



Is the origin of the hemianopic line bisection error purely visual? Evidence from eye movements in simulated hemianopia

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ARTICLE INFO

Article history:

Received 5 December 2008

Received in revised form 1 April 2009

Keywords:

Hemianopia

Simulation

Line bisection

Eye movements

Visual field

ABSTRACT

It is still unclear whether the contralateral line bisection error in unilateral homonymous hemianopia is caused by the visual field defect, strategic oculomotor adaptation or by additional extrastriate brain injury. We therefore simulated hemianopia in healthy participants using a gaze-contingent display paradigm and investigated its effects on manual and ocular line bisection performance and eye-movements. Although simulated hemianopia impaired line bisection and induced the adaptive oculomotor eye-movement pattern of hemianopic patients, it did not induce the contralateral bisection error, suggesting that neither the visual field defect nor oculomotor adaptation to it are the primary causes of the hemianopic bisection error.

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1. Introduction

Unilateral homonymous hemianopia (HH) is a visual field disorder in which vision is lost in both monocular hemifields contralateral to the side of brain injury. It is caused by postchiasmatic visual pathway injury that is frequently accompanied by extrastriate lesions; posterior cerebral artery infarction is the most common aetiology (Hebel & von Cramon, 1987; Zhang, Kedar, Lynn, Newman, & Biousse, 2006; Zihl, 2000). Hemianopic patients commonly complain of persistent and severe impairments of reading (Schuett, Heywood, Kentridge, & Zihl, 2008) and visual exploration (Zihl, 2000). Evidence suggests that these functional impairments are determined both by the visual field defect and by the degree of strategic oculomotor adaptation to visual field loss. The hemianopic reading and visual exploration impairments have therefore been interpreted as disorders of the visual bottom-up and attentional top-down control of visual processing and eye-movements, which masquerade as failures of vision (Schuett, Kentridge, Zihl, & Heywood, 2009a).

It is rather striking that these patients also frequently seem to suffer from a spatial distortion which is reflected by a reliable contralateral deviation in the manual bisection of horizontal lines towards the side of their blind hemifield. This contralateral hemianopic bisection error may be understood as a disorder of the egocentric visual midline in the horizontal plane which becomes manifest as a systematic, contralateral shift of the visual

midline or subjective straight-ahead direction in visual-spatial judgements as well as in spatial orientation problems in daily life, such as difficulties with maintaining the straight-ahead direction during walking (Ferber & Karnath, 1999; Kerkhoff, 1999; Zihl, 2000). The hemianopic bisection error is not a deficit in an everyday life task but an indicator of a potentially underlying visual-spatial deficit in HH and therefore also needs to be distinguished from the hemianopic reading and visual exploration impairments. Thus, the line bisection task is a diagnostic and experimental tool to investigate this apparent visual-spatial disorder.

Such a visual-spatial disorder would not be expected with a pure visual-perceptual deficit such as HH and it is therefore not surprising that unfortunately, and despite a much longer history, this contralateral hemianopic line bisection error is less well-known than the ipsilateral bisection error that is frequently associated with visuospatial neglect (Kerkhoff & Bucher, 2008). Axenfeld (1894) was the first to report the hemianopic bisection error. Liepmann and Kalmus (1900) confirmed his report a few years later and termed this contralateral bisection error “hemianopic measurement error”. This error is significantly larger than that of normal observers, who typically bisect horizontal lines more or less accurately (Jewell & McCourt, 2000; for the first report on line bisection in normal observers, see Wolfe, 1923). The contralateral bisection error represents a robust symptom that is frequently associated with HH and persists even years after the occurrence of brain injury (Barton, Behrmann, & Black, 1998; Barton & Black, 1998; Doricchi et al., 2005; Hausmann, Waldie, Allison, & Corballis, 2003; Kerkhoff, 1993; Zihl, 2000; Zihl & von Cramon, 1986).

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The origin of the hemianopic bisection error, however, remains unclear. Barton and Black (1998) investigated line bisection in a small group of hemianopic patients as well as in patients with unilateral cerebral hemispheric lesions who showed normal visual fields. Based on their finding that the contralateral bisection error was present only in hemianopic patients but not in those with normal visual fields, they suggested two possible explanations for the hemianopic bisection error, which, however, have never been investigated.

The first explanation is that the hemianopic bisection error is a direct consequence of the visual field defect. The contralateral bisection error results from a non-veridical spatial representation within a visual hemifield, since in HH the line is viewed in only one hemifield (Barton & Black, 1998). Evidence from hemifield line bisection in normal participants seems to support the visual origin of the hemianopic bisection error, i.e. that the field defect is a necessary prerequisite for the contralateral bisection error. Bisection lines viewed in only one hemifield by instructing participants to fixate the left or right line end induces the contralateral bisection error found in hemianopic patients (Best, 1910a, 1910b; Nielsen, Intriligator, & Barton, 1999). Yet, Best (1910b) found that the bisection error in hemianopic patients was significantly larger than that of healthy observers during hemifield line bisection and therefore dismissed his original hypothesis of a visual origin of the contralateral bisection error. Observations of dissociations between HH and the contralateral bisection error also suggest that the hemianopic visual field defect may not be a necessary condition that causes the contralateral bisection error (Best, 1919; Zihl, 1988, 2000).

According to Barton and Black's (1998) second explanation, the hemianopic bisection error is a manifestation of strategic oculomotor adaptation to visual field loss. Patients who show oculomotor adaptation to visual field loss consistently shift their gaze and, thus, their visual field border, into the area corresponding to their blind hemifield, enabling them to regain sufficient reading and visual exploration performance (Zihl, 2000). Oculomotor adaptation becomes manifest as a change of oculomotor patterns and is possibly best explained as a functional reorganisation of the attentional top-down eye-movement control in reading (Schuett et al., 2008) and visual exploration (Zihl, 2000). Oculomotor adaptation to visual field loss possibly indicates an adaptive attentional bias to contralateral hemispace, which might cause the contralateral line bisection error (Barton & Black, 1998). The slight leftward error normal observers typically show during line bisection (i.e. pseudo-neglect), has also been interpreted as reflecting an attentional bias to left hemispace (Fischer, 2001; Jewell & McCourt, 2000). Barton et al. (1998) studied eye-movements in seven hemianopic patients showing the contralateral bisection error. In contrast to the fixation pattern of normal observers that is concentrated around the centre of the line (Barton et al., 1998; Ishiai, Furukawa, & Tsukagoshi, 1987, 1989), all patients showed a contralateral deviation in the pattern of eye-movements. Although this finding seems to support Barton and Black's (1998) second explanation, that an adaptive attentional bias to contralateral hemispace is a necessary prerequisite for the contralateral bisection error, their assumption was challenged by observations of dissociations between oculomotor adaptation to visual field loss and the contralateral bisection error (Gassel & Williams, 1963a, 1963b; Williams & Gassel, 1962).

Thus, although the contralateral bisection error is frequently associated with HH, it seems to be separable from both the visual field defect and oculomotor adaptation to it. Alternatively, it has been suggested that additional extrastriate brain injury to regions that are involved in visual-spatial perception might result in the hemianopic bisection error (Best, 1919; Ferber & Karnath, 1999; Kerkhoff, 1993; Zihl, 2000). However, the critical lesion location remains to be investigated. It may include posterior occipito-temporal structures (Best, 1919; Ferber & Karnath, 1999; Kerkhoff, 1993;

Zihl, 2000) and/or cortical and subcortical white matter pathways, particularly splenial fibres (Hausmann et al., 2003). The high frequency of extrastriate lesions in patients with HH resulting from postchiasmatic visual pathway injury (Hebel & von Cramon, 1987) may explain why the contralateral bisection error is frequently associated with, but separable from, HH and oculomotor adaptation to it.

In summary, it is still unclear whether the contralateral line bisection error in HH is caused by the visual field defect and/or oculomotor adaptation to visual field loss, or whether hemianopic patients additionally have to deal with the consequences of a visual-spatial deficit caused by additional extrastriate brain injury. Yet, as long as the origin of the hemianopic bisection error is unknown, our understanding of functional impairment in visual field loss remains incomplete and current practice of assessment and rehabilitation imperfect. The purpose of the reported experiments therefore was to identify the visual and adaptive oculomotor (and thus attentional) components that may constitute the hemianopic bisection error and to establish the extent to which this bisection error is purely visually elicited. To do this, we simulated HH in healthy participants by means of a gaze-contingent display. Simulating HH allows the study of behavioural changes associated with the hemianopic visual field defect in the absence of brain injury (Schuett et al., 2009a; see also Schuett, Kentridge, Zihl, & Heywood, 2009b).

In Experiment 1, we investigated the effects of simulated HH on manual line bisection performance and associated eye-movements. Measurement of eye-movements helps to elucidate the role of adaptive oculomotor (and thus attentional) factors in causing the hemianopic bisection error. For the same purpose, we also examined whether the point of bisection may be predicted by the ocular fixation at the time of bisection. We further devised a computerised manual line bisection task and determined whether it resembles the conventional paper-and-pencil task that is commonly used to assess line bisection in hemianopic patients.

In Experiment 2, we studied the effects of simulated HH on line bisection performance and associated eye-movements, not only in a manual bisection task but also in an ocular bisection task without a manual response ("line bisection task by fixation", see Ishiai, Koyama, & Seki, 1998). This enabled us to establish both the role of adaptive oculomotor factors in causing the hemianopic bisection error, as well as examine the assumption that the point of bisection may be predicted by the ocular fixation at the subjective line centre. Comparing ocular and manual line bisection performance and eye-movements also allows us to disentangle the contributions of adaptive oculomotor/attentional factors from the possible impact of manual motor factors. In addition, we investigated whether performing the ocular bisection task may influence line bisection performance in a subsequent manual bisection task (and vice versa).

2. Experiment 1: the effects of simulated HH on manual line bisection

2.1. Methods

2.1.1. Participants

In Experiments 1 and 2 we tested two different groups of naïve, healthy participants with normal or corrected-to-normal vision. We included only right-handed participants with a laterality quotient of >80 in the Edinburgh Handedness Inventory (Oldfield, 1971) in order to eliminate the effects of handedness, which is a significant factor modulating bisection performance in line bisection (Jewell & McCourt, 2000). Participants were native English speakers and had no reading disorders, visual disorders or any other neurological disease or psychiatric condition, and gave their informed consent in accordance with the Declaration of Helsinki

and with local ethical committee approval. In Experiment 1, we tested twelve participants (9 males, 3 females; mean age: 32.0 years (SD: 13.3); years of education: 11.2 years (SD: 3.5)).

2.1.2. Eye-movement recording and simulating HH

Eye-movements were recorded using a pupil and dual Purkinje image video eye-tracker (HS-VET, Cambridge Research Systems). The position of the right eye (binocular viewing) was recorded at a sampling rate of 250 Hz. Eye-movement calibration using a sixteen-point grid was carried out before each recording session and repeated before each task and block of trials. For stimulus presentation, we used an Eizo FlexScan F56 monitor (100 Hz, 17", 800 × 600 pixels) upon which a Keytech touch screen (KTMT-1700, 17") was mounted. At a viewing distance of 38 cm, the screen subtended 40° horizontally and 32° vertically and participants' eye level was at the screen's centre. Participants' heads were fixed by a circular head holder that was firmly attached to a forehead- and chinrest. Ambient room illumination was 1 lux. We used a visual stimulus generator (Cambridge Research Systems) running custom software integrated with our eye-tracker for controlling stimulus presentation.

For simulating left- and right-sided HH (LHH, RHH) in healthy participants, we used a gaze-contingent display paradigm which we have shown to induce the reading and visual exploration impairments found in hemianopic patients (Schuett et al., 2009a). Based on current eye position (acquired at 2.5 times frame rate), the screen to the left (LHH) or right (RHH) assumed the colour of the background. Visual field sparing of the simulated HH was 1°, i.e. 1° between foveal eye position and the left or right visual field boundary remained visible (Fig. 1). Screen update occurred within a single frame (maximum lag: 10 ms). When gaze was directed at positions outside the registration area, the complete screen area was blanked.

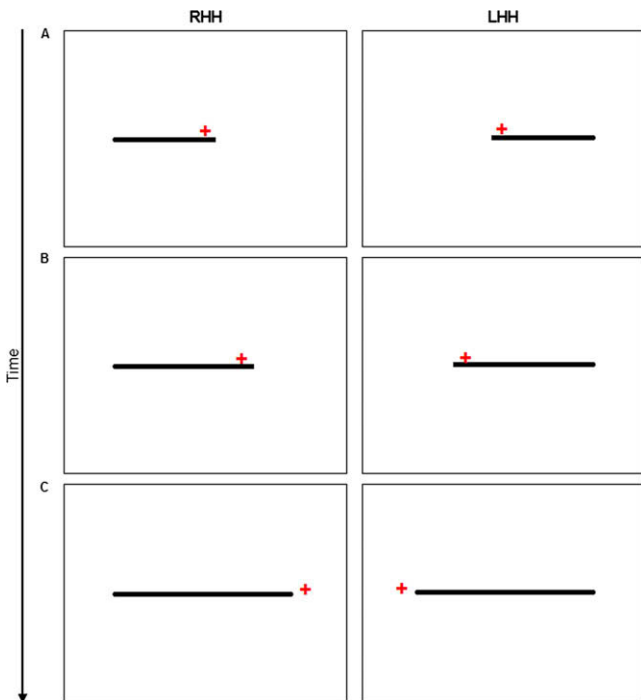


Fig. 1. Schematic illustration of right- and left-sided simulated hemianopia during line bisection (RHH, LHH); our gaze-contingent display paradigm blanks the side to the right or left of current fixation (visual field sparing: 1°). Potential fixation sequences are illustrated (the red cross indicates potential fixation positions of a participant); RHH: scanning the line from the centre (A) to its right end (C), LHH: scanning the line from the centre (A) to its left end (C).

Before each task and block of trials we validated the calibration and accuracy of the simulated visual field boundary by assessing the offset between actual and measured eye position using a nine-point grid. Calibration and validation procedures were repeated if the validation error was greater than 1° on average or greater than 0.5° at each point. During trials, we continuously monitored the accuracy of the simulated visual field boundary on a control display and, in cases of mismatch between actual and measured eye position, calibration and validation procedures were repeated. Trials with >20% loss of eye-movement data (resulting from lid closures or saccades to positions outside the registration area) were discarded from the analyses.

2.1.3. Assessment of manual line bisection

For assessing manual line bisection and associated eye-movements we devised a computerised manual line bisection task that resembles the conventional paper-and-pencil bisection task in which lines are presented on a paper sheet and are bisected using a pencil; this task is typically used with hemianopic patients (for the only exceptions, see Barton et al., 1998; Kerkhoff, 1993). We did not use the most common computerised approach in which lines are bisected using a mouse-controlled cursor since this task has different cognitive and motor demands than line bisection that involves a reaching action (Dellatolas, Vanluchene, & Coutin, 1996; Luh, 1995; Rolfe, Hamm, & Waldie, 2008).

Short (5.3 cm, 8° of visual angle), medium (8.1 cm, 12°) and long (10.9 cm, 16°) horizontal lines (width: 0.3 cm) were presented, one at a time, in the centre of a touch-sensitive monitor screen. Luminance of the black lines was 0.2 cd/m², against a white background of 27 cd/m². Ten lines of each length were presented in randomised sequence. The centre of each line was aligned with the participants' midsagittal plane. Participants were instructed to touch the centre of each line (i.e., subjective line centre) as accurately as possible by using a fine touch screen pen (Palm Inc.). There was no preceding fixation dot. They were asked to make sure to have seen the entire line, i.e. both line ends, before touching the position they perceived to be its centre (Liepmann & Kalmus, 1900). Viewing time was unlimited and participants were free to move their eyes. Touching the line initiated the next trial (ISI = 1000 ms). Participants received no visual feedback on their touch position or its accuracy in order to eliminate practice effects and to ensure that subsequent bisections were not biased. Eye-movement recording started with the onset of line presentation and ended after the participant touched the line.

For assessing line bisection performance we used the response position and calculated the deviation from the left or right of the objective line centre. We report the signed error (°) as a measure of error direction. A negative or positive value indicates a leftward or rightward bisection error, respectively. In addition, we report the absolute error (°) as a measure of error magnitude. We also measured the time required to bisect each line, i.e. time elapsed between onset of line presentation and the response (bisection time).

For assessing eye-movements during line bisection we analysed the horizontal positions (°) of the following fixations, which indicate the horizontal fixation distribution: (1) the bisection fixation (i.e. the fixation at the time of bisection), (2) the maximum fixation (i.e. the fixation with the longest duration), and (3) the left- and right-most fixations (negative and positive values indicate fixation positions to the left and right of the lines' centre, respectively). In addition, we analysed the (4) horizontal fixation range (the distance between left- and right-most fixation positions) as well as the (5) number and (6) duration (ms) of left- and right-hemisphere fixations (i.e. the fixations spent in left and right hemisphere defined with respect to the centre of the screen). In addition to analysing measures indicating the horizontal fixation distribution, we ana-

lysed the (7) number and (8) mean amplitude ($^{\circ}$) of left- and rightward saccades, which indicate the direction of the eye-movements used to inspect each line. We also report the (9) scanpath length (the sum of saccadic amplitudes) ($^{\circ}$), which indicates the efficacy of visual information extraction in visual field loss (Zihl, 2000).

2.1.4. Assessment of touch position measurement accuracy and paper-based line bisection

For assessing the accuracy of our measurement of touch position in the manual line bisection task, we used the manual line bisection task but presented pre-transected lines in which the lines' centres were marked with small, vertical transection marks (data were obtained from participants in Experiment 2 ($n = 20$) who performed this task at the end of the experiment). This pre-transected manual line bisection task is similar to the "Landmark Task" (Milner, Brechmann, & Pagliarini, 1992), except that the transection marks were always at the centre of each line and participants were instructed to touch the centre-mark of each presented line as accurately as possible. We calculated the absolute deviation of each touch position to the centre mark.

To investigate whether our computerised bisection task resembles the conventional paper-and-pencil task, we also assessed paper-and-pencil line bisection performance. Materials, instruction and procedure were identical to those used in the computerised manual bisection task, except that lines were presented in the centre of separate white paper sheets, one at a time; test sheets were aligned with the participant's midsagittal plane. After marking the subjective line centre, the experimenter immediately exchanged the test sheet and presented the next line. The paper-and-pencil line bisection task was performed under normal daylight conditions. We measured the position of each bisection mark to 0.5 mm (0.08°) accuracy and expressed it in $^{\circ}$.

2.1.5. Procedure

Participants were instructed to bisect each line using their right hand in order to eliminate the effects of hand use, which is also a significant factor modulating bisection performance (Jewell & McCourt, 2000). To control the initial starting position of oculomotor and gross motor scanning participants were instructed to begin visually scanning the line in the centre of the screen and to rest their hand on the table in a position aligned with the screen centre between trials. All participants performed the computerised manual line bisection task with simulated LHH, RHH and in a normal viewing condition, i.e. without any simulated HH (N). Task performance in the normal viewing condition was obtained at the end of the task. The sequence of simulation-conditions (starting with LHH or RHH) was counterbalanced across participants to eliminate order effects. After completion of the computerised manual line bisection task and a short break, participants performed the conventional paper-based line bisection task under normal viewing conditions.

2.1.6. Data analysis

To evaluate whether line bisection performance in the computerised and paper-and-pencil bisection task is comparable we performed a repeated measures ANOVA on the measurements of signed and absolute error, with task (computerised, paper-based) and line length (small, medium, long) as within-subject factors. To investigate the effects of simulated HH on line bisection performance and eye-movements, we performed repeated measures ANOVA with simulation-condition (LHH, RHH, N) and line length (small, medium, long) as within-subject factors. Where sphericity assumptions were violated as assessed by Mauchly's W test, we applied the Greenhouse-Geisser correction to the degrees of freedom. Post-hoc paired comparisons between

simulation-conditions, line lengths and tasks were performed using repeated measures t -tests. As multiple tests were carried out, the significance level was adjusted using a Bonferroni correction to an alpha-level of 0.05 for multiple comparisons. In addition, we calculated Pearson's correlations (two-tailed) between the horizontal bisection point and the position of the fixation at the time of bisection for each simulation-condition. 3.4% of trials were excluded from the analyses.

2.2. Results

2.2.1. The effects of simulated HH on manual line bisection performance

Before assessing the effects of simulated hemianopia on line bisection we first test the accuracy of our touch-screen system using the pre-transected line bisection task. The mean absolute error between the marked centres and the measured touch positions was 0.10° (SD: 0.04) for all simulation conditions. Moreover, our touch-screen based manual line bisection task can also reasonably be used a substitute for the conventional paper-based bisection task since there were no differences in error magnitude (absolute error) and direction (signed error) between tasks (larger $F_{(1.0,11.0)} = 0.36$, $p = 0.561$). The significant effect of line length for absolute error ($F_{(1.5,16.3)} = 26.05$, $p < 0.001$) disappeared when the error was expressed as a proportion of line length (largest $F_{(1.3,14.3)} = 3.54$, $p = 0.072$) as would be expected given Weber's Law for Position.

In standard (non pre-transected) manual line bisection our results demonstrate that simulated HH of either sort induced an ipsilateral bisection error (i.e. towards the intact hemifield), as well as increased bisection times (see Table 1); although contralateral errors did occur, they were less frequent and smaller than ipsilateral errors (RHH: $t_{(10)} = 3.16$, $p = 0.010$, non-significant for LHH: $t_{(9)} = -1.83$, $p = 0.147$; two-tailed repeated measures t -tests). Under normal viewing conditions, in contrast, lines were bisected quickly and more or less accurately; although we obtained a slight leftward error, it was significantly smaller than the bisection errors induced by simulated HH (significant effect of simulation-condition; smallest $F_{(2,22)} = 5.25$, $p = 0.014$). Leftward errors were more frequent but not larger than rightward errors (see Table 1; $t_{(9)} = 0.90$, $p = 0.393$; two-tailed repeated measures t -test). These results are substantiated by the finding that error direction was determined by simulation-condition ($\chi^2_{(4)} = 28.00$, $p < 0.001$; two-tailed Pearson's chi-square test). Line length had no effect on line bisection performance. Although errors increased with increasing line length (absolute error: $F_{(1.1,12.6)} = 11.00$, $p < 0.001$; signed error: $F_{(1.3,14.3)} = 3.73$, $p = 0.065$), errors remained invariant across line lengths when expressed as a proportion of line length (largest $F_{(1.4,14.9)} = 1.82$, $p = 0.20$).

2.2.2. The effects of simulated HH on eye-movements during manual line bisection

Under normal viewing conditions, participants showed a symmetrical distribution of fixations that was concentrated around the objective centre of the line. Simulated HH of either sort induced a contralateral deviation of the eye-movement pattern (significant effect of simulation-condition for all oculomotor parameters; smallest $F_{(2,22)} = 9.19$, $p = 0.001$) (see Table 2). Analysing the left- and right-most fixation positions revealed that participants scanned further into their blind hemifield than into their intact field; the fixation with the longest duration also showed a contralateral deviation. Consistent with this observation we found a contralaterally skewed horizontal fixation distribution during line bisection with simulated HH of either sort. Participants made significantly more fixations on the side of space corresponding to their blind hemifield (smaller $t_{(11)} = 4.95$, $p < 0.001$). Under normal

Table 1
Manual line bisection performance in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Overall bisection error signed error (°)	+0.4 (1.0)	−0.4 (0.7)	−0.1 (0.2)	*	*	*
[% of line length]	[+3.4 (8.3)]	[−3.9 (5.9)]	[−0.8 (1.7)]			
Absolute error (°)	0.7 (0.8)	0.6 (0.6)	0.2 (0.1)	*	*	n.s.
[% of line length]	[6.2 (6.5)]	[5.2 (4.9)]	[1.5 (1.1)]			
Leftward bisection error (%)	42.1	75.4	66.7	*	n.s.	*
(°)	0.3 (0.3)	0.7 (0.6)	0.2 (0.1)	*	*	*
[% of line length]	[3.3 (2.3)]	[6.0 (5.2)]	[1.7 (1.2)]			
Rightward bisection error (%)	57.3	24.0	29.9	*	n.s.	*
(°)	1.0 (1.0)	0.3 (0.2)	0.1 (0.1)	*	*	*
[% of line length]	[8.4 (7.7)]	[2.5 (2.4)]	[1.2 (0.8)]			
Correct bisections (%)	0.6	0.6	3.4	n.s.	n.s.	n.s.
Bisection time (s)	6.6 (3.5)	7.1 (2.6)	4.4 (2.8)	*	*	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples *t*-tests, except for frequency of left- and rightward errors and correct bisections: two-tailed Pearson's chi-square test). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

Table 2
Eye-movements during manual line bisection in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Horizontal position (°) of the						
Bisection fixation	−1.3 (1.6)	+1.6 (1.7)	−0.1 (0.6)	*	*	*
Maximum fixation	−3.7 (2.3)	+2.6 (2.4)	−0.2 (0.7)	*	*	*
Leftmost fixation	−8.9 (3.4)	−4.0 (2.3)	−3.9 (3.8)	*	n.s.	*
Right-most fixation	+3.1 (2.9)	+9.3 (3.2)	+3.0 (3.3)	n.s.	*	*
Fixation range (°)	12.0 (4.9)	13.3 (4.2)	6.9 (5.8)	*	*	n.s.
Right-hemisphere fixations						
Number	17.9 (15.2)	58.2 (21.9)	9.89 (9.9)	*	*	*
Duration (ms)	500.6 (311.7)	453.7 (159.9)	419.2 (170.1)	*	*	*
Left-hemisphere fixations						
Number	48.3 (23.3)	22.4 (12.1)	9.36 (7.0)	*	*	*
Duration (ms)	560.7 (270.4)	448.9 (165.3)	493.5 (269.1)	*	*	*
Rightward saccades						
Number	34.6 (17.9)	38.8 (13.4)	10.4 (7.9)	*	*	n.s.
Amplitude (°)	2.7 (1.1)	3.5 (1.5)	2.3 (1.0)	n.s.	*	*
Leftward saccades						
Number	30.4 (16.6)	43.5 (16.1)	8.7 (7.0)	*	*	n.s.
Amplitude (°)	3.5 (1.9)	2.4 (0.6)	2.5 (1.1)	*	n.s.	*
Scanpath length (°)	191.5 (113.1)	229.1 (89.6)	50.0 (49.0)	*	*	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples *t*-tests). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

viewing conditions, however, fixations were equally distributed in left- and right-hemisphere ($t_{(11)} = -0.28$, $p = 0.788$) (two-tailed repeated measures *t*-tests).

Although we did not obtain a significant effect of simulation-condition on fixation duration and saccadic amplitudes (largest $F_{(1,4,15,1)} = 2.50$, $p = 0.105$), post-hoc comparisons revealed that also these measures were significantly and differentially affected by simulated HH (see Table 2). During line bisection with simulated HH fixation durations increased and participants made larger saccades towards the blind field than towards the intact hemifield (RHH: $t_{(11)} = -2.55$, $p = 0.027$; LHH: $t_{(11)} = 1.88$, $p = 0.087$); under normal viewing conditions, however, saccadic amplitudes did not differ between directions ($t_{(11)} = 1.29$, $p = 0.225$) (two-tailed repeated measures *t*-tests). As would be expected given these results, we found that the spatial range covered by fixations was considerably larger, scanpaths significantly longer and participants made more saccades (both to the left and right) during line bisection

with simulated HH than under normal viewing conditions (see Table 2).

The horizontal range of fixations increased with increasing line length under normal viewing conditions (significant difference between the small and long line; $t_{(11)} = -8.07$, $p < 0.001$) but remained constant across lengths during line bisection with simulated HH (RHH: largest $t_{(11)} = -1.19$, $p = 0.260$; LHH: largest $t_{(11)} = -2.14$, $p = 0.056$); we obtained the same effect for the positions of the left- and right-most fixation positions (significant main and interaction effect line length smallest $F_{\text{int}(4,44)} = 3.41$, $p = 0.016$). Line length did not affect the contralateral deviation of the leftmost fixation in LHH or that of the right-most fixation in RHH (largest $t_{(11)} = 0.70$, $p = 0.499$). It did, however, affect the right-most fixation in LHH and the leftmost fixation in RHH as well as both fixation positions under normal viewing conditions; both fixations were shifted further to the left or right, respectively, with increasing line length (smallest $t_{(11)} = -2.85$, $p = 0.016$).

2.2.3. The relationship between the point of bisection and the fixation at the time of bisection

Simulated HH of either sort induced a contralateral deviation of the fixation at the time of bisection (see Table 2). During line bisection with RHH, the same large deviation was present irrespective of the direction of the bisection error (largest $t_{(10)} = 0.42$, $p = 0.686$). During line bisection with LHH, the magnitude of the contralateral deviation depended on error direction; it was significantly larger for contralaterally deviated bisections than for ipsilateral bisections ($t_{(9)} = -2.41$, $p = 0.039$). Under normal viewing conditions, the fixation at the time of bisection showed only a slight deviation whose direction depended on the direction of the error. For leftward bisections, it was shifted to the left; for rightward bisections, it was shifted slightly to the right. Yet, the magnitude of this deviation did not differ between left- and rightward bisections ($t_{(9)} = -1.20$, $p = 0.260$) (two-tailed repeated measures t -tests).

There was a significant correlation between the position of the fixation at the time of bisection and the manual bisection position for both types of simulated HH (smaller $r = 0.17$, $p = 0.001$) and under normal viewing conditions ($r = 0.11$, $p = 0.047$). These effects nevertheless differed depending on direction of the bisection error with simulated HH. During line bisection with simulated HH, we only found correlations when subjects made ipsilateral bisection errors (smaller $r = 0.24$, $p < 0.001$) and not contralateral ones (larger $r = -0.13$, $p = 0.127$). Under normal viewing conditions we only found correlations for rightward errors ($r = 0.20$, $p = 0.045$) and not for leftward ones ($r = -0.01$, $p = 0.929$).

2.3. Discussion

Our results demonstrate that simulated HH of either sort induced an ipsilateral bisection error that was significantly larger than the typical, small leftward bisection error we obtained under normal viewing conditions (Jewell & McCourt, 2000). The contralateral bisection errors that did occur were smaller and less frequent than ipsilateral errors. These effects differ from the common observation of a reliable and much larger contralateral bisection error in hemianopic patients (Barton & Black, 1998; Barton et al., 1998; Doricchi et al., 2005; Hausmann et al., 2003; Kerkhoff, 1993; Zihl, 2000; Zihl & von Cramon, 1986). Although simulated HH did not induce the bisection error found in hemianopic patients it produced the same contralateral deviation in the pattern of eye-movements that is shown by patients during line bisection; this deviation suggests the presence of strategic oculomotor adaptation to contralateral hemispace (Barton et al., 1998; Ishiai et al., 1987, 1989).

Our observation of large, predictive overshooting saccades into the blind hemifield (i.e. a contra-directional saccadic bias) further supports the presence of oculomotor adaptation to simulated HH (Gassel & Williams, 1963a; Meinenberg, Zangemeister, Rosenberg, Hoyt, & Stark, 1981; Williams & Gassel, 1962; Zangemeister, Oechsner, & Freska, 1995; Zangemeister & Utz, 2002; Zihl, 2000). By shifting gaze, and thus the simulated visual field boundary, towards the blind hemifield participants can bring obscured visual information about the extent of the presented line into their seeing hemifield. We recently demonstrated that oculomotor adaptation to simulated HH occurs spontaneously and rapidly, even in the absence of any instruction aimed at improving participants' performance (Schuett et al., 2009a, 2009b). Our finding of a symmetrical and centred oculomotor scanning pattern under normal viewing conditions confirms prior observations that healthy participants mainly scan the centre of the lines (Barton et al., 1998; Ishiai et al., 1987, 1989).

Fixation position at the time of bisection may be an important factor in predicting the ipsilateral bisection error in simulated HH as indicated by the significant correlations we found between

the ipsilaterally deviated point of bisection and the position of the fixation at bisection. The contralateral deviation of this fixational measure was more pronounced for contralateral errors but these are not to be predicted by the fixation at the time of bisection. Under normal viewing conditions, the fixation at the time of bisection deviated in the same direction as the bisection error but it seems only to predict the bisection positions in rightward errors. Our findings are consistent with evidence from line bisection in visual neglect suggesting that the placement of the bisection mark may be predicted by an ocular fixation at the time of bisection (Ishiai et al., 1989, 1998).

3. Experiment 2: the effects of simulated HH on ocular line bisection

To investigate further the significance of oculomotor (and thus attentional) factors in line bisection with simulated HH and to establish the extent to which line bisection performance is determined by the manual motor component of the bisection task, we conducted Experiment 2. Here we studied line bisection both in computerised and paper-based manual bisection tasks as well as in an ocular bisection task without manual response (Ishiai et al., 1998). In addition, we investigated whether performing the ocular bisection task may influence line bisection performance in a subsequent manual bisection task (and vice versa).

3.1. Methods

3.1.1. Participants

We tested twenty participants (12 males, 8 females; mean age: 19.1 years (SD: 1.3); years of education: 12.4 years (SD: 0.7)).

3.1.2. Eye-movement recording and simulating HH

Methods for eye-movement recording and simulating HH were identical to those used in Experiment 1.

3.1.3. Assessment of ocular line bisection

For examining ocular line bisection we devised a computerised version of Ishiai et al.'s (1998) "line bisection task by fixation". Our ocular line bisection task was identical to the manual line bisection task used in Experiment 1, except that the response-mode was ocular; in addition, we used longer lines (small: 13.6 cm (19.7°), medium: 16.6 cm (23.6°), long: 19.6 (27.3°)) and presented five instead of ten lines for each length. Participants were instructed to fixate the centre of each presented line as accurately as possible. Upon stable fixation of the position they perceived to be the line's centre, the next trial was initiated via mouse-click. Eye-movement recording started with the onset of line presentation and ended by mouse-click.

The analysis of ocular line bisection performance and eye-movement parameters was identical to Experiment 1, except that we used the horizontal positions of the 'bisection'-fixation instead of the touch positions.

3.1.4. Assessment of manual line bisection

For assessing manual line bisection performance and eye-movements we used the same manual line bisection task as in Experiment 1. The analysis of performance and oculomotor parameters was also identical to Experiment 1.

3.1.5. Assessment of 'bisection'-fixation and touch position measurement accuracy and paper-based line bisection

In order to assess the accuracy of 'bisection'-fixation and touch position measurements we used the pre-transected manual line bisection task described in Experiment 1, except that for assessing 'bisection'-fixation position measurement accuracy (pre-transect-

ed ocular line bisection task) participants were instructed to fixate the centre-mark of each presented line as accurately as possible. The results of the manual version of the task have already been presented in Experiment 1.

To establish the extent to which paper-based line bisection performance is predicted by the manual motor component of the bisection task, we additionally assessed paper-based line bisection performance. We used the same paper-and-pencil line bisection task as in Experiment 1, except that we used longer lines (small: 13.6 cm (19.7°), medium: 16.6 cm (23.6°), long: 19.6 (27.3°)) and presented five instead of ten lines for each length.

3.1.6. Procedure

All participants performed the ocular and manual line bisection task with LHH, RHH and in a normal viewing condition, i.e. without any simulated HH (N). Normal viewing condition was the final test condition for every participant. The sequence of simulation-conditions (starting with LHH or RHH) was counterbalanced across participants to eliminate order effects. Since performing the ocular bisection task may influence line bisection performance in a subsequent manual bisection task (and vice versa), participants were randomly allocated into two equal groups ($n = 10$); Group A first performed the manual, then the ocular line bisection task (mean age: 19.4 years (1.7); years of education: 12.5 (0.8); 2 females, 8 males), Group B performed the tasks in the opposite order (mean age: 18.8 years (0.6); years of education: 12.3 (0.6); 6 females, 4 males). After completion of the computerised line bisection tasks, we assessed the baseline accuracy of manual and ocular line bisection performance with pre-transected lines. Finally, participants performed the paper-and-pencil line bisection task under normal viewing conditions.

3.1.7. Data analysis

The analyses for testing the effects of simulated HH on ocular and manual line bisection performance and eye-movements were identical to Experiment 1, except that we used task-sequence (Groups A, B) as an additional between-subject factor. We conducted the same analysis for testing the effects of response-mode by including response-mode (manual, ocular) as an additional within-subject factor. In addition, we compared bisection performance between the computerised manual, ocular and paper-and-pencil bisection task (signed and absolute error under normal viewing conditions) by performing a repeated measures ANOVA with task and line length as within-subjects factors. Task-sequence was a between-subject factor in both analyses. Post-hoc paired comparisons between simulation-conditions, tasks and line lengths were performed using repeated measures t -tests. Corrections for violations of sphericity assumptions and multiple comparisons were identical to those used in Experiment 1. The analyses to further investigate the hypothesis that the point of bisection may be predicted by the ocular fixation at the subjective line centre were also identical to those used in Experiment 1; in addition we calculated Pearson's correlations (two-tailed) between the manual and ocular signed bisection errors. 1.3% of trials were excluded from the analyses of the manual line bisection data, 2.3% of trials from the analyses of the ocular line bisection data.

3.2. Results

3.2.1. The effects of simulated HH and task-sequence on ocular and manual line bisection performance, and the effects of response-mode

3.2.1.1. The effects of simulated HH and task-sequence on ocular line bisection. The accuracy of the 'bisection'-fixation position measurements in the pre-transected ocular line bisection task was 0.15° (SD: 0.21) for all viewing conditions (mean absolute deviation for all line lengths).

The patterns of effects of simulated HH on the magnitude and direction of the bisection error and bisection time during ocular line bisection were identical to those observed in Experiment 1, except that ocular bisection errors were slightly larger. We also obtained the same slight leftward error under normal viewing conditions (see Table 3; significant effect of simulation-condition, smallest $F_{(1.2,22.3)} = 15.00$, $p < 0.001$; $\chi^2_{(4)} = 75.20$, $p < 0.001$). The ipsilateral errors during line bisection with a simulated HH of either sort were not only more frequent (see Table 3) but also significantly larger than the contralateral errors (smaller $t_{(16)} = -3.26$, $p = 0.005$). Under normal viewing conditions, the leftward errors were more frequent (see Table 3) but not larger than rightward errors ($t_{(15)} = 1.24$, $p = 0.233$) (repeated measures t -tests). As with manual line bisection, ocular line bisection was not affected by line length (largest $F_{(1.4,26.1)} = 0.95$, $p = 0.372$).

We found no effect of the order in which participants undertook the manual and ocular bisection tasks on ocular bisection performance (the largest task-sequence main or interaction effects is non-significant $F_{(2,36)} = 2.06$, $p = 0.143$).

3.2.1.2. The effects of simulated HH and task-sequence on manual line bisection. Although we replicated the effects of simulated HH on the magnitude of the manual bisection error and bisection time found in Experiment 1 (see Table 4; significant effect of simulation-condition; smaller $F_{(2,36)} = 34.57$, $p < 0.001$) as well as the non-significant effect of line length (largest $F_{(2,36)} = 2.50$, $p = 0.10$), we did not obtain the ipsilateral bisection error during line bisection with simulated HH ($F_{(1.1,20.0)} = 0.02$, $p = 0.919$); ipsi- and contralateral errors were equally frequent (see Table 4) and of equal magnitude (larger $t_{(16)} = 0.19$, $p = 0.850$; repeated measures t -tests). We observed a slight leftward error not only under normal viewing conditions but also for line bisection with simulated HH (see Table 4). The leftward errors under normal viewing conditions were slightly larger than rightward errors ($t_{(18)} = 1.95$, $p = 0.068$, marginal; repeated measures t -test). These results are substantiated by the finding that error direction was not determined by simulation-condition ($\chi^2_{(4)} = 4.54$, $p = 0.371$; two-tailed Pearson's chi-square test).

We examined whether the absence of an ipsilateral bisection error during line bisection with simulated HH was accounted for by task-sequence. We replicated the main findings of Experiment 1 in participants who performed the ocular bisection task first ($n = 10$). They showed slightly more and larger ipsilateral than contralateral bisection errors during manual line bisection with simulated HH (LHH: $t_{(8)} = 3.88$, $p = 0.006$; non-significant for RHH: $t_{(8)} = -1.11$, $p = 0.297$); these effects were not evident in participants who first performed the manual bisection task (larger $t_{(8)} = 0.89$, $p = 0.401$) (repeated measures t -tests).

Moreover, we found that participants who first performed the ocular bisection task showed slightly smaller bisection errors during line bisection with simulated HH (RHH: 0.70° (SD: 0.42), LHH: 0.79° (SD: 0.29)) than those who performed the manual bisection task first (RHH: 1.04° (SD: 0.53), LHH: 0.84° (SD: 0.41)) although this difference only reached marginal significance for RHH ($t_{(18)} = 1.89$, $p = 0.075$; LHH: $t_{(18)} = 0.46$, $p = 0.652$); this tendency was not evident under normal viewing conditions ($t_{(18)} = -0.48$, $p = 0.641$) (independent samples t -tests; significant interaction between task-sequence and simulation condition: $F_{(2,36)} = 3.72$, $p = 0.034$).

3.2.1.3. The effects of response-mode. The differences in the effects of simulated HH on line bisection performance between the ocular and manual line bisection task obtained in the present experiment are substantiated by a significant effect of response-mode for the absolute error (measure of error magnitude) and its significant interaction with simulation-condition for the signed error

Table 3

Ocular line bisection performance in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Overall bisection error Signed error						
(°)	+1.0 (1.7)	−1.4 (1.6)	−0.4 (0.8)	*	*	*
[% of line length]	[+4.2 (7.1)]	[−5.8 (7.1)]	[−1.5 (3.5)]			
Absolute error						
(°)	1.4 (1.4)	1.6 (1.4)	0.7 (0.6)	*	*	n.s.
[% of line length]	[6.0 (5.7)]	[6.9 (6.1)]	[2.9 (2.5)]			
Leftward bisection error						
(%)	23.7	80.6	64.1	*	n.s.	*
(°)	0.9 (0.7)	1.8 (1.4)	0.8 (0.6)	n.s.	*	*
[% of line length]	[3.8 (2.8)]	[7.9 (6.3)]	[3.5 (2.8)]	n.s.	*	*
Rightward bisection error						
(%)	73.9	16.3	31.7	*	*	*
(°)	1.6 (1.5)	0.8 (0.6)	0.5 (0.3)	*	*	*
[% of line length]	[7.0 (6.1)]	[3.3 (2.8)]	[2.1 (1.4)]	*	*	*
Correct bisections (%)	2.4	3.1	4.1	n.s.	n.s.	n.s.
Bisection time (s)	7.0 (3.3)	7.2 (3.7)	4.6 (2.4)	*	*	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples *t*-tests, except for frequency of left- and rightward errors and correct bisections: two-tailed Pearson's chi-square test). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

Table 4

Manual line bisection performance in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Overall bisection error signed error						
(°)	−0.07 (1.0)	−0.05 (1.2)	−0.03 (0.4)	n.s.	n.s.	n.s.
[% of line length]	[−0.3 (4.2)]	[−0.3 (4.7)]	[−0.1 (1.7)]			
Absolute error						
(°)	0.8 (0.6)	0.9 (1.2)	0.3 (0.3)	*	*	n.s.
[% of line length]	[3.3 (2.6)]	[3.5 (3.1)]	[1.3 (1.0)]			
Leftward bisection error						
(%)	56.0	50.7	52.0	n.s.	n.s.	n.s.
(°)	0.8 (0.8)	0.9 (0.7)	0.3 (0.2)	*	*	n.s.
[% of line length]	[3.2 (2.1)]	[3.7 (3.0)]	[1.4 (0.9)]	*	*	n.s.
Rightward bisection error						
(%)	43.7	49.0	45.7	n.s.	n.s.	n.s.
(°)	0.9 (0.7)	0.8 (0.8)	0.3 (0.3)	*	*	n.s.
[% of line length]	[3.5 (3.1)]	[3.3 (3.1)]	[1.3 (1.1)]	*	*	n.s.
Correct bisections (%)	0.3	0.3	2.3	n.s.	n.s.	n.s.
Bisection time (s)	6.9 (2.7)	6.8 (2.5)	3.6 (1.5)	*	*	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples *t*-tests, except for frequency of left- and rightward errors and correct bisections: two-tailed Pearson's chi-square test). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

(measure of direction and magnitude) (smaller $F_{(1,18)} = 32.35$, $p < 0.001$).

Conducting the same analysis (i.e. repeated measures ANOVA with response-mode, simulation-condition and length as within-subject factors and task-sequence as a between-subject factor) but using the manual line bisection data obtained in Experiment 1 showed, however, that line bisection performance with simulated HH did not differ between the ocular and manual task. In contrast to the previous analysis, the significant main and interaction effects only indicate a difference in magnitude but not in direction between ocular and manual bisection errors with simulated HH (Tables 1 and 3; smaller $F_{(2,22)} = 7.35$, $p = 0.004$).

Despite these differences we obtained significant correlations between ocular and manual bisection errors for line bisection with simulated HH of either sort (smaller $r = 0.33$, $p = 0.009$) but not under normal viewing conditions ($r = -0.12$, $p = 0.356$). Moreover, participants required the same amount of time for manual and ocular line bisection (Tables 3 and 4; larger $F_{(1,18)} = 2.61$, $p = 0.124$).

Comparing computerised ocular, manual and paper-based line bisection performance under normal viewing conditions revealed a slight leftward bisection error, irrespective of the task used to assess bisection performance. This error was largest in the ocular bisection task (smaller $t_{(19)} = -4.24$, $p < 0.001$) and did not differ between the two manual bisection tasks ($t_{(19)} = -0.61$, $p = 0.552$) (repeated measures *t*-tests); significant effect of task: absolute error $F_{(1,2,21.8)} = 17.93$, $p < 0.001$, signed error $F_{(1,2,21.8)} = 3.88$, $p = 0.055$). The significant effect of line length for absolute error ($F_{(1,8,32.7)} = 5.61$, $p = 0.010$) disappeared when expressed as a proportion of line length ($F_{(1,8,32.3)} = 2.01$, $p = 0.154$); there was no effect of task-sequence (largest $F_{(1,4,44.2)} = 1.68$, $p = 0.165$).

3.2.2. The effects of simulated HH and task-sequence on eye-movements during ocular and manual line bisection, and the effects of response-mode

3.2.2.1. The effects of simulated HH and task-sequence on ocular and manual line bisection. The use of longer lines explains the greater left- and rightward deviation of fixational measures, the larger range of fixations and the longer scanpaths that we obtained in

the present experiment when compared to Experiment 1. Eye-movement patterns during ocular line bisection with simulated HH showed the same contralateral deviation that we obtained during manual line bisection in the previous and present experiment (Tables 5 and 6) (significant main effect of simulation-condition for all oculomotor parameters; ocular: smallest $F_{(2,36)} = 6.02$, $p = 0.006$; manual: smallest $F_{(2,36)} = 4.54$, $p = 0.017$). In contrast to manual line bisection, however, the horizontal range of fixations did not differ between viewing conditions ($F_{(1,5,26,3)} = 0.24$, $p = 0.785$) and the differences in scanpath length were less consistent ($F_{(2,36)} = 3.03$, $p = 0.061$).

Hemisphere analyses revealed the differential effect of simulated HH on the horizontal fixation distribution for ocular (Table 5) and manual line bisection (Table 6). Fixations were more frequent in contralateral than in ipsilateral hemisphere (ocular: smaller $t_{(19)} = 4.39$, $p < 0.001$; manual: smaller $t_{(19)} = -10.76$, $p < 0.001$). Under normal viewing conditions fixations were symmetrically distributed during manual line bisection ($t_{(19)} = -0.55$, $p = 0.586$). During ocular line bisection, however, participants showed a tendency to fixate more frequently in left- than right-hemisphere ($t_{(19)} = 1.80$, $p = 0.088$) (repeated measures t -tests). We also obtained a differential effect for fixation durations during ocular line bisection that was not evident during manual line bisection (Table 5). Simulated HH of either sort induced significantly longer fixation durations in ipsilateral than in contralateral hemisphere (RHH: $t_{(19)} = 3.79$, $p = 0.001$; LHH: $t_{(19)} = -0.53$, $p = 0.603$ (the non-significant result may possibly be due to a large variation in individual fixation durations)). Under normal viewing conditions left-hemisphere fixation duration was significantly longer than right-hemisphere fixation duration ($t_{(19)} = 2.46$, $p = 0.023$) (repeated measures t -tests). This result is consistent with our finding of ipsilateral ocular bisection errors during line bisection with simulated HH and leftward bisection errors under normal viewing conditions.

We also replicated the interaction between simulation-condition and line length for the left- and right-most fixation positions and the range of fixations during manual line bisection and additionally confirmed this effect for the maximum fixation position (smallest $F_{(4,72)} = 3.28$, $p = 0.016$; marginal significance for fixation-range: $F_{(4,72)} = 2.12$, $p = 0.087$). During ocular line bisection, however, this length effect was present in all simulation-conditions (smallest $F_{(1,8,32,5)} = 4.19$, $p = 0.028$).

Although performing the ocular bisection task had a considerable effect on manual line bisection performance (but not *vice versa*), eye-movement measures were not significantly affected by task-sequence (non-significant main and interaction effects; largest $F_{(1,18)} = 1.48$, $p = 0.240$). Eye-movement patterns during ocular line bisection also did not differ between participants who first performed manual line bisection and those who first performed ocular bisection (largest $F_{(1,18)} = 2.14$, $p = 0.161$), except that the maximum fixation position showed a slight rightward deviation in the former group but a leftward deviation in the latter group ($F_{(1,18)} = 7.37$, $p = 0.014$).

3.2.2.2. The effects of response-mode. The differences between ocular and manual line bisection in the effects of simulated HH on the range of fixations, scanpath length and left- and right-hemisphere fixations are confirmed by a significant interaction of response-mode and simulation-condition (smallest $F_{(2,36)} = 3.67$, $p = 0.035$): the increased fixation range and longer scanpaths were present only during manual line bisection whereas the differential effect on fixation durations was associated with ocular line bisection only. In addition we found that simulated HH induced a greater deviation of the maximum fixation position during manual line bisection than during ocular bisection (Tables 4 and 6; $F_{(2,36)} = 5.69$, $p = 0.007$). Eye-movement patterns under normal viewing conditions were not, however, affected by response-mode (largest $F_{(1,18)} = 3.56$, $p = 0.075$), except that bisecting lines by fixation seemed to induce a slight leftward deviation in oculomotor patterns that was not present during manual line bisection as well as slightly larger saccades (significant effect of response-mode for left-hemisphere fixations and saccadic amplitudes, smallest $F_{(1,18)} = 4.79$, $p = 0.042$).

3.2.3. The relationship between the point of bisection and the fixation at the time of bisection during manual line bisection

We replicated the contralateral deviation of the fixation at the time of bisection during manual line bisection with simulated HH and the slight leftward deviation under normal viewing conditions (Table 6; $F_{(2,36)} = 16.12$, $p < 0.001$). Our observation that ipsilateral errors were accompanied by a smaller fixational deviation (LHH: -1.6° (SD: 3.6), RHH: 1.4° (SD: 2.8)) than contralateral errors (LHH: -2.6° (SD: 3.2), RHH: 1.9° (SD: 3.9)) is also consistent with

Table 5
Eye-movements during ocular line bisection in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Horizontal position ($^\circ$) of the						
Maximum fixation	-3.0 (4.2)	+2.4 (4.5)	-0.2 (4.1)	*	*	*
Leftmost fixation	-15.9 (2.6)	-9.6 (5.2)	-13.2 (2.3)	*	*	*
Rightmost-fixation	+9.7 (4.4)	+16.6 (2.6)	+12.3 (2.3)	*	*	*
Fixation range ($^\circ$)	25.6 (6.1)	26.2 (6.5)	25.5 (4.3)	n.s.	n.s.	n.s.
Right-hemisphere fixations						
Number	24.4 (21.4)	38.2 (19.6)	16.9 (9.8)	n.s.	*	*
Duration (ms)	389.0 (121.2)	316.2 (92.0)	298.8 (109.5)	n.s.	n.s.	n.s.
Left-hemisphere fixations						
Number	40.7 (19.6)	28.5 (31.1)	21.5 (15.8)	*	n.s.	*
Duration (ms)	366.1 (175.6)	468.7 (239.8)	353.7 (157.8)	n.s.	*	n.s.
Rightward saccades						
Number	31.2 (12.5)	30.8 (19.7)	20.6 (13.2)	*	*	n.s.
Amplitude ($^\circ$)	5.4 (1.2)	4.9 (1.8)	6.7 (2.7)	*	*	n.s.
Leftward saccades						
Number	33.8 (25.4)	35.9 (26.1)	17.9 (10.5)	*	*	n.s.
Amplitude ($^\circ$)	3.9 (1.2)	4.6 (1.4)	6.0 (2.0)	*	*	n.s.
Scanpath length ($^\circ$)	295.2 (168.1)	290.6 (181.2)	226.0 (121.4)	n.s.	n.s.	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples t -tests). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

Table 6

Eye-movements during manual line bisection in left- and right-sided simulated hemianopia (LHH, RHH) and in the normal viewing condition (N) [means (SD) calculated over all line lengths].

	LHH	RHH	N	N-LHH	N-RHH	LHH-RHH
Horizontal position (°) of the						
<i>Bisection fixation</i>	−2.1 (4.5)	+1.7 (4.7)	−0.2 (0.6)	*	*	*
<i>Maximum fixation</i>	−6.5 (3.9)	+6.8 (4.5)	−0.5 (4.5)	*	*	*
<i>Leftmost fixation</i>	−16.5 (2.8)	−10.3 (5.1)	−11.4 (4.3)	*	n.s.	*
<i>Rightmost fixation</i>	+11.0 (4.0)	+17.4 (2.7)	+11.6 (3.8)	n.s.	*	*
Fixation range (°)	27.5 (6.1)	27.7 (6.7)	23.0 (7.6)	*	*	n.s.
Right-hemisphere fixations						
<i>Number</i>	17.9 (10.9)	46.4 (22.6)	15.8 (9.7)	n.s.	*	*
<i>Duration (ms)</i>	324.8 (82.9)	341.5 (94.4)	280.0 (92.3)	*	*	n.s.
Left-hemisphere fixations						
<i>Number</i>	50.5 (25.8)	17.5 (12.5)	15.1 (8.9)	*	n.s.	*
<i>Duration (ms)</i>	355.3 (84.0)	376.0 (123.0)	345.1 (129.7)	n.s.	n.s.	n.s.
Rightward saccades						
<i>Number</i>	34.1 (15.7)	29.7 (17.1)	16.3 (9.0)	*	*	n.s.
<i>Amplitude (°)</i>	4.8 (1.5)	5.8 (1.6)	5.9 (2.5)	n.s.	n.s.	n.s.
Leftward saccades						
<i>Number</i>	34.3 (17.2)	34.2 (15.7)	14.6 (8.1)	*	*	n.s.
<i>Amplitude (°)</i>	4.8 (1.5)	5.3 (1.4)	6.0 (2.7)	n.s.	n.s.	n.s.
Scanpath length (°)	358.1 (202.2)	344.6 (188.9)	182.8 (114.6)	*	*	n.s.

Statistical comparisons were made between LHH, RHH, and N (two-tailed dependent samples *t*-tests). * indicates $p < 0.017$ (α_{corr}), n.s. indicates non-significant comparisons.

Experiment 1. These differences did not, however, reach statistical significance (larger $t_{(16)} = 1.17$, $p = 0.261$). We also found that the fixation at the time of bisection deviated in the same direction as the point of bisection under normal viewing conditions ($t_{(18)} = -4.03$, $p = 0.001$) (repeated measures *t*-tests).

Since performing the ocular bisection task led to improvements in subsequent manual line bisection performance (but not *vice versa*), we investigated whether participants might have used the bisection-by-fixation strategy they must have adopted during ocular line bisection to perform manual line bisection. Although the position of the fixation at the time of bisection was not affected by task-sequence (largest $F_{(2,72)} = 2.01$, $p = 0.149$), we found that only participants who first performed the ocular bisection task ($n = 10$) showed the relationship between this fixational measure and the point of bisection during line bisection with simulated HH (smaller $r = 0.19$, $p = 0.018$; manual task first: larger $r = 0.09$, $p = 0.264$). Consistent with Experiment 1, this relationship was more pronounced for ipsilateral errors (smaller $r = 0.19$, $p = 0.099$) than for contralateral errors (larger $r = -0.02$, $p = 0.891$). Under normal viewing conditions, however, we obtained this relationship irrespective of whether participants first performed the ocular or manual bisection task (smaller $r = 0.31$, $p < 0.001$). Yet, in the former group, it reached statistical significance for rightward errors only ($r = 0.30$; $p = 0.014$) (as in Experiment 1); in the latter group, it was significant for leftward errors only ($r = 0.25$, $p = 0.023$).

3.3. Discussion

Although we could not fully replicate the ipsilateral manual bisection error found in Experiment 1, we showed again that simulated HH induces the contralaterally deviated eye-movement pattern of hemianopic patients during line bisection (Barton et al., 1998; Ishiai et al., 1987, 1989) but not their contralateral line bisection error (Barton & Black, 1998; Barton et al., 1998; Doricchi et al., 2005; Hausmann et al., 2003; Kerkhoff, 1993; Zihl, 2000; Zihl & von Cramon, 1986). Interindividual differences on the impact of a simulated visual field defect (Schuett et al., 2009a; Zangemeister & Utz, 2002) and the use of longer lines, which increases the difficulty of line bisection with a visual field defect, may account for the differences between experiments.

Studying ocular line bisection in simulated HH demonstrated that the ipsilateral bisection error and the contralateral deviation in the pattern of eye-movements found in Experiment 1 also occur without manual response. The significant correlation between ocular and manual bisection errors and the finding that ocular and manual line bisection require the same amount of time is consistent with this finding. Moreover, irrespective of whether we used the ocular, manual or the classic paper-and-pencil bisection task to assess line bisection performance under normal viewing conditions, participants showed the same bisection times, the small leftward bisection error and the symmetrical oculomotor scanning pattern that is typical of healthy subjects (Barton et al., 1998; Ishiai et al., 1987, 1989; Jewell & McCourt, 2000). Although ocular bisection errors were slightly larger and we obtained a slight leftward directional bias in the otherwise symmetrical eye-movement patterns under normal viewing conditions, this result nevertheless suggests that the manual motor component of the line bisection task, i.e. the actual hand movement, seems not to be critical to the bisection error and oculomotor behaviour of healthy participants when confronted with a pure visual field defect or under normal viewing conditions. This conclusion is supported by findings from ocular line bisection in visual neglect indicating that the placement of the bisection mark is predicted by the fixation at the time of bisection (Ishiai et al., 1989, 1998). Based on these findings the “line bisection task by fixation” has been proposed as a substitute for the manual line bisection test (Ishiai et al., 1998) which may be particularly useful in cases where upper extremity disorders impede the assessment of line bisection performance. Examining ocular line bisection in simulated HH has shown that this task might also be a useful experimental and diagnostic tool for assessing line bisection in patients with visual field loss.

The importance of oculomotor factors in line bisection with simulated HH is further emphasised by the effects of ocular line bisection on subsequent manual bisection. Performing the ocular line bisection task led to smaller bisection errors and seemed to increase the frequency and magnitude of ipsilateral relative to contralateral errors. Performing the manual bisection task, in contrast, had no effect on subsequent ocular bisection. These findings suggest that participants may adopt the bisection-by-fixation strategy they used during ocular line bisection for performing the manual bisection task with simulated HH. Participants may use

an ocular fixation to guide their manual bisection response, which seems to improve manual line bisection performance. The significant correlation we obtained between the fixation at the time of bisection and the point of bisection during manual line bisection with simulated HH only after participants had performed the ocular bisection task supports this assumption. It remains possible, however, that these improvements did not result from adopting a specific bisection strategy but from increased oculomotor adaptation to simulated HH or from simple practice effects. Yet, line bisection performance and eye-movements as well as the close relationship between the fixation at the time of bisection and the bisection position under normal viewing conditions remained unchanged after performing the oculomotor task. Moreover, ocular line bisection did not improve after performing the manual bisection task, neither when participants were confronted with simulated HH nor under normal viewing conditions. These findings contradict the latter two explanations and that line bisection performance has found to be robust to retest effects further supports our assumption (Kerkhoff & Marquardt, 1998; Pierce, Jewell, & Menneker, 2003).

4. General discussion

The purpose of the present study was to identify the visual and oculomotor (and thus attentional) components that may constitute the hemianopic bisection error as well as to establish whether the origin of the contralateral bisection error in hemianopic patients is purely visual.

Our results demonstrate that a pure hemianopic visual field defect does not induce the reliable contralateral deviation during line bisection that has been reported for hemianopic patients (Barton & Black, 1998; Barton et al., 1998; Doricchi et al., 2005; Hausmann et al., 2003; Kerkhoff, 1993; Zihl, 2000; Zihl & von Cramon, 1986). Although it induced significantly larger bisection errors than under normal viewing conditions, these errors were smaller than those of hemianopic patients and participants showed both, contra- and ipsilateral errors; ipsilateral errors were even larger and more frequent than contralateral errors, resulting in an overall ipsilateral error. Although the presence of a pure hemianopic visual field defect impairs line bisection performance in healthy participants, it seems not sufficient for the reliable contralateral bisection error to emerge. This finding contradicts the assumption that the hemianopic bisection error is a direct consequence of the visual field defect (Barton & Black, 1998; Barton et al., 1998; Best, 1910a; Nielsen et al., 1999).

Yet the presence of strategic oculomotor adaptation to visual field loss indicating an attentional bias to contralateral hemispace also does not seem to be the causative factor in hemianopic bisection error. We demonstrated that line bisection with simulated HH was associated with a contralateral deviation in the pattern of eye-movements. This deviation indicates strategic oculomotor (and thus attentional) adaptation to visual field loss and mirrors the oculomotor behaviour of hemianopic patients during line bisection (Barton et al., 1998; Ishiai et al., 1987, 1989). Despite strategic oculomotor adaptation to contralateral hemispace, our participants did not show the reliable bisection error in the same direction. Thus, compensatory shifts of eye-movements towards the blind field and the contralateral bisection error can dissociate. This finding challenges the view that the hemianopic bisection error arises from oculomotor adaptation indicating an adaptive attentional bias to contralateral hemispace (Barton & Black, 1998; Barton et al., 1998).

Although neither the visual field defect, nor oculomotor adaptation to it, seems to be the causative factor in hemianopic bisection error, they may nevertheless contribute to it. The line bisection task has long been used as an experimental tool to study the per-

ceptual, attentional and motor factors affecting visuospatial performance both in patients with visual neglect and normal subjects (Fischer, 2001) but, surprisingly not in patients with visual field loss. Thus, it remains unknown exactly which factors determine line bisection performance in visual field loss. Investigating the role of the visual field defect in relation to perceptual, attentional and (ocular and manual) motor factors seems to be of particular interest in this regard, not least since patients with visual neglect frequently show a concomitant visual field disorder (Walker, Findlay, Young, & Welch, 1991).

The fact that the magnitude and direction of the bisection errors we observed in simulated HH are not the same as in real HH suggests a differential contribution of visual and adaptive oculomotor (and thus attentional) factors to the respective bisection errors. Since error magnitude does not differ between left- and right-sided visual field loss, either in real HH (Kerkhoff, 1993; Zihl, 1995, 2000; Zihl & von Cramon, 1986) or in simulated HH, it may be the severity of the visual field defect that determines the magnitude of the bisection error. If the visual field defect contributes to the error, the degree of visual field sparing should be negatively correlated with error magnitude (Barton & Black, 1998). Although preliminary evidence suggests that there is no such relationship in hemianopic patients (Kerkhoff, 1999; Zihl, 2000), no systematic study has been carried out thus far, and since we studied line bisection in simulated HH with a constant visual field sparing, this relationship still requires further investigation in both real and simulated HH. The side of the visual field defect seems to determine the direction of the error in hemianopic patients; patients with a left-sided HH show leftward errors, patients with a right-sided HH show rightward errors (Barton & Black, 1998; Barton et al., 1998; Doricchi et al., 2005; Hausmann et al., 2003; Kerkhoff, 1993; Zihl, 2000; Zihl & von Cramon, 1986). In simulated HH, however, the relationship between side of visual field loss and error direction was less pronounced. The effect of the side of visual field loss on the hemianopic contralateral bisection error may not be visual. It may rather be the side of brain injury that determines error direction but masquerades as a visual effect.

It is also important to consider the possibility that hemianopic visual field defects result in a chronic differential lateralised or asymmetric visual-sensory input and, thus, an imbalance in visual-spatial processing efficiency, which can give rise to an attentional bias in the direction of the seeing hemifield, i.e. to ipsilateral hemispace (Tant, Kuks, Kooijman, Cornelissen, & Brouwer, 2002). Such ipsilateral attentional bias arising from a visual-sensory deficit might explain the ipsilateral bisection errors our participants showed when confronted with a simulated HH. Another factor contributing to the ipsilateral errors found in our participants may be a geometric bias that is introduced by the fact that the visual angles subtended by each of the two halves of a line are unequal when the line is viewed in one hemifield on a flat surface perpendicular to the direction of gaze at fixation. Although the error arising from this geometric bias is in the wrong direction to account for the ipsilateral bias in simulated HH, its magnitude is comparable to that of the ipsilateral error in our participants. Since its magnitude also increases with increasing line length, this error could account for the absence of a consistent ipsilateral bias when longer lines were used (Experiment 2). The difference in distance from the eye to the two halves of the line with a flat display is another potential influence on line length perception (Norman, Todd, Perotti, & Tittle, 1996), however, again the difference in distance between the near and far end lines in our tasks is negligible compared to the depth differences one would expect in order to account for the ipsilateral bisection errors found in our study (Norman et al., 1996). It nevertheless remains possible that retinal eccentricity effects on perceived line length may contribute to these errors. Bisecting lines viewed in only one hemifield by instructing participants to fixate

the left or right line end induces a contralateral bisection error which has been explained as being mediated by the relationship between retinal eccentricity and cortical magnification. The representation of space may be distorted in the periphery and the portion of the stimulus in central vision may be overestimated (central magnification) (Nielsen et al., 1999). The similarities in magnitude between the errors found in hemifield line bisection and the errors associated with simulated HH seem to support this argument. Yet, since both errors were in opposing directions, it remains to be seen exactly which factors determine a systematic change in the bias (in addition to the systematic change in the accuracy) of position judgments as eccentricity increases.

Although the bisection error in simulated and real HH does not seem to be a manifestation of strategic oculomotor adaptation indicating an adaptive attentional bias to contralateral hemispace, oculomotor factors may nevertheless contribute to the resulting bisection error. We identified the fixation at the time of bisection as an important oculomotor factor that seems to be critical to the ipsilateral bisection error found in simulated HH. The significance of oculomotor factors in manual line bisection is further supported by our findings from ocular line bisection in simulated HH and under normal viewing conditions. Participants showed the same line bisection error and oculomotor behaviour as in the manual line bisection task indicating that the manual motor component seems not to be integral to the ipsilateral bisection error associated with simulated HH and the small leftward error under normal viewing conditions. Significant correlations between ocular and manual bisection errors are consistent with this view. Further investigation is required in order to determine the extent to which the fixation at the time of bisection and the manual motor component contribute to the contralateral bisection error found in hemianopic patients.

The finding that performing the ocular bisection task with simulated HH, i.e. bisecting lines by fixating instead of marking the subjective line centre, improved performance in the subsequent manual bisection task but not *vice versa*, provides additional evidence for the importance of oculomotor factors in manual line bisection. However, since we observed no improvements under normal viewing conditions, oculomotor factors may be of particular importance if vision is compromised. Performing ocular line bisection with simulated HH may allow participants to adopt an oculomotor strategy that helps guiding their manual bisection response in a condition where lines can never be seen in their entirety. The consequent improvements in line bisection suggest that this strategy alleviates the line bisection impairment caused by this pure visual field defect. It remains to be determined whether such oculomotor strategies suffice to alleviate the contralateral line bisection error in hemianopic patients.

In conclusion, our findings suggest that the hemianopic visual field defect and its adaptive oculomotor (and thus attentional) consequences may contribute to the contralateral bisection error found in hemianopic patients but they do not seem to be its primary causes. The bottom-up restriction of the visual field clearly affects line bisection performance, suggesting that the ability to accurately bisect lines requires visual information extraction from the parafoveal and peripheral visual field. If vision in these visual field regions is affected, either by simulated HH or by brain injury, lines are only partly visible, which impairs efficient line bisection. However, a pure hemianopic visual field defect and its adaptive oculomotor (and thus attentional) consequences did not suffice to induce the contralateral bisection error. Thus, the basis of the hemianopic bisection does not seem to be purely visual. These results are consistent with reports that the contralateral bisection error can dissociate from visual field loss (Best, 1919; Zihl, 1988, 2000) as well as from successful strategic oculomotor adaptation indicating an adaptive attentional bias to contralateral hemispace

in patients (Gassel & Williams, 1963a, 1963b; Williams & Gassel, 1962). Although the contralateral bisection error is frequently associated with HH, it is separable from both, the visual field defect and its adaptive oculomotor (and thus attentional) consequences.

The hemianopic line bisection impairment is not simply a failure of vision but an indicator of a visual–spatial deficit which is frequently associated with HH but not primarily caused by it. It seems to require additional extrastriate brain injury, possibly to regions that are involved in visual–spatial perception. Axenfeld (1894) advocated the line bisection task as “a simple method to diagnose hemianopia”, particularly in cases where there is no access to a perimeter or when patients are not able to undergo perimetric visual field testing (see also Liepmann & Kalmus, 1900). The dissociability of the contralateral line bisection error and HH indicates, however, that the diagnostic value of the line bisection task in the assessment of HH is limited. Yet, although the line bisection task is not an appropriate substitute for perimetric testing and can only complement perimetric diagnosis, it is an important tool to assess visual–spatial perception which is frequently impaired in hemianopic patients. Since visual–spatial deficits interact with visual deficits and increase resulting functional impairments, studying visual–spatial deficits in patients with visual field loss, as well as developing effective treatment methods, is of great importance. Although strategic oculomotor adaptation and the contralateral bisection error can dissociate, treatment-induced oculomotor adaptation in reading and visual exploration (Zihl, 2000) may help patients to overcome their shift of the egocentric visual midline. Yet, evidence from patients with visual neglect suggests that visual–spatial deficits require specific treatment for their improvement (Kerckhoff, 1998). It is also therefore important to study the natural course of the visual–spatial deficit associated with visual field loss since spontaneous recovery of perception of spatial axes has been reported in patients with right posterior cerebral infarctions (Zihl, 2000).

Acknowledgments

Susanne Schuett was supported by a PhD scholarship from the German Academic Exchange Service (DAAD). We wish to thank John Findlay for his valuable advice on eye movement analysis and Robert Metcalf for writing the software programs for the analysis of the eye-movement data. We also would like to thank the two anonymous reviewers for their helpful comments and suggestions on an earlier version of this manuscript.

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