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CENTRIPETAL VERSUS CENTRIFUGAL BIAS IN VISUAL LINE BISECTION: FOCUSING ATTENTION ON TWO HYPOTHESES

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1. ABSTRACT

A variety of stimulus factors have been shown to influence the degree of leftward displacement of perceived line midpoint (i.e., pseudoneglect), which typifies the performance of normal subjects in line bisection tasks [M.E. McCourt & G. Jewell: *Neuropsychologia* 37, 843-855 (1999); G. Jewell & M.E. McCourt: *Neuropsychologia* 38, 93-110 (2000)]. One such factor is the position of lines within the visual field, where two conflicting patterns of bisection error have been reported. Some authors report a *centrifugal* pattern of error, where perceived line midpoint shifts away from the vertical midline, regardless of line position, i.e., relatively leftward for leftward displaced lines and vice versa. Others have reported a *centripetal* pattern of bisection error, where perceived line midpoint is always displaced centrally, toward the vertical midline, regardless of line position. There is no satisfactory explanation for these discrepant findings. An experiment using a tachistoscopic forced-choice line bisection protocol is described which discloses that neurologically normal right-handed subjects (N=82) typically display a centrifugal pattern of bisection error when lines are azimuthally displaced over a relatively small range, whereas a centripetal pattern is observed when lines are displaced over a wider range. Results from ancillary control experiments, in which eye position was measured during testing, confirm that systematic differences in gaze direction do not occur as a function of line position, and thus cannot account for the different patterns of bisection error. We conclude that stimulus context significantly modulates the strategy with which observers deploy spatial attention. When line position is constant, or varies over a narrow range, observers hold attention steady and widen its aperture to accommodate the relevant range of spatial location. Centrifugal bisection error is thus produced by the asymmetric cueing effect of laterally displaced lines, according to the activation-orientation theory [M. Kinsbourne: *Acta Psychologica* 33, 193-201 (1970)]. When the range of line position exceeds the aperture of focal attention, we hypothesize that observers adopt a strategy in which attention is dynamically scanned in the direction of azimuthally displaced lines. The effects of attentional scanning on line bisection performance are quite robust. The centripetal scanning proposed to occur for widely displaced lines is consistent with the centripetal pattern of bisection error in this condition.

2. INTRODUCTION

2.1. Visuospatial Hemineglect

The syndrome of visuospatial hemineglect entails difficulty reporting, responding or orienting towards stimuli located within contralesional hemispace, as defined in terms of retinocentric (space-based), egocentric (body-referenced) or allocentric (object-based) coordinate systems (1-19). Left hemispatial neglect occurs most frequently subsequent to right inferior parietal or temporoparietal lobe damage, but may also derive from lesions to the frontal or cingulate cortex, or to a variety of subcortical structures (20-33). The phenomenon of neglect has attracted considerable interest on the part of both clinicians and behavioral neuroscientists because understanding its etiology offers the potential to both advance the basic knowledge of the neural substrates of spatial attention, as well as to ameliorate the often severe disabilities of patients affected by this disorder.

2.1.1. Line Bisection

Line bisection tasks are frequently employed to assay asymmetries in spatial attention. Neglect patients typically bisect horizontal lines of moderate length significantly to the right of veridical center (e.g., as if they either ignore the majority of the left-hand side of the stimulus or are, alternatively, as if they are hyperattentive to the right-hand side).

2.2. Pseudoneglect

Neurologically normal right-handed subjects also systematically misbisect space or objects such as lines (34-38). This latter phenomenon has been termed “pseudoneglect" (34). This term refers to an asymmetric perception of space (or objects) that occurs in the absence of neural pathology. It is opposite in direction to the attentional asymmetry of neglect patients, meaning that normal subjects typically misbisect line stimuli to the left of veridical center or, on a cancellation task, may fail to cancel stimuli on the right-hand side of stimulus arrays (39). Controlling for the confounding influences of limb and oculomotor (intentional) factors, tachistoscopic forced-choice psychophysical techniques (40-43) have revealed that pseudoneglect has a significant perceptual component, and is a statistically significant and reliable visuoperceptual asymmetry possessing an effect size of approximately 1.25 (43).

2.2.1. Relationship to Hemineglect

The phenomena of neglect and pseudoneglect, as their names suggest, are often discussed together as phenomena that reveal a common and fundamental hemispheric asymmetry in the neural substrates of attention (43). Supporting this idea are experiments illustrating that a variety of stimulus and task-related variables modulate the magnitude and direction of both neglect and pseudoneglect in a complimentary manner (41). An enhanced understanding of pseudoneglect may therefore contribute to research and discovery concerning neglect syndrome.

2.2.2. Centrifugal versus Centripetal Bias in Pseudoneglect

One stimulus manipulation known to modulate the magnitude of pseudoneglect is the azimuthal position of lines within the visual field. Several authors (40, 44-47) report a *centrifugal* pattern of bisection error, where perceived line midpoint shifts relatively leftward for lines presented partly within the left hemifield, and relatively rightward for lines presented in the right hemifield. A number of studies, however, have reported a *centripetal* pattern of bisection error (9, 34, 48, 49) in which subjects commit relatively rightward bisection errors for lines appearing partly or wholly within the left visual field, and leftward errors for lines in the right hemifield. The majority of authors reporting centrifugal biases have explained these results in terms of the activation-orientation hypothesis (50-52). Neilsen, Intriligator & Barton (49) offered a functional anatomical explanation for the centripetal pattern of bisection error they observed in terms of differential cortical magnification across the visual field. No single study, however, has reported both centripetal and centrifugal patterns of bisection biases, and none has attempted to explain the discrepancy in terms of either theory or methodology.

The goal of this report is to replicate both the centrifugal and centripetal patterns of bisection error, if possible, and to further assess whether individual differences and/or methodological or procedural differences might underlie these discrepant patterns of performance. We report that individual subjects demonstrate both centrifugal and centripetal patterns of error, and that these patterns are systematically related to differences in experimental procedure. An explanation of our results is offered which attempts to reconcile the discrepant patterns of performance within a unified theoretical framework.

3. MATERIALS AND METHODS

3.1. Subjects

Subject laterality was assessed using a standard questionnaire (53) on which a composite score of −100 denotes exclusive left-handedness, and +100 denotes exclusive right-handedness. A total of 82 right-handed subjects (42 male, mean age = 22.0 years, mean laterality score = +80.6; 40 female, mean age = 21.6 years, mean laterality score = +75.6) participated in at least one of the three Experimental Conditions. Twenty-five subjects participated in all three conditions of the experiment (15 male, mean age = 23.0 years, mean laterality score = +73.0; 10 female, mean age = 23.1 years, mean laterality score = +77.5). Twenty-four subjects participated only in Conditions 1 and 2 (8 male, mean age = 20.1 years, mean laterality score = +89.3; 16 female, mean age = 20.4 years, mean laterality score = +84.7). Thirty-three subjects participated in Condition 3 only (17 male, mean age = 22.1 years, mean laterality score = +83.2; 16 female, mean age = 21.8 years, mean laterality score = +65.3). There was no significant difference in either mean age or laterality score across male and female subjects, $t(80) = 0.51$, $p > .05$ and $t(80) = 1.12$, $p > .05$, respectively. Further, there was no significant difference in mean age or laterality score across the three independent groups of subjects who participated in all three Experimental Conditions (1, 2 and 3), two Conditions (1 and 2 only), or the single Condition (3 only): for subject age, $F(2, 79) = 2.66$, $p>.05$; for subject laterality score $F(2, 79) = 2.86$, $p>.05$. When a common group of subjects participates in more than one experimental condition, repeated-measures inferential statistics are most frequently employed. However, because a sizable number of subjects participated in fewer than all three conditions, for across-condition comparisons independent-groups statistics are reported throughout. This approach is justified for two reasons. First, the groups are relatively homogeneous; there are no significant differences in age or laterality score between the groups of subjects participating in the various conditions, as indicated above. Second, independent-groups comparisons are recognized to be a more conservative test for differences among dependent measures (e.g., bisection performance) than are repeated-measures comparisons. We note that in all cases where significant results from independent-groups statistical tests are reported, the repeated-measures tests performed independently on those subsets of subjects for which they are warranted produce substantively equivalent results. All subjects possessed normal or corrected-to-normal vision, and reported no neurological abnormalities.

3.2. Instrumentation and Calibration

Subject responses were sensed and collected, and stimuli were presented as 640x480 pixel images on IBM-compatible computers equipped with 17” flat-screen monitors with frame refresh rates of 60 Hz. The generation and sequencing of stimuli and the collection of subject responses were accomplished using the ERTS software package (54). Luminance and contrast calibrations were made using a photometer (Tektronix, model J17). In some experimental conditions eye position measurements were obtained using an infrared eye-tracker (Applied Science Laboratories, model 5000).

3.3. Stimuli

3.3.1. Constant Line Midpoint (Experimental Condition 1)

A facsimile of a line stimulus used in the constant line midpoint condition is illustrated in Figure 1(a). The legend below the panel indicates length and position in degrees visual angle. In this condition, stimuli were horizontally oriented lines of 100% Michelson contrast presented binocularly on a gray background (approximately 30 cd/m^2), viewed with natural pupils. Viewed from a distance of 45 cm the lines subtended 22.3° in width by 0.39° in height. The true midpoints of all lines were centered with respect to the center of the display (0°), which also coincided with the vertical midline and the subjects' midsagittal plane. All lines appeared at 0° vertical eccentricity, along the horizontal midline. All lines were pretransected; transectors assumed 25 positions ranging from ±0.88° relative to veridical line midpoint. This range of transectors is sufficient to produce asymptotic "left" or "right" transector location judgments in nearly all neurologically normal subjects. The line illustrated in Figure 1(a) is transected at the veridical midpoint. Lines could possess two contrast polarities, defined by whether the upper left quadrant of the transected line was white (e.g., lines illustrated in Figure 1b) or black (e.g., lines illustrated in Figure 1c). Lines with opposite contrast polarities appeared with equal frequency. The order of appearance of lines with different transector locations and contrast polarities were randomized within blocks of trials.

3.3.2. Narrow Line Midpoint Variation (Experimental Condition 2)

Facsimiles of line stimuli used in the narrow line midpoint variation condition are illustrated in Figure 1(b). The legend below the panel indicates length and position in degrees visual angle. In this condition, stimuli were horizontally oriented lines of 100% Michelson contrast presented binocularly on a gray background (approximately 30 cd/m^2) viewed with natural pupils. Viewed from a distance of 45 cm the lines subtended 22.3° in width by 0.39° in height. Lines could appear at seven locations possessing azimuthal midpoints at ±2.43°, ±0.48°, ±0.24°, and 0^o with respect to the center of the display (0^o), which coincided with the vertical midline and the subjects' midsagittal plane. Although separated vertically for purposes of illustration, in the actual experiments all lines appeared at 0^o vertical eccentricity, along the horizontal midline. As illustrated in Figure 1(b), all line stimuli in the narrow line midpoint variation condition straddle the vertical midline. All lines were pretransected; transectors assumed 25 positions ranging from ±0.88° relative to veridical line center. This range of transectors is sufficient to produce asymptotic "left" or "right" transector location judgments in nearly all neurologically normal subjects.

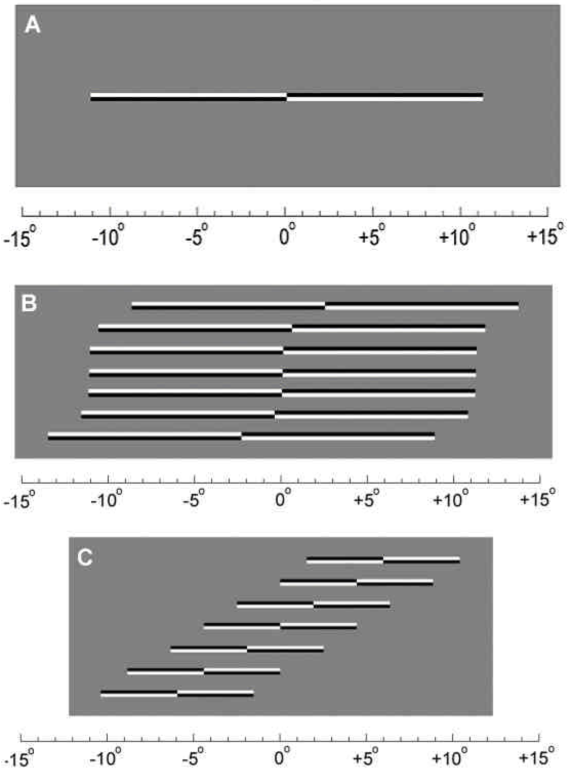

Figure 1. A: A facsimile of a line stimulus used in the constant line midpoint condition (Experimental Condition 1). The legend indicates length and position in degrees visual angle. Viewed from a distance of 45 cm, lines subtended 22.3° in width by 0.39° in height. B: Facsimiles of line stimuli used in the narrow line midpoint variation condition (Experimental Condition 2). Viewed from a distance of 45 cm the lines subtended 22.3° in width by 0.39° in height. Lines could appear at seven locations possessing azimuthal midpoints at: ±2.43°, ±0.48°, ±0.24°, and 0° with respect to the center of the display (0°), which coincided with the vertical midline and the subjects' midsagittal plane. C: Facsimiles of line stimuli used in the wide line midpoint variation condition (Experimental Condition 3). Viewed from a distance of 69 cm the lines subtended 8.9° in width by 0.31° in height. Lines could appear at seven locations possessing azimuthal midpoints at: ±5.94°, ±4.41°, ±1.92°, and 0° with respect to the center of the display (0°), which coincided with the vertical midline and the subjects' midsagittal plane.

Lines with opposite contrast polarities appeared with equal frequency. The order of appearance of lines with different transector locations, contrast polarities and azimuthal positions was randomized within blocks of trials.

3.3.3. Wide Line Midpoint Variation (Experimental Condition 3)

Facsimiles of line stimuli used in the wide line midpoint variation condition are illustrated in Figure 1(c). The legend below the panel indicates length and position in degrees visual angle. In this condition, stimuli were horizontally oriented lines of 100% Michelson contrast presented binocularly on a gray background (approximately 30 cd/m^2) viewed with natural pupils. Viewed from a distance of 69 cm the lines subtended 8.9° in width by 0.31° in height. Lines could appear at seven locations possessing azimuthal midpoints at ±5.94°, ±4.41°, ±1.92°, and 0° with respect to the center of the display (0°), which coincided with the vertical midline and the subjects' midsagittal plane. As illustrated in Figure 1(c), the three central-most line stimuli in the wide line midpoint variation condition straddle the vertical midline, as did all lines in Experimental Condition 2. However, the four most eccentric line stimuli fall entirely within the left and right visual fields. Although separated vertically for purposes of illustration, in the actual experiments all lines appeared at 0° vertical eccentricity, along the horizontal midline. All lines were pretransected; transectors assumed 27 locations ranging from ±0.70° relative to veridical line midpoint. Lines with opposite contrast polarities appeared with equal frequency. The order of appearance of lines with different transector locations, contrast polarities and azimuthal positions was randomized within blocks of trials.

3.4. Procedures

All experiments utilized a forced-choice tachistoscopic line bisection paradigm (40-42). This method has been found to successfully isolate the visuoperceptual and attentional components of line bisection, while effectively controlling for many confounding variables inherent to traditional manual line bisection (i.e. systematic visual scanning, gross motor cueing, etc.). The forced-choice methodology is, moreover, a significantly more sensitive measure of attentional asymmetry in normal subjects. Left-error in tachistoscopic forced-choice experiments possesses an effect size (Cohen's d-statistic) of 1.25 [$d = 2t/\sqrt{df}$, according to the formula of Cooper & Hedges (55)] as opposed to a value of 0.35 for traditional manually performed method-of-adjustment measures (43).

Subjects were seated upright in comfortable armless task chairs whose height was pneumatically adjustable. Their midsagittal planes were aligned with the display monitor; control of head alignment and viewing distance was secured by the use of a table-mounted chin-rest. On each trial subjects made single-interval forced-choice decisions regarding transector location relative to veridical line midpoint by depressing either the left or right mouse button as appropriate. Button orientation corresponded to the axis of perceptual discrimination (i.e., the “left” response button was to the left of the “right” response button). Lines were presented for 150 ms; inter-trial intervals were variable since subsequent trials began 750 ms following previous responses.

Subjects made eight "left-right" judgments at each transector location. Determinations of subjective line midpoint for each line stimulus condition were thus based on 200 (25 transector locations x 8 judgments per location) forced-choice bisection trials in Experimental Conditions 1 and 2, and on 216 (27 transector locations x 8 judgments per location) in Experimental Condition 3. Subjects depressed mouse buttons with their right hands on half the trials; on the other half, the left hand was used. Hand used to respond was blocked and order was counterbalanced within and across subjects. For subjects participating in two or more Experimental Conditions, order of participation was counterbalanced.

3.5. Design and Analysis

3.5.1. Descriptive Phase

The dependent measure in all Experimental Conditions was the percent of trials on which subjects indicated that the transector was located to the “left” of line midpoint. Psychometric functions were derived by plotting percent "left" judgments against transector location for each subject. Nonlinear least-squares regression was performed to fit a cumulative Gaussian distribution to each psychometric function. The cumulative Gaussian function is described by the equation:

$$f(\mathrm{x},\alpha,\beta,\sigma) = \alpha[50+50(\mathrm{erf}((\mathrm{x}-\beta)/2^{0.5}\,\sigma))]$$

where "x" is transector location, α is an overall gain parameter, β is the x-axis location corresponding to the mean of the underlying Gaussian density function (i.e., the transector location at which left-right responses occur with equal frequency), and parameter σ is its standard deviation. The error function (erf) is a polynomial approximation to the cumulative Gaussian distribution, for which there is no closed-form analytical expression.

3.5.2. Inferential Phase

Based on these least-squares regressions, transector locations corresponding to a 50% left response rate (parameter β), and standard deviations (parameter σ) were extracted. The value of parameter β is a measure of bisection accuracy, and indexes the transector location at which left/right responses occur with equal frequency. This location is known as the “point of subjective equality” (p.s.e.), and is an objective measure of perceived line midpoint. Perceived line midpoint can be accurate (i.e., veridical), or biased left or right. Negative values of β correspond to leftward error. The value of parameter σ, on the other hand, is a measure of bisection precision. The primary inferential statistical analyses were performed on accuracy measures (p.s.e. values); secondary analyses were performed on the precision measures, i.e., the standard deviations (σ) of subjects’ underlying Gaussian distributions. Comparisons of mean p.s.e. and standard deviation values were analyzed using appropriate ANOVA models and post-hoc tests, as warranted by the particular experimental design.

3.5.3. Eye Position Analysis

In all Experimental Conditions subjects were specifically instructed to hold their gaze as steadily as possible at the center of the display screen, however, no fixation point was present on screen either during or between trials. In order to determine whether systematic eye gaze deviations occurred in Experimental Condition 3 (Wide Line Midpoint Variation), eye position data were collected during the experiment from eight subjects (3 males, 5 females). Eye position and pupil size were continuously monitored via a remote infrared eye-tracker (Applied Science Laboratories, model 5000), and were sampled at a rate of 60 Hz. The dependent measure of interest was eye position during the 150 ms time interval during which line stimuli were displayed on the CRT monitor. Eye position data were analyzed offline, using one-way independent-groups or repeated-measures ANOVA's as appropriate, to determine whether mean eye position varied systematically as a function of azimuthal line position.

4. RESULTS

4.1. Analyses of Bisection Accuracy (p.s.e.)

4.1.1. Constant Line Midpoint (Experimental Condition 1)

The black symbols in Figure s 2(a) and 2(c) plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 1. The dashed horizontal lines in panels (a) and (c) indicate veridical line midpoint; leftward error is denoted by negative values, and rightward error is denoted by positive values. Figure 2(a) plots mean p.s.e. in absolute units (degrees visual angle); Figure 2(c) expresses these same data in relative units (% line length). Expressed in either unit, a single-sample t-test (evaluated against the hypothesis of veridical bisection, i.e., 0^{o}) reveals a significant mean leftward deviation in perceived line midpoint (-0.25^{o}; -1.13%), $t(48) = -7.62$, $p < .001$.

4.1.2. Narrow Line Midpoint Variation (Experimental Condition 2)

The gray symbols in figure s 2(a) and 2(c) plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 2. A one-way repeated-measures ANOVA reveals a significant overall effect of azimuthal line position on perceived line midpoint, $F(6, 288) = 24.92$, $p < .001$. Single-sample t-tests (evaluated against the hypothesis of veridical bisection) revealed significant mean leftward deviations of perceived line midpoint for lines positioned at -2.43^{o} (-0.46^{o}; -2.05%), $t(48) = -5.79$, $p < .001$; -0.48^{o} (-0.22^{o}; -0.97%), $t(48) = -6.98$, $p < .001$; -0.24^{o} (-0.22^{o}; -0.97%), $t(48) = -7.06$, $p < .001$; 0.0^{o} (-0.20^{o}; -0.90%), $t(48) = -8.00$, $p < .001$; $+0.24^{o}$ (-0.19^{o}; -0.84%), $t(48) = -5.88$, $p < .001$; and $+0.48^{o}$ (-0.16^{o}; -0.73%), $t(48) = -4.96$, $p < .001$. A significant rightward bisection error exists for lines positioned at $+2.43^{o}$ ($+0.24^{o}$; $+1.08\%$), $t(48) = 3.94$, $p < .001$. The pattern of bisection errors in the Narrow Line Midpoint Variation condition is consistent with a centrifugal bias.

4.1.3. Wide Line Midpoint Variation (Experimental Condition 3)

The open symbols in figure s 2(a) and 2(c) plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 3. A one-way repeated-measures ANOVA reveals a significant overall effect of azimuthal line position on perceived line midpoint, $F(6, 342) = 5.44$, $p < .001$. Single-sample t-tests

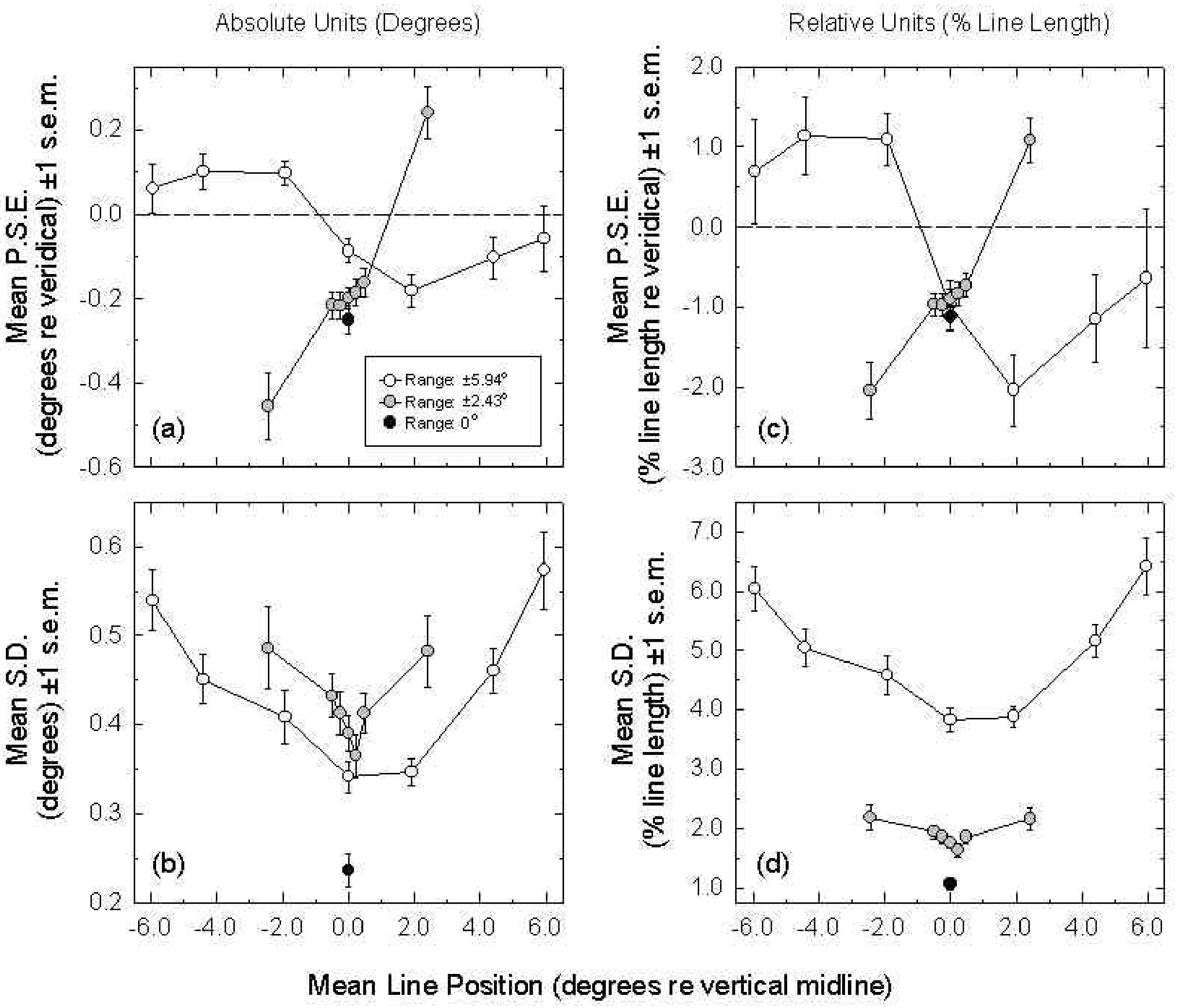

Figure 2. A,C: The black symbols plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 1. The dashed horizontal lines indicate veridical bisection; leftward error is denoted by negative values, and rightward error is denoted by positive values. Panel (a) plots mean p.s.e. in absolute units (degrees visual angle); panel (c) expresses these same data in relative units (% line length). The gray symbols plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 2. The pattern of bisection errors in this condition is consistent with a centrifugal bias. The open symbols plot mean p.s.e. values (±1 s.e.m.) as a function of mean azimuthal line position in Experimental Condition 3. The pattern of bisection errors in this condition is consistent with a centripetal bias. B,D: The solid symbols plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) in Experimental Condition 1. The gray symbols plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) as a function of mean azimuthal line position in Experimental Condition 2. Bisection precision is significantly greater for lines positioned near the vertical midline, and systematically worsens with increasing eccentricity. The open symbols plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) as a function of mean azimuthal line position in Experimental Condition 3. Bisection precision is significantly greater for lines positioned near the vertical midline, and systematically worsens with increasing eccentricity.

(evaluated against the hypothesis of veridical bisection) reveals a non-significant rightward deviation of perceived line midpoint for lines positioned at −5.94° (+0.06°; +0.07%), t(57) = 1.06, p > .05. Significant rightward deviations exist for lines positioned at −4.41° (+0.10°; +1.14%), t(57) = 2.37, p = .021; and −1.92° (+0.09°; +1.09%), t(57) = 3.33, p = .002. Significant leftward deviations occur for lines positioned at 0.0° (−0.09°; −0.98%), t(57) = −3.14, p = .003; +1.92° (−0.18°; −2.04%), t(57) = −4.56, p < .001; and +4.41° (−0.10°; −1.16%), t(57) = −2.10, p = .040. Finally, there was a non-significant leftward error for lines positioned at +5.94° (−0.06°; −0.65%), t(57) = −0.75, p > .05. The pattern of bisection errors in the Wide Line Midpoint Variation condition is consistent with a centripetal bias.

4.1.4. Across-Condition Comparisons

4.1.4.1. Absolute Units

The azimuthal line position of (0^o) is common to all three Experimental Conditions. As illustrated in Figure 2(a), when measured in absolute units (degrees), a one-way independent-groups ANOVA reveals a significant difference in perceived line midpoint for lines presented at the vertical midline as a function of Experimental Condition, F(2, 153) = 8.77, p < .001. Post-hoc independent-groups t-tests reveal that, expressed in either absolute or relative units, bisection errors in Experimental Conditions 1 and 2 are not significantly different, t(96) = 1.23, p > .05. However, leftward bisection error (in degrees) is significantly smaller in Experimental Condition 3 than in either Conditions 1 or 2, t(105) = –7.93, p < .001, and t(105) = –7.58, p < .001, respectively.

4.1.4.2. Relative Units

When expressed in relative units (% line length, Figure 2c), a one-way independent-groups ANOVA reveals no significant difference in perceived line midpoint for lines presented at vertical midline across Experimental Condition, F(2, 153) = 0.25, p > .05. As mentioned previously, a within-subjects analysis performed on that subset of 25 subjects who participated in all three Experimental Conditions supports identical conclusions.

4.2. Analyses of Bisection Precision (s.d.)

4.2.1. Constant Line Midpoint (Experimental Condition 1)

The solid symbols in **Figure** s 2(b) and (d) plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) in Experimental Condition 1.

4.2.2. Narrow Line Midpoint Variation (Experimental Condition 2)

The gray symbols in Figure s 2(b) and (d) plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) as a function of mean azimuthal line position in Experimental Condition 2. A one-way repeated-measures ANOVA reveals a significant overall effect of azimuthal line position on bisection precision, F(6, 288) = 3.88, p = .001. Contrast-analysis confirms that the trend is quadratic, F(1, 48) = 11.10, p = .002. Bisection precision is significantly greater for lines positioned near the vertical midline, and systematically decreases (s.d. increases) with increasing eccentricity.

4.2.3. Wide Line Midpoint Variation (Experimental Condition 3)

The open symbols in **Figure** s 2(b) and (d) plot mean s.d. values (in degrees and % line length, ±1 s.e.m., respectively) as a function of mean azimuthal line position in Experimental Condition 3. A one-way repeated-measures ANOVA reveals a significant overall effect of azimuthal line position on bisection precision, F(6, 342) = 13.50, p < .001. As in Experimental Condition 2, contrast-analysis confirms that the trend is quadratic, F(1, 57) = 57.45, p < .001. Bisection precision is significantly greater for lines positioned near the vertical midline, and systematically decreases (s.d. increases) with increasing eccentricity.

4.2.4. Across-Condition Comparisons

4.2.4.1. Absolute Units

The azimuthal line position of (0^o) is common to all three Experimental Conditions. As illustrated in Figure 2(b), when measured in absolute units (degrees), a one-way independent-groups ANOVA reveals a significant difference in bisection precision for lines presented at the vertical midline as a function of Experimental Condition, F(2, 153) = 16.53, p < .001. Post-hoc independent-groups t-tests reveal that bisection precision in Experimental Condition 1 is significantly better than in either Conditions 2 or 3, t(96) = –5.60, p < .001, and t(96) = –4.09, p < .001, respectively. Bisection precision does not differ significantly, as measured in degrees, between Experimental Conditions 2 and 3, t(105) = 1.82, p > .05.

4.2.4.2. Relative Units

When expressed in relative units (% line length, Figure 2d), a somewhat different conclusion is supported. Here, a one-way independent-groups ANOVA also reveals a significant difference in bisection precision for lines presented at midline across Experimental Condition, F(2, 153) = 102.99, p < .001. Post-hoc independent-groups t-tests, however, reveal that bisection precision is significantly better in the constant midpoint condition (1) than in either Condition 2 or 3, t(96) = –5.60, p < .001, and t(96) = –12.03, p < .001, respectively. Also, bisection precision in Condition 2 is significantly better than in Condition 3, t(96) = –8.91, p < .001. A within-subjects analysis performed on that subset of 25 subjects who participated in all three Experimental Conditions supports identical conclusions.

4.3. Measures of Individual Variation

4.3.1. Eye Position Variation

Based on pupil size measurements, eye position data associated with blink artifacts were rejected. The number of samples rejected on this basis accounted for approximately 3% of all eye position readings. Figure s 3(a-i) plot mean eye position (±3 s.e.m.) during line presentation epochs for three male observers (panels a-c), five female observers (panels d-h), and the mean aggregated across observers (panel i), as a function of azimuthal line position. Based on a total of 1505 eye position samples[1], the effect of line position is not significant for subject MEM (panel a), F(6, 1498) = 0.64, p >. 05. Based on a larger set of eye position samples the effect of line position is significant for subjects TMH (panel b), F(6, 13538) = 5.38, p < .001, and JMF (panel c), F(6, 13554) = 9.32, p < .001. Similarly, for female subjects, the effect of line position is significant for subjects TMS (panel d), F(6, 11283) = 7.64, p < .001; KAS (panel e), F(6, 11676) = 6.44, p < .001; BJS (panel f), F(6, 13366) =5.50, p < .001; ALB (panel g), F(6, 13245) = 3.29, p = .003; and NJB (panel h), F(6, 12454) = 2.40, p = .025. Panel (i) plots mean eye position versus azimuthal line position collapsed across all eight observers, where a one-way repeated measures ANOVA reveals no significant effect of line position on mean eye position, F(6, 42) = 0.45, p > .05. Seven of eight individual observers possess fixation biases which depart significantly from veridical screen center: MEM [mean = $–0.41^o$, t(1504) = –12.2,

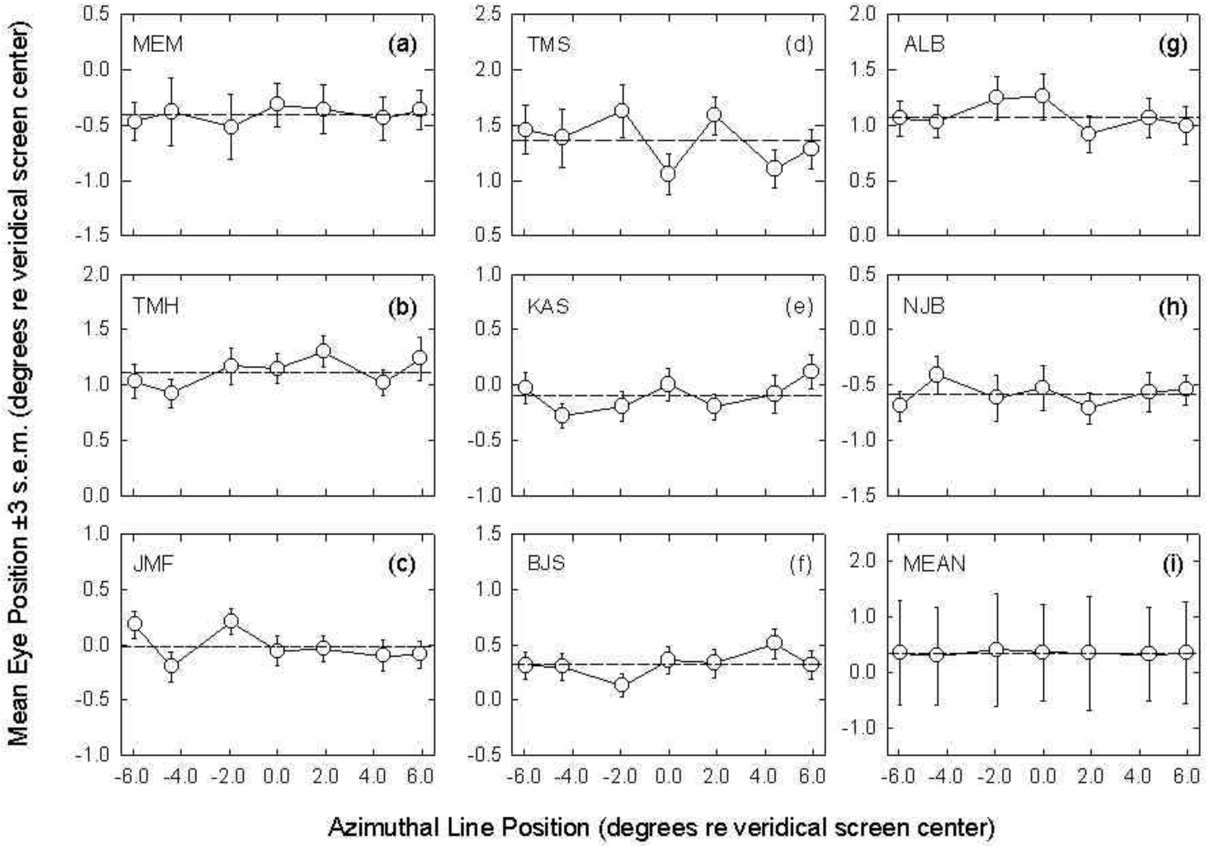

Figure 3. Panels (a-i) plot mean eye position (±3 s.e.m.) during line presentation epochs for three male observers (panels a-c), five female observers (panels d-h), and the mean aggregated across observers (panel i), as a function of azimuthal line position.

p < .001]; TMH [mean = +1.12^o, t(13544) = 51.3, p < .001]; JMF [mean = –0.001^o, t(13554) = –.69, p > .05]; TMS [mean = +1.37^o, t(11289) = 45.0, p < .001]; KAS [mean = –0.09^o, t(11676) = –4.6, p < .001]; BJS [mean = +0.32^o, t(13366) = 17.9, p < .001]; ALB [mean = +1.08^o, t(13245) = 41.8, p < .001]; and NJB [mean = –0.58^o, t(12460) = –23.0, p < .001]. The mean fixation bias aggregated across all eight observers is displaced slightly (but significantly) to the right (+0.35^o) of veridical screen center, t(55) = 3.6, p = .001. None of the means associated with individual line positions, however, differs significantly from veridical screen center: –5.94°, t(7) = 1.31, p > .05; –4.41°, t(7) = 1.16, p > .05; –1.92°, t(7) = 1.38, p > .05; 0°, t(7) = 1.43, p > .05; +1.92°, t(7) = 1.16, p > .05; +4.41°, t(7) = 1.34, p > .05; +5.94°, t(7) = 1.33, p > .05.

4.3.2. Centrifugal versus Centripetal Patterns of Bisection Error

Although the pattern of aggregate bisection errors in Experimental Conditions 2 and 3, as illustrated in Figure 2, are statistically unambiguous, a considerable degree of variability is nevertheless observed between the patterns of bisection error of individual subjects. In order to facilitate a between-subject comparison, a succinct univariate index of bisection performance (and hence, variability) in each condition was obtained by computing the slope of the p.s.e versus azimuthal line position function for individual subjects. Figure s 4(a) and (b) illustrate this procedure as applied to a small sample of representative subjects. The p.s.e. versus azimuthal line position data from Experimental Conditions 2 and 3 were subjected to linear regression analysis. Both the slope of the function and the coefficient of determination (r^2 – a measure of goodness-of-fit) were computed individually for each subject. Figure 4(a) shows that in Experimental Condition 2 (narrow range), slopes for individual subjects (values shown in the figure legend) varied from negative (i.e., a centripetal pattern) to positive (a centrifugal pattern). The mean coefficient of determination (r^2) for the linear regressions of the 49 subjects in Experimental Condition 2 was 0.741 (s.e.m. = 0.039). Because the pattern of bisection error in Experimental Condition 3 (wide range) is curvilinear over the entire range of azimuthal line positions (see Figure 2), p.s.e. versus line position slopes in this condition were calculated over a truncated azimuthal line position range (±1.92^o), where the trend is more nearly linear. Figure 4(b) shows that in Experimental Condition 3 (wide range) there is also considerable between-subject variation in the pattern of bisection error, with some subjects expressing positive slopes (centrifugal pattern) and some possessing negative slopes (centripetal pattern). The coefficient of determination (r^2) for the regressions for the

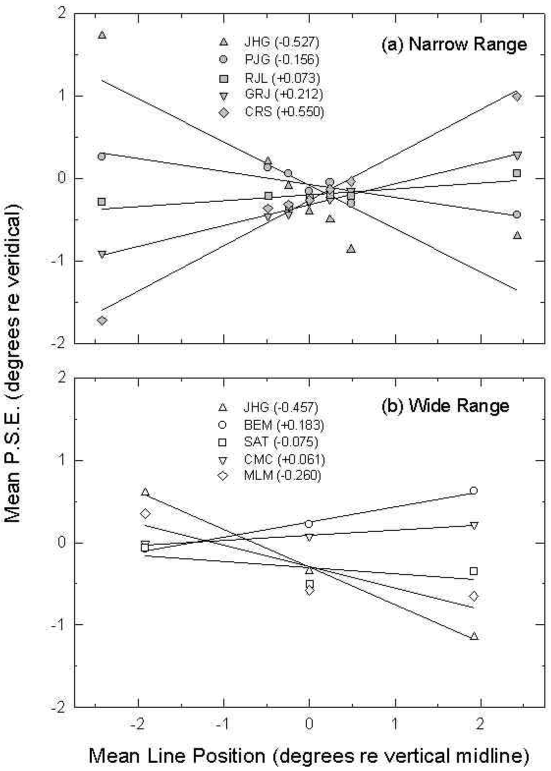

Figure 4. Panel (a) shows that in Experimental Condition 2 (narrow range), slopes for individual subjects (values shown in the figure legend) varied from negative (i.e., a centripetal pattern) to positive (a centrifugal pattern). Panel (b) shows that in Experimental Condition 3 (wide range) there is also considerable between-subject variation in the pattern of bisection error, with some subjects expressing positive slopes (centrifugal pattern) and some possessing negative slopes (centripetal pattern). In both conditions, the slope parameters derived from the linear regression analysis capture nearly 75% of the total variance associated with the effect of azimuthal line position on perceived line midpoint.

58 subjects in Experimental Condition 3 averaged 0.736 (s.e.m. = 0.043). Thus, in both conditions, the slope parameters derived from the linear regression analysis capture nearly 75% of the total variance associated with the effect of azimuthal line position on perceived line midpoint.

Figure s 5(a) and (b) present frequency distributions (bin width = 0.01) of slope parameters for all subjects in Experimental Conditions 2 and 3, respectively. One-sample Kolmogorov-Smirnov tests reveal that in neither condition 2 nor 3 does the distribution of slopes depart significantly from normality, Z(49) = 0.923, p = 0.362, and Z(58) = 1.090, p = 0.185, respectively. The solid lines in figures 4(a) and (b) denote the normal distributions which best describe the two frequency histograms. These distributions possess means (and standard deviations) of +0.140 (0.183), and –0.089 (0.138), respectively. A t-test for independent samples confirms that the means of the two distributions are significantly different, t(105) = 7.37, p < .001. The vertical dashed lines in figures 4(a) and (b) indicate the slope of the p.s.e. versus azimuthal line position functions computed from the aggregate means illustrated in Figure 2, which agree nearly perfectly with the mean of the slopes computed from individual subject data.

We tested the hypothesis that the variability observed in the pattern of bisection error across individual subjects might be related to differences in subject laterality. Figure s 6(a) and (b) plot the slope parameters of subjects in Experimental Conditions 2 and 3, respectively, against individual laterality scores. In neither condition was there a significant correlation: Condition 2, r(47) = 0.170, p > .05; Condition 3, r(56) = 0.048, p > .05. Solid lines in each panel are linear regression; dashed lines enclose 95% confidence intervals for each regression line.

5. DISCUSSION

5.1. Centrifugal versus Centripetal Bisection Error

A consistent and significant pattern of leftward error (pseudoneglect) was observed in all three Experimental Conditions for lines presented at the vertical midline (0^o). This result replicates those of numerous other investigators, as recently reviewed by Jewell & McCourt (43). The centrifugal pattern of bisection error revealed in the Narrow Midpoint Range condition (Experimental Condition 2) replicates the earlier finding of McCourt and Jewell (41), as well as the majority of previous reports detailing the influence of line position on bisection error (43).

5.1.1. Differential Cortical Magnification Hypothesis

The centripetal pattern of bisection error found in the Wide Midpoint Range condition (Experimental Condition 3) replicates, in part, the report of Nielsen et al. (49), who offered an explanation for centripetal bisection errors for lines presented entirely within a single visual hemifield based on a consideration of the mapping of the visual fields onto striate cortex. Specifically, they note that there is a relatively magnified representation of the central visual field in the retinostriate projection. Thus, lines presented eccentrically are subject to a nonlinear visuotopic remapping in which the portion of the line nearest the fovea enjoys a larger cortical representation than do portions of the line located at increasingly greater eccentricities. Assuming that perceived length is directly related to the magnitude of cortical representation, they reason that the length of the centrally represented portion of the line will be overestimated relative to the more peripherally represented portion, resulting in a bias of perceived midpoint toward the over-represented (central) side. While this hypothesis can account for the data presented by Nielsen *et. al.* (49), there are several problems with generalizing this hypothesis to account for the data of the present experiment. First, this explanation offers no account for the reliably observed leftward error in the perceived midpoint (pseudoneglect) when lines are presented at the vertical midline, where perceptual distortions imposed by differential cortical representation should be entirely symmetrical, and hence, offsetting. Nielsen *et. al.* (49) did not address this potential objection

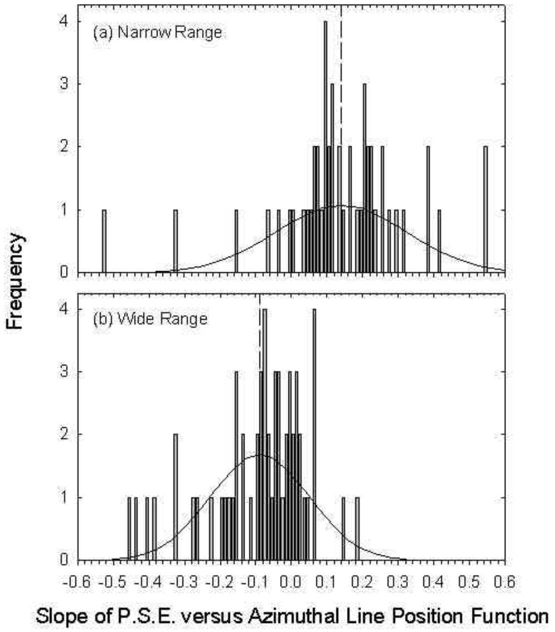

Figure 5. Panels (a) and (b) present frequency distributions of slope parameters for all subjects in Experimental Conditions 2 and 3, respectively. The solid lines denote the normal distributions which best describe the two frequency histograms. These distributions possess means (and standard deviations) of +0.140 (0.183), and –0.089 (0.138), respectively. The vertical dashed lines indicate the slope of the p.s.e. versus azimuthal line position functions computed from the aggregate means illustrated in Figure 2, which agree nearly perfectly with the mean of the slopes computed from individual subject data.

because their subjects displayed no leftward error in perceived line midpoint for centrally presented lines. A recent meta-analysis of the line bisection literature, however, reveals that the vast majority of reports (including this one) confirm the existence of leftward error (43). Second, this explanation predicts a centripetal bias in perceived line midpoint for *all* lines azimuthally displaced from the vertical midline. The data from Experimental Condition 2, as well the prior experiments of McCourt & Jewell (41), and from a host of studies reviewed by Jewell & McCourt (43), establish that reliable and significant patterns of *centrifugal* bisection error are obtained under certain experimental conditions. Finally, this explanation does not readily account for a critical aspect of the present results from Experimental Condition 3, *viz.*, that there is a *decrease* in centripetal bias with increasing line midpoint eccentricity.

5.1.2. Role of Eye Position

Clarifying an understanding of the mechanisms underlying our results, our analysis of eye position data confirms that centrifugal bisection error does *not* result from systematic deviations in eye position during line presentation. We find that such deviations in eye position are modest (typically less than one degree) in comparison to the entire range of line midpoint variation (±5.94°). Further, while significant differences in eye position do obtain for most subjects, such variations are not systematic, and therefore cannot account for systematic differences in perceived line midpoint with varying line position. An extremely interesting finding resulting from the analysis of eye position, however, is that individual subjects tend to fixate at locations slightly eccentric to veridical display (and hence line) midpoint. This begs the question whether such fixation biases might constitute an important source of the presently unexplained individual variation observed in bisection performance for lines presented at the vertical midline (2, 5, 40, 43, 56-59). Note that small systematic displacements in eye position are equivalent to small azimuthal line displacements. Such modest displacements, as shown in Experimental Condition 2, can significantly influence perceived line midpoint. Thus, subjects prone to a leftward fixation bias might be expected, on average, to display p.s.e. values which are displaced relatively rightward compared to those with rightward fixation biases.

5.2. Role of Stimulus Context

The fact that individual subjects could display a centrifugal pattern of bisection error in Experimental Condition 2, and a centripetal pattern in another, closely related condition (Experimental Condition 3), strongly suggests that stimulus context plays a critical role in determining how spatial attention is allocated. Marshall, Lazar, Krakauer & Sharma (60) recently demonstrated the effect of context on perceived line midpoint in bisection experiments involving manipulations of line length. They were concerned with the so-called "crossover effect", which refers to the apparently paradoxical finding that whereas neglect patients misbisect lines of moderate length significantly to the *right* of veridical midpoint, the bisection errors of these same patients, when confronted with short lines, "crossover" to the *left* of center. McCourt & Jewell (41) report a complimentary crossover effect in the bisection performance of normal observers, where left errors for lines longer than approximately 4^{o} gives way to rightward error for shorter lines. In a free viewing, manual bisection task Marshall *et. al.* (60) presented lines of various lengths (from 3-12 cm; equivalent to lengths of 3.0-15.2^{o} if a viewing distance of 45 cm is assumed) to neglect patients in two contexts: one in which lines of different lengths were intermixed within a single block of trials, and another in which line length was held constant throughout individual blocks. The principal result of these experiments was the disclosure of a profound context effect on bisection performance. Thus, compared to the perceived midpoint of reference lines when they were presented in blocks where line length was held constant, the perceived midpoint of reference lines shifted relatively leftward when they were intermixed with longer lines, and shifted relatively rightward when intermixed with shorter lines. The results of Marshall *et. al.* (60), taken together with the present results, imply that a context-dependent lability in the deployment of spatial attention may be responsible for the transition from a *centrifugal* pattern of bisection errors when line position is varied over a narrow range, to a *centripetal* pattern of error when the range of line position is widened.

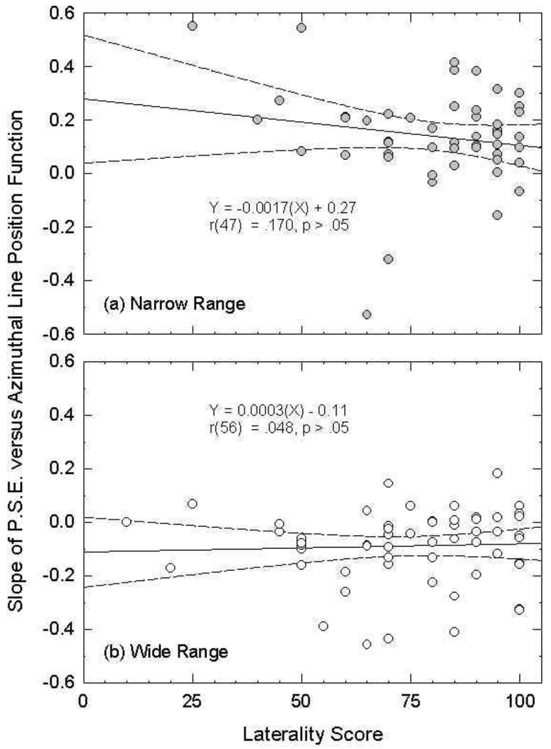

Figure 6. Panels (a) and (b) plot the slope parameters of subjects in Experimental Conditions 2 and 3, respectively, against individual laterality scores. In neither condition was there a significant correlation between slope and laterality score.

5.3. Attentional Scanning Hypothesis

Spatial attention has been variously characterized in terms of "spotlight" (61), "floodlight" (62) or "zoom-lens" analogies (63, 64). Attention has been argued to improve the spatial resolution of the visual system within the region "illuminated" or "viewed" through its application (65). Attentional enhancement of spatial resolution offers a parsimonious explanation of the bisection precision data of Figure 2. At least some of the overall decrease in bisection precision (reflected by increasing s.d. values) with increasing line midpoint eccentricity in Experimental Conditions 2 and 3 must reflect the coarser grain of the retinostriate projection with increasing distance from the fovea. Between-condition comparisons of bisection precision for centrally (0° eccentricity) presented lines, on the other hand, clearly illustrate the putative role of spatial attention. Thus, in Experimental Condition 1, where there was no variation in the location of line stimuli, subjects were free to concentrate their attention over a (relatively) narrow and fixed region of space, since each line's mean location could be anticipated with complete certainty. Here, the standard deviations of the psychometric functions were quite small (mean = 0.24°). In Experimental Conditions 2 and 3, however, confronted on a trial-by-trial basis with lines whose midpoints varied over a range of ±2.43° and ±5.94° respectively, subjects reported having to simultaneously attend to a larger region of space. Their bisections were consequently significantly less precise, even for lines presented at the vertical midline (means = 0.39° and 0.34°, respectively).

The notion of a directed attentional "spotlight" possesses utility in accounting for the centripetal pattern of bisection error observed in Experimental Condition 3. Recall that subjects were instructed to hold their gaze centered within the display (and were largely successful at doing so according to the eye position records). Let us assume that at its widest aperture (i.e., in a "floodlight" mode) the breadth of focal attention is nevertheless still too narrow to encompass the entire 12° range of line midpoints that appeared within blocks of trials in Experimental Condition 3.[2] The brief presentation of eccentric line stimuli might therefore be followed by a covert redirection (e.g., scanning) of the attentional spotlight toward the (former) location of the (now extinguished) stimulus, i.e., and attentional "saccade". As reviewed by Jewell & McCourt (43), one of the largest effects revealed by the meta-analytic treatment of the line bisection literature is the effect of *overt* visual scanning, where bisection errors are powerfully biased in the direction from which scanning is initiated. Thus, subjects scanning lines from left-to-right err significantly to the left of veridical line midpoint relative to non-scanning trials, whereas subjects scanning from right-to-left generally make rightward errors of smaller magnitude.[3] If the covert attentional scanning we are proposing has an influence similar to overt scanning, then lines presented at leftward eccentricities will be covertly scanned from right-to-left (thus producing rightward error) and lines presented at rightward eccentricities will be covertly scanned from left-to-right (thus producing leftward error). The net result will be a *centripetal* pattern of bisection error for eccentrically presented lines. The *centrifugal* pattern of bisection error found for the majority of subjects in Experimental Condition 2 suggests, however, that the breadth of the attentional "spotlight" may be sufficiently wide to encompass all relevant portions of those line stimuli without necessitating (or involuntarily invoking) covert scanning maneuvers. This could occur by virtue of the narrower range of line midpoints (assuming space-based attention), which allows relevant regions of lines of different positions to be grasped simultaneously, rather than sequentially. As mentioned above, it might also derive from a broader "tuning" of attention to the longer line length itself (assuming object-based attention). Considering the heterogeneity of the p.s.e. versus azimuthal line position slopes illustrated in Figure 5, however, it is tempting to speculate that subjects who displayed a centripetal pattern of bisection error (i.e., negative slopes) correspond to those who utilized a strategy involving narrowly focused attention and attentional scanning (as in Experimental Condition 3), whereas those subjects with a centrifugal pattern (i.e., positive slopes) correspond to those who employed a wide-focus, non-scanning strategy.

5.4. Attentional Recruitment Hypothesis

The attentional scanning hypothesis appears to provide a cogent explanation for the overall centripetal bisection pattern observed in Experimental Condition 3, as well as accounting for individual departures from this pattern, but what of the centrifugal pattern of bisection error observed in Experimental Condition 2. McCourt & Jewell (41) reported similar results in an identical experiment and noted that they were consistent with an activation-orientation or activation-arousal hypothesis (26, 47, 50-52). Briefly stated, this hypothesis applies to line bisection as follows. The leftward error of normal right-handed subjects in line bisection tasks derives from a hemispheric asymmetry in the allocation of attention to the line itself (object-based attention) or to the space within which the centrally presented line is located (space-based attention). The right hemisphere is presumed dominant with respect to the allocation of attention, such that the contralateral (left) line-half is "magnified", relative to the right half, by the excess attention devoted to it. The perceived midpoint of lines is therefore drawn into the "magnified" line-half, displacing it leftward.

If another sensory stimulus (e.g., visual, auditory, somatosensory) is delivered such that the right hemisphere is further activated, such activation will act to increase the relative "magnification" of the left line-half, and will produce a greater leftward error. Conversely, activating the left hemisphere, causing the right line-half to be relatively "magnified", decreases leftward error and, for large activations, may actually induce rightward errors. For example, in normal subjects, leftward bisection error is significantly greater for lines viewed monocularly through the left versus right eye, presumably due to the left eye's greater subcortical connections with the right hemisphere (66, 67). Bisections made using the left hand (controlled by the right hemisphere) generally possess greater leftward error than bisection made using the right hand (68; see 43 for review). When bisecting wedge-shaped lines (e.g., ≅ or 0), bisection errors are powerfully biased toward the taller side (42), suggesting that spatial attention is differentially recruited according to stimulus attributes such as shape, size and spatial contrast (41). Similarly, the delivery of visual cues located near the left- or right-hand line ends strongly biases bisection errors toward the cued line end (69; see 43 for a review of cueing effects). Finally, many types of contralesional stimulation have been shown to ameliorate the severity of neglect (70-81) presumably by recruiting attention toward the neglected hemispace.

Within this general framework, the activation-orientation hypothesis predicts that lines with midpoints displaced to the left or right of the vertical midline will differentially activate the right or left hemispheres, respectively. Lines displaced leftward will favor activation of the right hemisphere, drawing the perceived line midpoint leftward, and vice versa. The centrifugal pattern of bisection error predicted by this hypothesis is precisely what is observed in Experimental Condition 2. The same logic applies to the lines in Experimental Condition 3. That a centripetal pattern of bisection error nevertheless prevails in that condition suggests that the activation produced by directional attentional scanning (an active process) is larger than that produced by mere lateralized stimulus presentation (a more passive process). The differential hemispheric activation produced by lateralized stimulus presentation will increase as a greater proportion of the stimulus falls entirely within one visual hemifield. Such an increase in activation (which by itself is hypothesized to produce a centrifugal pattern of bisection error) may, however, explain the decreasing magnitude of centripetal bisection error observed for the two most laterally displaced lines in Experimental Condition 3 (midpoints at ±4.41° and ±5.94°), both of which are confined entirely to a single visual hemifield (see Figure 1c).

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Footnotes:

[1] The smaller number of eye position samples for subject MEM reflects the fact that eye position was sampled for this subject only during a 20 ms epoch coincident with stimulus onset, rather than over the entire 150 ms stimulus duration.

[2] Since spatial attention is in part object-based (1, 19; see 41 and 42 for evidence of object-based attention in line bisection tasks), its aperture might be significantly influenced by object size, i.e., line length. Lines in Experimental Condition 3 measured only 8.9°, whereas in Experimental Condition 2 they subtended 22.3° in length. Thus, despite a wider range of line midpoints, the modal aperture of attention in Experimental Condition 3 could conceivably have been much narrower than in Experimental Condition 2.

[3] Using a backward masking paradigm, McCourt & Jewell (41) tested and disconfirmed the hypothesis that left-to-right covert attentional scanning of this kind might be responsible for the leftward bisection error in bisection tasks (e.g., Experimental Condition 1) for lines of constant location. This does not discount the hypothesis, however, that covert directional scanning might occur when line position itself is varied over a considerable range on a trial-by-trial basis.

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