Relative localization in the human fovea: radial–tangential anisotropy

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A distinction is drawn between two intrinsic directions within a simple spatial configuration. The line joining two elements is the radial direction and orthogonal to it is the tangential direction. Separation and bisection discrimination and just-detectable differences in line length are examples of radial thresholds. Vernier and alignment detection are tangential thresholds. Neural processing along these two intrinsic directions differs. There is a strong ‘oblique effect’ for tangential thresholds and virtually none for radial thresholds. Flank interaction impairs tangential but not radial thresholds.

Keywords: oblique effect; vernier; orientation discrimination; bisection; inhibitory interaction

1. INTRODUCTION

Our capability for perceiving simple geometrical relationships within a small target configuration is remarkable and far better than if it were based solely on the spatial local signatures of individual retinal receptors. This hyperacuity is the result of sophisticated signal processing, the detailed neural apparatus of which is still largely unexplained.

In the first instance two kinds of these fine visual spatial discriminations can be distinguished. The first is exemplified by vernier acuity, which is judgement of the alignment of two picture elements; here the discrimination concerns the direction at right angles to the line joining the elements. An example of the second is discrimination of the elements’ separation, i.e. the length of the real or virtual line joining them. In a detailed investigation, Westheimer & McKee (1977*b*) were able to show that, under optimal conditions, the thresholds for these two tasks are the same and that their performance puts both in the hyperacuity class.

In the simplest scheme it might be supposed that these discriminations start with determination of the absolute position of each picture element within the sensory manifold. However, vernier acuity, for example where the alignment of two collinear lines can be judged with a precision of up to one-tenth of a receptor’s diameter, evidently does not fit a scheme in which locations are firmly established first and their spatial relationship subsequently extracted. Several lines of evidence are relevant here.

- (i) Relative localization is seriously distance dependent, being impaired as the separation of the elements increases beyond 8–10 arcmin in the fovea (Westheimer & McKee 1977*b*).
- (ii) Even a 30–50 ms asynchrony of the onset of the components reduces thresholds (Westheimer & McKee 1977*a*).
- (iii) Performance is robust to common motion of the whole configuration, which can slip across at least 100 receptors in 200 ms without deterioration of thresholds (Westheimer & McKee 1975).

Thus, one is led towards the view that there is dynamic processing of a configuration as a group based on a set of

synchronous signals from its elements. In order to simplify the terminology and, at the outset, decouple the inherent geometry of the stimulus from the meridian–eccentricity polar coordinate framework usually applied to the retina, the word *radial* is assigned here to the direction separating two picture elements and the word *tangential* to the orthogonal direction, e.g. that of misalignment of vernier stimuli. The radial and tangential directions are orthogonal but intrinsic to the configurations, the relative locations of the elements of which are being judged, i.e. the coordinate axes are ordained by the stimuli themselves, regardless of orientation and retinal location (figure 1*a*).

In a general examination of the cues for spatial arrangement, Watt (1984) came to the conclusion that the radial and tangential dimensions (he used the term orthoaxial for the latter) have to be dealt with separately. Here, a further question is raised of whether, because of the similarities in threshold, the processing of vernier and bisection tasks, which are emblematic of the two dimensions, is subserved by the same kind of neural substrate. There is some evidence against this view. For example, contrast reduction impairs vernier acuity and separation discrimination unequally (Morgan & Regan 1987; Westheimer *et al.* 1999). Improvement through training in the retinal periphery in one of these tasks does not transfer to the other (Crist *et al.* 1997) and, to the extent that they play a role here, the contextual interactions in the primary visual cortex, where receptive fields are elongated, are not the same when tested along the preferred orientation of the cell or lateral to it (Kapadia *et al.* 2000).

The present study reports on experiments that show two additional differences in signal processing in the two intrinsic, spatial, cardinal directions of a stimulus. One involves the ‘oblique effect’, i.e. impairment in visual performance when the orientation of the task is not in the retinal horizontal or vertical meridians. Line orientation (Orban *et al.* 1984), line vernier (Corwin *et al.* 1977), grating contrast (Camisa *et al.* 1977), grating resolution (Emsley 1925) and angle (Heeley & Buchanan-Smith 1996) are among the visual discriminations that manifest an oblique effect. The other type of test applied in examining possible differences in performance for the radial

Figure 1. (a) Schematic diagram illustrating the concept of the two cardinal directions intrinsic to a stimulus configuration. For simplicity, a two-dot configuration is used at an arbitrary orientation and in an arbitrary retinal location. The line joining the two elements defines the radial direction. Separation discrimination, line-length discrimination and bisection are examples of thresholds in the radial direction. Orthogonal to the latter is the tangential direction. Vernier and alignment discrimination exemplify tangential thresholds. (b) Configurations used in tangential thresholds. (i) Orientation discrimination of lines. (ii) Two-dot vernier pattern. (c) Configurations used in the experiments involving radial thresholds. (i) Three-line bisection thresholds. (ii) Length discrimination of a line. (d) Five-dot pattern used in the experiment described in §3(b). In the null position, the outer dots are 10 arcmin from the centre and there is strict horizontal and vertical alignment. Bisection measurements involve a common horizontal displacement of the three vertically aligned dots. The task is the detection of the direction of displacement of the central dot with respect to two outer horizontal dots, which remain fixed; the two outer vertical dots are displaced along with the centre dot. Alignment thresholds involve the common horizontal displacement of the three horizontally aligned dots. Judgement is of the alignment of the central dot with respect to the two outer vertical dots, which remain fixed; the two outer horizontal dots move along with the centre dot. The two control experiments are pure bisection (using only three horizontally arrayed dots) and pure three-dot alignment (using only three vertically arrayed dots).

and tangential directions is the use of interaction phenomena, in which neighbouring stimuli interfere with discrimination. It will be seen that both of these tools help in distinguishing the radial from the tangential processing mechanism.

2. METHODS

Observers were shown patterns on computer monitors for 300 ms and had to make a binary discrimination in each trial. Each trial consisted of the presentation of a comparison pattern followed by the test pattern after an interval of 600 ms. The method of constant stimuli was used in which at each trial the observer was shown a test pattern selected at random from an array of seven equally spaced around the comparison value of the test parameter. For example, to measure length discrimination at an orientation of 45° , a 12 arcmin line at 45° was shown first. It was followed after a 600 ms interval by a line also at 45° that would have length randomly in the range 11 to 13 arcmin. For each condition, threshold measurements were usually based on three runs of 150 responses each, spread over at least two days. The data were analysed by the method of probits, which yields a threshold, defined as half the difference between the 25 and 75% points on the psychometric curve, with a standard error. The orientation and kind of pattern and task, e.g. two-dot alignment or line-length discrimination, remained unchanged for each run of 150 trials. There were no null-pattern comparisons in the individual trials in the second experiment because the patterns were self-referential.

Patterns were generated by an IBM-type computer on 15 inch (1 inch = 0.0254 m) Sony Trinitron monitors, and were made up of white lines that were *ca.* 0.5 arcmin wide. The luminance of their components, which was measured on a patch of the screen with a Minolta LS110 meter, was *ca.* 50 cd m^{-2} against a dark ($1\text{--}2 \text{ cd m}^{-2}$) background in a dimly lit room. An anti-aliasing procedure produced smooth lines in all orientations. The standard optometric convention for orientation was employed. The horizontal meridian was $0\text{--}180^\circ$ and zero was to the left as seen by the observer.

All participants had normal vision corrected with spectacles or contact lenses and observed the monitor binocularly with natural pupils at a distance of 5 m. They were experienced in this kind of psychophysical experiment and had completed several thousand trials by the time data accumulation for this project was started. There were no indications of training changes during the experiments. There were three sessions of 150 trials in most conditions and these did not show any consistent improvement during the course of the study. The observers included the author and four undergraduates in their early 20s who were naive as to the purpose of the study.

3. RESULTS

(a) *Orientation dependence of thresholds in the tangential and radial directions*

The just-detectable difference in orientation was measured for lines lying in eight equally spaced meridians. The lines were 12 arcmin long. Each trial, in runs of 150 trials, started with the presentation of a line of the designated orientation followed by the test line; the observer had to indicate, if necessary by guessing, whether the latter appeared tilted clockwise or counter-clockwise with respect to the comparison. The data (figure 2) show the well-documented oblique effect—there is better orientation discrimination for lines in and around the horizontal and vertical meridians. In a companion experiment, which was otherwise identical, the lines were replaced by small dots at their end-points (figure 1b). The results are also expressed in angular

Figure 2. Orientation dependency of two kinds of tangential threshold in three observers: (a) G.W., (b) M.J.L. and (c) K.Y. Just-detectable difference in the orientation of a 12 arcmin foveal line (filled squares) and alignment of two dots 12 arcmin apart (open circles). For ease of comparison, the same units of measurement are used in both, namely the just-detectable angular difference between the line ends and the dots, respectively, in degrees. The duration of exposure was 300 ms. A two-interval, forced-choice, psychophysical method allowed for comparison with a standard in each trial. All observers show a prominent oblique effect.

measure and, as far as meridional anisotropy is concerned, there is virtually no difference in the tangential thresholds whether the line is fully drawn out or merely indicated by the end-points.

In the next set of experiments, thresholds were obtained in eight meridians in two tasks involving spatial judgements in the radial direction. One was length discrimination

of lines with base length 12 arcmin. The other was bisection acuity in which a comparison had to be made between the width of the two spatial intervals of base width 20 arcmin, which were demarcated by three parallel lines of 12 arcmin length (see figure 1c for sketches of the patterns). For comparison purposes, each trial in the length discrimination task included presentation of a standard-length line followed by the test line, which randomly differed from it in length. Because the bisection pattern allowed comparison within itself, there was only a single presentation in each trial. Neither of the two radial thresholds exhibits the pronounced meridional anisotropy or oblique effect of the tangential thresholds, as can be seen in figure 3.

(b) *Flank interference in the radial and tangential thresholds*

Laterally placed flanking lines interfere with both vernier (Westheimer & Hauske 1975) and line-orientation (Westheimer *et al.* 1976) discrimination. The next set of experiments was designed to determine whether this flank-induced threshold increase also exists in the radial direction. Using a balanced configuration, the observers had to make judgements of bisection, which is a radial threshold, and, separately, of alignment, which is a tangential threshold. The pattern consisted of a central dot, the relative horizontal shift of which had to be judged by the observer. This test dot was flanked both vertically and horizontally by a dot on either side (figure 1d). In the null configuration all flank distances were 10 arcmin. In the bisection experiments, the central dot was randomly displaced to the right or left and the observer had to indicate the direction of the shift using, as criteria, the outer horizontal dots, the positions of which remained fixed. The outer vertical dots, which were acting as flanks, shared the middle dot's displacement. In the alignment experiments, the observer also had to indicate the direction of the middle dot's horizontal shift, but this time with reference to the outer vertical dots, the positions of which now remained fixed. However, here the outer horizontal dots acted as flanks and were displaced along with the middle dot. This arrangement had the virtue that the stimulus and response variables were a horizontal perturbation of the middle dot's position throughout, thereby factoring out any possibly orientation and position unevenness. For controls, thresholds were also measured in a three-dot, horizontal, bisection task, i.e. omitting the two outer vertical dots and in a three-dot, vertical, alignment task, i.e. omitting the two outer horizontal dots.

The results for these four conditions—alignment with and without flanks and bisection with and without flanks—are depicted in figure 4 for three observers and show the pronounced difference between the two tasks. In bisection, which is judgement in the radial direction, the presence of flanks only produces an insignificant threshold impairment; the average with-flank-to-without-flank ratio for the three observers is 1.12. On the other hand, in the alignment task, just as had been observed previously with the vernier and line-orientation discrimination, which are other examples of tangential thresholds, the flanks cause a pronounced impairment. Here the average with-flank-to-without-flank ratio for the three observers is 2.21.

Figure 3. Orientation dependence of two kinds of radial threshold in the same three observers: (a) G.W., (b) M.J.L. and (c) K.Y. Just-detectable difference in the length of a line 12 arcmin long (open circles) and bisection thresholds for a configuration of three lines 12 arcmin long and 20 arcmin apart (filled squares). The duration of exposure was 300 ms. A two-interval, forced-choice, psychophysical method allowed for comparison with a standard in each trial.

4. DISCUSSION

As a first step in the study of form discrimination, sensitivity to differences in simple geometrical patterns with an axis of symmetry was examined by partitioning it into perception of the separation of feature components and perception of shear or misalignment. The human

Figure 4. Flank interaction in the bisection and alignment tasks (pattern shown in figure 1*d*) (base dot separations 10 arcmin). The radial task was the threshold for precision with which observers could judge whether the middle dot bisected the distance between the two outer horizontal dots when these three horizontally arrayed dots were shown alone and when the middle dot was accompanied by two vertical dots, i.e. the flanks. Similar data are shown on the right side of the graph for detection of whether the middle dot was aligned with respect to the virtual vertical line joining the top and bottom dots when these three vertically arrayed dots were shown alone and also when the middle dot was accompanied by a flanking dot to its right and left. The duration of exposure was 300 ms and there were three observers. The alignment (tangential) but not bisection (radial) thresholds are impaired by flanks.

observer is highly sensitive, at a hyperacuity level, to both; nevertheless they seem to be subserved by somewhat different neural mechanisms. Two more differences are added here to the previously demonstrated difference in robustness to contrast and lack of transfer of perceptual training between the two: only tangential thresholds (misalignment, vernier and line orientation) and not radial ones (spatial-interval discrimination and bisection) are afflicted with an oblique effect and exhibit a pronounced impairment by flanking stimuli. This radial-tangential anisotropy is in a different category from the orientational anisotropy of the oblique effect because, unlike the latter, which goes through two cycles in 180° , it goes through only one and, moreover, it is taken as intrinsic to the stimulus pattern, whatever this pattern's meridional orientation.

The experiment in § 3(b) has the virtue that it concentrates on the horizontal displacement of a single dot and shows that the effect of flanks depends on whether the task is alignment or spatial-interval judgement. Attention has been refocused from an apparatus by which the dot's absolute location is established to the ones through which its relative position with respect to other components of the stimulus pattern emerge. It turns out that the processing apparatus for the relationship intrinsic to the configuration, i.e. divorced from its absolute position and orientation, is distinguishably different.

If one adds the previous demonstration for the need for synchrony for the best performance, there develops the concept of a spatial differencing apparatus, here examined within configurations with a minimum of stimulus elements acting as markers. The relative immunity to the

actual nature of these demarcating elements (dots, lines, etc.) goes some way towards delineating the mechanism. The immediate impulse would have been to postulate a single kind of differencing apparatus, but now that there is convincing evidence of a radial–tangential dichotomy, modelling approaches will have to be more nuanced.

Andrews (1967) proposed that vernier alignment discrimination is in fact a variant of orientation discrimination. The virtually identical oblique effect in three observers for discrimination of orientation of a line and the tangential shift of well-separated dots (figure 2) lends support to the view that their processing apparatus has something in common. A popular interpretation of the oblique effect in line orientation is that there is a relative underrepresentation of obliquely orientated neurons in the primary visual cortex (Celebrini *et al.* 1993). However, from what is known about the response of cortical cells with elongated receptive fields, they are not well addressed by just two dots along their preferred direction. Hence, it does not necessarily follow that the neural substrates for all tangential discriminations reside in the primary visual cortex. Nevertheless, neurons in the primary visual cortex will surely participate in the signal processing of the tasks studied here. Recent analysis of a surround effect on their responses (Kapadia *et al.* 2000) is, therefore, relevant. Firing of these units can be potentiated by suitably placed collinear stimuli, i.e. stimuli that lie just outside the classical receptive field along their orientation axis. Laterally placed flanking stimuli always cause inhibition. And, inhibition by lateral flanks is precisely what tangential thresholds manifest and radial thresholds lack.

Combining these neurophysiological findings with the psychophysical ones in this paper and the lack of transfer of training between the two stimulus categories then leads to a view that places the processing of tangential thresholds (line-orientation discrimination and vernier acuity) at a different neural level from spatial-interval discrimination or bisection. The latter are not only immune to the oblique effect and to flank inhibition, but they are also more robust to contrast reduction. One can conclude that the processing of form in simple configurations is already decoupled from the fixed local sign of elements of the retinal mosaic, and proceeds by separate mechanisms dedicated to two intrinsic orthogonal directions.

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