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Retinal Electrophysiology

Correlations between observability of the spatial frequency doubled illusion and a multi-region pattern electroretinogram

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ABSTRACT

A glaucoma screening device based on the visibility of the spatial frequency doubled (FD) Illusion will be marketed by Welch Allyn Ltd in the next year (ANU Patents (Australia) 611 585, (USA) 5 065 767 and application PL 3130. An underlying assumption of the method is that retinal processes are being tested. To test this assumption we compared the visibility of the FD Illusion over a range of conditions and in the same spatial locations as a multi-region pattern electroretinogram (PERG). Grating speed and contrast were good predictors of the psychometric functions and PERG amplitude and phase.

Key words: magnocellular multi-region, non-linear; pattern electroretinogram rectifying, sandwich model, spatial frequency doubled illusion, sum of sinusoids, Y cells.

A subset of the retinal ganglion cells (RGC), the Y-like cells of the primate magnocellular visual pathway (M_y cells) are strongly affected by retinal gain control[1] and are thus analogous to the Y cells of the cat. The gain control affecting RGC enhances responses when moderate to high contrast visual stimuli move quickly.[2] One way of achieving isolation of M_y responses may be through the exploitation of the spatial frequency doubled (FD) illusion.[3,4] When a coarse grating pattern has its contrast reversed at a high rate, people perceive the pattern as having twice as many stripes (i.e. having twice the spatial frequency).[5] There are several lines of evidence suggesting that it is the M_y cells that are the source for this illusion.[4,6]

The characteristic second harmonic components of Y cell responses arise from non-linear subunits in the Y cell receptive field.[7,8] These small subunits have full-wave rectified responses and are distributed over a region coextensive with the linear centre-surround components.[7] The rectification has the form[7-9] response $\propto$ |stimulus|x, with x = 0.8-0.9. The FD illusion is known to be formed by a similar process.[5] Work by Victor and Shapley[10] indicated that both X and Y cells are subject to a gain control. The critical experiments involved the temporal modulation of a stationary sine grating by a sum-of-sinusoids stimulus, in which the temporal contrast modulation signal is the sum of several temporal sinusoidal waves. X cell responses to increasing contrast at 2 Hz and below are weak, but between 8 and 15 Hz response amplitudes increase proportionally with input contrast. Response phase also increases with increasing temporal frequency.[10] These effects of increasing contrast are even greater in the Y cell, the mean phase advance for the non-linear response component Y cells being twice that seen in X cells, indicating that the non-linearity is well described by a squaring operation. The gain control mechanism appears to be governed by the signal arising from non-linear summation component of Y cell responses.

The following study endeavours to isolate M_y cell activity in the human by using a variant of the sum-of-sinusoids technique. If these cells generate the non-linear component of the pattern electroretinogram (PERG) response, increasing image contrast should result in increasing phase advances. Large phase shifts in the second harmonics should occur when the FD illusion is strong, namely in response to low spatial and high temporal frequency stimuli.

METHODS

Each region of the visual stimulus (Fig. 1) contained an achromatic (6500 °K) sinusoidal grating (mean luminance of 45 cd/m^2). The default spatial frequencies of gratings in the outer, middle and centre regions were 0.125, 0.250 and 0.750 c.p.d., respectively. The other spatial frequencies

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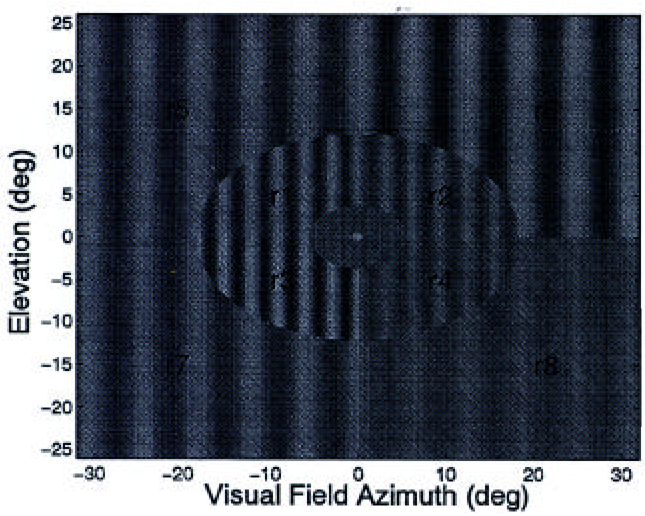

Figure 1. Illustration of the visual stimuli used for both the pattern electroretinogram and psychophysical experiments depicting a single frame in the stimulus sequence. As the temporal modulations in each region are asynchronous, the contrasts of the regions differ in this single frame.

tested were obtained by multiplying the default spatial frequencies by 1/4, 1/2 1, 2 and 4. Gratings were presented at two contrasts, 0.4 and 0.8. The resulting 10 stimulus sets were presented in randomized order for the Right eyes of subjects were recorded from by standard methods and informed consent was obtained under ANU protocol M881. The recording epoch (40.35 s) provided a frequency resolution (dF) of 0.0248 Hz. The temporal frequencies applied to the nine regions were defined as dF*((889, 893, 898, 904, 911, 921, 935, 947, 955) - N*75), where N = (1,3,5,9), providing non-overlapping bands of frequencies 1.8 Hz apart. Further details of the visual stimuli and the methods for calculating the significance of the responses have been given elsewhere.[4]

The conditions required to see the FD illusion were determined in psychophysical experiments. Subjects matched the apparent spatial frequency of temporally modulated gratings with an unmodulated grating having twice the spatial frequency (i.e. that of the FD illusion). Gratings were modulated at the middle (fifth) frequency from each of the temporal frequency sets of the PERG experiments + 2, providing test frequencies of 5.82, 9.54, 13.25, 16.97, 20.69, 24.40 and 28.12 Hz. In each trial the modulated grating was presented for 1 s. After a 1 s blank period, the unmodulated grating was presented for 0.5 s. Subjects indicated whether the modulated pattern had appeared coarser than the matching pattern. Stimulus presentations were randomized, the four subjects each completing 12 repetitions of each of the 35 test conditions and nine regions for both contrasts.

Canonical variate analysis (SPSS; SPSS Inc., Chicago, IL, USA) was used to probe for the presence of relationships between dependent and independent variables from the psychophysical and PERG experiments. This was revealed by correlations between these variables and the calculated canonical variates. Separate regression analysis (SPSS) was conducted on the raw data at each contrast (e.g. absolute phase lag, probability of seeing the illusion) and also for data that were the differences between the dependent variables obtained at contrast 0.8 and 0.4, such as phase difference.

RESULTS

Figure 2, describing the probability of seeing the FD illusion at contrast 0.4 and 0.8, is the mean of psychometric functions from four subjects and over the eight outer regions of the stimulus. The dots indicate the spatial and temporal frequencies at which the multi-region PERG was assessed in the same subjects for comparison. As both temporal and spatial frequency vary together along the diagonal, we sometimes describe the stimuli in terms of the ratio of the spatial and temporal frequencies, which can be thought of as image speed.

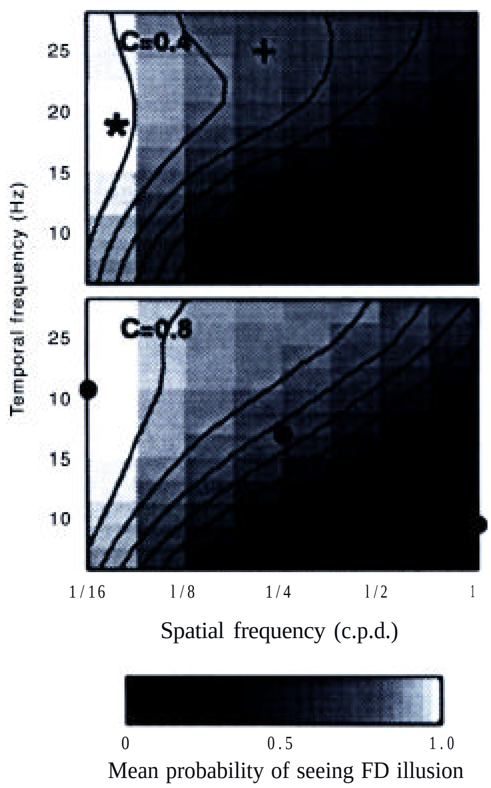

Figure 2. Average psychometric functions describing the probability of seeing the frequency doubled (FD) illusion at contrasts (C) 0.4 and 0.8. Contours are in steps of 0.1 beginning at P=0.9 and running down to P=0.1. The spatial frequencies appearing on the abscissa relate to the inner four regions (rl-r4, Fig. 1). Dots in lower panel indicate pattern electroretinogram test conditions.

Table 1. Correlations between the Independent variables speed and contrast and the dependent variables (psychophysical probability, pattern electroretinogram phase and amplitude) with the canonical variates for both absolute data and differences obtained at contrasts *0.4* and 0.8

Variable	Canonical variate 1 (absolute)	Canonical variate *2* (absolute)	Canonical variate 1 (difference)
Psychophysical	0.991	0.011	0.098
Amplitude	*-0.264*	*0.946*	*-0.978*
Phase	-0.315	*-0.020*	*0.578*
Speed	1.000	-0.001	-
Contrast	*-0.008*	*11.000*	-

There was a strong correlation (0.991) between the psychophysical data (i.e. the probabilities of seeing the FD illusion) and canonical variate one (CV 1, Table 1) and CV 1 was correlated with speed (1.000). There was a similar relationship between contrast and PERG amplitude with CV2 A separate analysis revealed that differences in phase and amplitude were related to speed (Table I). Multiple regression analysis of phase differences obtained at contrast *0.4* and 0.8 against several independent variables indicated that input temporal frequency (or speed) was a significant determinant of phase advance (mean (±SEM) 2.15±0.427 °/Hz, P= 0.0000, t=5.038, d.f.=93) once the independent effects of visual field region were subtracted (temporal visual field yielded 13.7±3.55° larger advances at all frequencies; P<0.0002).

DISCUSSION

The largest PERG phase advances with increasing contrast occur at speeds requisite for seeing the FD illusion, consistent with Y cell responses being modified by retinal gain control. Differences in mean phase advance, which where independent of speed or temporal frequency, were also observed, such that the temporal retina provided larger overall phase shifts, consistent with hemi-retinal anatomical differences." While we saw no naso/temporal effect in the psychometric functions as that in the phase shift data, this has been previously reported in related experiments6 on more subjects. The psychometric functions, however, indicate the possibility of two generators of the illusion, one occurring at very low spatial frequencies and medium temporal frequencies, which is robust with decreasing contrast, and a second occurring at high contrasts over a range of spatial frequencies provided the temporal frequency is high.

REFERENCES

1 Bernardete EA, Kaplan E, Knight BW. Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Vis. Neurosci.* 1992; 8: 483-6.
2 Shapley RM, Victor JD The effect o fcontrast on the nonlinear response of the Y-cell. 1J Pbysiol. 1980; 302: 535-47.
3 Maddess T, Henry GH. Nonlinear visual responses and visual deficits in ocular hypertensive and glaucoma subjects. Clin. *Vis. Sci.* 1992; 7: 371-83.
4. James AC, Maddess T, Rouhan K, Bedford S, Snowball M. Evidence for M_y-cell involvement in the spatial frequency doubled illusion as revealed by a multiple region PERC for glaucoma. J. Opt. Soc. Am. *VSIA Tech. Dig.* 1995; 1: 3 14-l 7.
5 Kelly DH. Frequency doubling in visual responses. J. *Opt. Soc.* Am. 1966; 56: 1628-33.
6. Maddess T, James AC, Hemmi J. Aliasing effects reveal apparent sampling density of human nonlinear retinal ganglion cells. Vision Res. 1997 (in press).
7 Hochstein S, Shapley RM. Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. J. Physiol. 1976; 262: *265-84.*
8 Victor JD, Shapley RM. The nonlinear pathway of Y ganglion cells in the cat retina. J. Gen. *Physiol. 1979, 74:* 671-89.
9. Victor JD. The dynamics of the cat retinal Y cell subunit. J. *Physiol.* 1988; 405: 289-320
10 Shapley RM, Victor JD. The effect o fcontrast on the transfer properties of cat retinal ganglion cells. J. Pbysiol. 1978; 285: 275-98.
11 Connolly M, Van Essen D. The representation of the visual field in parvicellular and magnicellular layers of the lateral geniculate nucleus. J. Comp. Neurol. 1984, 226: 544-64.