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Low spatial frequency channels and the spatial frequency doubling illusion

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ABSTRACT

Purpose: This study examined the number and nature of spatio-temporal channels in the region where the frequency-doubling (FD) illusion would be expected to occur at 8 locations spanning the central 30° of the visual field.

Methods: The probability of seeing the FD illusion was examined in 17 subjects. Stimuli were presented at 5 octaves of low spatial frequencies, at each of 7 flicker frequencies in the range 5.65 to 27.95 Hz. In a single trial subjects matched the apparent spatial frequency of the flickering test pattern using a 2 Alternative Forced Choice method. Thirteen subjects were examined for stimuli presented at contrast 0.95. Three or 4 subjects were examined at each of the contrasts 0.2, 0.4 and 0.8. A factor analysis was conducted on the psychometric functions, quantifying the number and possible spatio-temporal tuning of neural channels present.

Results: At contrast 0.95 three factors were able to explain 79.3% of the total variance in the psychometric responses to the 35 test conditions. This simple form of three broad spatiotemporal channels was also found at the other contrasts, and for different subjects. The Factor Scores showed differential distribution of the Factors onto the 8 different visual field locations. Thus the expression of the 3 channels differed somewhat across the visual field.

Conclusions: The results support earlier reports, that several low spatial frequency channels exist below 1 cpd in the periphery. The results may have implications for the FDT and Matrix perimeters.

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INTRODUCTION

Spatial frequency doubling (FD) occurs when low spatial frequency sinusoidal gratings have their contrast rapidly modulated. Under those conditions the spatial frequency appears to be approximately twice the original value¹⁻⁷. The FD effect has recently been employed in the diagnosis of glaucoma^{8,9}, with some evidence being presented that the FDT perimeter provides earlier diagnosis^{10,11}. As discussed by Vallam & Metha⁷, there is still a lack of concordance regarding the mechanisms for the generation and the perception of the FD illusion.

The evidence for the numbers of channels subserving low spatial frequencies also remains equivocal. Blakemore and Campbell¹² reported that spatially specific adaptation could not be found below 3 cpd. Other research findings provide evidence for the existence of separately adaptable and maskable mechanisms from 0.2 to 1.0 cpd¹³⁻¹⁷. There is also support for the notion that temporal sensitivity is subserved by only a few mechanisms each having a quite broad bandwidth e.g. ^{18,19}. Hess and Plant²⁰ gave evidence for two broadly tuned and directionally selective temporal mechanisms but Hammett and Smith²¹ claimed that an additional temporal channel at low spatial frequencies is due to an artefact of differences in the rate of perceptual fading as a function of temporal frequency.

Thus far little work has been done to examine under what conditions the FD illusion is seen at different visual field locations^{7,22}, and no examination of how many channels might contribute to perception in that spatio-temporal region has been conducted. Therefore we examine those issues here using factor analysis of psychometric functions from many subjects^{6,23-26}.

METHODS

Subjects

Seventeen normal subjects were included in the study, 10 were women. The subjects' ages ranged from 19 to 47 years. The subjects had corrected visual acuities of 6/9 or better, with no history of clinical visual problems. No visual field defects were detected in any subject using an FDT perimeter (Full Threshold C-20 Program). The study followed the tenets of the Declaration of Helsinki. Written informed consent was obtained from each subject.

[Figure 1 about here please]

Visual Stimuli

Stimuli could be presented at one of eight visual field locations (Fig. 1). The stimulus layout is related to that used in several studies including some of our published multifocal ERG studies using FD stimuli^{27, 28}. The layout also is identical to that of a companion dichoptic mfVEP study²⁹ and a published mfVEP study on Multiple Sclerosis³⁰ using FD stimuli, and is similar to the layout of the FDT perimeter stimulus ensemble. A secondary objective of the present study therefore was to understand the channels possibly contributing to the mfERG and mfVEP signals in the same regions. Subjects viewed the video monitor at a distance of 30 cm as maintained by a chin rest, and a fixation spot was presented at the screen centre. Each of the 8 regions could display an achromatic (color temperature 6500° K) sinusoidal grating. The mean luminance was 45 cd/m². The basal spatial frequencies used were 0.25 cpd (inner regions) and 0.125 cpd (outer regions) and as such were roughly M-scaled, i.e. scaled with respect to cortical magnification³¹. Five different test ensembles were obtained by multiplying these basal frequencies by 0.25, 0.5, 1.0, 2.0 or 4.0. All subjects were tested using their right eye, their left eye being covered by a patch.

The psychophysical tests were conducted using a temporal two alternative forced choice method (2AFC) wherein a single presentation sequence consisted of three grating patterns that were shown consecutively (Fig. 2) at one of the 8 possible locations. Within each of those presentation sequences the contrast of the gratings was increased from 0 to the test contrast and then back down to 0. Each temporal window was based on a Blackman function⁶. The first pattern in the test sequence was a flickering test pattern of duration 2.5 seconds, followed by two non-flickering comparison patterns (Fig. 2, inserts). The flickering test gratings adopted sinusoidal contrast modulation frequencies at one of 5.65, 9.37, 13.08, 16.80, 20.52, 24.23 or 27.95 Hz. The two static comparison gratings were presented at contrasts designed to be subjectively similar to the flickering test patterns.

[Figure 2 about here please]

The two static comparison patterns had either the same spatial frequency as the modulated test pattern (F) or twice of that (2F). Subjects indicated which of the comparison patterns had a spatial frequency which was closest to that of the test pattern. Thus, the resulting psychometric functions (e.g. Figs. 3, 4) indicate the probability that the test pattern displayed a spatial frequency doubled appearance. During the test procedure, the same task could be repeated if the subject is undecided, or missed a stimulus. The presentation order of the F and 2F comparison patterns was randomized on all trials.

The experiments were completed for grating contrasts of 0.2, 0.4, and 0.8 for 3 or 4 experienced subjects. Those psychometric functions were derived from 12 repeats of each of the 35 conditions for each region and subject (N=3360 per subject). For the other experiments on 13 subjects, the flickering stimulus had contrast 0.95. For these 13 subjects the psychometric functions were derived from 5 repeats of each of the 35 conditions per region (N=1400 per subject). For the contrast 0.95 stimuli the comparison contrasts were 0.50, 0.43, 0.37, 0.30, 0.23, 0.17, and 0.10 for test modulations of 5.65 to 27.95 Hz respectively.

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For lower flicker contrast the comparison gratings had their contrasts lowered proportionately. Software for data acquisition, analysis and display was written in Matlab (Matlab; The Mathworks, Natick, MA). Stimulus generation was controlled by a Vista Graphics Board (Truevision, Shadeland Station, IN).

Factor Analysis

In order to estimate how many spatio-temporal channels might contribute to the psychometric functions, and their possible form, we applied factor analysis to our measured psychometric functions. This is now a fairly standard technique used by ourselves^{6, 32} and others²³⁻²⁶. Of particular interest here was the spatio-temporal form and number of channels present in the spatio-temporal domain in which the FD illusion has been reported. Also of interest was the relative influence of any such channels for each part of the visual field. In principle relatively few channels might dominate the spatio-temporal domain, their influences possibly being revealed by the covariance (or cross-correlation) between the responses of different subjects to the relatively large numbers of test conditions involved (35 per stimulus region). Factor analysis attempts to exploit such covariance to provide information about any such channels. Simply stated, factor models can present simplified representations of the many data variables in terms of a small number of unobservable variables: in the present case putative spatio-temporal channels that determine the form of the measured psychometric functions. The basic equation of a Factor analysis is:

$$X = S L' + E \quad (\text{Eq. 1})$$

where X is data matrix, in the present case its rows were observations (psychometric functions) for the 35 spatio-temporal test conditions defining the columns. S is the matrix of factor *scores*, i.e. the estimated responses of the channels to each stimulus³³. L is the matrix of factor *loadings*: the loadings are weights that are used to combine the factor scores into the psychometric variables (X), here representing the putative influences of the channels (factors)

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upon the points of the spatiotemporal domain studied³³. The loadings were computed from R , the correlation matrix of X by singular value decomposition (SVD), such that $R = F \times D \times G$ providing:

$$L = F \times \text{diag}(D)^{0.5} \quad (\text{Eq. 2})$$

and the factor scores were given by,

$$S = XL(L'L)^{-1} \quad (\text{Eq. 3})$$

The columns of F (or G , they are equal in this case) are the eigenvectors of R and the elements of the diagonal matrix D are the eigenvalues. The eigenvalues provide the proportion of the variance in R provided by each eigenvector. Commonly the eigenvalues are sorted and plotted. If some small number of factors determine the observed variables then a sharp step should occur in this *scree* plot (e.g. Figs. 7G,H), the number of eigenvalues before the step providing an indication of the number (k) of factors to consider, the remaining small components being discarded as noise. Note that before Eqs. 2 and 3 are computed k columns of F and D , that provide the k highest eigenvalues, are selected to provide a k -factor model, the selected eigenvectors being the estimated *factors*; these truncated matrices will be called F^* and D^* . We will refer to this SVD based method as a Principle Components (PC) factor analysis.

The adequacy of these models is determined by computing the proportions of variance accounted for and the *communalities*³³. The communalities are akin to r^2 -values and indicate what proportion of each of the original variables is accounted for by the factor model, hence the communalities for each of the points in the spatio-temporal domain examined should be uniformly high if the factor model accounts well for all the input variables (e.g. Fig. 7D,F). Before forming L (Eq. 2) the loadings were rotated according the Varimax method³³. Through the Varimax method each rotated factor is a combination of only the highly

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interdependent input variables. That is the factors tend to be loaded onto (i.e. reflect) the input variables.

Note that in X the 2D psychometric functions were first drawn out into a vector of length 35, hence the analysis had no knowledge of the spatio-temporal relationship of points in the psychometric functions. *Therefore any factors that appear as reasonable looking spatio-temporal channels are due only to correlations in the data, and not the form of the analysis.*

A reconstructed correlation matrix $R^* = F^* \text{diag}(D) F^{*'}$ can be estimated³³. An adjunct to the PC method is a maximum likelihood (ML) method which, via an iterative process, modifies F^* such that the error between R and R^* is minimized³³. The ML method was used here as a confirmatory technique because the ML method provides the possibility of less constrained (non-orthogonal) factors. Major differences in the outcomes for the two methods might call into question the validity of the PC method.

[Figure 3 about here please]

RESULTS

The mean psychometric functions (across 13 subjects) obtained at contrast 0.95 are shown in Figure 3. The presented functions are based on a linear interpolation of the original mean psychometric functions to yield twice the density of points. This was reasonable given that data from 13 subjects was used and so the final number of interpolated points is many fewer than the raw data. The mean psychometric functions (averaged across subjects and stimulus regions) for contrast 0.95 and the three lower contrasts are shown in Figure 4.

[Figure 4 about here please]

A large number of psychometric functions from different subjects (and or stimulus regions) are required for factor analysis. In our initial factor analysis for the contrast 0.95 condition (13 subjects), all the regional psychometric functions were transformed into the rows of the matrix X in Equation 1; thus the resulting factors and factor loadings will contain information about what is happening across stimulus regions, as well as across subjects. We will call this *grand* model Type-G. A step in the scree plot indicated that 6 factors might be the minimum number to consider (Fig. 7G). We found that even when 6 factors were included the factor loadings were complex (Fig. 5A) and the communalities were uniformly low (mean communalities, 0.59; median communalities, 0.61; Fig. 7C,E). The percentages of variance accounted for by the first six factors were 26.7, 9.97, 8.67, 5.77, 4.51 and 3.84 (total, 59.4%). Note that the maximum number of factors to consider is often thought to be those encompassing at least one variable's worth of variance, in this case $1/35 = 2.86\%$, so the 6 factor model was not unreasonable on these grounds. More factors would need to be included to improve the communalities and proportion of variance accounted for. A possible explanation for the need for a relatively complex model of 6 or more factors was that somewhat different mechanisms were operating in different regions; alternatively there could be large individual differences (variability) between subjects.

[Figure 5 about here please]

In order to address these possibilities, we either averaged the data across subjects or across regions, before entering it into the factor analysis. We refer to the models based on subject-wise averages as Type-S models. For these models the factor loadings remained complex (Fig. 5B), the proportion of variance accounted for was low (68%), and the communalities were unevenly distributed (not shown). Averaging across subjects eliminated between subject variance, so that cannot be the major source of the complexity of the Type-G models.

[Figure 6 about here please]

We next averaged the psychometric data across stimulus regions, referred to as Type-R models (Fig. 6). For 6 factors the Type-R models were found to produce uniformly high communalities (mean communalities, 0.92; median communalities 0.94), indicating that all points of the psychometric data were well explained by the factors. Further restricting the model to only three factors still yielded good communalities (mean communalities, 0.79; median communalities 0.83, and Fig. 7D,F). The proportions of variance from the three factor Type-R model were 46.8%, 18.7% and 13.9% (total, 79.3%). The factor loadings for PC and ML factor models were very similar (cf. Figs. 6A,B).

Figures 7C to F examine communalities and variances accounted for by Type-G and Type-R models. The communalities obtained from the PC model (Figs. 7C,D) and ML model (Figs. 7E,F) are presented here for point-wise comparison to the mean psychometric data for region 1 (Fig. 7A) and the same data for subject 1 (Fig. 7B). Note that the each communality indicates the proportion for variance accounted for by the model in each of the 35 data points of the original psychometric data. The communalities were uniformly high for the data that were averaged across regions (Type-R model, Fig. 7D,F), but not for Type-G models (Fig. 7C,E), indicating that all parts of the psychometric functions were equally well accounted for

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by the factor models. Also, both the PC and ML models explain the psychometric the functions very similarly. The scree plots of percent eigenvalues indicated that the proportion of the total variance in the data accounted for by each possible factor in the Type-G and –R PC models.

[Figure 7 about here please]

As alluded to earlier a way to examine what is happening by region is to examine the *factor scores* for the Type-G model (Fig. 8). These indicate in which visual field locations the 6 factor loadings (channel tunings) of Figure 5a have their strongest influence. Results from the first 6 factors are shown from left to right; one plot per factor. Strong negative or positive weights are indicated by either very dark (negative) or very light (positive) tones, while weights close to 0 are grey.

We also constructed three factor Type-R models of the data obtained at lower contrasts. The resulting factor loadings are shown with those of Figure 6A (for contrast 0.95) replotted for comparison (Fig. 9). The results are quite consistent across contrasts despite the fact that only one subject was common to the contrast 0.95 and lower contrast data sets, providing a degree of cross-validation.

[Figure 8 about here please]

[Figure 9 about here please]

DISCUSSION

The initial Type-G models were complex, with at least 6 factors required, and even those produced a somewhat complex distribution of factor scores (channel influences) across the visual field (Fig. 8). The Type-S and -R models were examined in order to understand the sources of that complexity. Models examining psychometric data averaged across subjects (Type-S), examined variation across regions only, however, many factors were still required to explain a reasonable proportion of the variance and the loadings were complex (Fig. 5B). Evidently the initial complexity of Type-G models was mainly due to differences across regions, rather than across subjects. Models examining psychometric data averaged across stimulus regions (Type-R), examined variation across subjects only. In this case the models were simple, even three factors explaining about 80% of the variance. Importantly the putative channel influences, the factor loadings, were very similar for different groups of subjects, and at different contrasts (Fig. 9). As mentioned in the Methods, since the analysis had no information about the relative position of the psychometric data within the tested spatio-temporal domain; any reasonable looking loadings are purely a product of the variance structure of data and not the model.

Taken together these data suggest that the basic mechanisms were simple but with small variations due to visual field location (Fig. 8). A partial explanation for this variation might be that the different scaling of the gratings in inner and outer regions was not exactly M-scaled, despite detailed testing³¹, however differences also occurred at each eccentricity (Fig. 8). The presumption in the scaling used here is that the magnification factor should be like that reported for parasol retinal ganglion cells³¹, which may not be correct. Even the results from Type-G models indicate that no more than 6 independent mechanisms are needed to explain most of variance in the 280 data points of the psychometric functions.

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Examining Figure 9 it is apparent that the parts of the spatio-temporal domain in which the FD illusion is seen are influenced by up to three independent mechanisms. The first factor loading is reminiscent of the high probability region in the psychometric data at low contrasts (*cf.* Fig. 4D). Frequency doubling has been reported to be better seen as contrast is reduced to threshold levels^{2, 6}, at least for the spatial and temporal frequencies examined in those studies. The data of Figure 9 provide a degree of cross validation given that only one subject was common between the group test and contrast 0.95 and the group tested at lower contrasts.

Wilson et al.³⁴ reported that 6 spatial frequency tuned mechanisms were required to fit central vision over the range 0.25 to 22.0 cpd; three of those channels had their peaks under 4 cpd, the lowest two possibly having more transient responses. Simpson & McFadden²⁶ found evidence for three broadly tuned bandpass channels peaking at 4, 8 and 16 cpd. According to Hess and Howell³⁵, the lowest spatial channel is reported to be around 0.2 cpd rather than 2 cpd as reported earlier¹². While there is a growing support that spatial sensitivity is subserved by a moderately large number of detectors, each with relatively limited spatial bandwidths; temporal sensitivity is thought to be subserved by only a few detectors with broader temporal bandwidths¹⁹.

It has been postulated that temporal vision is subserved by only two broadly tuned detectors labelled for temporal frequency^{36, 37}. A third high temporal frequency detector was suggested after discovering that temporal frequency discrimination using 2 cpd gratings supports the existence of two temporally selective mechanisms, and there may be an additional higher temporal frequency mechanism at about 0.2 cpd²⁰. Other reports suggest three or more temporal selective channels exist^{18, 19, 38, 39}. This notion was challenged by Hammett and Smith²¹ who suggested that perceptual fading might account for the improvement of discrimination at high temporal frequencies. Results from Waugh and Hess⁴⁰

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suggest otherwise; improvement in temporal discrimination still persists without perceptual fading. It is interesting to see that perhaps these high temporal detectors for low spatial frequencies as suggested by Hess and Plant²⁰ are displayed in Figures 5 and 6.

In conclusion, our results support earlier reports that at least 2 spatial frequency channels exist below 1 cpd^{15, 17}, and lend support for a third high temporal frequency channel as suggested by other reports¹⁸⁻²⁰, as opposed to the postulate that temporal vision is subserved by only two broadly tuned temporal channels^{36, 37}. Secondly each visual field region responds somewhat differently, even regions at the same eccentricity. Thus far estimating channel characteristics has tended to exploit independent variations across subjects, so the present results suggest the possibility of exploiting within subject variation across parts of the visual field to infer channels within subjects. The results may be important for clinical devices such as the FDT perimeter which tacitly assumes that similar mechanisms operate at all visual field locations. One option would be to examine the sensitivity and specificity of the different mechanisms implied here. This could lead to the use of stimuli that scaled with visual field eccentricity, or that have different flicker rates in particular field locations. That could be a problem for a perimeter because the different sorts of stimuli might be confusing to subjects so the potential benefits might be swamped by increased variability. This is not an obstacle to multifocal methods where visual responses are recorded objectively, and multifocal PERGs using M-scaled FD stimuli have been demonstrated^{27, 28}.

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LEGENDS

FIGURE 1. An illustration of the visual stimulus layout comprising eight possible stimulus regions, only one of which was presented in any trial. The gratings are presented here at different contrasts to permit the eight regions to be distinguished. The small cross indicates the fixation spot presented at the screen centre. The symbols r1 to r8 indicate the numbering scheme of the regions.

FIGURE 2. Illustration of the temporal evolution of the 2AFC test sequences. The flicker test was displayed for 2.5 seconds, followed by two optional stimuli. The subject's task was to choose which of the two test pattern options had the subjectively the closest spatial frequency to the flickering test pattern. For aesthetic purposes the sinusoidal modulation frequency of the test grating illustrated here varies more slowly than any used in the tests. *Inserts upper.* Each panel illustrates the visual appearance of the stimuli in the 2AFC test sequences. The left grating has noise added to it simulating the appearance of test pattern modulated by a high temporal frequency. The middle and right gratings indicate static grating patterns whose contrast has been previously determined to be subjectively similar to the contrast of the flickering test pattern.

FIGURE 3. The psychometric functions obtained at a contrast of 0.95 averaged across the thirteen subjects. The functions describe the probability of seeing the frequency doubled illusion, light shades represent higher probabilities of seeing the illusion (see calibration bar at bottom). Contours are in steps of 0.1, the highest being 0.9. The symbols r1 to r8 indicate the 8 stimulus regions, as indicated in Fig. 1. Note that the layout of the figure roughly follows that of the stimulus ensemble, with data for the inner 4 regions presented centrally. Note that the abscissa labels correspond the spatial frequencies of the inner regions, the outer regions having $\frac{1}{2}$ those frequencies.

FIGURE 4. Comparisons of psychometric functions averaged across subjects and the 8 visual field regions for contrasts 0.95, 0.8, 0.4, 0.2 (A to D). The regions which are lightly shaded correspond to the regions where the probability of seeing the frequency doubling is much highest (see calibration bar at the bottom). As contrast decreases, the region where the FD is seen well contracts to the left towards the lowest spatial frequencies.

FIGURE 5. Factor loadings indicating at what spatial and temporal frequencies each factor strongly influences the psychometric data. A) when all the data from each region and subject is entered in a grand analysis (Type-G model) at least 6 factors are required to explain a reasonable proportion of the variance (see text, and scree plot Fig. 7G). B) Factor loadings obtained from data averaged across the 13 subjects (Type-S model). For both Model types even 6 factors produced only fair communalities (see Fig. 7C,E).

FIGURE 6. Three sets of factor loadings from data from thirteen subjects averaged across regions (Type-R model). A) the top row shows the loadings indicating the influences of each factor at each spatial and temporal frequency pair for PC factors. B) bottom row, shows the ML loadings. The ML loadings for factors 2 and 3 have been switched (compared to the order that the proportion of variance would indicate), and the sign of the middle set of data has been inverted, to match their PC counterparts. The median communalities for the PC factors were 0.92 and 0.94, and were uniformly high for both PC and ML factors (e.g. Fig. 7C-F). For 3 factors, as shown here, the values were still 0.79 and 0.83 respectively.

FIGURE 7. Variances explained by Type-G and –R models. The top row shows exemplary psychophysical results for comparison with the corresponding communalities for Type-G and Type-R models. Communalities indicate the proportion of variance explained for each point in the psychometric function, uniform communalities mean the factors explain the psychometric function well at all points. A) results from region 1 for data averaged across repeats at contrast 0.95. B) psychometric data from region 1 of subject 1. The communalities

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for the PC (C, D) and ML factor analyses (E,F) uniformly explain the points of the whole psychometric function, both where FD is seen and where it is not (cf. A,B and C-F). The communalities are higher for the Type-R models. Scree plots indicating the proportion of variance in the correlation matrix explained by each PC factors for 6 (G) and 3 (H) component models. In both cases there is a distinct step after 3 factors indicating that these first 3 are not noise.

FIGURE 8. The mean factor scores across subjects from the Type-G analysis. Strong weights are indicated by either very dark or very light tones, while weights close to 0 are grey (see calibration bar). While the mean factor scores are broadly similar for a given factor there are differences across quadrants, and centrally versus peripherally. This suggests the spatiotemporal influences of the factors, as indicated by the factor loadings, vary across the visual field.

FIGURE 9. Comparisons of factor loadings at for data obtained at different contrasts for Type-R models. The loadings suggest that as contrast decreases (from contrast 0.95, top row) the loadings remain similar supporting the existence of three independent channels. The sign of the third set of loadings was allowed to vary. The numbers of subjects from A to D were: 13, 4, 4, 3. Note that only one subject was common to all four data sets making the similarity between the loadings all the more remarkable.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9