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RESEARCH ARTICLE

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Perceptual distortions in the neural representation of visual space

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Abstract The visual mechanism by which human observers determine the separation between objects has long been of interest. This study examines the extent to which separation in visual space can be misperceived in foveal and extrafoveal vision. Foveally, vertical separations were consistently overestimated relative to horizontal separations, a result which is consistent with the well-documented horizontal-vertical illusion (HVI). Extrafoveally, much larger misrepresentations of visual space were perceived. In addition, separations tangential to fixation were consistently perceived as being greater than separations in a radial direction. These marked misperceptions of visual space which occur in extrafoveal vision take the form of a radial/tangential anisotropy combined with an overestimation of vertical distance. The results have important implications for meridional anisotropies which have previously been documented in a number of visual performance tasks.

Key words Separation · Radial · Tangential · Anisotropy

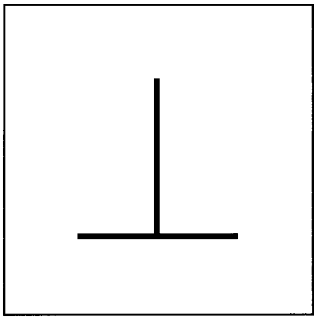
Introduction

The human visual system is acutely sensitive to comparisons involving spatial length or intervals (Westheimer 1979). Thresholds for such tasks are commonly smaller than the separation between foveal photoreceptors and less than 5% of the length of the interval being judged. The precision of such judgments has led to them being placed among a set of spatial discriminations given the group label “hyperacuity” (Westheimer 1979). While the fractional changes in length or spatial distance that human vision can detect are impressive, they should not lead one to conclude that the system displays a high level of absolute accuracy. Thresholds are related to the ability of an observer to detect a just-noticeable-difference in a physical parameter of the stimuli. The acute ability to perform such tasks often co-exists in the presence of large perceptual errors (Morgan et al. 1990). For example, it is known that normal human observers display a constant error in the estimation of spatial distance or length depending upon orientation. An example of this type of perceptual error is shown in Fig. 1. In this arrangement a vertical line is misperceived as being considerably longer than a horizontal line despite the two being of identical physical length. This well-known effect is often referred to as the horizontal-vertical illusion (Fick 1852).

Illusions are a ubiquitous feature of human spatial vision and have, for centuries, provided a perceptual window into processing mechanisms in the normal visual system. An understanding of such misperceptions is important, since examples of non-veridical visual performance provide a mechanism to infer relevant structural and processing limitations of early visual coding. Indeed, the legitimacy of models of early visual processing can be judged by their ability to explain classical illusions (Morgan and Moulden 1986; Lulich and Stevens 1989; Morgan and Casco 1990; Morgan and Baldassi 1997).

In the literature devoted to vision, meridional anisotropies are one of the most frequently encountered sets of misperceptions. Since the initial description of the horizontal-vertical illusion by Fick (1852), a number of studies have documented a perceptual asymmetry be-

Fig. 1 Example of the horizontal-vertical illusion. The vertical line appears perceptually longer than the horizontal line of the pattern, despite the fact that both are physically identical



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tween horizontally and vertically oriented visual stimuli (Valentine 1912; Künnapas 1955, 1957). Several theories have been advanced in an attempt to explain this perceptual phenomenon. These include the astigmatic theory of Valentine (1912) and the elliptical visual field theory of Künnapas (1957). However, none of the early theories provides a satisfactory explanation of the illusion. Furthermore, there is evidence that this type of meridian-dependent spatial misperception varies as a function of visual field location (Pearce and Taylor 1962; Pearce and Matin 1969; Thompson and Schiffman 1974) although a detailed investigation of this phenomenon has never been documented.

In this study, we measure misperceptions in spatial distance at the fovea, and extensively in the peripheral visual field. These data are used to construct a plot of the compressions and expansions normally encountered in the neural representation of visual space. Finally, the underlying structure of physiological mechanisms in the visual pathway, and their role in generating these misperceptions, is discussed.

Materials and methods

Stimuli

Observers were presented with two luminance-defined Gaussian patches, separated by a baseline separation at one of four orientations [horizontal (0°), oblique right (45°), vertical (90°) and oblique left (135°)]. Each of the four orientations is represented in Fig. 2. The cross indicates the observer's fixation point under conditions of peripheral viewing. The mathematical description of the Gaussian patches is given by:

$$L_{\mathrm{mean}}+A\exp(-(x^2+y^2)/2\sigma^2) \quad (1)$$

where L_{mean} is the mean luminance of the background, A is the luminance amplitude and σ is the standard deviation of the Gaussian envelope. The vertical and horizontal distances from the peak of the Gaussian envelope are denoted by x and y.

Stimuli were generated using the macro capabilities of the public domain software "NIH Image 1.61 ppc" (developed at the U.S. National Institutes of Health and available from the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from the National Technical Information Service, Springfield, Virginia, part number PB95–500195GEI). Stimuli were presented on a CTX 17" colour monitor at a mean luminance of 22 cd/m^2 and a frame rate of 75 Hz. The non-linear luminance response of the display was linearised using the inverse function of the luminance response as measured with a Minolta CS-100 photometer. The host computer was a Power Macintosh 7200/90.

Procedure

On a single 200-ms presentation, any one of seven predetermined separations was displayed for each orientation. Following each presentation the subject was required to indicate whether the separation was perceived to be greater or smaller than the mean of all the previous presentations (Westheimer and McKee 1977; Morgan 1992). The results of the first 20 trials were discarded to allow the subjects to construct their own internal metric with which to compare each trial. Tasks such as this, in which a single standard is maintained across a dimension such as orientation, can be performed with relative ease. The alternative situation is outlined by Morgan (1992), who has shown that observers can maintain appropriate discrimination of multiple concurrent standards. Bootstrap analysis (Foster and Bischof 1991) was applied to the resulting psychometric functions for each orientation to define the point of subjective equality (50% response level) and the threshold (difference between the 84% and 50% response levels).

The experiment was conducted monocularly with the stimuli centred on fixation (foveal condition) and also centred at 32 extrafoveal locations – 8 equally spaced visual field meridia at 4 eccentricities (1.875°, 3.75°, 7.5° and 15°). Increases in eccentricity were achieved by keeping peripheral fixation constant and changing viewing distance. The separation of the Gaussian blobs as a function of increasing eccentricity was therefore 1.25°, 2.5°, 5° and 10°.

Observers

The two authors acted as observers. Each observer used their dominant eye for observation and undertook several practice sessions prior to data collection. Experimental trials were carried out in a dimly lit room to avoid monitor reflections. Both observers were pre-presbyopic and wore appropriate distance refractive correction where necessary. No additional refractive correction was provided for peripheral observations since off-axis aberrations have a minimal effect on peripheral visual performance over the central 25° of the visual field (Jennings and Charman 1981).

Results

Foveal data

Analysis of the point of subjective equality (PSE) from the foveal psychometric functions is used to provide a measure of the perceptual bias or magnitude of the illu-

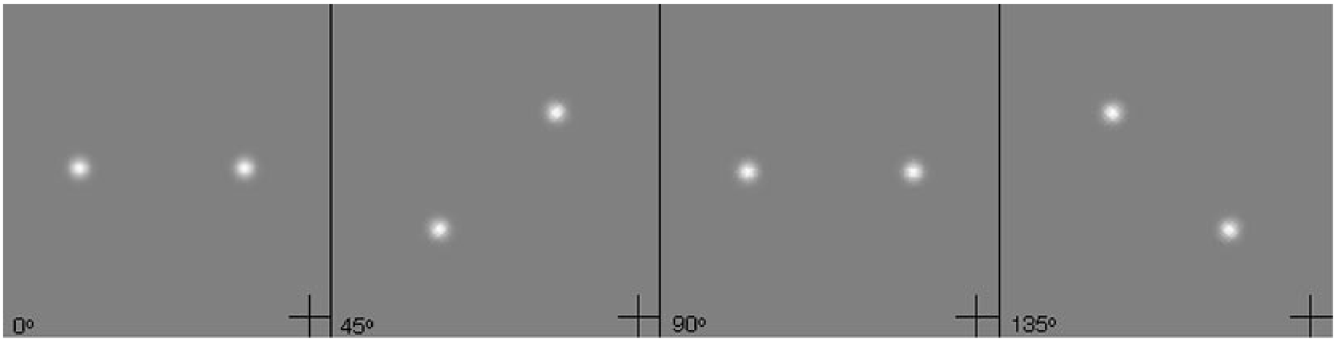

Fig. 2 Examples of the Gaussian patch stimuli used in the experiment. Two patches were presented in one of four possible orientations (horizontal, oblique right, vertical, oblique left). The *cross in the bottom right-hand corner* of each pair of stimuli represents the observer's fixation point for peripheral viewing at one visual field position

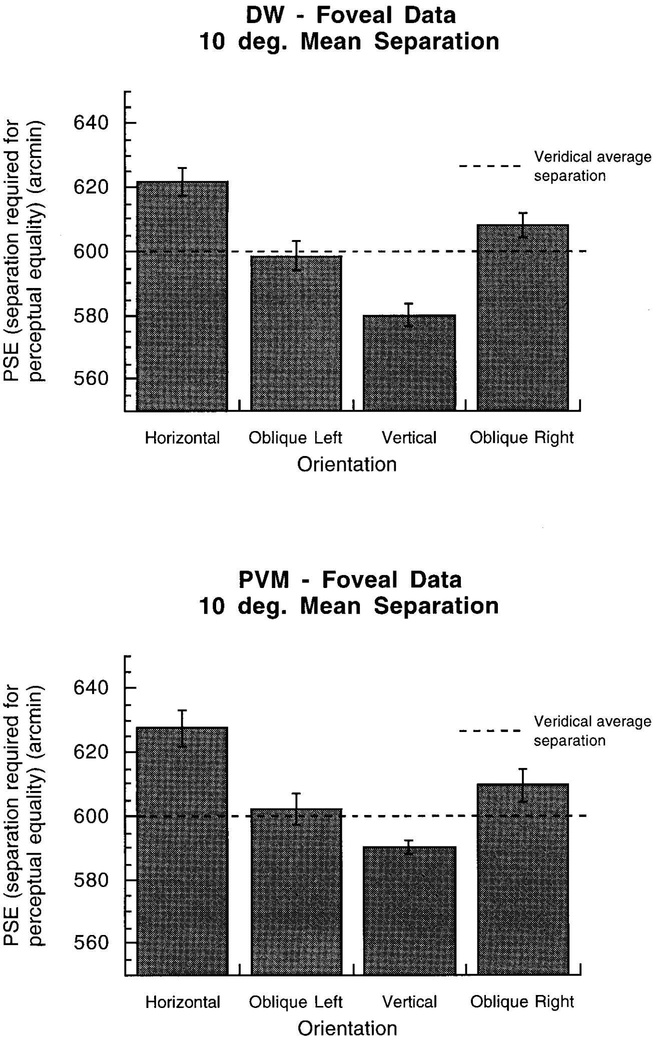

Fig. 3 Orientational misperceptions of spatial separation in foveal viewing for two subjects. The graph indicates that for both subjects, a horizontally orientated pattern must be physically larger in order to appear perceptually equivalent to a vertically oriented pattern. Oblique separations fall in between perceived horizontal and vertical separations

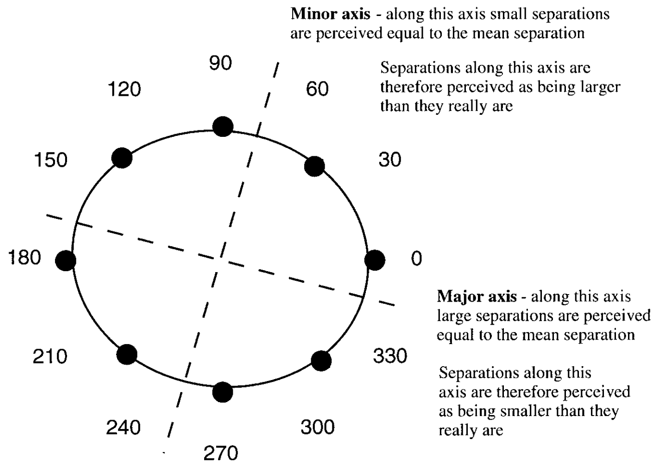

Fig. 4 An ellipse was fitted by a method of least squares to the combined data for the four stimulus orientations (horizontal, vertical, oblique right and oblique left). From this procedure, the magnitude of the overestimation of spatial separation in percentage terms (difference in PSEs between major and minor axes divided by the mean PSE) and the orientation at which the misperception is greatest (the minor axis of the ellipse) are derived (see text for details)

sion. For stimuli centred on the fovea (Fig. 3), a larger separation is required in the horizontal meridian in order to be perceptually equivalent to a vertical separation. This is consistent with the horizontal-vertical illusion (HVI). The data of Fig. 3 represent an HVI of 6.9% for subject DW and 6% for PVM for a baseline separation of 10 deg. The magnitude of the foveal illusion for both observers remained relatively unchanged for other baseline separations. Along oblique meridia (oblique left and oblique right), separations are perceived as having a magnitude somewhere between the vertical and horizontal meridional separations and close to the veridical separation.

Thresholds refer to the ability of the observer to perceptually detect just-noticeable-differences in the stimuli, and represent the accuracy with which objects in visual space may be localized. For foveal spatial interval discrimination Weber's law for position is known to hold (Levi et al. 1988), dictating that thresholds are directly proportional to the separation giving rise to the threshold. This permits thresholds to be conveniently expressed as Weber fractions (threshold/separation). Foveal thresholds for interval discrimination were measured at four different baseline separations (1.25°, 2.5°, 5° and 10°) and, averaged across separation, gave a mean Weber fraction of 6.1% and 5.1% (for observers PVM and DW respectively). The size of the illusion in foveal vision is therefore slightly greater than the threshold (expressed in Weber terms) for discriminating perceptual changes in the magnitude of the spatial interval.

Extrafoveal data

Extrafoveally, analysis of the PSEs reveals much larger misrepresentations of visual space (at least 20%). Furthermore, these misperceptions were not necessarily consistent with the HVI, but instead depended upon the orientation of the separated blobs relative to fixation. In order to quantify the magnitude and the orientation of these misperceptions, ellipses were fitted to the PSE separation data of the four oriented stimuli (horizontal, vertical, oblique right, oblique left) by a method of least squares (Fig. 4). The elliptical function fitted to the data from the four stimulus orientations is given below:

$$(\delta\mathrm{PSE}\times\sin^2(\alpha-\alpha_{\mathrm{minor}}))+(\mathrm{PSE}_{\mathrm{mean}}-(\delta\mathrm{PSE}/2)) \qquad (2)$$

where $\mathrm{PSE}_{\mathrm{mean}}$ represents the mean PSE across orientations, $\delta\mathrm{PSE}$ represents the difference in PSE between its maximum and minimum values, α is the orientation of the stimuli and α_{minor} is the orientation at which the PSE

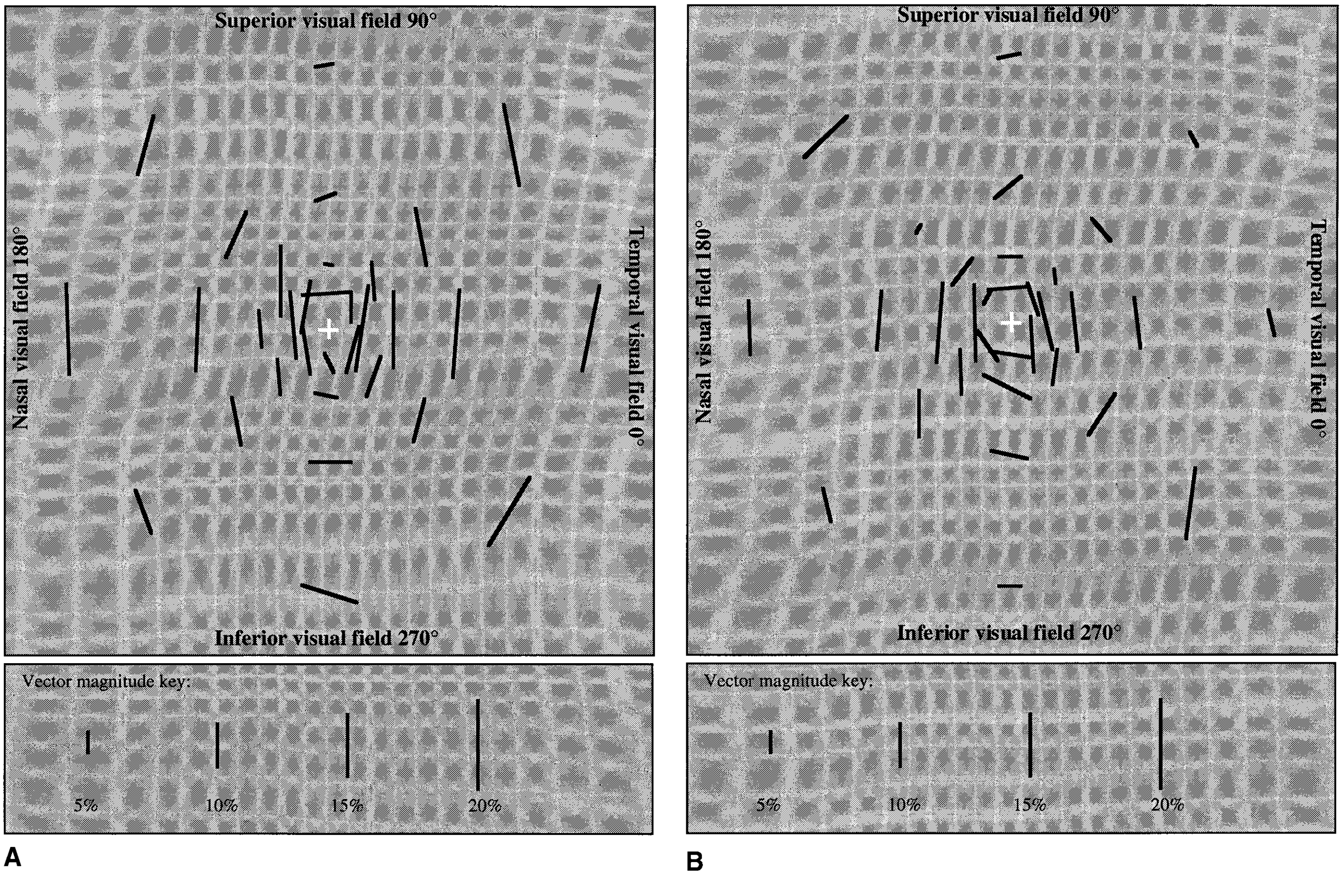

Fig. 5 Field plots of spatial misperceptions in separation for subjects DW **(A)** and PVM **(B)**. The length of the vector is related to the size of the misperception, and can be graded from the key provided below the field plots. The orientation of the vector represents the meridian where the misperception of separation was greatest

is at a minimum, i.e. the orientation at which separation is perceived as being greatest (Fig. 4).

From this, the magnitude of the misperception was calculated in percentage terms as:

$$\frac{\delta \mathrm{PSE}}{\mathrm{PSE}_{\mathrm{mean}}} \times 100 \qquad (3)$$

Vectors corresponding to the percentage magnitude and direction of the overestimation of spatial separation are plotted in Fig. 5A,B. These figures show field plots of the magnitude and orientation of spatial misperceptions in the 32 extrafoveal field locations examined. For clarity, the foveal data have been omitted from both plots, but lie between 4.5% and 7% for each baseline separation and are oriented either vertically or very close to the vertical (i.e. the traditional HVI).

Despite an overall vertical dominance, the vectors representing the more extrafoveal field locations demonstrate a tendency towards a tangential arrangement with regard to fixation. Interestingly, the vectors along the vertical midline are oriented close to the horizontal meridian (i.e. horizontal separations are perceived as larger than vertical – a reversal of the traditional HVI). The plots of both observers show qualitatively similar effects. The magnitude of the illusion was significantly greater in the lower visual field than the upper visual field for one observer (PVM $F_{1,11}$=15.82, P=0.002), but not for the other (DW $F_{1,11}$=0.065, P>>0.05). This highlights inter-individual differences in the extent of spatial anisotropies, which have been a feature of a number of previous studies (Yap et al. 1987; Bennett and Banks 1991; Toet and Levi 1992).

Thresholds also demonstrated a tendency towards a radial/tangential arrangement. When expressed in Weber terms, thresholds were fairly constant across eccentricity (approximately 6%). Both radial and tangential thresholds at each eccentricity were examined along the four principal meridians (vertical, horizontal, oblique right, oblique left). A repeated measures analysis of variance showed that thresholds for stimuli oriented radially were significantly lower than those oriented tangentially to fixation (PVM $F_{1,7}$=9.10, P=0.019; DW $F_{1,7}$=11.67, P=0.011). No significant differences in thresholds were found between different meridia (vertical, horizontal or either oblique) (PVM $F_{3,21}$=0.89, P>>0.05; DW $F_{3,21}$=0.54, P>>0.05). In addition, there was no significant interaction effect between meridian and stimulus orientation (PVM $F_{3,21}$=2.78, P>0.05; DW $F_{3,2}$=0.61, P>>0.05), indicating that the radial/tangential differences in threshold were maintained across meridia.

Discussion

Marked misperceptions of visual space occur in extrafoveal vision. These appear to take the form of a combination of horizontal/vertical and radial/tangential anisotropies. Along the horizontal meridian, these individual anisotropies summate to produce large overestimations of vertical visual space. Along the vertical meridian, the traditional HVI is reversed to produce an overestimation of horizontal visual space. Thus, depending upon the visual field location, this radial-tangential illusion can enhance, diminish, or even reverse the HVI.

Contrary to previous reports involving other length misperceptions (Morgan et al. 1990), we find that changes in perceptual bias are accompanied by concurrent changes in threshold. The results show that tangential expansions of visual space are accompanied by an increase in thresholds for stimuli oriented tangentially to fixation. Therefore, the processes which cause the perceptual bias in spatial interval tasks subsequently add uncertainty to the observers' judgements in the same direction as the bias. This is perhaps to be expected, given that spatial interval thresholds are known to be directly proportional to separation. Any perceptual increase in separation would therefore be expected to affect threshold, provided the misperception arose at a relatively early stage of visual processing.

Previous examinations of length judgements in the peripheral visual field have suggested that the horizontal-vertical illusion may be combined with a radial-tangential illusion to produce the perceptual output (Pearce and Taylor 1962). The present study adds weight to this proposal with both observers showing an overall vertical dominance in their maps. Whereas previous studies were unable to conclusively establish the presence of this phenomena due to the limited number of test positions (Pearce and Taylor 1962; Thompson and Schiffman 1974), our present data confirm the existence of a combined radial/tangential and horizontal/vertical illusion across the central visual field. The reversal of the horizontal-vertical illusion along the vertical meridian was previously reported by Pearce and Matin (1969). However, this reversal was asymmetric, occurring to a greater extent in the superior field than the inferior field. Moreover, the reverse illusion increased in magnitude as a function of vertical eccentricity. Interestingly, Pearce and Matin (1969) also reported reverse illusions along the horizontal meridian. In contrast, the present study finds a reverse illusion only along the vertical meridian and the magnitude of the reverse illusion remains reasonably constant across eccentricity.

Neurons involved in the early stages of visual processing do not show true orientation specificity as the term is understood when applied at a cortical level. However, there is considerable evidence to show that the receptive fields of retinal ganglion cells (Rodieck and Stone 1965; Levick and Thibos 1982) and lateral geniculate neurons (LGNs) (Vidyasagar and Urbus 1982; Shou et al. 1986) show an orientation bias. This bias is commonly greater for radial orientations, i.e. stimuli which are oriented parallel to a line connecting the receptive field centre and the centre of the visual field (Levick and Thibos 1982; Vidyasagar and Urbus 1982). Furthermore, other studies have shown that the major axis of the dendritic fields of retinal neurons is elongated in a radial direction with respect to the area centralis in cats (Leventhal and Schall 1983) and the fovea in humans and macaque (Rodieck et al. 1985; Schall et al. 1986). Interestingly, the over-representation of orientations radial to the centre of the visual field is preserved beyond the retina and LGN into the visual cortex itself (Leventhal 1983, 1984). The level in the visual cortex to which this representation is maintained is a matter of some debate, but the relationship is preserved at least as far as the primary visual cortex of cats and monkeys (Payne and Berman 1983; Bauer and Dow 1989).

The neurophysiological evidence outlined above allows us to construct a physiologically plausible model for peripheral radial-tangential anisotropies. The details of the model are outlined in Fig. 6. The assumption is made, based on neurophysiological data, that the neural representation of the radially elongated dendritic fields is maintained in the visual pathway up to the level at which separation discrimination takes place. Schematic neural units corresponding to the neural representation of elongated dendritic fields are represented by overlapping ellipses (see Fig. 6). The aspect ratio of each neural unit is derived from that of the elongated dendritic fields reported by Schall et al. (1986). Superimposed on each array of neural units are two bar stimuli – each bar is identical in size but oriented orthogonally. The linking hypothesis of the model is that perceived size or distance is related to the number of neural units stimulated by an object falling on it. For example, in Fig. 6, the array oriented along the horizontal has a cross pattern, stimulating neural units in both the horizontal and vertical directions. Due to the radial elongation of the neural units, the vertical bar covers a greater number of units than the horizontal bar (Fig. 6A). The presumed perceptual consequence of this pattern of stimulation is that vertical space appears expanded relative to horizontal space. Since the elongation of the neural units is always radial to fixation, as the visual field location is changed the expansion of space changes from a vertical/horizontal anisotropy along the horizontal meridian to a tangential/radial anisotropy, where a tangential expansion of visual space is present relative to radial orientations (Fig. 6B,C). The model outlined in Fig. 6 also indicates scale invariance of the perceptual distortions of spatial metric. Figure 6 shows a smaller array closer to fixation along the horizontal orientation. If scale invariance holds, one would expect the magnitude of the illusion, in percentage terms, to remain approximately uniform as eccentricity is increased along a particular meridian. Examination of the field plots for both observers (Fig. 5A,B) shows that the magnitude of the illusion is indeed relatively constant with increasing eccentricity.

Another factor which warrants consideration is radial stretching of the retina during eye growth (Cheng et al.

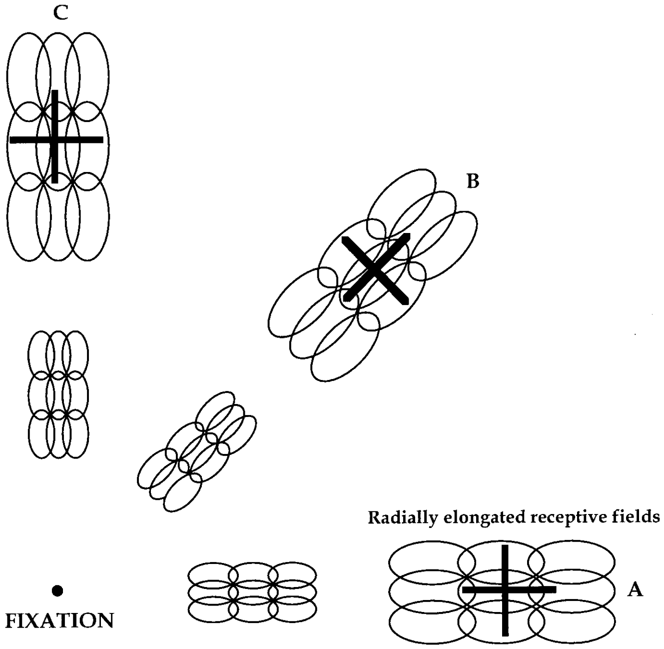

Fig. 6A–C A model of radial/tangential anisotropies. Visual space is tiled with the receptive fields of neural units. The fields are oriented and elongated in a radial direction. The neural unit aspect ratios (2) have been taken from elliptical fitting procedure of *P*-alpha (aspect ratio=2) and *P*-beta (aspect ratio=1.5) ganglion cells carried out by Schall et al. (1986). **A** A cross pattern impinges the array. Due to the spatial arrangement of the fields in the array, the vertical limb of the pattern stimulates more neural units than the horizontal limb. The consequence of the differential activity is that the perceptual size of the vertical limb is increased. **B, C** As the fields of the neural units are always oriented towards fixation, a change in the visual field location results in an increase in the number of tangential neural units being stimulated relative to units oriented in a radial direction. Scale invariance of this expansion of visual space is a result of having symmetrically scaled arrays closer to fixation

1992; Troilo et al. 1996). This may cause the spacing between retinal units to be increased in a radial orientation but maintained in a tangential orientation. If this radial separation increase is preserved in the neural representation at a higher level, similar effects to those produced in the model would be predicted. In Fig. 6A the elliptical units would be separated in a radial direction but their spatial relations would be maintained in the tangential direction. It would be of interest to investigate the peripheral radial/tangential anisotropies reported here in axial anisomyopes (subjects who are more myopic in one eye than the other), who will have differing amounts of retinal stretch in each eye, to examine the influence of this factor on the magnitude of the illusion.

Schall et al. (1986) attempted to ascertain whether the orientation of each dendritic field was related to its position on the retina. To do this they calculated the angular difference between the orientation bias of the dendritic field and the polar angle of a line connecting the centre of the field to the centre of the fovea. They found that, although there was a significant tendency for the dendritic fields to be oriented radially to the fovea, there was a tendency for most cells to be oriented more horizontally than their polar angle (Leventhal and Schall 1983). The consequence for the model of this horizontal bias in neural representation is that the radial-tangential anisotropies found in the peripheral visual field are likely to be combined with an overall expansion of vertical space. This would seem to be confirmed in the spatial field plots of both observers (Fig. 5), who show an overall dominance in vertical expansion. Another interesting aspect of the study by Leventhal and Schall (1983) is that radial elongation of dendritic fields, and presumably their neural representation, is greatest for cells on or close to the horizontal meridian. This would predict that the greatest perceptual expansions of visual space should be located along the horizontal meridian, and smaller expansions should be found along the vertical meridian. Inspection of the plots of both observers indicates that this prediction is qualitatively borne out in the psychophysical data.

The radial/tangential anisotropies reported here carry considerable implications for visual experiments conducted in the peripheral visual field. Visual researchers almost invariably quantify the size, separation, spatial frequency, velocity, etc. of their stimuli on the basis of their angular subtense at the eye, thereby representing stimuli according to an optical definition of spatial magnitude. As the present data show, perceptual visual space is compressed or expanded relative to optical space depending upon the visual field location and the meridian of interest. Visual field location therefore becomes an important consideration when using oriented stimuli.

Meridional anisotropies have been shown to occur in a number of spatial tasks. Fahle (1986) reported that the ability to detect curvature of a line was superior when the line was oriented towards the fovea. Performance was therefore found to be optimal when the discrimination cue was oriented tangentially to fixation. Similar findings are reported by Yap et al. (1987), who used a three-dot bisection task oriented either radially or tangentially to fixation. Performance was significantly better when the three dots (and therefore also the spatial offset required to solve the task) were oriented tangentially to fixation. Scobey and van Kan (1991) measured the ability to detect spatial displacements of a small object within the visual field. Once again, displacements in a tangential direction were more reliably identified than orthogonal displacements. In addition to these positional tasks, anisotropies have also been reported in spatial resolution. Both Rovamo et al. (1982) and Temme et al. (1985) reported that resolution performance was significantly better for gratings whose orientation pointed towards fixation. The same findings also hold for the discrimination of symmetry using compound gratings (Berardi and Fiorentini 1991; Bennett and Banks 1991).

Interestingly, all of these previously documented anisotropies are qualitatively predictable from the anisotropies of visual space presented here. However, attempts to provide quantitative analysis are confounded by two major factors. Firstly, there exist substantial inter-individual differences in the extent of the meridional anisotropies in several of these tasks (Yap et al. 1987; Bennett and Banks 1991; Toet and Levi 1992). Secondly, there are conflicting views as to the range of eccentricities over which anisotropies exist. The majority of reports document a consistent orientation anisotropy across the visual field (Temme et al. 1985; Yap et al. 1987; Scobey and van Kan 1991; Toet and Levi 1992). However, it has also been reported that anisotropies are maximal close to the fovea (Berardi and Fiorentini 1991), or alternatively can only be found at relatively large eccentricities (Rovamo et al. 1982).

When one takes into account the perceptual distortions of visual space which we have reported, the large body of psychophysical anisotropies described above are not, in themselves, surprising. Instead, such findings are to be expected given the discrepancy between optical and neural definitions of visual space, an observation supported by both physiological and psychophysical considerations.

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