CRITICAL FLICKER FREQUENCY AND M-SCALING OF STIMULUS SIZE AND RETINAL ILLUMINANCE

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(Received 3 November 1983; in revised form 16 April 1984)

Abstract—Using various stimulus areas and luminances we measured monocular critical flicker frequency (CFF) as a function of eccentricity in the temporal visual field. With constant stimulus area and luminance, CFF was not independent of visual field location. When stimulus area was scaled by the magnification factor of the human striate cortex to produce equal cortical stimulus areas from different retinal locations, CFF increased monotonically with increasing eccentricity. Hence, CFF cannot be made independent of visual field location by spatial M-scaling. However, when also retinal illuminance was M-scaled by reducing stimulus luminance in inverse proportion to Ricco's area at each eccentricity, CFF became independent of visual field location.

Human vision Peripheral vision Perimetry Flicker Cortical magnification factor

INTRODUCTION

The visual field is represented topographically in the striate cortex. The scale of the map changes with visual field location: the central parts have a much larger representation than peripheral regions. The scale, called cortical magnification factor (M), indicates the length, in millimetres along the cortical surface, that corresponds to one degree of arc in the visual field (Daniel and Whitteridge, 1961).

With increasing eccentricity (angular distance from the center of the visual field) photopic visual acuity decreases in direct proportion to the human cortical magnification factor (Cowey and Rolls, 1974; Virsu and Rovamo, 1979). Our recent results suggest that even the local anisotropy of monocular M within ocular dominance columns is reflected in the resolution of gratings oriented along and across meridians in peripheral vision (Rovamo et al., 1982). The slowest velocity needed for perceiving movement increases with eccentricity in inverse proportion to the human cortical magnification factor (Johnston and Wright, 1983). Thus, when a stimulus is magnified at peripheral locations in inverse proportion to the cortical magnification, it becomes equally visible across the visual field.

Contrast sensitivity too becomes independent of visual field location when grating areas, velocities and spatial frequencies are scaled by the human cortical magnification factor so that gratings produce computationally equivalent cortical representations from different retinal locations (Rovamo et al., 1978; Virsu et al., 1982; cf. Koenderink et al., 1978a). In addition, M-scaling applies to luminance-modulated, chromatic gratings (Rovamo, 1983), to colour contrast (Noorlander et al., 1983), to fine-grain movement illusion (Foster et al., 1981), to pattern-reversal evoked potentials (Meredith and Celesia, 1982), to

detection of coherent movement in random-dot patterns (van de Grind et al., 1983), to differential motion detection and velocity discrimination (McKee and Nakayama, 1984), and to temporal integration (Rovamo et al., 1984).

There are, however, other measures, such as the Vernier acuity (Westheimer, 1982), orientation discrimination (Scobey, 1982), stereoacuity (Fendick and Westheimer, 1983), fusional vergence response (Hampton and Kertesz, 1983), and temporal order detection (Westheimer, 1983), that evidently cannot be made independent of visual field location by *M*-scaling spatial stimulus parameters. In agreement with Virsu and Rovamo (1979), these complications suggest that spatial *M*-scaling as such is incomplete.

This paper extends M-scaling to luminance by taking into account the amount of luminous flux collected by retinal ganglion cells (Enroth-Cugell and Shapley 1973a, b). Both the spatial stimulus parameters and retinal illuminance were M-scaled and the effects were tested by measuring critical flicker frequency (CFF) as a function of eccentricity in the temporal visual field.

METHODS

Apparatus and stimuli

Flicker was generated with a low-frequency sinusoidal oscillator (hp 202C) on a green (P31) cathoderay screen (Tektronix 620) with a frame frequency of 3.2 kHz produced by combining a ramp with a triangular wave of 2 MHz, both from a function generator (Exact 7260). To guarantee a homogenous stimulus field the screen was blanked during the return of the ramp. The luminance response of the screen was measured with Spectra Spot Photometer and linearized (r = 0.970) with a multifunction con-

verter (National Semiconductor LH0094). Measurements with a phototransistor (Texas Instruments TIL81) showed that within 20-70 Hz flicker was sinusoidal (r = 0.990) with a modulation of 30%. The average luminance of the screen was 50 phot. cd/m² which is equivalent to 114 scot, cd/m² on our display. The screen was limited with black cardboard to a square stimulus field with a desired area. Average retinal illuminance was varied by inserting neutral density filters (Agfa-Gevaert) in front of the right eye; the left eye was covered with a black eye-pad. Longterm dilatation of the right pupil was induced with four drops of 10% phenylephrine hydrochloride. which leaves accommodation unaffected. The centre of the stimulus field was fixated in foveal experiments and a small spot of green light served as a fixation point in extrafoveal experiments. Experiments were performed in a dark room. A bite-board was used to stabilize the head. Viewing distance was 28.6 cm.

Procedures and subjects

To minimize local adaptation to flicker (Ginsburg, 1966), monocular critical flicker frequency (CFF) was determined as follows: Using a flicker frequency of 90 Hz, which always appeared steady, each retinal location was first adapted to the average luminance of the stimulus field. Thereafter the frequency was manually reduced until flicker was perceived. The highest frequency that produced visible flicker was recorded as an estimate of CFF. The frequency was then set at 90 Hz for 2 min. After this the frequency was quickly reduced to a value that produced clearly visible flicker. Then the frequency was slowly increased until flicker disappeared. The lowest frequency that annihilated flicker was recorded as another estimate of CFF. Thereafter the frequency was again set at 90 Hz for 2 min. Six estimates of CFF were recorded in succession, and they were averaged.

To avoid the adverse effect of fading of peripheral stimuli, the subject closed his eyes for a moment or made a rapid eye movement when the stimulus field tended to fade. Four experienced subjects (aged 25–38 years) participated in the experiments. Their results were similar.

RESULTS

In the experiment of Fig. 1 the stimulus field had a constant area at different eccentricities. Retinal illuminance was also constant at eccentricities of 0-80 deg because the retinal area per one solid degree of visual field and the effective pupillary area decrease similarly when eccentricity increases from 0 to 80 deg (Bedell and Katz, 1982). As Fig. 1 shows, critical flicker frequency (CFF) was not independent of eccentricity but first increased and then decreased with increasing eccentricity (cf. Hartmann et al., 1979).

In the experiment of Fig. 2, the stimulus area was M-scaled (Rovamo and Virsu, 1979): the area was

increased with eccentricity in inverse proportion to the square of the human cortical magnification factor to keep the calculated cortical projection area of the stimulus field constant at all visual field locations; the values of cortical magnification, in mm deg⁻¹, were obtained from equation $M = 7.99 (1 + 0.29E + 0.000012E^3)^{-1}$, where E is eccentricity in degrees of visual angle. As Fig. 2 shows, CFF now increased monotonically with eccentricity. The result means that CFF cannot be made independent of visual field location by M-scaling the spatial stimulus parameters.

The human cortical magnification factor has been estimated by assuming that cortical magnification is directly proportional to the square-root of retinal ganglion-cell receptive-field density (Rovamo and Virsu, 1979). Thus, M-scaling of spatial stimulus parameters compensates only for the decrease of sampling density of ganglion cells with increasing eccentricity. On the other hand, CFF of single feline ganglion cells increases with flux defined as retinal illuminance multiplied by the area of receptive field centre (Enroth-Cugell and Shapley, 1973a, b). This

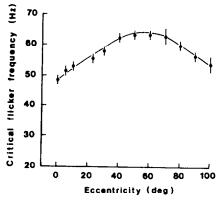


Fig. 1. Critical flicker frequency (mean ± SD) as a function of eccentricity in the temporal visual field of the right eye. Stimulus area was 88.4 deg², pupillary diameter 8 mm, retinal illuminance 2510 phot. td, and subject A.R.

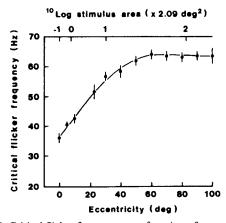


Fig. 2. Critical flicker frequency as a function of eccentricity when stimulus area was *M*-scaled. Other details as in Fig. 1.

suggests that, with M-scaled stimulus area, the increase of CFF with eccentricity in Fig. 2 results from the increase of receptive field size towards the retinal periphery (De Monasterio and Gouras, 1975), because in the experiments of Fig. 2 retinal illuminance and the number of ganglion cells stimulated were the same at all eccentricities from 0 to 80 deg. This hypothesis can be tested by reducing retinal illuminance in inverse proportion to the area of receptive field centre.

Ricco's area provides an estimate for the area of receptive field centre in man: by pooling together the results of Wilson (1970) and Inui et al. (1981) from the nasal visual field we found, in agreement with Virsu and Rovamo (1979), that the radius (R) of Ricco's area, in degrees, is linearly related (r = 0.987)to the inverse of cortical magnification: R = 0.0263 $(1+3.15\,M^{-1})$. Thus, at the eccentricity of 0 deg the radius of Ricco's area is 0.293 mm when projected onto the striate cortex whereas at the eccentricity of 100 deg the cortical projection of the radius is 0.0878 mm. This suggests that, when expressed in cortical millimetres, the size and overlap of receptive fields are largest in foveal vision and decrease with increasing eccentricity. Our previous results (e.g. Rovamo et al., 1978; Virsu et al., 1982) indicate, however, that the spatial frequency producing the maximal contrast sensitivity is at all eccentricities directly proportional to the human cortical magnification factor.

In the rhesus-monkey striate-cortex the mean receptive-field size (F) is also linearly related to the inverse of cortical magnification: Fig. 6 from Hubel and Wiesel (1974) indicates that F = 0.156 $(1 + 5.08 M^{-1})$ for eccentricities of 1-22deg whereas according to Dow et al. (1981) F = 0.209 $(1 + 1.53 M^{-1})$ for eccentricities of 0-2.5 deg. Both equations suggest that the product, magnification multiplied by aggregate field size, decreases with increasing eccentricity. However, only Dow et al. (1981) verified this suggestion experimentally; according to Hubel and Wiesel (1974) the product is practically independent of visual field location. On the other hand, Dow et al. (1981) found that the foveal value of magnification is about 30 mm deg⁻¹ whereas the estimates of Daniel and Whitteridge (1961) and Hubel and Wiesel (1974) are 5-6 mm deg⁻¹, in accordance with our estimate of 8 mm deg⁻¹ for man (Rovamo and Virsu, 1979). The results of Dow et al. (1981), obtained from binocularly fixating awake monkeys, may, however, be unreliable because of several reasons: for example, the number and density of penetrations into the cortical representation of the fovea was excessive in all four hemispheres studied and the control of eye position and optical effects was inadequate.

In the experiment of Fig. 3 the area of the stimulus field was kept constant at all eccentricities but retinal illuminance was M-scaled: stimulus luminance was reduced with increasing eccentricity in inverse pro-

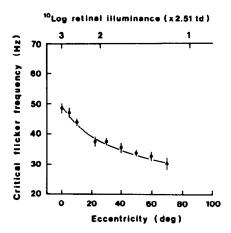


Fig. 3. Critical flicker frequency as a function of eccentricity when retinal illuminance was M-scaled. Other details as in Fig. 1.

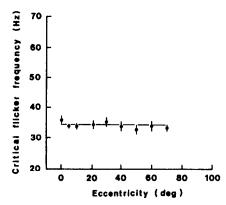


Fig. 4. Critical flicker frequency as a function of eccentricity when both the stimulus area and retinal illuminance were *M*-scaled. Other details as in Fig. 1.

portion to Ricco's area. Measurements could not be performed at eccentricities larger than 70 deg because within 80-100 deg the stimulus field was masked by the edge of the rack for neutral density filters. As Fig. 3 shows, CFF decreased now monotonically with increasing eccentricity. The decrease evidently results from the decrease of cortical projection area and ganglion cell density with increasing eccentricity, because retinal illuminance was M-scaled.

In the experiment of Fig. 4 both the stimulus area and retinal illuminance were *M*-scaled. Now CFF became independent of visual field location. The result is surprising because there is evidence that in primates ganglion cells with different temporal properties dominate in peripheral and central retina (De Monasterio *et al.*, 1976) and that each retinal location contains a range of receptive field sizes (Troscianko, 1982).

DISCUSSION

In agreement with previous studies (cf. Hartmann et al., 1979), our experiments showed that with

constant stimulus area and luminance, critical flicker frequency (CFF) is not independent of visual field location. Our experiments also showed that (1) with M-scaled stimulus area, CFF increased monotonically with eccentricity and (2) with M-scaled retinal illuminance, CFF decreased monotonically with increasing eccentricity. These results suggest that with constant stimulus area and luminance, the variation of CFF with visual field location results from two counteracting factors: the decrease of ganglion cell density towards the retinal periphery tends to reduce CFF and the increase of receptive field size towards the retinal periphery tends to enhance CFF.

In addition, our results showed that CFF can be made independent of visual field location only by M-scaling both the stimulus area and retinal illuminance. Thus, our results support the view that spatiotemporal information processing is qualitatively similar for stimuli presented at different locations of the visual field and that quantitative differences result from retinotopical differences in the density, size and overlap of sampling apertures i.e. ganglion-cell receptive-fields. Also, eye movements (Carpenter, 1977) and ocular optics (Jennings and Charman, 1981) evidently contribute to quantitative differences: Receptive field size grows with increasing eccentricity (De Monasterio and Gouras, 1975). Therefore, during steady fixation peripheral stimuli are more stabilized than foveal stimuli. On the other hand, peripheral image quality exceeds the requirements of neural sampling (Jennings and Charman, 1981), which may result in aliasing distortions (cf. Williams and Collier, 1983).

In the present experiments temporal modulation was 30%, retinal illuminance was always above 90 scot. td, and CFFs were at least 30 Hz. This indicates (Conner, 1982) that the contribution of rods was negligible.

CFF is known to increase within increasing stimulus area and luminance (van de Grind et al., 1973). Our results, however, imply that in the classical Granit-Harper law stimulus area should be replaced by the number of ganglion cells stimulated, and in the classical Ferry-Porter law stimulus luminance should be replaced by the flux collected by ganglion cells.

We calculated flux as retinal illuminance multiplied by Ricco's area whereas Koenderink et al. (1978b) assumed that flux is directly proportional to M^{-2} . However, in agreement with Koenderink et al. (1978b), our results suggest that, at least in cone vision, the state of adaptation at different eccentricities is not determined by retinal illuminance but by the flux collected by ganglion cells.

Flicker fusion perimetry has been used for clinical investigation of visual fields (see Miles, 1950). With moderate success Weekers and Roussel (1946) have already tried to reduce the eccentricity-dependent variation of CFF by adjusting stimulus size. The invariance of CFF obtained by changing both the stimulus area and luminance with visual field location

provides, however, a novel method for clinical investigation of visual fields. In this optimal perimetry normal thresholds as a function of visual field location are horizontal lines called perimetrograms. Consequently, visual field defects are readily recognized as pits, as in an audiogram.

The invariance principle presented above takes into account both the luminous flux and the number of ganglion cells stimulated. Thus it is an extension of an earlier invariance principle (Rovamo et al., 1978; Koenderink et al., 1978; Virsu and Rovamo, 1979) that took into account only the number of ganglion cells stimulated.

We thank Oskar Oflund and Paulo Foundations and Finnish Broadcasting Company for support and T. Lammi for technical assistance.

REFERENCES

Bedell H. E. and Katz L. M. (1982) On the necessity of correcting peripheral target luminance for pupillary area. Am. J. Optom. Physiol. Opt. 59, 767-769.

Carpenter R. H. S. (1977) Movements of the Eyes. Pion, London.

Conner J. D. (1982) The temporal properties of rod vision. J. Physiol. 332, 139-155.

Cowey A. and Rolls E. T. (1974) Human cortical magnification factor and its relation to visual acuity. *Expl Brain Res.* 21, 447-454.

Daniel P. M. and Whitteridge D. (1961) The representation of the visual field on the cerebral cortex in monkeys. J. Physiol. 159, 203-221.

De Monasterio F. M. and Gouras P. (1975) Functional properties of ganglion cells of the rhesus monkey retina. J. Physiol. 251, 167-195.

De Monasterio F. M., Gouras P. and Tolhurst D. J. (1976) Spatial summation, response pattern and conduction velocity of ganglion cells of the rhesus monkey retina. Vision Res. 16, 674-678.

Dow B. M., Snyder A. Z., Vautin R. G. and Bauer R. (1981) Magnification factor and receptive field size in foveal striate cortex of the monkey. Expl Brain Res. 44, 213-228.

Enroth-Cugell C. and Shapley R. M. (1973a) Adaptation and dynamics of cat retinal ganglion cells. J. Physiol. 233, 271-309.

Enroth-Cugeli C. and Shapley R. M. (1973b) Flux, not retinal illumination, is what cat retinal ganglion cells really care about. J. Physiol. 233, 311-326.

Fendick M. and Westheimer G. (1983) Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. Vision Res. 23, 145-150.

Foster D. H., Thorson J., McIlwain J. T. and Biederman-Thorson M. (1981) The fine-grain movement illusion: a perceptual probe of the neuronal connectivity in the human visual system. *Vision Res.* 21, 1123-1128.

Ginsburg N. (1966) Local adaptation to intermittent light as a function of frequency and eccentricity. Am. J. Psychol. 79, 296-300.

Hampton D. R. and Kertesz A. E. (1983) Fusional vergence response to local peripheral stimulation. J. opt. Soc. Am. 73, 7-10.

Hartmann E., Lachenmayr B. and Brettel H. (1979) The peripheral critical flicker frequency. Vision Res. 19, 1019-1023.

Hubel D. H. and Wiesel T. N. (1974) Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor. J. comp. Neurol. 158, 295-305.

- Inui T., Mimura O. and Kani K. (1981) Retinal sensitivity and spatial summation in the foveal and parafoveal regions. J. opt. Soc. Am. 71, 151-154.
- Jennings J. A. M. and Charman W. N. (1981) Off-axis image quality in the human eye. Vision Res. 21, 445-455.
- Johnston A. and Wright M. J. (1983) Visual motion and cortical velocity. *Nature* 304, 436-438.
- Koenderink J. J., Bouman M. A., Bueno de Mesquita A. E. and Slappendel S. (1978a) Perimetry of contrast detection thresholds of moving spatial sine-wave patterns. III. The target extent as a sensitivity controlling parameter. J. opt. Soc. Am. 68, 854-860.
- Koenderink J. J., Bouman M. A., Bueno de Mesquita A. E. and Slappendel S. (1978b) Perimetry of contrast detection thresholds of moving spatial sine-wave patterns. IV. The influence of the mean retinal illuminance. J. opt. Soc. Am. 68, 860-865.
- McKee S. P. and Nakayama K. (1984) The detection of motion in the peripheral visual field. Vision Res. 24, 25-32.
- Meredith J. T. and Celesia G. G. (1982) Pattern-reversal visual evoked potentials and retinal eccentricity. *Electro-encephalogr. clin. Neurophysiol.* 53, 243-253.
- Miles P. W. (1950) Flicker fusion fields. Am. J. Ophthal. 33, 1069-1077.
- Noorlander C., Koenderink J. J., den Ouden R. J. and Edens B. W. (1983) Sensitivity to spatiotemporal colour contrast in the peripheral visual field. *Vision Res.* 23, 1-11.
- Rovamo J. (1983) Cortical magnification factor and contrast sensitivity to luminance-modulated chromatic gratings. *Acta Physiol. Scand.* 119, 365-371.
- Rovamo J. and Virsu V. (1979) An estimation and application of the human cortical magnification factor. *Expl Brain Res.* 37, 495-510.
- Rovamo J., Virsu V. and Näsänen R. (1978) Cortical magnification factor predicts the photopic contrast sensitivity of peripheral vision. *Nature* 271, 54-56.

- Rovamo J., Leinonen L., Laurinen P. and Virsu V. (1984) Temporal integration and contrast sensitivity in foveal and peripheral vision. *Perception*. In press.
- Rovamo J., Virsu V., Laurinen P. and Hyvärinen L. (1982) Resolution of gratings oriented along and across meridians in peripheral vision. *Invest. Ophthal. visual Sci.* 23, 666-670.
- Scobey R. P. (1982) Human visual orientation discrimination. J. Neurophysiol. 48, 18-26.
- Troscianko T. (1982) A given visual field location has a wide range of perceptive field sizes. Vision Res. 22, 1363-1369.
- van de Grind W. A., Grüsser O.-J. and Lunkenheimer H.-U. (1973) Temporal transfer properties of the afferent visual system. In *Handbook of Sensory Physiology*, Vol. VII/3A. Springer, Berlin.
- van de Grind W. A., van Doorn A. J. and Koenderink J. J. (1983) Detection of coherent movement in peripherally viewed random-dot patterns. J. opt. Soc. Am. 73, 1674-1683.
- Weekers R. and Roussell F. (1946) Introduction a l'etude de la frequence de fusion en clinique. Ophthalmologica 112, 305-319.
- Westheimer G. (1982) The spatial grain of the perifoveal visual field. Vision Res. 22, 157-162.
- Westheimer G. (1983) Temporal order detection for foveal and peripheral visual stimuli. Vision Res. 23, 759-763.
- Williams D. R. and Collier R. (1983) Consequences of spatial sampling by a human photoreceptor mosaic. Science 221, 385-387.
- Wilson M. E. (1970) Invariant features of spatial summation with changing locus in the visual field. J. Physiol. 207, 611-622
- Virsu V. and Rovamo J. (1979) Visual resolution contrast sensitivity and the cortical magnification factor. *Expl Brain Res.* 37, 475–494.
- Virsu V., Rovamo J., Laurinen P. and Näsänen R. (1982) Temporal contrast sensitivity and cortical magnification. Vision Res. 22, 1211-1217.