with $0.40 = (0.15 + 0.08)/(1.58 - 1)$ from above).

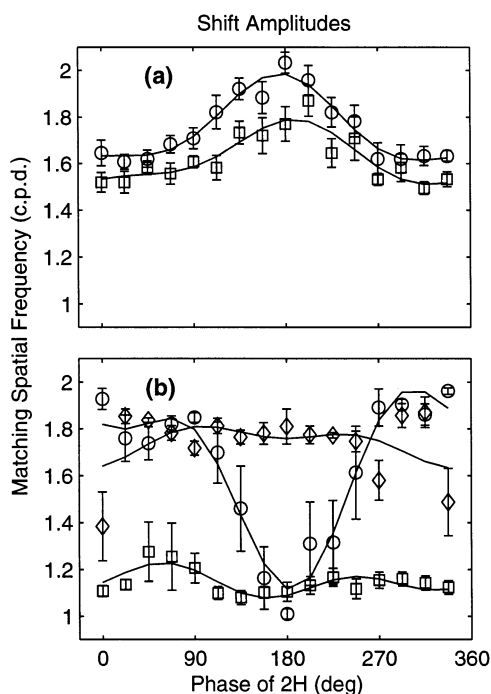


Fig. 5. Amplitude of mean and $2H$ phase dependent apparent fineness. Subjects matched the apparent fineness of $F + 2H$ gratings to spatial frequency scalable reference gratings. (a) Two matching functions for (TM) where the initial spatial frequency of the reference gratings was set at random (uniform distribution) to one of 128 spatial frequencies in the adjustment range 0.67–3.0 c/deg (circles), or to 1.5 c/deg (squares). (b) Matching functions for three naïve subjects where the initial reference grating frequency was 1.5 c/deg. All solid curves are the best fitting (least-squares) regression models comprising a mean fineness shift component and apparent fineness modulations at one and two cycles per 360° of $2H$ phase ($M + P + 2P$). Error bars are S.E. for $n \geq 6$ trials.

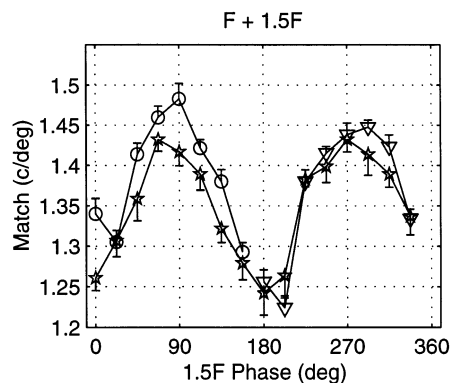


Fig. 6. Data from three experiments on TM where the summed components had spatial frequencies 1 and 1.5 c/deg ($F + 1.5F$). In the three experiments either the full range of phases (stars, $n = 6$), or half the range (circles and triangles, $n = 12$) were conducted. Error bars are S.E. and only the upper or lower bars are presented to reduce clutter.

We also examined the magnitude of the apparent fineness changes with the same spatial frequency matching paradigm but for spatial sums of $F + 1.5F$, where F was 1 c/deg. Results from three experiments on TM showed similar modulation of apparent fineness for this case (Fig. 6). The full $M + P + 2P$ model was required: mean magnitude being 1.36 c/deg and the amplitudes of P and $2P$ being 0.029 and 0.088 c/deg, respectively (mean $F = 111.4$, $df_{2,139}$)

The possibility of apparent fineness components modulated at one and two cycles per 360° (P and $2P$) found for the data of Figs. 5 and 6 made us re-examine the data from the nine subjects of Fig. 2 obtained with the 2AFC procedure. Fitting the raw 2AFC data for each subject or the mean subject response functions produced the same outcomes. We report statistics for the fits to the raw 2AFC data here. Overall, the simpler regression model $M + P$, produced slightly better fits on average (a mean F of 26.4 on average df of 2 and 112), than did fits to $M + 2P$ (a mean F of 19.2 on the same df). The full $M + P + 2P$ model was significantly better than the $M + P$ for one subject ($P = 0.03$, $F = 3.54$ $df_{2,139}$), and marginally better for two others ($P = 0.09$ and 0.11).

We also fit the data of Figs. 3 and 4 with the same models. For Fig. 3 $M + P + 2P$ was better or marginally better in 4 of the data sets ($0.005 < P < 0.082$), otherwise $M + P$ was on average a better fit than $M + 2P$ (mean F s of 25.8 and 22.7, both on df of 2 and 115, mean $P < 0.0000$). For the data set of Fig. 4 the data of JK for contrast 0.4 was best fit by the full model, $M + P + 2P$ ($P = 0.04$), while for contrasts 0.1 and 0.2 the full model was only marginally better than the simpler $M + 2P$ model ($P = 0.09$ and 0.19, respectively). The data of TM were all decidedly better fit by $M + 2P$.

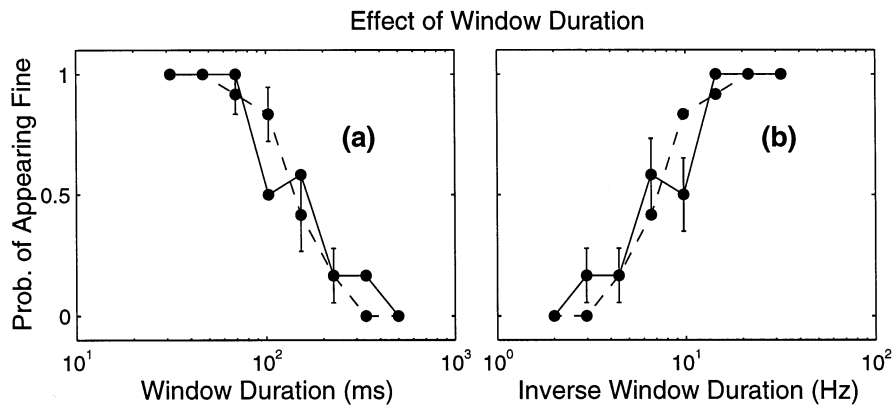


Fig. 7. $F +$ illusory $2H$. Effect of reducing presentation time. (a) As presentation time (Blackman window τ , Section 2) is reduced the apparent fineness is biased toward $2H$ (TM, solid; JK dashed). (b) Shows the data set of (a) presented on an inverse time (frequency) axis. The S.E. ($n = 12$) are shown for TM in (a) and JK in (b).

3.2. Illusory $2H$

In the study of Kulikowski (1975) an illusory $2H$ component was induced by brief presentations of low spatial frequency sinusoidal grating patterns. The situation is related to our experiments above because it is well known that the input spatial F component is also present, even when the illusory $2H$ is very vivid. Kelly (1981) and Kulikowski (1975) both showed that the illusory $2H$ component could be substantially nulled with a static phase reversed $2H$ grating, leaving a strong F component visible. We wished to examine this case of compound gratings consisting of F added to an illusory $2H$. Fig. 7 shows that as stimulus duration for a 0.5 c/deg grating ($= F$, no real $2H$ was presented) dropped below 200 ms the apparent fineness moved from being intermediate to that of the illusory $2H$ grating. The appearance of the central grating for the intermediate presentation times was sometimes similar to that of the central grating in Fig. 1 and at other times like $F + 2H$ sums with other phase relations such as those shown at the top of Fig. 2, some of which look quite like a single grating. We also examined the effect of lowering the F grating contrast for the presentation duration 0.125 s (Fig. 8). Again only a single frequency 0.5 c/deg sinusoidal test grating was presented. As contrast was reduced below 0.2 the probability of seeing the flashed grating as the illusory $2H$ pattern increased to 1.

4. Discussion

All subjects reported that the $F + 2H$ gratings had an apparent fineness between that of its component parts (Fig. 1). Similar apparent fineness shifts are observed for F frequencies between 0.25 and 4.0 c/deg and contrasts from 0.05 to 0.4 (Figs. 3 and 4). The reader can check that the effect is not due to the possible

inference of a vertical texture gradient in the test patterns, or the relative placement of the F and $2H$ comparison gratings, by covering one of the comparison gratings of Fig. 1 and/or inverting the page. An interesting feature of the 2AFC data was the variability across and within subjects in the phase dependence of the effect (Figs. 2a, 3).

We also examined the magnitudes of apparent fineness shifts using a MOA spatial frequency matching paradigm. These experiments showed a mean apparent fineness shift of 1.58 ± 0.11 S.E. c/deg when the F grating was 1 c/deg. For all five cases examined significant additional modulation of apparent fineness was found at both one and two cycles per 360° of $2H$ grating phase (i.e. the P and $2P$ components). Similar modulations were also observed for $F + 1.5F$ compound gratings (Fig. 6). Re-examination of the 23 response functions of 2a, 3 and 4 indicated that for three cases the full model, $M + P + 2P$, was justified, and was only marginally worse than simpler $M + P$ or $M + 2P$ models in seven cases.

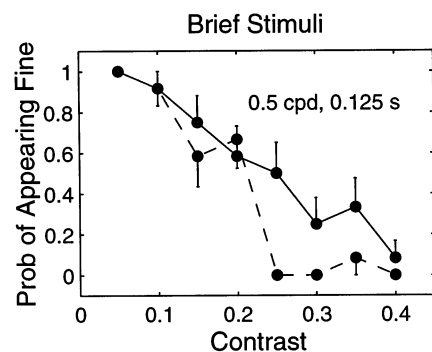


Fig. 8. For 125 ms stimuli (τ , Section 2) the percept becomes completely biased toward $2H$ as the contrast of F falls below 0.1. Only the upper or lower S.E. ($n = 12$) are shown for each subject (TM, solid; JK dashed).

When the data of 2a, 3 and 4 were fit with the full model the amplitudes of the P and $2P$ components were, respectively: Fig. 2a, 0.63 ± 0.17 and 0.78 ± 0.12 S.E.; Fig. 3, 0.76 ± 0.32 and 0.30 ± 0.09 S.E.; Fig. 4, 0.09 ± 0.02 and 0.42 ± 0.05 S.E. The range of the 2AFC data was 0–1 so these can be compared directly with the amplitudes obtained for the matching procedure of Fig. 5: 0.15 ± 0.06 and 0.076 ± 0.03 S.E. c/deg. Overall, evidence for modulation of apparent fineness by the relative phase of the $2H$ grating is excellent, the full $M + P + 2P$ model being required for the nine MOA data sets (Figs. 5 and 6), and either required (seven of 23 cases) or not inconsistent the 2AFC data.

Following the test of Fig. 5a, TM repeated the experiment of Fig. 4 three times and again obtained results like those of Fig. 4 (not shown). The experiment of Fig. 5a was repeated a third time after the data of Fig. 6 were obtained, again with the original result (i.e. like Fig. 5a) being reproduced. Thus, while one might expect the response functions of 4 and 5a to have more similar shapes, it would appear that something increased TM's the probability of seeing a modulation of fineness at one cycle per 360° of $2H$ phase. Fig. 7 shows that the stimulus duration used for Fig. 4 (2 s) was far too long for any contribution by an illusory $2H$ component. At the same time afterimage effects in the standing compound grating also seem unlikely to have contributed to the relative salience of either of the components of the compound grating since these effects are largely non-existent at 1 c/deg and above (Burbeck & Kelly, 1984).

Several models have been proposed to explain apparent spatial frequency shifts produced in other experimental paradigms with static patterns (Blakemore et al., 1970; Klein et al., 1974). The present results suggest that perhaps the simplest notion is that a variety of image components, whether they be illusory nonlinear distortion products, or real objects, are submitted for analysis to a set of overlapping, broad band, spatial frequency channels (King-Smith & Kulikowski, 1975a,b). Any such two-component patterns, with frequencies separated by less than a single channel's bandwidth, would thus be perceived as having an intermediate spatial periodicity equal to the peak tuning of the most excited channel. This is in the spirit of the work of Richards and Polit (1974) who showed that convincing matches to low pass filtered random 1D textures can be made by the sum of a small set of spatial frequencies, so called textural "pseudometamers". A similar argument has been made to account for temporal frequency discrimination (Mandler & Makous, 1984). It is interesting that for the spatial case when subjects are forced to make long range estimates of the distance between the stripes of such gratings they correctly estimate the distance (Nyman & Rovamo, 1980). The present results indicate

that the model proposed here extends to the case where one textural component is the illusory FD pattern (Figs. 5 and 6). This case of illusory stimulus components will be discussed further below.

The case of simultaneously induced shifts of apparent fineness for spatially separated inducers and test patterns (both static) (MacKay, 1973; Klein et al., 1974) could be similarly explained as long as the receptive fields of the channel units were a few wavelengths across and the perceived spatial frequency of the adjacent regions was determined by the frequencies present at the boundaries, that is by a textural density version of the Craik–O'Brien-cornsweet effect, as reported by MacKay (1973). As predicted from this argument the simultaneous spatial frequency shift for centre-surround stimuli is found to be greatly reduced if the border region is interfered with (Klein et al., 1974). Opponency between channels more than one octave apart is required to explain apparent texture density effects where the major components are more widely separated in spatial frequency (MacKay, 1973; Klein et al., 1974), such opponent interactions being well known, e.g. Tolhurst (1972a,b).

Many studies of opponent interaction have employed interactions between gratings and their third harmonic ($3H$). For this reason we did some experiments including a $3H$ component. In these experiments either the $2H$ component was fixed and the $3H$ phase was varied or the reverse. In either case the $3H$ component seemed to have little effect on the perceived textural fineness of the compound grating pattern. It would be interesting to repeat these experiments with moving gratings, where a special role for $3H$ phases has been demonstrated for the perception of moving edges (Anderson, 1993; Bex & Edgar, 1995).

The use of factor analysis to look for inherent structure in the variation of psychometric functions has proved to be very effective (Peterzell & Teller, 1996). It is interesting that the analysis presented here indicates functions with well-behaved shapes, given that functions of any shape constructable from eight points were possible. The three putative phase tuning functions also account for 92.5% of the variance in the nine subject's data. The structure suggests four broad equi-spaced phase channels spanning $0-360^\circ$. This is in agreement with Field and Nachmias (1984) who employed a completely different method. The results also reinforce the idea of bar and edge detecting mechanisms (Kulikowski & King-Smith, 1973; Shapley & Tolhurst, 1973), see also Kulikowski (1991).

On the other hand the covariance which underlies the putative phase channels could be produced by competing effects that happened to modulate the apparent fineness at one and two cycles per 360° of $2F$ or $1.5F$ phase, particularly if different subjects interpreted these competing effects somewhat differently. The data sum-

marised in Figs. 5 and 6 suggest that the *mean* apparent fineness (M) may correspond to the carrier frequency $[F + H]/2$ present in our compound gratings (Burton, 1972; Badcock & Derrington, 1985). These possibilities assume the textural fineness of the patterns is extracted by a nonlinear mechanism leading to a product between the input F and $2H$ components. There is abundant evidence that texture discrimination and recognition are mediated by nonlinear processing (Beck, Sutter & Ivry, 1987; Chubb & Sperling, 1991; Landy & Bergen, 1991; Victor & Conte, 1991; Graham & Sutter, 1996).

One possibility then is that the additional modulation of the apparent fineness could then be explained by terms arising from the retinal contrasts of the F and $2H$ gratings not being equal. The idea can be summarised as follows. If the contrasts, A and B , of the two components are not equal then the compound waveform can be described by two equivalent expressions. Both expressions have a term that is the product of the carrier and envelope frequencies but they differ in having an additive phase dependent term in one of the input frequencies having contrasts $A - B$ or $B - A$ (Eqs. (4) and (6)). Since it has not appeared in the literature we give the details of this process in the Appendix A. Since both expressions are equally valid subjects' percepts might flip spontaneously between the two states as in the bistable percepts of a Necker cube. This process might lead to a phase dependence and correlation between subjects' responses to similar phases. In our experiments, however, the contrasts of the summed gratings were always equal (except for Fig. 3) and so any difference in the contrasts would have to be due to demodulation by the optics. Given that the spatial frequencies of our patterns were so low there is unlikely to be a large differential demodulation of the summed components, and therefore the contrasts $A - B$ and $B - A$ would be very small. Moreover, in the case of the experiments of Fig. 3, when the $2H$ contrast was half that for F , there appeared to be little difference between these data and any other collected in the equi-contrast condition.

Human discrimination of small relative phase changes within compound gratings has been shown to be due to relative brightness discriminations (Badcock, 1984a,b). That work does not eliminate the prospect of phase channels for rather gross discriminations of relative phase (Burr, 1980; Caelli & Bevan, 1982). The strong implication of local brightness changes in fine phase discriminations, however, indicates that we should consider the possibility of our observed modulation of apparent contrast being due to a similar mechanism.

We investigated this possibility in two ways. These methods were motivated by the observation by several subjects that they were using the width of bright stripes or the slope of the brightness change in the region of

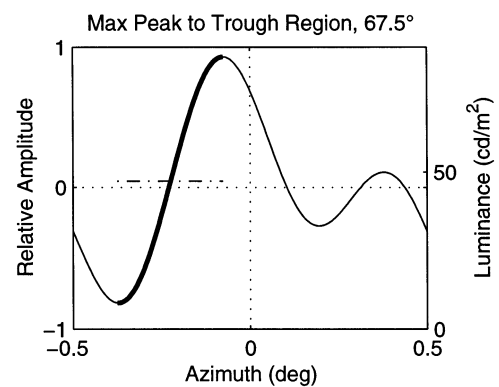


Fig. 9. A unit cycle, i.e. the repeated unit, of the brightness profile of a $F + 2H$ grating. Each component has contrast 0.5 and the $2H$ phase is 67.5° (as in the middle figures of Fig. 2 top). The thicker line segment indicates the region of greatest peak to trough brightness change. The short horizontal dash-dot line segment indicates the mean luminance of the selected grating sub-region which differs from the grand mean.

the biggest peak to trough change in brightness as the cue to the apparent fineness. For example, examination of the two leftmost unit cycle patterns shown at the top of Fig. 2 indicates that the bright stripe of the 67.5° pattern is narrower than that of the 0° pattern. This agrees with the whole 67.5° grating pattern being often reported to have a high apparent fineness. We therefore extracted the biggest trough to peak change within one cycle of the brightness profiles of compound gratings (Fig. 9) and either did a linear regression on the carrier frequency f_c (and its phase) or an iterative nonlinear regression where the frequency was allowed to change. The results for the $F + 2H$ ($= F + 2F$) and $F + 1.5F$ compound gratings are shown in Fig. 10a, b. In the case of regression on f_c the fitted amplitude varies with phase (circles) and so, as with our psychometric functions, we fitted the waveforms of Fig. 10a, b with models containing M , P and $2P$ components. In both cases the full $M + P + 2P$ model was required to fit the data (solid lines). Thus, if subjects attended to these small grating regions and confounded f_c amplitude with apparent fineness we would get the required sort of modulation of apparent fineness. This process would however require the brain to identify f_c , possibly by a nonlinear mechanism, and then stick doggedly to trying to fit the amplitude of that frequency, which seems unlikely.

Perhaps a more physiologically realistic outcome was obtained from the nonlinear fitting process. Here we see that the fitted frequency, while being close to f_c , varies (solid lines, Fig. 10c, d) as in the observed psychometric functions. Again, the $M + P + 2P$ model was required to fit the data (not shown). This model corresponds roughly to a winner take all response by a set of local linear channels having differing spatial frequency tunings. Notice that no nonlinear distortion product is

required as the very local peak to trough region actually has a spatial frequency near f_c . The finding that there is no need to consider nonlinear distortion products is in accord with the literature on relative phase detection within compound gratings (Badcock & Derrington, 1985, 1989). In fact it would be a two-stage process where only the channels examining the most contrasting sections of the grating compete to decide on the spatial frequency. Another pleasing result was that the amplitude of the best fitting frequency (circles, Fig. 10c, d) had a reversed form to that of the frequencies. This could lead to cases where the most active channels lead to response functions like those of Fig. 5a, or psychometric curves which look like they are produced by some kind of competition between the effects of the best frequency and amplitude (Fig. 5b). Also, these relationships would impart the sort of correlations between frequencies which lead the factor analysis to generate something that looks like phase channels in strict quadrature relationships. Thus, the most physiological model explains much of the range of our observed behaviour while at the same time precluding the need for phase channels, in agreement with the work on relative phase discrimination in compound gratings (Burr, 1980; Badcock, 1984a,b; Badcock & Derrington, 1985, 1989; Derrington & Badcock, 1986).

The dynamic production of a $2H$ pattern in the form of the FD illusion is now of strong clinical relevance given its very successful application to the diagnosis of glaucoma (Maddess, 1991; Maddess & Henry, 1992; Johnson & Samuels, 1997) and the consequent introduction of the frequency doubling technology (FDT) perimeter being marketed jointly by Humphrey Instruments Ltd. and Welch Allyn Ltd. Some earlier studies of transient presentation of low spatial frequency gratings examined the issue of the perceptual fineness of these patterns by having subjects match the transiently presented pattern to a single spatial frequency (Tynan & Sekuler, 1974; Virsu, Nyman & Lehtio, 1974; Kulikowski, 1975; Thompson & Murphy, 1978; Nyman & Rovamo, 1980; Parker, 1981; Georgeson, 1985). As spatial and temporal frequency (or flash presentation time) are varied subjects match the resultant pattern to a range of spatial frequencies between F and $2H$.

There are two possible interpretations of these results. The first is that the observed pattern is always a single sinusoidal grating having a particular intermediate spatial frequency. The second interpretation is that some form of compound pattern is seen ($F + 2H$) and that pattern has a particular apparent fineness. It is well known that linear response components are present even when the FD illusion is vivid. For example Kelly

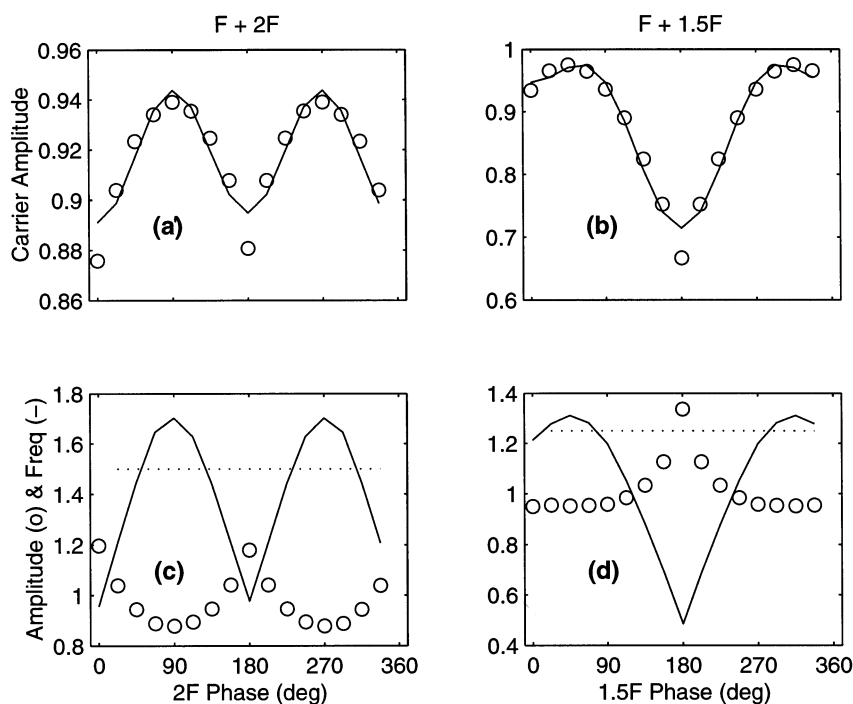


Fig. 10. Summary of fits to the maximum peak to trough regions (Fig. 9) of $F + 2F$ (a, c) and $F + 1.5F$ (b, d). (a, b) Amplitudes obtained from linear regression on the carrier frequency f_c (circles) and fitted $M + P + 2P$ (solid curves) models (Section 2). (c, d) Best fitting spatial frequencies (solid lines) and their amplitudes (circles) obtained from a nonlinear iterative fit to the maximum peak to trough region for (c) $F + 2F$ ($2H$) gratings and (d) $F + 1.5F$ gratings. The dotted horizontal lines in (c) and (d) represent f_c . As in Fig. 9 the component sinusoidal gratings each had contrast 0.5.

(1981) and Kulikowski (1975) both showed that the $2H$ component could be substantially nulled with a static counterphase pattern leaving a strong F component visible. The presence of other harmonic components during transient presentation is precisely why Kulikowski (1975) coined the term *apparent fineness* because the pattern seen during transient presentation is at times not clearly a single sinusoid. Thus, for a range of stimulus conditions one would expect both F and $2H$ components to be present, in various admixtures, leading to a range of percepts having various grades of intermediate apparent fineness. That both F and $2H$ are present in different add mixtures is most easily seen by approaching a monitor from a distance where a low spatial frequency is shown modulated at 20–30 Hz. As one approaches the monitor stripes contributed by the FD effect emerge from between the strips of the stimulus grating, producing a range of $F + 2H$ percepts.

That F and $2H$ components might be present in various admixtures for the case of transiently presented coarse gratings is in agreement with retinal ganglion cell physiology. The basic hypothesis behind the use FD stimuli for glaucoma diagnosis (Maddess, 1991; Maddess & Henry, 1992) is that the illusion is largely produced by the effects of retinal gain control (Shapley & Victor, 1978, 1981) upon cells of the magnocellular visual pathway. The hypothesis is that Y-like magnocellular cells (M_y -cells) are particularly involved (Maddess, Hemmi & James, 1998). The existence of these Y-like cells in primates (Blakemore & Vital-Duran, 1981; Kaplan & Shapley, 1982; Marrocco, McClurkin & Young, 1982; Derrington & Lennie, 1984) and their analogous physiology to that of cat Y-cells (Derrington & Lennie, 1984; Bernardete, Kaplan & Knight, 1992) is well established, as are possible cortical correlates (Kulikowski & Vidyasagar, 1986). The combined effects of high temporal and low spatial frequency stimuli upon Y-cells produces very strong quadratic nonlinear responses (Victor & Shapley, 1979b; Shapley & Victor, 1980; Victor, 1988), where the nonlinear component can have ten times the amplitude of the linear response component (Victor & Shapley, 1979a). At the same time primate P-cells do not experience such gain control (Bernardete et al., 1992) and have very low contrast gain (Kaplan & Shapley, 1986). Thus the expectation from the physiology is that as spatiotemporal conditions are biased toward those for optimal enhancement of nonlinear responses from M_y -cells, the visual percept would become increasingly dominated by a $2H$ component: the temporal frequency doubling leading to a spatial frequency doubling (Tyler, 1974; Kelly, 1981). It is not surprising that the quadratic response persists to low contrasts (Kulikowski, 1975) given that the underlying nonlinearity is rectification which is hard down to zero stimulus input (Victor & Shapley, 1979a; Victor, 1988). Indeed, the measured shape of the rectifying response is

essentially the same for both Y-cell physiology (Victor & Shapley, 1979a,b; Victor, 1988) and the FD illusion (Kelly, 1981) being proportional to $|\text{Contrast}|^z$ (where $z \approx 0.7$ and negative contrasts are defined as those darker than average). Kulikowski (1975) also stressed that this effect appears at spatial frequencies associated with the mechanism generating apparent motion, a mechanism that in turn is highly nonlinear (Kulikowski & Tolhurst, 1973; King-Smith & Kulikowski, 1975b). Perceptual observation also backs up the idea of gain being increased under these conditions because as contrast is lowered the $2H$ component can appear to be more vivid than the fundamental which produced it, the so called *over-contrast* effect (Kulikowski, 1972; Georgeson, 1985).

Several lines of evidence suggest that the second harmonic distortion responsible for the FD illusion is retinal in origin. Studies of spatial aliasing with FD gratings indicate that the units responsible for the production of the illusion have a spatial sampling density equal to that expected for M_y -cells from 0 to 40° retinal eccentricity (Maddess et al., 1998). Also, novel PERG studies indicate that the ERG signal becomes dominated by responses having the characteristics of Y-cell activity being modified by contrast gain control (James et al., 1995; Bedford, Maddess, Rose & James, 1997; Maddess et al., 1997). Finally the large size of M_y -cells and their sparse distribution of the retina (for discussion see Maddess et al., 1998) mean that they should be both easily damaged by glaucoma (Quigley, Sanchez, Dunkelburger, L'Hernault & Baginski, 1987; Quigley, Dunkelburger & Green, 1988, 1989; Glovinsky, Quigley & Dunkelburger, 1991; Glovinsky, Quigley & Pease, 1993; Smith, Chino, Harwerth, Ridder, Crawford & DeSantis, 1993) and such damage should be easy to detect as appears to be the case (Maddess & Henry, 1992; Johnson & Samuels, 1997).

In conclusion the effect shown in Fig. 1 suggests that a variety of visual inputs including linear and nonlinear retinal streams, are all valid inputs to a system of linear spatial frequency tuned channels, at least as far as the estimation of periodicity is concerned. The resulting competition between linear broadband channels leads to a perception of $F + 2H$ compound gratings having intermediate apparent fineness. Modulation of that apparent fineness with component grating phase seems likely to be a natural consequence of the local nature of the analysis. This appears to hold for both static stimuli and stimuli where an illusory $2H$ component is generated by transient or high temporal frequency modulation of contrast.

Acknowledgements

We are grateful for the reviewers' comments that made us focus on the causes of the phase dependent modulation of the apparent fineness.

Appendix A

Consider a compound grating with spatial frequencies in c/deg of f_1 and f_2 and differing contrasts A and B . To aid the readability of the equations, we express space, x , as $\omega = 2\pi x$. Since our F gratings had cosine phase with respect to the centre of the monitor we use the cosine versions.

$$L(\omega) = L_m(1 + A \cos(f_1\omega + \phi_1) + B \cos(f_2\omega + \phi_2)) \quad (1)$$

When $A = B = C$, then the commonly quoted result is obtained

$$L(\omega) = L_m(1 + 2C[\cos([f_1 - f_2]/2 \omega + [\phi_1 - \phi_2]/2) \times \cos([f_1 + f_2]/2 \omega + [\phi_1 + \phi_2]/2)]) \quad (2)$$

If $B < A$, then one way to treat the problem is to imagine the f_1 component is the sum of two parts having the same frequency and phase but with amplitudes $A - B$ and B .

$$L(\omega) = L_m(1 + (A - B)\cos([f_1\omega + \phi_1]) + B[\cos([f_1\omega + \phi_1]) + \cos([f_2\omega + \phi_2])]) \quad (3)$$

This permits us to do the same manipulation as in Eq. (2) for the two components having amplitude B , thus describing the compound grating as the sum of the modulated components and a scaled version of the f_1 grating. To make Eq. (3) more readable we made the substitutions: $[f_1 - f_2]/2 = f_e$, $[\phi_1 - \phi_2]/2 = \phi_e$, $[f_1 + f_2]/2 = f_c$, $[\phi_1 + \phi_2]/2 = \phi_c$ where the subscripts e and c denote the envelope and carrier components, then we can rewrite Eq. (1) as

$$L(\omega) = L_m(1 + (A - B)\cos([f_1\omega + \phi_1]) + 2B[\cos(f_e\omega + \phi_e) \times \cos(f_c\omega + \phi_c)]) \quad (4)$$

Of course f_e and f_c do not appear in the Fourier spectrum of the compound grating. Notice also, that we can equally well express f_2 as the sum of two components with amplitudes A and $B - A$.

$$L(\omega) = L_m(1 + A[\cos([f_1\omega + \phi_1]) + \cos([f_2\omega + \phi_2])] + (B - A)\cos([f_2\omega + \phi_2])) \quad (5)$$

Leading to the compound wave being interpreted as some amount of f_2 plus a larger ($2A > 2B$) modulated component.

$$L(\omega) = L_m(1 + (B - A)\cos([f_2\omega + \phi_2]) + 2A[\cos(f_e\omega + \phi_e) \times \cos(f_c\omega + \phi_c)]) \quad (6)$$

Since both Eq. (4) and Eq. (6) are valid descriptions of the compound wave it is perhaps reasonable to suggest

the brain might flip between states where it adopts Eq. (4) or Eq. (6) as being the valid percept, much as one interprets a Necker cube. If the process of extracting the apparent fineness was affected by a particular brightness cue one would then expect modulation of the fineness at one and two cycles per 360° of $2H$ grating phase (given that the cue would be repeated in each cycle of the compound grating). These two modulations would in turn induce correlations within our subject data that would appear as four phase channels per cycles per 360° of $2H$ grating phase.

References

- Anderson, S. J. (1993). Visual processing delays alter the perceived spatial form of moving gratings. *Vision Research*, 33, 2733–2746.
- Badcock, D. R. (1984a). How do we discriminate relative spatial phase? *Vision Research*, 24, 1847–1857.
- Badcock, D. R. (1984b). Spatial phase or luminance profile discrimination? *Vision Research*, 24, 613–623.
- Badcock, D. R., & Derrington, A. M. (1985). Detecting the displacement of periodic patterns. *Vision Research*, 25, 1253–1258.
- Badcock, D. R., & Derrington, A. M. (1989). Detecting the displacements of spatial beats: no role for distortion products. *Vision Research*, 29, 731–739.
- Beck, J., Sutter, A., & Ivry, R. (1987). Spatial frequency channels and perceptual grouping in texture segregation. *Computer Vision Graphics and Image Processing*, 37, 299–325.
- Bedford, S., Maddess, T., Rose, K. A., & James, A. C. (1997). Correlations between observability of the spatial frequency doubled illusion and a multi-region PERG. *Australia and New Zealand Journal of Ophthalmology*, 25, 91–93.
- Bernardete, E. A., Kaplan, E., & Knight, B. W. (1992). Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Visual Neuroscience*, 8, 483–486.
- Bex, P. J., & Edgar, G. K. (1995). Shifts in the perceived location of a blurred edge increase with contrast. *Perception and Psychophysics*, 57, 1187–1189.
- 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.
- Blakemore, C., & Vital-Duran, F. (1981). Distribution of X- and Y-cells in the monkey's lateral geniculate nucleus. *Journal of Physiology*, 320, 17P.
- Burbeck, C. A., & Kelly, D. H. (1984). Role of local adaptation in the fading of stabilized images. *Journal of the Optical Society of America A*, 1, 216–220.
- Burr, D. C. (1980). Sensitivity to spatial phase. *Vision Research*, 20, 391–396.
- Burton, G. J. (1972). Evidence for non-linear response processes in the human visual system from measurements on the thresholds of spatial beat frequencies. *Vision Research*, 13, 1211–1225.
- Caelli, T., & Bevan, P. (1982). Visual sensitivity to two-dimensional spatial phase. *Journal of the Optical Society of America*, 72, 1375–1381.
- Chubb, C., & Sperling, G. (1991). Texture quilts: basic tools for studying motion-from-texture. *Journal of Mathematical Psychology*, 35, 411–442.
- Derrington, A. M., & Badcock, D. R. (1986). Detection of spatial beats: non-linearity or contrast increment detection? *Vision Research*, 26, 343–348.

- Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 219–240.
- Field, D. J., & Nachmias, J. (1984). Phase reversal discrimination. *Vision Research*, *24*, 333–340.
- Georgeson, M. A. (1985). Apparent spatial frequency and contrast of gratings: separate effects of contrast and duration. *Vision Research*, *25*, 1721–1727.
- Glovinsky, Y., Quigley, H. A., & Dunkelburger, G. R. (1991). Retinal ganglion cell loss is size dependent in experimental glaucoma. *Investigative Ophthalmology and Visual Science*, *32*, 484–491.
- Glovinsky, Y., Quigley, H. A., & Pease, M. E. (1993). Foveal ganglion cell loss is size dependent in experimental glaucoma. *Investigative Ophthalmology and Visual Science*, *34*, 395–400.
- Graham, N., & Sutter, A. (1996). Effect of spatial scale and background luminance on the intensive and spatial nonlinearities in texture segregation. *Vision Research*, *36*, 1371–1390.
- Heeley, D. W. (1979). A perceived spatial frequency shift at orientations orthogonal to adapting gratings. *Vision Research*, *19*, 1229–1236.
- James, A. C., Maddess, T., Rouhan, K., Bedford, S., & Snowball, M. (1995). Evidence for M_y-cell involvement in the spatial frequency doubled illusion as revealed by a multiple region PERG for Glaucoma. *Journal of the Optical Society of America and VSIA Technical Digest*, *1*, 314–317.
- Johnson, C. A., & Samuels, S. (1997). Screening for glaucomatous visual field loss with frequency doubling perimetry. *Investigative Ophthalmology and Visual Science*, *38*, 413–425.
- Johnson, R. A., & Wichern, D. W. (1992). *Applied multivariate statistical analysis*. Englewood Cliffs, NJ: Prentice Hall.
- Kaplan, E., & Shapley, R. M. (1982). X and Y cells in the lateral geniculate nucleus of macaque monkeys. *Journal of Physiology*, *330*, 125–143.
- Kaplan, E., & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Science USA*, *83*, 2557–2755.
- 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., & Kulikowski, J. J. (1975a). The detection of gratings by independent activation of line detectors. *Journal of Physiology*, *247*, 237–271.
- King-Smith, P. E., & Kulikowski, J. J. (1975b). Pattern and flicker detection analysed by subthreshold summation. *Journal of Physiology*, *249*, 519–548.
- Klein, S., Stromeyer III, C. F., & Ganz, L. (1974). The simultaneous spatial frequency shift: a dissociation between the detection and perception of gratings. *Vision Research*, *14*, 1421–1432.
- Kulikowski, J. J. (1972). Relation of psychophysics to electrophysiology. *Trace (Paris)*, *6*, 64–69.
- Kulikowski, J. J. (1975). Apparent fineness of briefly presented gratings: balance between movement and pattern channels. *Vision Research*, *15*, 673–680.
- Kulikowski, J. J. (1991). What really limits vision? Assessment of visual function and the role of interacting channels. In J. J. Kulikowski, V. Walsh, & I. J. Murray, *Limits of vision* (pp. 286–329). London: Macmillan.
- Kulikowski, J. J., & King-Smith, P. E. (1973). Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. *Vision Research*, *13*, 1455–1478.
- Kulikowski, J. J., & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. *Journal of Physiology*, *232*, 149–162.
- Kulikowski, J. J., & Vidyasagar, T. R. (1986). Space and spatial frequency: analysis and representation in macaque striate cortex. *Experimental Brain Research*, *65*, 5–18.
- Landy, M. S., & Bergen, J. R. (1991). Texture segregation and orientation gradient. *Vision Research*, *31*, 679–691.
- MacKay, D. M. (1973). Lateral interactions between neural channels sensitive to texture density. *Nature*, *245*, 159–161.
- Maddess, T. (1991). Method and apparatus for use in diagnosis of glaucoma. *USA Patent No. 5*, 295, 495.
- Maddess, T., Bedford, S., James, A. C., & Rose, K. A. (1997). A multiple frequency, multiple region pattern electroretinogram investigation of nonlinear retinal signals. *Australian and New Zealand Journal of Ophthalmology*, *25*, 94–97.
- Maddess, T., Hemmi, J., & James, A. C. (1998). Evidence for spatial aliasing effects in the Y-like cells of the magnocellular visual pathway. *Vision Research*, *38*, 1843–1859.
- Maddess, T., & Henry, G. H. (1992). Nonlinear visual responses and visual deficits in ocular hypertensive and glaucoma subjects. *Clinical Vision Science*, *7*, 371–383.
- Mandler, M. B., & Makous, W. (1984). A three channel model of temporal frequency perception. *Vision Research*, *24*, 1881–1887.
- Marrocco, R. T., McClurkin, J. W., & Young, R. A. (1982). Spatial summation and conduction latency classification of cells of the lateral geniculate nucleus of macaques. *Journal of Neuroscience*, *2*, 1275–1291.
- Nyman, G., & Rovamo, J. (1980). Perceived spatial frequency of flickering gratings: a local spatial distortion. *Perception*, *9*, 403–409.
- 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.
- Peterzell, D. H., & Teller, D. Y. (1996). Individual differences in contrast sensitivity functions: the lowest spatial frequency channels. *Vision Research*, *36*, 3077–3085.
- Quigley, H. A., Dunkelburger, G. R., & Green, W. R. (1989). Studies of retinal ganglion cell atrophy correlated with automated perimetry in human eyes with glaucoma. *American Journal of Ophthalmology*, *107*, 453–464.
- Quigley, H. A., Dunkelburger, G. R., & Green, W. R. (1988). Chronic human glaucoma causing selectively greater loss of large optic nerve fibres. *Ophthalmology*, *95*, 357–363.
- Quigley, H. A., Sanchez, R. M., Dunkelburger, G. R., L'Hernault, N. L., & Baginski, T. A. (1987). Chronic glaucoma selectively damages large optic nerve fibres. *Investigative Ophthalmology and Visual Science*, *28*, 913–920.
- Richards, W., & Polit, A. (1974). Texture matching. *Kybernetik*, *16*, 155–162.
- Shapley, R., & Tolhurst, D. J. (1973). Edge detectors in human vision. *Journal of Physiology*, *229*, 165–183.
- Shapley, R. M., & Victor, J. D. (1978). The effect of contrast on the transfer properties of cat retinal ganglion cells. *Journal of Physiology*, *285*, 275–298.
- Shapley, R. M., & Victor, J. D. (1980). The effect of contrast on the non-linear response of the Y-cell. *Journal of Physiology*, *302*, 535–547.
- Shapley, R. M., & Victor, J. D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *Journal of Physiology*, *318*, 161–179.
- Smith III, E. L., Chino, Y. M., Harwerth, R. S., Ridder III, W. H., Crawford, M. L. J., & DeSantis, L. (1993). Retinal inputs to the monkey's lateral geniculate nucleus in experimental glaucoma. *Clinical Vision Science*, *8*, 113–139.
- Tabachnick, B. G., & Fidell, L. S. (1996). *Using multivariate statistics*. New York: HarperCollins.
- Thompson, P., & Murphy, B. J. (1978). Adaptation to a spatial frequency doubled stimulus. *Perception*, *9*, 523–528.
- Tolhurst, D. J. (1972a). Adaptation to square-wave gratings: inhibition between spatial frequency channels in the human visual system. *Journal of Physiology*, *226*, 231–248.

- Tolhurst, D. J. (1972b). On the possible existence of edge detector neurones in the human visual system. *Vision Research*, 12, 797–804.
- Tolstov, G. P. (1962). *Fourier series*. New York: Dover.
- 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.
- Victor, J. D. (1988). The dynamics of the cat retinal Y cell subunit. *Journal of Physiology*, 405, 289–320.
- Victor, J. D., & Conte, M. M. (1991). Spatial organization of nonlinear interactions in form perception. *Vision Research*, 31, 1457–1488.
- Victor, J. D., & Shapley, R. M. (1979a). The nonlinear pathway of Y ganglion cells in the cat retina. *Journal of General Physiology*, 74, 671–689.
- Victor, J. D., & Shapley, R. M. (1979b). Receptive field mechanisms of cat X and Y retinal ganglion cells. *Journal of General Physiology*, 74, 257–298.
- Virsu, V., Nyman, G., & Lehtio, P. K. (1974). Diphasic and polyphasic temporal modulations multiply apparent spatial frequency. *Perception*, 3, 323–336.