Masking, aftereffect, and illusion in visual perception of curvature

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Masking, aftereffect, and illusion paradigms were used to establish the spatial selectivity of curvature detectors in human vision. Arcs with the same chord orientation mask each other maximally when they are identical in radius and direction of curvature. There is gradual reduction in masking over an extensive spatial range as arcs diverge in curvature. The transition from convexity to concavity does not produce discontinuity in the masking function. The extent to which a straight line appears curved also depends on the curvature of arcs shown previously (aftereffect) or at the same time (illusion). It is suggested that these effects could occur through selective adaptation of detectors responsive to either global curvature or the orientation of local straight-line approximations within an arc. Evidence is reviewed in support of the latter interpretation.

Microelectrode studies have shown that single cells in the cat and monkey visual cortex have maximum response restricted to particular spatial properties. The neural operations by which contour orientation, image motion, spatial frequency, and binocular disparity are processed have received detailed attention, but little has been established about the basis of curvature analysis in the visual system. Cells in the frog retina (Lettvin, Maturana, McCulloch, & Pitts, 1959) and the pigeon retina (Maturana & Frenk, 1963) respond selectively to different degrees of convexity. However, electrophysiological study of the cat and monkey visual cortex (Hubel & Wiesel, 1965, 1968), superior colliculus (Cyander & Berman, 1972; Sterling & Wickelgren, 1969), and infero-temporal cortex (Gross, Rocha-Miranda, & Bender, 1972) has failed to isolate a class of cell that is more effectively excited by arcs of specific radius, direction of curvature, and chord orientation than by other spatial configurations.

This apparent lack of curvature detectors may be artifactual; the microelectrode data at present available may be biased through concentrated use of straight lines as exploratory stimuli in establishing the trigger function of cells. Whether this is the case can be best determined by study of the response of a large sample of cells to arcs that are systematically varied in their spatial properties. An alternative, but less direct, approach to the question involves psychophysical paradigms that give data that can be related to analytical and integrative operations in the visual system. These paradigms include spatial masking, aftereffect, and illusion. Masking refers to elevation in the threshold for detection of one pattern (target

stimulus) as the consequence of exposure to another pattern (inducing stimulus). Aftereffects involve a shift in the apparent spatial properties of an above-threshold target following exposure to the inducing stimulus. In illusions, the target appears distorted when it is shown at the same time as the inducing pattern.

The present experiments examine spatial selectivity in masking, aftereffect, and illusion in the perception of curvature. The rationale by which psychophysical data obtained using these paradigms might provide information about feature detection is outlined prior to description of the experiments, and is considered more critically in the General Discussion.

EXPERIMENT I

Gratings mask each other maximally when they are identical in orientation (Campbell & Kulikowski, 1966), spatial frequency (Blakemore & Campbell, 1969), and stereospatial disparity (Blakemore & Hague, 1972), and less so as they differ in terms of the dimension in question. The spatial selectivity of masking has in each case been taken as evidence that there are specialized visual detectors for the particular dimension. The general argument is that exposure to the inducing stimulus renders specific neural detectors inactive for a period of time afterwards. If detectors normally engaged in signaling the target stimulus are now in an adapted state, the signal-noise ratio that is critical for detection can be maintained only by an increase in the energy level of the target stimulus. In these terms, psychophysical data provide an index of the breadth of tuning of neural detectors, because exposure to one stimulus is able to impair detection of another stimulus only to the extent that the two stimuli are represented by common neural units.

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Masking data suggest that spatial detectors in human vision are tuned over an orientation range of ± 15 deg (Campbell & Kulikowski, 1966), a range of ± 1 octave in spatial frequency (Blakemore & Campbell, 1969), and a range of ± 12 minarc in binocular disparity (Blakemore & Hague, 1972). Curvature-specific masking is studied in Experiment I; the question of interest is whether the visibility of a target arc is selectively impaired as a function of the direction and extent of curvature of inducing arcs to which the subject was previously exposed.

Method

Apparatus and Procedure. Curvature-specific masking was measured by comparing the threshold for detection of an arc following exposure to curved lines and a homogeneous field of equivalent space-average luminance. Forward masking was studied, with a fixation point (shown for 1 sec), the inducing stimulus (120 msec), and the target stimulus (duration manipulated as the dependent variable of the experiment) exposed in succession in separate channels of a Gerbrands three-field tachistoscope (Model T-3B-1). The inducing stimulus, which subtended 2 deg 38 min square, was either a homogeneous field (luminance 3.7 cd/m²) or a square-wave grating of arcs with vertical chords and uniform curvature.¹ The spatial frequency of the grating was 2.7 cycles/deg, the contrast was .8, and the space-average luminance, 3.7 cd/m². The four curvature values of the inducing stimulus in the experiment were 2 deg 2 min convex, 2 deg 2 min concave, 6 deg 45 min convex, and 6 deg 45 min concave. The target stimulus was a field that was either homogeneous or contained a single line (luminance 13.6 cd/m²) subtending 2 deg 38 min x 8 min. The line was either straight and vertical or curved (with a vertical chord) at one of the following radii: 1 deg 21 min, 1 deg 42 min, 2 deg 2 min, 2 deg 42 min, 4 deg 3 min, 6 deg 45 min, or 13 deg 30 min convex or concave.

The target line was shown on some trials and the associated blank field on other trials. The subject's task was to report which of these conditions had been displayed. The experiment determined the period of exposure required for the line and blank conditions to be differentiated with 75% accuracy. Masking reflected the difference between detection measures obtained for each combination of inducing and target curvature and values found for each target when the homogeneous inducing field was shown in place of the grating.

Contour masking was measured using a blockwise tracking method adapted from Houlihan and Sekuler (1968). Thresholds were established for each combination of the inducing stimulus (four curvature values and the homogeneous field) and the target line (15 values). For a given combination, a block of 12 target trials (six line presentations and six blank presentations, in random order) was initially given at a fixed exposure level, and the period of display was increased or decreased in 2-msec steps until the subject achieved 75% accuracy over a single block or bracketed this value between successive blocks.

The 16 subjects were undergraduate students with normal or corrected-to-normal vision. They were divided into four groups such that measures were obtained from a subject at each target value with the homogeneous inducing field and a single curvature value of the inducing grating. The order of testing under the experimental (exposure to grating) and control (exposure to homogeneous field) conditions was counterbalanced between subjects, and a Latin square was used to vary the sequence in which the target values were tested between subjects.

Results and Discussion

The threshold for contour detection under each stimulus condition was taken as the period the target

needed to be exposed for 75% accuracy in differentiation of line and blank trials. Thresholds were determined by interpolation when necessary. For each subject, a masking ratio was calculated for each combination of inducing and target curvatures by dividing the threshold produced with exposure to the inducing grating by the threshold found when the homogeneous field was shown in place of the grating. A ratio greater than 1.0 indicated that the target line was less detectable as the result of exposure to the grating, and for values less than 1.0, exposure to the grating had facilitated detection of the target line.

It is obvious from inspection of the mean ratios shown in Figure 1 that curvature-specific masking occurred. The target line was most difficult to detect (relative to control measures) when it was the same curvature as the inducing arcs, and the extent of masking was reduced as the inducing and target lines differed in curvature. An analysis of variance, together with multiple comparisons between means by Duncan's test, based on the data shown in Figure 1 supported this conclusion. In addition, the analysis confirmed that adaptation to slightly curved arcs (6 deg 45 min radius) produced a significantly higher peak level of masking as well as greater differentiation of masking in the proximity of the peak value than adaptation to extremely curved arcs (2 deg 2 min radius). However, in both cases the masking functions were selective to curvature over almost the total range of values employed in the experiment. Masking functions resulting from exposure to convex and concave arcs of common curvature were mirror-image reflections of each other, and there was no sharp discontinuity in masking in the transition from convexity to concavity.

All of the masking ratios shown in Figure 1 exceed

Figure 1. Mean masking ratios as a function of inducing curvature (signified by arrows) and target curvature.

1.0. Thus, the target lines were more difficult to detect (whatever their curvature) after exposure to the grating (whatever its curvature) than to the homogeneous field of equivalent luminance. This result is unlikely to reflect restriction in the stimulus range used in the experiment in that the target lines varied almost over the total possible curvature range from a convex semicircle through a straight line to a concave semicircle. It is possible that inappropriate control levels were used; however, this factor would not be at the basis of the graded selectivity in masking over virtually the total curvature range. The further alternative is that mechanisms that process curvature within the visual system have broad tuning, such that a single detector is responsive over the complete curvature range irrespective of the spatial value it most prefers.

Masking data by themselves can at best provide indirect identification of feature detecting operations in the visual system. The present results show that spatial masking is selective to curvature, but they do not necessarily establish that there are visual detectors that are primarily responsive to this dimension. Attention is later given to alternative neural logics by which the present data could result.

EXPERIMENT II

In addition to altering the threshold for detection of a target (masking), exposure to an inducing stimulus can modify the apparent spatial properties of an above-threshold target that is viewed at the same time (illusion) or immediately afterwards (aftereffect). For example, a vertical line appears tilted counter-clockwise when seen against a background of clockwise-tilted lines (tilt illusion) or following exposure to the lines (tilt aftereffect). In both cases, the magnitude of the distortion depends on the orientation difference between the inducing and target stimuli (Gibson, 1937; Gibson & Radner, 1937). Recent accounts have attributed tilt (see Coltheart, 1971), motion (Sekuler & Pantle, 1967), spatial frequency (Blakemore, Nachmias, & Sutton, 1970), and binocular depth (Blakemore & Julesz, 1971) aftereffects to selective adaptation of feature detectors. In the case of the tilt aftereffect, it has been assumed that the perceived tilt of the target reflects the mean of the distribution of excitation by which the line is represented within a population of orientation-selective detectors. If detectors excited by the inducing stimulus are suppressed for a period of time afterwards, the distribution of excitation resulting when the target is shown will be skewed and its mean shifted.

This analysis supposes that an aftereffect occurs only if there is overlap in the neural representation of the inducing and target stimuli. For this reason, there should be consistency between indices of spatial selectivity determined with masking and aftereffect

paradigms. It is possible to consider tilt (Carpenter & Blakemore, 1973), motion (Over & Lovegrove, 1973), and spatial frequency (MacKay, 1973) illusions within the same framework by assuming that these distortions result from inhibitory interaction between feature detectors by which simultaneously displayed inducing and target stimuli are signaled in the visual system.

Coltheart (1971) has suggested that selective adaptation of curvature-tuned detectors may underlie the aftereffect in which a straight line appears bowed in the opposite direction to previously inspected curved lines (Bales & Follansbee, 1935; Gibson, 1933; Wilson, 1965). The curvature illusion, in which a straight line appears bowed in the opposite direction to curved lines against which it is displayed, could similarly be attributed to inhibitory interaction among curvature detectors. The present experiment measures the size of the curvature aftereffect and illusion as a function of the direction and extent of curvature of the inducing stimulus. Spatial selectivity as measured with these paradigms is later considered in relation to the masking functions reported in Experiment I.

Method

Curvature aftereffect. The aftereffect was measured by determining the curvature required for a target line to appear straight following exposure to curved lines. On each trial, the subject was exposed in succession to a fixation point (shown for 1 sec), an inducing field (120 msec), a dark interval (10 msec), and a target line (30 msec). The 15 gratings used as inducing stimuli were similar to those described in Experiment I, except that the radii were 1 deg 51 min, 2 deg 18 min, 2 deg 45 min, 3 deg 42 min, 5 deg 30 min, 9 deg 15 min, and 18 deg 30 min convex and concave and there was also a grating of vertical straight lines. The induction gratings subtended 3 deg 36 min square. The target line subtended 3 deg 36 min x 11 min; its luminance was 13.6 cd/m² and the contrast, .8. The curvature of the test line could be changed by the experimenter in steps of .8-mm lateral displacement of the ends relative to the center, and at each curvature the chord remained vertical.

Sixteen undergraduate students with normal or corrected-to-normal vision were tested. On each trial, the subject was required to judge whether the target line appeared convex or concave; he was not allowed to report that the line appeared straight. Under a given inducing condition, a straight line was shown as the target on the first trial, and on subsequent trials the curvature of the target line was varied in .8-mm steps (convex or concave displacement), in accord with a random staircase procedure, until six reversals in judgment had occurred between successive curvature values. The intertrial interval was 10 sec. Each subject was tested under all inducing conditions, with two sets of measures obtained using the straight-line grating. A Latin square was used to vary the sequence in which the inducing conditions were presented across subjects.

Curvature illusion. The same stimulus values and general procedures were used to measure the illusion except that the inducing and target stimuli were shown simultaneously (for 60 msec) rather than in succession. Sixteen undergraduate subjects were tested.

Results and Discussion

Under both aftereffect and illusion conditions, the target line was treated as having appeared straight at the position midway between displacements to which

the subject gave opposite curvature judgments. Measures found with the curved-line inducing gratings were subtracted from measures obtained with the straight-line inducing grating. These difference scores reflect the displacement within the target required to nullify the curvature distortion produced by the inducing arcs. In the aftereffect and illusion functions shown in Figure 2, + is scored when concave displacement was needed for the test line to appear straight and - when convex displacement was required.

The results in Figure 2 show that, except at slight inducing curvatures, a physically straight line appears bowed in the opposite direction to curved lines displayed immediately beforehand or at the same time. An analysis of variance showed that the mean distortion considered without regard for the direction of displacement varied significantly as a function of the radius of the inducing arcs, $F(7,210) = 214.4$, $p < .01$. The direction of curvature (convex vs. concave) had no influence on the magnitude of displacement, $F(1,30) = .02$, $p > .05$; this variable instead determined the direction of displacement. The mean aftereffect and illusion did not differ significantly, $F(1,30) = .16$, $p > .05$, but the interaction between aftereffect/illusion and the radius of the inducing arcs was significant, $F(7,210) = 6.4$, $p < .01$.

The maximum aftereffect and illusion were obtained when the inducing stimulus was a grating of strongly curved arcs (radius 2 deg 45 min or 3 deg 42 min, convex or concave). Inducing arcs that were less curved produced markedly less distortion, while inspection of more strongly curved arcs resulted in a slightly decreased aftereffect and illusion than that produced by the 2 deg 45 min and 3 deg 42 min arcs (see Figure 2). It was earlier suggested that curvature aftereffects and illusions may reflect interactions

between the neural correlates of inducing and target stimuli. In these terms, there would be greatest perceptual distortion when adaptation or inhibition produced by the inducing stimulus results in maximal skew in the distribution of excitation by which the target stimulus is signaled. The present data suggest that there is maximum interaction between the neural representation of straight lines and strongly curved arcs (i.e., of radius 2 deg 45 min and 3 deg 42 min). This confirms the conclusion drawn from Experiment I that visual mechanisms engaged in curvature analysis are broadly tuned across the dimension of radius.

It is tempting to conclude from the present data that there are detectors primarily tuned to curvature in human vision. In these terms, a straight line would be signaled by the relative response rates of convexity and concavity detectors, and an aftereffect would occur whenever one class of detector has been adapted by prior exposure. The illusion would occur because convex inducing arcs would inhibit the convexity detectors by which the target is normally signaled, but have no influence on the response of the concavity detectors. One would, in fact, be following a well-established strategy for the identification of feature detectors (see Blakemore & Julesz, 1971; Blakemore, Nachmias, & Sutton, 1970; Sekuler & Pantle, 1967) in proposing, from the present data, that curvature is a basic dimension of visual analysis. The question now to be considered is whether such a conclusion can be validly drawn from the present results.

GENERAL DISCUSSION

The ability to distinguish arcs in terms of their radius, direction of curvature, and chord orientation clearly requires that the visual system is capable of analyzing and differentiating these properties. The question of present interest is whether masking, aftereffect, and illusion data can be used to establish the characteristics of the neural mechanisms that undertake analysis of curvature. In considering this issue, it should be clearly recognized that psychophysical data merely relate the inputs and outputs of the visual system, and do not by themselves provide direct information about intervening operations. Any one of a number of operations might underlie detection of curvature within the visual system. For example, arcs might be processed on a global basis such that single detectors prefer curved lines more than any other spatial configuration, with response controlled by the direction and degree of curvature. Alternatively, an arc might be processed on a segment-by-segment basis in terms of the orientation of straight-line approximations; curvature would then be represented by the distribution of excitation over a population of detectors that are tuned primarily to contour orientation.

Figure 2. Mean aftereffect (solid line) and illusion (dotted line), with standard errors, as a function of inducing curvature.

There are at least two ways in which inferences about feature detection developed from psychophysical functions can be validated. The most direct approach involves reference to microelectrode data. For example, orientation has become recognized as a basic property in feature analysis through demonstrations that many single cells in the cat and monkey cortex prefer straight lines to other stimuli, and respond differentially as orientation is varied around a preferred value. Orientation selectivity in contour masking in human vision approximates the tuning functions reported for single cells in microelectrode studies (see Leibowitz & Harvey, 1973), and such similarity provides support for the proposition that selective adaptation of tilt detectors underlies the masking functions. Claims that motion, spatial frequency, and binocular depth are primary dimensions of information analysis in the human visual system have been validated in a similar manner. However, this approach provides limited support for any claim that there are specialized curvature detectors.

A detector that undertakes global analysis of curvature would be triggered optimally by an arc of specific radius, direction of curvature, and chord orientation, and it would show generalization in response over each of these dimensions. It might be inferred from the present psychophysical data that mechanisms broadly tuned to curvature function in human vision and can be selectively adapted or inhibited. Cells with such specialization have not, however, been found in microelectrode studies. Simple cortical cells respond best to straight lines and they are insensitive to variation in curvature (see comment by Hubel in Henry & Bishop, 1972, p. 368). Hypercomplex cells can signal curvature (but not with high selectivity) if they have inhibitory regions at both ends of their receptive fields, but the cells also respond to the orientation of straight lines and they in no way prefer curves in the manner that simple cells prefer straight lines. In this connection, Hubel and Wiesel (1968, p. 215) have commented: "The hypercomplex cell can, in a sense, serve to measure curvature: the smaller the activating part of the field, the smaller the optimal radius of curvature would be. To term such cells 'curvature detectors' seems unwise, however, since the term neglects the importance of the orientation of the stimulus, and does not capture the essential importance of a line stimulus to one region and the absence of a line stimulus to an adjacent, antagonistic region. Similar objections would apply to terms like 'corner units.'"

The second approach to identification of feature detectors is less direct in that it relies on the consistency of inferences developed from psychophysical functions obtained over several paradigms or across stimulus transforms within a paradigm. This approach has been used by Appelle (1972), for example, in specification of the properties of

orientation detectors in human vision. Attention can now be given to data suggesting that curvature selectivity in masking, aftereffect, and illusion is best conceptualized in terms of adaptation and inhibition of orientation detectors that signal straight-line approximations within an arc rather than mechanisms that undertake global analysis of curvature.

Blakemore and Over (1974) found that a curvature aftereffect is not induced if the subject has made continuous eye movements in the direction of the chord of the adaptation arc. This condition exposes a given part of the retina equally to orientation information of opposite sign over the inspection period. An aftereffect is produced with constant fixation or eye movements at right angles to the chord. Under the latter condition, there has been differential adaptation to orientation over the extent of the retina to which the target line is displayed, and the curvature aftereffect might therefore reflect variation in the direction and size of local tilt aftereffects. Curvature illusions have, by the same logic, been attributed to variations in orientation-selective inhibition along the length of the target line (Crassini & Over, 1974).

In a similar manner, the curvature-specific color aftereffects attributed by Riggs (1973) to selective adaptation of wavelength-sensitive curvature detectors do not occur if there have been systematic eye movements along the chord of the adaptation arc during inspection (MacKay & MacKay, 1974). In addition, curvature-specific color aftereffects produced by fixation of the inducing stimulus are variegated rather than uniform in appearance in a manner consistent with selective adaptation of orientation information within the display. Aftereffects induced with arcs also transfer to gratings (and vice versa) in accord with orientational similarities (Crassini & Over, 1975). These data suggest that curvature-specific color aftereffects are merely complex forms of the orientation-specific color aftereffects that were first described by McCollough (1965).

If arcs are analyzed in terms of the orientations of local straight-line approximations, it should be possible to develop a model of the integrative operations by which gradients of orientation are processed to result in curvature perception. The masking, aftereffect, and illusion data reported in the present experiments might profitably be used in conjunction with evidence on orientation selectivity as a basis for estimating these operations.

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NOTE

1. The stimuli used in the experiments were selected to cover a range of curvatures from a convex arc () almost forming a semicircle, through vertical straight, to a concave arc () of the same dimensions. The stimulus series covered approximately equal steps of curvature defined as the reciprocal of radius. However, following the convention adopted by Riggs (1973) and others, curvature values are expressed throughout this paper in terms of radius (degrees of visual angle) rather than the reciprocal of radius.

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