

MATCHING VELOCITY IN CENTRAL AND PERIPHERAL VISION

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Abstract—The apparent velocity of peripheral, drifting sinusoidal gratings was measured as a function of eccentricity and viewing distance. Gratings appeared to move more slowly in the periphery. Apparent velocities in fovea and periphery could be matched by an appropriate spatial scaling of peripheral gratings. This scaling factor provides a psychophysical measure of the changing spatial grain of the visual system with eccentricity. Scaling factors were found to be the same for lower threshold of motion and for velocity matching with standard gratings of 2 and 6 Hz. The finding generalised over a range of standard temporal frequencies (<7 Hz) and spatial frequencies (1.2–9 c/deg). The psychophysically determined scaling factors were found to be proportional to the square root of macaque mean cortical receptive field area as a function of eccentricity. The data support a ratio strategy for encoding motion in which motion information is expressed relative to the changing spatial grain of the visual system. Locations for the apparent identity of physically identical grating motion fell along a straight line in space, prompting an explanation of these visual field effects in terms of the acquisition of environmental information from optic flow.

Psychophysics Grating velocity Visual field Optic flow

INTRODUCTION

Perceived velocity decreases with eccentricity (Lichtenstein, 1963; Campbell and Maffei, 1979, 1981; Tynan and Sekuler, 1982). The changes in contrast threshold with eccentricity can be compensated (Rovamo *et al.*, 1978) if peripheral gratings are enlarged by a scale factor. The scale factors used were assumed to compensate for changes with eccentricity in the human cortical magnification factor (M), expressed in millimetres of visual cortex per degree of visual space (Rovamo and Virsu, 1979). Similarly, lower threshold for motion velocity is equalised across the visual field if expressed relative to the changing spatial grain of the visual system as indexed by Rovamo and Virsu's estimates of M^{-1} (Johnston and Wright, 1983, 1985).

At suprathreshold stimulus levels, stimulus velocities required to cancel the motion after effect conform to the M -scaling pattern (Johnston and Wright, 1983; Wright and Johnston, 1985a) as do thresholds for detecting the spatial displacement of a grating stimulus (Wright and Johnston, 1985b), D_{\min} (Baker and Braddick, 1985) and the discrimination of coherent motion from random noise (van de Grind *et al.*, 1983). Other indices of motion analysis, D_{\max} (Braddick, 1974; Baker and Braddick, 1985) and V_m

(van de Grind *et al.*, 1983), which describe the spatial limits for the detection of coherent motion in random dot patterns, do not scale in accordance with the Virsu and Rovamo estimates. Using an alternative technique, McKee and Nakayama (1984) found that differential velocity thresholds at differing visual field locations could be equated by expressing their data with reference to the fall in grating acuity with eccentricity (resolution units/sec). Acuity scaling and scaling using Rovamo and Virsu's (1979) estimates of M^{-1} should provide similar results but we note grating displacement detection in a unreferenced dark field does not appear to scale in proportion to acuity measures (Levi *et al.*, 1984).

To estimate human cortical magnification Drasdo (1977) and Rovamo and Virsu (1979) used the assumption that M is directly proportional to the square root of the density of ganglion cell receptive fields. This does not agree well with all the available data (Cowey and Rolls, 1974) and must be seen as an approximation. An additional difficulty for the cortical scaling technique arises from Dow *et al.* (1981) and Van Essen *et al.* (1984) who have shown that monkey inverse cortical magnification is not proportional to mean cortical receptive field size, challenging the principle of cortical uni-

formity (Hubel and Wiesel, 1974, 1977). Psychophysical equivalence may depend upon scaling relative to cortical extent or relative to mean field size. In the central 10 deg, Levi *et al.* (1985) report that the change in performance with eccentricity in hyperacuity tasks can be related to macaque inverse cortical magnification while grating acuity can be related to cone density.

What is required is a means of obtaining a psychophysical indication of the changing spatial scale of peripheral vision as an alternative to methods which depend on measurements of anatomical or physiological variation across the visual field. Derived scaling functions can subsequently be related to the anatomy and physiology of the retino-striate pathway. We enlarged the retinal extent of a peripheral stimulus systematically by changing viewing distance to determine the spatial transformation required to produce a correspondence in visual performance across the visual field. We have applied this method to the lower threshold of motion (LTM) for gratings, and to a velocity matching task to determine whether the changes in apparent motion in the periphery could be related quantitatively to anatomical and physiological variation.

LOWER THRESHOLD OF MOTION SPATIAL SCALING FUNCTION

Methods

Techniques for measuring lower threshold of motion have been described previously (Johnston and Wright, 1985). A horizontal sinusoidal grating (contrast 0.5 and mean luminance 100 cd/m²) was viewed through a semi-circular aperture in a mask (mean luminance 40 cd/m²). The outer circular border of the grating patch was covered by a 5 mm overlay of tracing paper attenuating contrast at the grating edges. The radius of the grating aperture subtended 1.5 deg of arc at 300 cm and was positioned in the nasal visual field with fixation at the center of the straight, vertical edge for central fixation. Viewing was monocular and gratings were viewed in the nasal field of the dominant (right) eye. Spatial frequency and the angular subtense of the grating were varied conjointly by varying viewing distance. A fixation spot was placed at eye level along the line of sight at the same distance from the eye as the peripheral stimulus. The correct positions of oscilloscopes and fixation marker were readily determined by

placing them on a horizontal deck marked in polar coordinates centred on the eye.

LTM was measured by a method of adjustment. There were one 6 sec and five 4 sec periods during which the observer could control the drift rate of a grating by means of a multi-turn potentiometer. The frame rate of the grating display was 128 Hz. The rate of drift was increased during the first 6 sec interval until movement of the grating could just be discerned; the five 4 sec intervals allowed further fine adjustments of this setting, and the observation corresponding to the last interval was taken as the best estimate of threshold. Intervals during which adjustments could be made were interlaced with 4 sec periods in which the grating was held steady. Each data point is an average of four final threshold determinations of just discernable movement measured alternately in each of the two vertical directions of drift.

Results

Experiment 1

We measured lower threshold of motion (LTM) as a function of spatial frequency and eccentricity. The spatial frequency and angular subtense of grating patches were varied conjointly by varying viewing distance. This procedure provided a range of spatial frequencies from 1.5 to 12 c/deg for foveal stimuli and kept a constant 13.5 cycles on the screen throughout.

In Fig. 1(a), LTM, expressed as temporal frequency, is plotted against spatial frequency on log-log coordinates for a range of eccentricities in the visual field. Since velocity = temporal frequency · spatial frequency⁻¹, a line with a slope of one represents a constant velocity. LTM data points below the dashed line fell approximately along lines of constant velocity, confirming earlier studies (Johnston and Wright, 1983, 1985; Harris, 1985) which explored this stimulus range. At any eccentricity, the slope tended to increase for measurements at higher spatial frequencies. As expected, threshold velocity increased markedly with eccentricity; for a constant spatial frequency higher stimulus temporal frequencies are required to detect motion in the periphery.

The temporal properties of the visual system are invariant across the visual field (Koenderink *et al.*, 1978; Virsu *et al.*, 1982; Wright and Johnston, 1983, 1985a). Changes in apparent motion and motion threshold indicate therefore the variation in the spatial properties of the

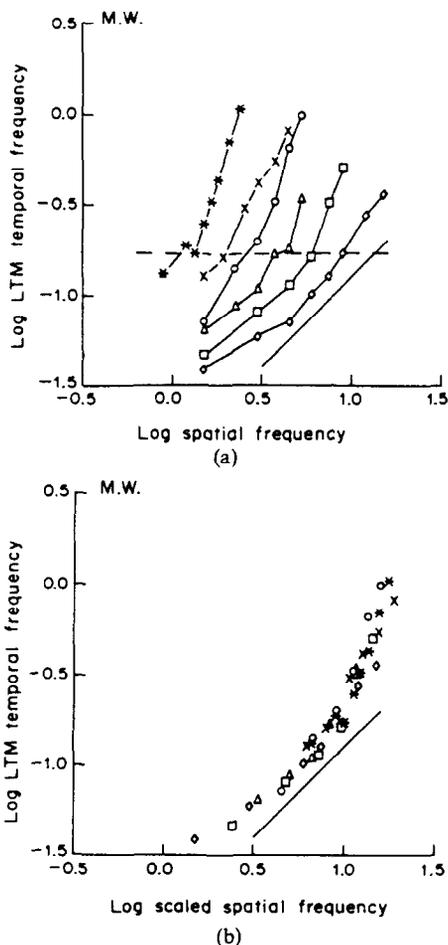


Fig. 1. (a) Lower threshold of motion (ordinate), expressed as temporal frequency, plotted as a function of spatial frequency (abscissa), for different eccentricities in the visual field. (Diamonds) = 0 deg. (squares) = 3 deg. (triangles) = 6 deg. (circles) = 10 deg. (crosses) = 16 deg. (stars) = 25 deg. Spatial frequency is varied by changing the viewing distance of the screen with the number of cycles on the screen kept constant at 13.5. The data are plotted on log-log coordinates. The slope of the solid diagonal line represents a constant velocity and horizontal line represents a constant temporal frequency. LTM data lie roughly along a line of constant velocity. (b) The same data have been transposed along the spatial axis until they superimpose. The amount of transposition required at each eccentricity gives the spatial scaling factor s .

visual system with eccentricity. We ask the question, if the temporal properties of a stimulus are kept constant, what spatial transformation will bring foveal and peripheral LTM functions into register? Peripheral LTM functions were matched to the foveal data by eye and the translation along the log spatial frequency axis recorded as the multiplicative scaling factor (s) for that eccentricity. Figure 1(b) shows the results of spatial scaling. The devi-

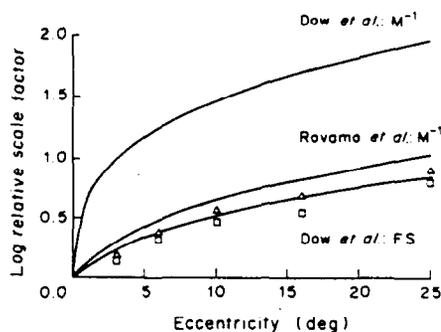


Fig. 2. Empirical spatial scaling factors for LTM are compared with scaling functions derived from primate cortical data and estimates of human inverse magnification: (triangles) = subject M.W., (squares) = subject A.J. Solid curves show, top; relative inverse cortical magnification [$M^{-1}(E)/M^{-1}(0)$] for macaque monkey (Dow *et al.*, 1981), middle; estimated human relative inverse cortical magnification (Rovamo and Virsu, 1979) and bottom; relative cortical receptive field width [$FS(E)/FS(0)$] from micro-electrode studies in macaque monkey (Dow *et al.*, 1981). The equations used were: $\log(M^{-1}) = 0.81 + 0.53x + 0.065x^2 + 0.079x^3$; $M^{-1}(0) = 2$ min/mm, $\log(FS^{-1}) = 1.14 + 0.19x + 0.071x^2 + 0.062x^3$; $FS(0) = 13.32$ min and $EM^{-1} = (1 + 0.33E + 0.00007E^3)EM(0)^{-1}$ where $x = \log(E) - 1.5$, M = cortical magnification, FS = cortical receptive field area^{1,2}, EM = estimated inverse magnification from the square root of ganglion cell density. E (eccentricity) and other measures are expressed with respect to minutes of visual angle in the first two equations and degrees of visual angle in the last equation.

ation from constant velocity threshold at high spatial frequency also shows spatial scaling. Note that when foveal and peripheral gratings are scaled to match the spatial grain of the visual field, lower motion threshold will be achieved at the same temporal frequency. The data could alternatively be expressed in scaled velocities by dividing temporal frequency by scaled spatial frequency ($f_s \cdot s^{-1}$).

In Fig. 2 the psychophysical spatial scaling factors from Experiment 1 are plotted against eccentricity. This is compared with a relative inverse magnification function [$M^{-1}(E)/M^{-1}(0)$] derived from Rovamo and Virsu's (1979) estimates of human inverse cortical magnification. Also included are a relative inverse magnification function derived from direct electrophysiological measurements of macaque cortical magnification [Dow *et al.*, 1981; $M(0) = 30$ mm/deg] and a similar treatment of mean receptive field size data taken from the same study. It can be seen that the scaling values for receptive field size are quite different from those for monkey cortical magnification. The Rovamo and Virsu (1979) scaling function

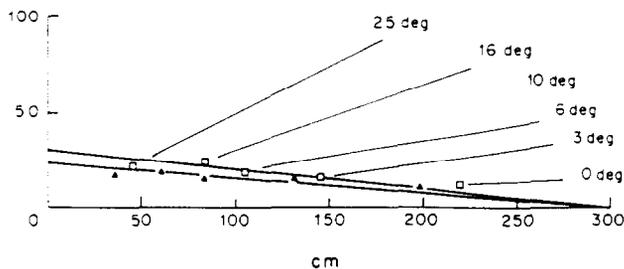


Fig. 3. Psychophysical scaling data plotted in the horizontal plane. The origin of the graph is the position of the eye, the x -axis represents distances in cm along the line of sight and the y -axis distances in cm along the axes orthogonal to the line of sight in the horizontal plane. Eccentricities along the horizontal meridian of the nasal field of the right eye are shown as lines radiating from the origin. Scaling distances ($300 \text{ s}^{-1} \text{ cm}$) for these eccentricities derived from the data of Fig. 1 are plotted (squares = M.W., triangles = A.J.). A straight line passing through the position of the foveal stimulus has been fitted to these data points by eye. The line through the data for A.J. has an aspect ratio of 10:1 and for M.W. 300:23. The scaling factor for each eccentricity lies close to a straight line in space passing through the fixation point and forming an acute angle with the line of sight. The graph can be understood as a plan view of the apparatus, in which the points represent the viewing distance for each eccentricity at which the stimulus must be placed for psychophysical equivalence.

differs substantially from the magnification scaling function but is close to the monkey field size scaling function. Although we can expect the absolute dimensions of the human and monkey striate cortex to differ, the relative scaling functions might be expected to be quite similar. The utility of the Rovamo and Virsu (1979) estimates may be in providing an approximate match between visual stimuli and mean receptive field size across the visual field.

A simpler description of our data can be arrived at by plotting the positions in the field of view which matches a physically invariant grating stimulus (as used in Experiment 1) to the psychophysically determined spatial scale of the visual system (Fig. 3). The points fall along a straight line making an acute angle to the line of sight at the location of the foveal stimulus. From Fig. 2 we can say that psychophysical scale factors covary with primate mean receptive field size. Combining Figs 2 and 3 it would appear that a physically invariant grating stimulus would match the spatial grain of the visual system as indexed by primate mean receptive field diameter if placed perpendicular to the eye along a line making an acute angle with the line of sight in our three-dimensional environment.

VELOCITY MATCHING

Methods

Two horizontal sinusoidal grating patches were viewed through semi-circular masked apertures with identical dimensions to those used in LTM determination. The mean luminance of

the gratings was 100 cd/m^2 . The standard grating stimulus was positioned in the nasal visual field with fixation at the centre of the straight, vertical edge. The distance of the standard grating was fixed at 300 cm. The adjustable grating could be placed at various distances and eccentricities in the nasal visual field. Again, viewing was monocular and subjects used their dominant, right eye. A darkened viewing enclosure and a chin and head rest was used to minimise distance cues (Brown, 1931). The spatial frequency and angular subtense of the test grating were, in most experiments, varied conjointly by varying viewing distance.

The task was to match the apparent velocity and direction of the peripheral grating to that of the standard stimulus. The observer could control the drift rate of the test grating by means of a multi-turn potentiometer. When a satisfactory match was achieved the subject initiated the next trial with a button press. Each trial consisted of 4 sec periods of grating motion interspersed with 4 sec periods with the gratings stationary. Generally, two or three such periods were required to achieve a setting. Ten or more trials were recorded automatically by computer and the mean displayed. The direction in which the standard grating drifted alternated 180 deg from trial to trial to guard against the build up of a directional after effect; the interspersed stationary grating served the same purpose. Pilot experiments revealed the importance of maintaining steady fixation while carrying out the velocity match. Tracking reduced the apparent velocity of the foveal stimulus (Brown,

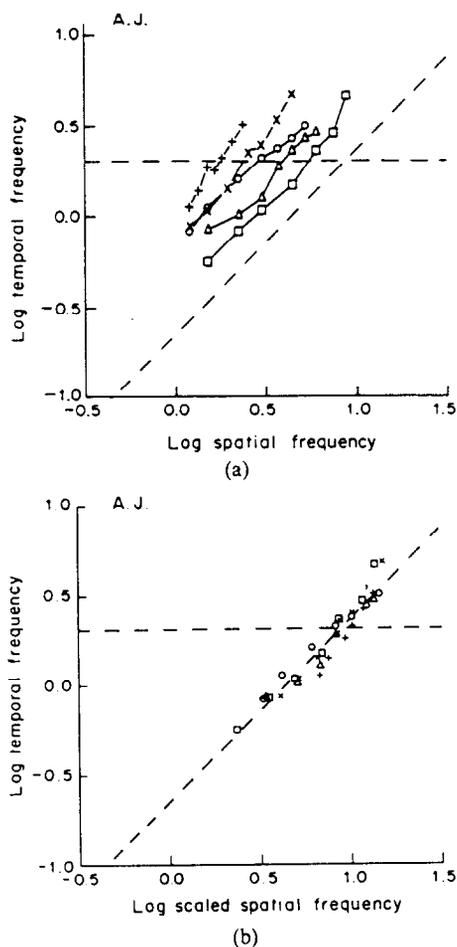


Fig. 4. (a) The temporal frequency of peripheral gratings whose apparent velocity is matched to that of a standard grating at the fovea (spatial frequency 9 c/deg, viewing distance 300 cm, temporal frequency 2 Hz) as a function of the spatial frequency of the test grating. The spatial frequency of the peripheral grating has been altered by varying viewing distance in the same way as in Fig. 1. Data are plotted on log-log coordinates. The dashed diagonal line represents the velocity of the standard grating and the dashed horizontal line represents its temporal frequency. Velocity matches have been made for eccentricities of 3 deg (squares), 6 deg (triangles), 10 deg (circles), 16 deg (X's) and 25 deg (crosses). (b) Data points have been transposed along the x -axis by the spatial scaling factors derived in Experiment (1). Each data point is the mean of 18 trials.

1931). The authors (A. J., M. W.) and one observer naive to the purpose of the experiments (A. McD.) served as subjects. Each experiment was conducted with at least two of the subjects. All had normal acuity (with appropriate refractive correction) and visual fields.

Results

Experiment 2

We measured the temporal frequency of peripheral gratings whose apparent velocity

matched that of a standard foveal grating as a function of the spatial frequency and eccentricity of the peripheral grating. The standard foveal grating, viewed at 300 cm, had a spatial frequency of 9 c/deg and temporal frequency of 2 Hz. At 300 cm the test grating matched the standard in all respects. The spatial frequency and angular subtense of the peripheral test grating were varied conjointly by changing viewing distance as in Experiment 1.

Figure 4(a) shows the temporal frequency of the test grating for a match to the standard as the spatial frequency of the test grating is varied by viewing distance, at each eccentricity. The velocity of the standard grating is represented on this graph as a line with a slope of one which passes through the point coincident with the standard temporal frequency (2 Hz) and spatial frequency (9 c/deg). For a given eccentricity, the temporal frequency of the test grating increases with spatial frequency according to a function with an approximately linear slope of one, showing the velocity of the peripheral grating required to match the foveal grating to be constant at a given eccentricity. Higher image velocities are required to match the peripheral stimulus to the foveal stimulus with increasing eccentricity as expected.

The data for eccentric viewing positions can be superimposed onto the standard velocity function [Fig. 4(b)] using the spatial translation function derived in Experiment 1. Thus the apparent velocity of a peripheral grating can be matched to that of a foveal grating by a purely spatial transformation of the retinal stimulus parameters of a peripheral stimulus with temporal parameters held constant. The scaling values determined psychophysically for LTM also apply to velocity matches. We have already seen that the LTM scaling function was close to the macaque relative field size function derived from Dow *et al.* (1981). Thus matching the spatial properties of moving gratings to monkey mean cortical receptive field size provides a psychophysical equivalence for both LTM and suprathreshold motion. An identical pattern of results was found for a standard grating of 9 c/deg and 6 Hz.

Experiment 3

There is a spatial scaling that can be applied to peripheral gratings so that central and peripheral gratings with the same temporal characteristics appear to be moving at the same velocity. Since subsequent experiments will in-

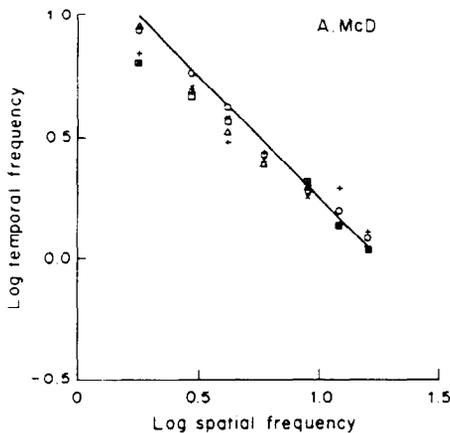


Fig. 5. The temporal frequency of test gratings (ordinate), placed at scaled viewing distances and different eccentricities (symbols as in Fig. 4), required to match the apparent velocity of a foveal standard grating, as a function of the spatial frequency of the standard grating (abscissa). The data are plotted on log-log coordinates. For subject A. McD. the peripheral grating is located at the average spatial scale distance for A.J. and M.W. (see Fig. 9). Each data point is the mean of 18 trials.

volve velocity matching with spatially scaled gratings we first confirm the findings of Experiment 2 that subjects match apparent velocities rather than veridical temporal frequency. Since the spatial frequency of rotating gratings influences angular velocity matches (Campbell and Maffei, 1979, 1981), an additional motive was to discover whether this finding extended to linear motion.

In Experiment 3 the temporal frequency and viewing distance of the standard grating was kept constant while its spatial frequency was systematically varied. The test gratings which had a spatial frequency of 9 c/deg at 300 cm were placed at the psychophysically determined spatial scaling locations for each eccentricity from Experiment 2. The temporal frequency of the peripheral grating for a satisfactory velocity match is plotted against the spatial frequency of the standard on log-log coordinates in Fig. 5. The velocity of the standard grating as a function of standard spatial frequency is shown as a solid line. The data points for a standard spatial frequency of 9 c/deg replicate Experiment 2; apparent velocity matches occur at a constant temporal frequency which is equal to the standard temporal frequency. When the velocity of the standard is changed to a different spatial frequency, apparent velocity matches continue to reflect the velocity of the test stimulus. The spatially scaled gratings are still related by a

constant temporal frequency but this now differs from the temporal frequency of the standard.

Experiment 3 confirms that matching occurs on the basis of apparent velocity not on the basis of veridical temporal frequency or some compromise between temporal frequency and velocity. The relative spatial frequency of test and standard gratings does not appear to have a significant influence on apparent velocity matches for linear motion.

Experiment 4

In this experiment the original finding that apparent motion is expressed relative to the changing spatial scale of the visual system is extended to a range of standard temporal frequencies. Peripheral gratings were placed at the spatial scaling locations. Central and peripheral gratings had the same display spatial frequency (13.5 cycles on the screen). In Fig. 6, The temporal frequency of the peripheral test grating is plotted as a function of the temporal frequency of the standard foveal grating (1, 3, 5 and 7 Hz). With appropriate spatial scaling data points for different eccentricities superimpose showing the finding to be independent of the temporal frequency of the standard across the range tested.

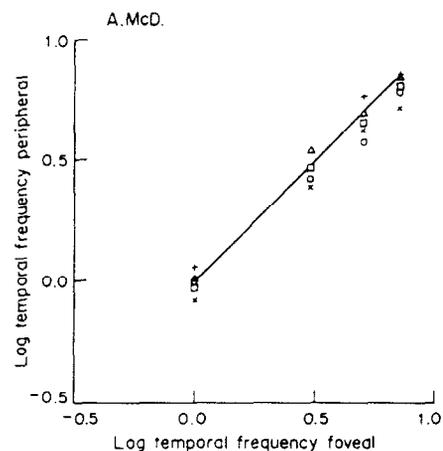


Fig. 6. The temporal frequency of peripheral test gratings, required to match the apparent velocity of a foveal standard grating, as a function of the temporal frequency of the standard foveal grating (1, 3, 5, 7 Hz). For subject A. McD. the peripheral gratings (symbols represent eccentricity values as in Fig. 4) are located at the average spatial scale distance for A.J. and M.W. (see Fig. 9). The solid diagonal line represents the prediction that a match for apparent velocity occurs when the temporal frequencies of central and peripheral gratings are identical. Spatial frequency of standard = 9 c/deg. Each data point is the mean of 18 trials.

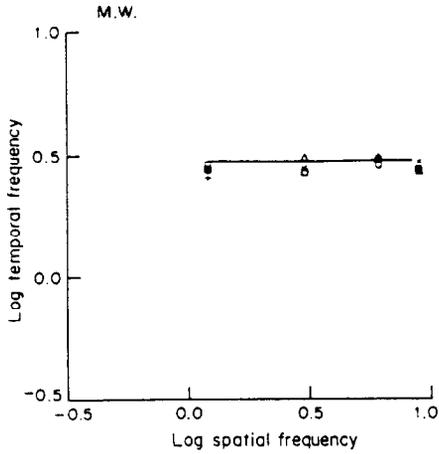


Fig. 7. The temporal frequency of peripheral gratings at psychophysically determined scaling locations (eccentricities as in Fig. 4) required to match the apparent velocity of a foveal grating for a range of standard spatial frequencies (1.2, 3, 6, 9 c/deg). Standard temporal frequency = 3 Hz. The match occurs at a constant temporal frequency regardless of the spatial frequency of the standard grating. Each data point is the mean of ten trials.

Experiment 5

Here the spatial scaling finding is extended to a number of standard spatial frequencies. At 300 cm the test grating matched the standard in all respects and spatial scaling of peripheral gratings was achieved by altering viewing distance. The solid diagonal line represents the prediction that for spatially-scaled gratings in the periphery, a match for apparent velocity occurs when the temporal frequencies of central and peripheral gratings are identical. In Fig. 7 we show the spatial scaling effect to extend to a range of base spatial frequencies.

Grating velocities in center and periphery appear matched when the spatial terms in the relation: $v = f_i \cdot f_s^{-1}$ are scaled appropriately with eccentricity. The main results of the study are

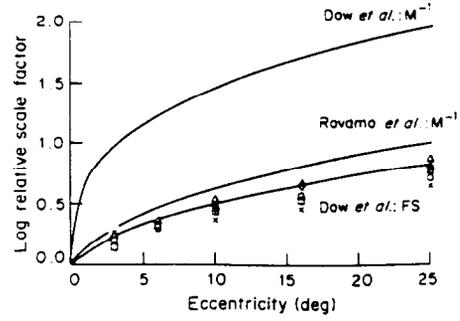


Fig. 8. Figure 2 is redrawn with the inclusion of spatial scaling values for apparent motion: (triangles) = LTM, M.W.; (diamonds) = velocity matching 2 Hz, M.W.; (squares) = LTM, A.J.; (circles) = velocity matching 2 Hz, A.J.; (crosses) = velocity matching 6 Hz, A.J.

summarised in Figs 8 and 9. Figure 8 collates the spatial scaling factors that have been determined psychophysically for lower threshold of motion and apparent velocity with separate derivation for Experiments 1 and 2 and both subjects. The data fall along the spatial scaling function derived from measurements of primate mean receptive field diameter (Dow *et al.*, 1981). The scaling factor (*s*) gives the ratio of the foveal stimulus distance to the distance of the peripheral stimulus from the eye required to provide the appropriately scaled retinal images for psychophysical equivalence.

To this point, as is usual in psychophysical studies, we have expressed stimulus dimensions and transformations in retinal terms since this is most appropriate for comparison with physiological and anatomical data. However a very simple interpretation of the data, which may offer a functional role for the variation in spatial grain with eccentricity, arises from a consideration of the physical properties of the stimuli. In measuring the position (or spatial scale factor) at which two physically identical gratings

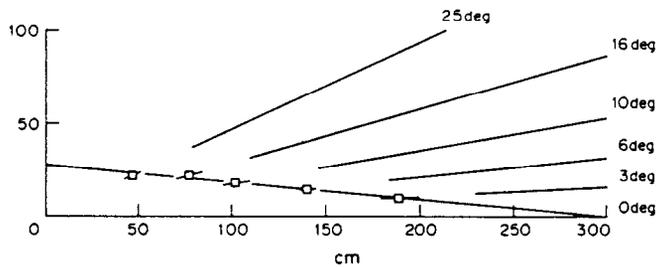


Fig. 9. Average spatial scaling distances using the data in Fig. 8, plotted as in Figure 3. The short line through each data point represents 1 SE above and below the mean. The straight line connecting the points has an aspect ratio of 300:28.

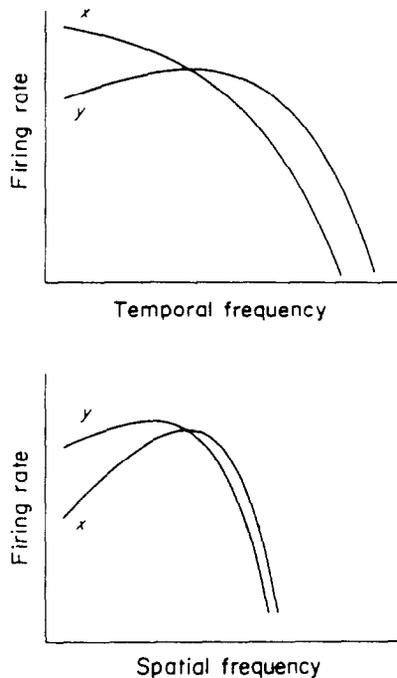


Fig. 10. Characteristic spatio-temporal filter functions for X-like and Y-like simple cells are plotted on arbitrary log-log axes. Following Marr and Ullman (1981) X-like and Y-like cells are assumed to combine smoothing and derivative operations and are modelled as spatio-temporal differentiating filters but we favour a different configuration and a ratio combination rule. $x_t = e^{-f_t}$, $x_s = f_s^2 \cdot e^{-f_s}$, $y_t = f_t \cdot e^{-f_t}$ and $y_s = e^{-f_s}$.

with the same temporal frequency have the same apparent velocity we also measure locations in the visual field where gratings with the same physical velocity appear to have the same apparent velocity. The relationship is a relative one but measured here with reference to a foveal grating at a distance of 300 cm. Figure 9 shows the average distance, with standard error bars, for which physically identical moving gratings appeared to have equivalent threshold for motion and equivalent apparent velocity. A straight line with an aspect ratio of 300:28 can be drawn through the data.

DISCUSSION

(a) Evidence for scaled encoding of velocity

Previous studies have demonstrated a decrease in apparent velocity with eccentricity in the visual field with a wide variety of stimuli (Lichtenstein, 1963; Campbell and Maffei, 1979, 1981; Tynan and Sekuler, 1981; MacKay, 1982). For example, Campbell and Maffei (1979, 1981) found that the apparent rotational velocity of

revolving patterns, including gratings, decreased with eccentricity as did the linear motion of a spot. Our results show that there is a similar decrease for linear motion of grating stimuli and that apparent velocities in the periphery are related to those in central vision by a spatial scaling factor. The same scaling factor applies across the range of grating motion tested.

Campbell and Maffei (1979, 1981) found when matching a test stimulus to a stimulus of constant angular velocity that apparent angular velocity first increased and then decreased with increasing test grating spatial frequency. Our results with linear motion of a grating behind an aperture do not show this effect. The matching velocity depended on the velocity of the standard and the eccentricity of the test stimulus and was independent of spatial frequency (Experiment 2). The independence from spatial frequency shown for LTM velocity (Johnston and Wright, 1983, 1985, present results) does break down at low contrast (Johnston and Wright, 1985) but grating contrast cannot explain the discrepancy since Campbell and Maffei used high contrast gratings. Regan and Beverley (1984) propose that separate mechanisms exist in the human visual system for the detection of linear and rotary motion. Campbell and Maffei's rotating grating is a complex stimulus in terms of the local analysis of linear components of motion and the precise cues utilised in judgements of rate of motion with their stimulus are probably different from those used in the present study. Changes in apparent motion with eccentricity however are consistent in both studies.

(b) Spatial scaling in the periphery

The scaling of velocity thresholds and matches with eccentricity admits at least two possible explanations. Thresholds may be equalised because scaled stimuli have an equivalent cortical extent or because they bear the same relation to the average spatial dimensions of cortical receptive fields. The electrophysiological data from macaque monkey (Dow *et al.*, 1981) used to generate the smooth curves of Figs 2 and 8 show that field size and inverse cortical magnification are not proportional contrary to the proposals of Hubel and Wiesel (1974) for parafovea and periphery. This has been confirmed for the macaque by Van Essen *et al.* (1984). Figure 8 collates spatial scaling factors from the lower threshold for motion and the velocity matching experiments for both

subjects. The data cluster around the scaling predictions from monkey cortical receptive field size data. This may be fortuitous but there are a number of reasons why a conclusion that spatial scaling matches stimuli to mean receptive field size might be warranted.

Firstly, while the absolute dimensions of receptive fields or striate cortex may differ between man and macaque and for individuals within species relative measurements might be expected to be similar. For the central 10 deg, direct estimates of human cortical magnification in the lower visual field made by Cowey and Rolls (1974) are consistent with monkey cortical magnification data (Levi *et al.*, 1985) and these measurements are good predictors of vernier acuity and stereoacuity (Levi *et al.*, 1985). If relative magnification is similar for man and macaque (Levi *et al.*, 1985) we might expect the relative variation in cortical field size in monkey and man to be similar.

The estimates of M by Rovamo and Virsu (1979) are based primarily on measurements of human ganglion cell density. M is assumed to be proportional to the square root of ganglion cell density, which is estimated from cone density in the macular area (Drasdo, 1977). In the cat, there is an approximate inverse relationship between ganglion cell field area and ganglion cell density (Peichl and Wässle, 1979) therefore the inverse of ganglion cell field diameter should be roughly proportional to the square root of ganglion cell density. If this was true of the primate, matching foveal and peripheral stimuli using Rovamo and Virsu's estimates of M^{-1} should primarily match visual stimuli to the gradient of ganglion cell receptive field diameter. We assume that since the sizes of ganglion cell dendritic fields in the cat (Peichl and Wässle, 1979) and in man (Rodieck *et al.*, 1985) fall into two discrete groups at any location in the retina, the relative, local, spatial gradient of the retino-cortical pathway at any level depends primarily upon ganglion cell morphology. Rovamo and Virsu's scaling function is of the right order but provides slightly higher values for spatial scaling than required for psychophysical equivalence in this study.

Finally Johnston and Wright (1985) argued that changes in apparent velocity with eccentricity must be explained with reference to the change in mean receptive field size. The finding that scaling factors for grating motion match the change in primate receptive field size is consistent with this view.

(c) *A ratio model*

A comprehensive model of motion analysis should account for both velocity encoding at a locus in the visual field and the gradual change in perceived speed with eccentricity. This second requirement provides an additional constraint on models of motion analysis which needs to be considered.

Velocity could be encoded by detecting spatial frequency and temporal frequency components in a moving image (Harris, 1980; Watson and Robson, 1981; Thompson, 1984) or encoded directly by a range of velocity tuned correlational detectors (Reichardt, 1961; van Doorn and Koenderink, 1982, 1983; van Santen and Sperling, 1984). In an identity coded system, the peak sensitivity of a single unit for some stimulus property "labels" a cell and the currently active cell within a population of labelled detectors governs sensory experience. Since a range of labelled detectors is required at any eccentricity there is no reason why identical foveal and peripheral stimuli should not activate identical labelled detectors. To accommodate changes in sensory experience with eccentricity an arbitrary renormalisation of peripheral labelled detectors would be required.

Alternatively, sensory experience might reflect relative activity in contrasting broad band velocity tuned units which had similar sensitivity to other sensory qualities like contrast or colour (Erickson, 1974). A shift in tuning towards higher velocities with eccentricity could explain our results but a velocity code may not be primary since striate cortical cells are spatio-temporally separable (Tolhurst and Movshon, 1975; Bisti *et al.*, 1985). Recent psychophysical evidence points to the existence of just two temporal frequency tuned components in the motion analysis system (Thompson, 1983; Moulden *et al.*, 1984) and the finding that the ratio of pattern to flicker threshold (Harris, 1980) is constant for a given stimulus velocity supports a constructive role for spatio-temporal filters in velocity encoding. However the problem of how a velocity coded system is constructed from spatio-temporal filters remains.

The spatio-temporal filter properties of striate cortical cells has been investigated and described. The velocity coding scheme outlined here utilises the response properties of spatio-temporally separable cells (Tolhurst and Movshon, 1975; Bisti *et al.*, 1985), with reciprocal spatio-temporal tuning (Ikeda and Wright,

1975) as found in area 17 in cat visual cortex. Figure 10 shows characteristic spatio-temporal frequency profiles for X and Y-like cortical simple cells drawn on log-log axes. Y-like cells, characterised by their transient temporal properties, are more responsive than X-like cells in the low spatial frequency range.

Notice that the ratio of Y-like to X-like simple cell activity tends to increase with velocity (Johnston and Wright, 1984). Since the response functions are drawn on a log-log graph the Y-like to X-like ratio is given by $y-x$. Clearly, with spatial frequency held constant the ratio of Y-like to X-like activity tends to increase with temporal frequency. With temporal frequency held constant the Y/X ratio tends to increase with decreasing spatial frequency. Thus increasing stimulus velocity by increasing temporal frequency and/or reducing spatial frequency increases the Y/X ratio. Since spatial and temporal influences combine multiplicatively in spatio-temporally separable cells the Y/X ratio will increase with stimulus velocity in an approximately monotonic fashion.

Because of the reciprocal relationship of band pass and low pass spatio-temporal filter functions, spatio-temporal information can be disambiguated and at the same time combined by computing the ratio of X-like and Y-like firing rates to give a signal which increases with velocity. This velocity coded mechanism would show independence from stimulus spatial frequency at superthreshold contrast and the scheme allows changes in perceived velocity with eccentricity to be explained in purely spatial terms. Motion is encoded relative to spatial grain with no compensation for the increased spatial extent of receptive fields and corresponding shifts in spatial tuning in peripheral X-like and Y-like cells.

(d) Optic flow

The visual system appears to make systematic mis-judgements about retinal image velocities. If there is one retinal location where image velocity is accurately encoded then there is a gradient of mis-information across the rest of the visual field. Like Campbell and Maffei (1981) we can turn to visual ecology in an attempt to find a functional role for this phenomenon. This apparent distortion is viewed from an ecological perspective taking locomotion as an example. If we look at a point along an even textured surface, texture elements close to the point of observation subtend a

greater visual angle at the eye (Gibson, 1950, 1979). During a lateral translation there is an increasing velocity gradient in the optic flow field from the fovea to the periphery. These image velocities are not encoded veridically since apparent velocity is influenced by retinal eccentricity. However, because of changes in apparent velocity with eccentricity, looking at some distance along the ground might compensate for the optic flow gradient and provide an invariant experience of motion across the visual field. Under these conditions our experience may reflect our motion relative to the environment rather than the variable retinal image velocities at the eye. Thus the grain of the visual system rather than causing sensory distortion may provide reliable information about our motion in a three-dimensional environment.

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