

Spatial attention: Differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes



Christopher S.Y. Benwell^{a,b}, Gregor Thut^a, Gemma Learmonth^b, Monika Harvey^{b,*}

^a Centre for Cognitive Neuroimaging, Institute of Neuroscience and Psychology, University of Glasgow, Glasgow 58 Hillhead Street, G12 8QB, United Kingdom

^b School of Psychology, University of Glasgow, Glasgow G12 8QB, United Kingdom

ARTICLE INFO

Article history:

Received 30 July 2013

Accepted 18 September 2013

Available online 25 September 2013

Keywords:

Attentional biases

Landmark

Line bisection

Hemispatial neglect

Lateralisation

ABSTRACT

Asymmetry in human spatial attention has long been documented. In the general population the majority of individuals tend to misbisect horizontal lines to the left of veridical centre. Nonetheless in virtually all previously reported studies on healthy participants, there have been subsets of people displaying rightward biases.

In this study, we report differential time-on task effects depending on participants' initial pseudoneglect bias: participants with an initial left bias in a landmark task (in which they had to judge whether a transection mark appeared closer to the right or left end of a line) showed a significant rightward shift over the course of the experimental session, whereas participants with an initial right bias shifted leftwards.

We argue that these differences in initial biases as well as the differential shifts with time-on task reflect genuine observer subtypes displaying diverging behavioural patterns. These observer subtypes could be driven by differences in brain organisation and/or lateralisation such as varying anatomical pathway asymmetries (Thiebaut de Schotten et al., 2011).

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1. Introduction

Asymmetry in human spatial attention has long been documented in both the lesioned and healthy brain (Vallar, 1998; Bowers and Heilman, 1980; Siman-Tov et al., 2007). In the general population, individuals tend to misbisect horizontal lines to the left of veridical centre (a phenomenon named 'pseudoneglect'), possibly as a consequence of right hemisphere specialisation for visuospatial attention (Bowers and Heilman, 1980; Schenkenberg, Bradford, and Ajax, 1980; Mesulam, 1999; Harvey, Pool, Roberson, and Olk, 2000; Jewell & McCourt, 2000; Thiebaut de Schotten et al., 2005; Benwell, Harvey, Gardner, and Thut, 2013).

It has further been suggested that arousal level influences spatial bias, with left bias associated with states of relatively high alertness and right bias associated with states of low alertness or fatigue (Bellgrove, Dockree, Aimola, and Robertson, 2004; Manly, Dobler, Dodds, and George, 2005; Fimm, Willmes, and Spijkers, 2006; Matthias et al., 2009; Newman, O'Connell, and Bellgrove, 2013). Moreover, specific to line bisection judgements, left to rightward shifts have been observed over the course of prolonged

performance on a landmark task. This has been labelled the 'Time-on-task' effect (Manly et al., 2005; Dufour, Touzalin, and Candas, 2007; Benwell et al., 2013) and it has been argued that attention is biased towards the left visual field in states of high alertness but that a reduction or even reversal of this bias occurs as right hemisphere dominance for task processing decreases with reduced alertness/increasing fatigue (Manly et al., 2005; Fimm et al., 2006; Dufour et al., 2007).

What is of interest, and its implications generally neglected so far, is that although most studies of spatial attention report the described left biases (see McCourt, 2001 and Jewell & McCourt, 2000 for a review of a large number of these studies), virtually all of these studies contain a subset of participants that display right biases. McCourt (2001) estimates that the true right bias in a population of young healthy right-handed participants is less than 5%. Nonetheless, a range of his groups' other studies reported numbers around 10% (see also very recent results by Szczepanski and Kastner, 2013) with yet other experiments resulting in figures as high as 30–50% (Cowie and Hamil, 1998; Braun & Kirk, 1999; Dellatolas, Coutin, and Agostini, 1996; Manning, Halligan, and Marshall, 1990).

McCourt (2001) emphasises that these performance differences are only meaningful if they reveal genuine observer subtypes rather than mere differences in the experimental methodology. There is in fact evidence from neuro-imaging that bilateral activation is frequently observed in studies of visuospatial function (Corbetta and

* Corresponding author. Tel.: +44 141 330 6174; fax: +44 141 330 4606.
E-mail address: Monika.Harvey@glasgow.ac.uk (M. Harvey).

Shulman, 2002; Corbetta et al., 2005; Siman-Tov et al., 2007; Szczepanski and Kastner, 2013). Moreover hemispatial neglect, a visuo-spatial attentional disorder leading to spatial biases in line bisection and landmark tasks (Vallar, 1998; Milner and Harvey 1995; Milner, Brechmann, and Pagliarini, 1992; Milner, Harvey, Roberts, and Forster, 1993; Harvey, Milner, and Roberts, 1995), although more frequent and severe after right hemisphere lesions (see Karnath & Rorden, 2012 and Harvey and Rossit, 2012 for recent reviews), is also present in up to 40% of patients suffering from left hemisphere damage (Beis et al., 2004). Further evidence that there may indeed be genuine observer subtypes was given in a recent study by Thiebaut de Schotten et al. (2011). For the first time, the authors showed that the relative hemispheric lateralisation of a parieto-frontal white matter pathway (superior longitudinal fasciculus II (SLF II)) predicts the degree of spatial bias across healthy participants. In line with previous studies, most of their participants showed a significant left bias in a line bisection task, whereas 30% (7/20) showed either no bias or a reversed right bias. Scores on the line bisection test correlated significantly with the lateralisation pattern of the SLF (II) in that participants with a larger right than left SLF II deviated more towards the left in the bisection task, whereas participants who showed no bias or a right bias showed a bilateral or reversed pattern of SLF II asymmetry. Individual differences in the relative lateralization of hemispheric dominance for spatial attention, and hence the direction and extent of behavioural spatial bias, have also been shown to be predicted by common DNA variation in dopamine system gene characteristics (Newman, O'Connell, Nathan, and Bellgrove, 2012; Bellgrove et al., 2007; Greene, Robertson, Gill, and Bellgrove, 2010). Moreover, in a recent fMRI study Cai, Van der Haegen, and Brysbaert (2013) investigated the relationship between functional lateralization of language production and visuospatial attention in healthy participants: they found that all those displaying (atypical) right hemispheric language production dominance, also displayed (atypical) left hemispheric visuospatial attention dominance. Additionally, all but one participant displaying typical left hemispheric language dominance also displayed right hemispheric dominance for spatial attention, suggesting the lateralization of language and spatial attention function to be functionally dependent.

Consistent with these arguments, in the current paper, we report the results of two experiments displaying differential time-on task effects depending on participants' initial pseudoneglect biases. Although authors investigating the time-on task effect have not discussed population differences in initial attention bias explicitly, predictions can be made from the time-on task vigilance/arousal hypothesis (Manly et al., 2005; Dufour et al., 2007; Benwell et al., 2013; Newman et al., 2013): if differences in pseudoneglect bias (left versus right) across the population are driven by fatigue levels (reduced leftward bias or cross over to the right due to decreased right hemisphere activation with reduced arousal/alertness), then participants with an initial right bias should show either no change, or an even greater rightward shift over time, i.e. should show a shift in the same direction as participants with an initial left bias. Interestingly what we report instead, is that although participants' initial left biases did indeed shift rightwards over time, participants who showed an initial right bias showed a shift in the opposite direction (leftward shift in bias), even though both groups did not differ in their initial alertness level and both groups reported a similar reduction of alertness over time. This pattern was replicated in two experiments (Experiments 1 and 2). Importantly, high test–retest reliability of initial (baseline) bias across days (as assessed in Experiment 3 over 3 sessions which were separated by 24 h minimum) supports the notion that the baseline bias represents a reliable and stable trait measure within individuals. This suggests that participants with right bias represent an observer subtype, rather than being at the tail end of a

homogenous group in terms of a right hemisphere driven spatial process.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty-eight right-handed participants (13 male, 15 female, mean age = 22.93 years; SD = 3.59, max = 37, min = 19) took part in the experiment. Written informed consent was obtained from each participant. All participants were volunteers naive to the experimental hypothesis being tested. All participants had normal or corrected-to-normal vision and reported no history of neurological disorder. The experiment was carried out within the Institute of Neuroscience & Psychology at the University of Glasgow and was approved by the local ethics committee.

2.1.2. Instrumentation and stimuli

Stimuli were presented using the E-Prime software package (Schneider, Eschman, and Zuccolotto, 2002) on a CRT monitor with a 1280 × 1024 pixel resolution and 85 Hz refresh rate. Adapted from Benwell et al., 2013, the paradigm represented a computerised version of the landmark task (Milner et al., 1993; Olk & Harvey, 2002). White lines on a grey background (luminance = 179, hue = 179) were briefly transected (35 ms) after a variable time period (from 150 ms to 6000 ms) using 100% Michelson contrast lines (see Fig. 1 for an example of the line stimuli, for details of procedure see Section 2.1.3 below and Fig. 2). Lines measured 30 cm in length by 0.5 cm in height and at a viewing distance of 100 cm subtended 17.06° (width) by .29° (height) of visual angle. Lines were transected at 1 of 17 points ranging symmetrically from ± 4.38% of absolute line length relative to veridical centre (see Fig. 1 for examples of line stimuli). This represented a range of −1.3° to 1.3° of visual angle relative to veridical centre.

2.1.3. Procedure

At the beginning and end of the experimental session, all participants completed the Stanford Sleepiness Scale (Hoddes, Zarcone, Smythe, Phillips, and Dement, 1973), a subjective measure of alertness ranging from 1 (fully alert) to 7 (asleep). Participants were then seated 100 cm from the screen and their mid-sagittal plane aligned with the display monitor. Viewing distance was kept constant using a chin rest.

Each experimental block consisted of 136 trials (8 judgements at each of the 17 transector locations). Fig. 2 depicts a schematic representation of the trial procedure. Each trial began with presentation of a plain grey screen (luminance = 179, hue = 179) for 1 s followed by presentation of the white line. Onset of the transected line (which appeared for 35 ms) was varied from trial to trial across 8 different stimulus onset asynchronies (SOAs: 150 ms, 857 ms, 1714 ms, 2571 ms, 3428 ms, 4285 ms, 5142 ms, 6000 ms). This SOA manipulation is the focus of another paper in preparation and is not considered any further here. After the 35 ms presentation of the transected line, the white line remained on the screen until the subject responded by pressing either the left or right response key. The subsequent trial began as soon as the response was made. Participants were instructed to pay attention to the white line throughout each trial. They were told

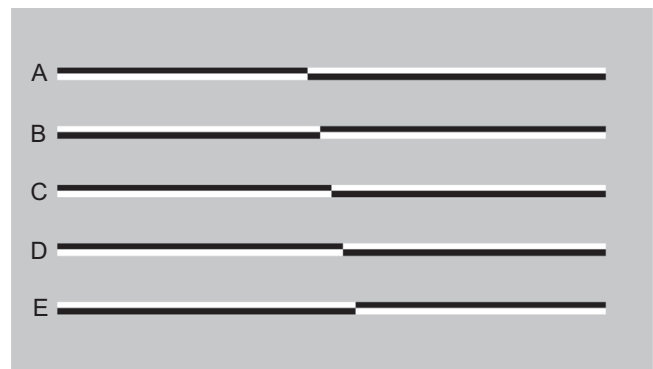


Fig. 1. Examples of line stimuli used in all experiments. Lines were transected at 1 of 17 locations ranging symmetrically from ± 4.38% (Experiment 1), or ± 4% (Experiments 2 and 3), of absolute line length relative to, and including, veridical centre (for full details of transector locations for each experiment, method Section 2.1.2 (Experiment 1) and Section 3.1.2 (Experiments 2 and 3)). Lines A and B are transected to the left of veridical centre, line C is veridically transected and lines D and E are transected to the right of veridical centre. Lines of varying contrast polarity appeared with equal frequency and the order of appearance was randomized.

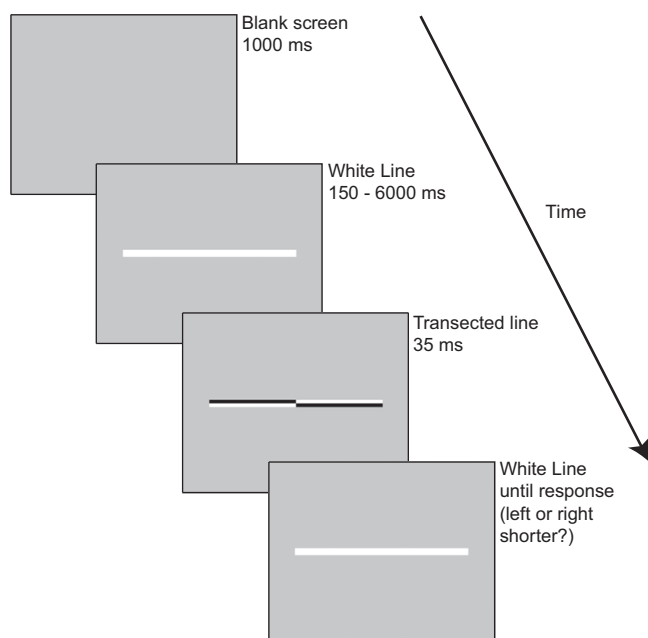


Fig. 2. A schematic representation of the trial procedure of Experiment 1. Onset of the transected line (which appeared for 35 ms) was varied from trial to trial across 8 different stimulus onset asynchronies (SOAs: 150 ms, 857 ms, 1714 ms, 2571 ms, 3428 ms, 4285 ms, 5142 ms, 6000 ms). The white line remained on the screen until the subject responded by pressing either the left or right (shorter) response key. The subsequent trial began as soon as the response was made.

that the line would be briefly transected (cut into two segments) at some point during the trial and that their task was to judge whether the transection mark appeared closer to the left end of the line or closer to the right end of the line. Participants responded using their dominant right hand (right index and middle finger respectively) and were instructed to hold their gaze on the centre of the screen throughout each trial. Trials lasted approximately 2–8 s with each block lasting 10–12 min. Trial type (location of transector in line) and SOA were selected randomly although each participant completed the same number of judgements for each transector location/SOA per block (1 judgement at each transector location per SOA during each block, i.e. 8 judgements per transector location when collapsed over SOA). A block of 20 practice trials was performed immediately prior to the beginning of the experimental blocks.

Each participant performed 8 blocks of the landmark task. Between blocks, participants were allowed to take short breaks. The entire experiment lasted approximately 70–80 min.

2.1.4. Experimental groups

Based on the bias displayed during the first block of the landmark task, participants were split into three experimental groups: an initial left bias group (LB Group: 7 male, 10 female, mean age = 22.47 years (max = 28, min = 19)), a group showing no initial bias (NB Group: 1 female, 4 males, mean age = 26 years (max = 37, min = 21)) and an initial right bias group (RB Group: 2 male, 4 female, mean age = 21.66 years (max = 23, min = 20)). Group assignment was based on the individually fitted psychometric functions (see Section 2.1.5 below) of the 1st block. A significant bias (either leftward or rightward) was judged to be present in any given participant if the 95% confidence interval for the estimated subjective midpoint did not include 0 (veridical centre) (95% confidence interval obtained from individually fitted psychometric function, see below).

2.1.5. Analyses

In order to obtain an objective measure of perceived line midpoint for each block in each participant, psychometric functions (PFs) were derived using the method of constant stimuli. The dependent measure was the proportion of trials on which participants indicated that the transector had appeared closer to the left end of the line. Non-linear least-squares regression was used to fit a cumulative logistic function to the data. The cumulative logistic function is described by the following equation:

$$f(\mu, x, s) = 1 / (1 + \exp((x - \mu) / s))$$

where x are the tested transector locations, μ corresponds to the x -axis location with a 50% 'left' and 50% 'right' response rate and s is the estimated width of the psychometric curve. The 50% location is known as the point of subjective equality (PSE) and represents an objective measure of perceived line midpoint. The width of the PF provides a measure of the precision of participants' line midpoint

judgements per block. For the purposes of the current study, transector location judgements were collapsed across the 8 SOA's prior to curve fitting. Inferential statistical analyses were performed on the individually fitted psychometric function PSE values and estimated widths, as well as the Stanford Sleepiness Scale ratings.

2.2. Results

2.2.1. Subjective alertness

Stanford Sleepiness Scale ratings confirmed a reduction in subjective alertness over the course of the experimental session, with the overall mean score on the Stanford Sleepiness Scale increasing from 2.9 (SD = 1.06) to 3.4 (SD = 1.49). A 2 (pre vs post experiment) \times 3 (group) factorial analysis of variance (ANOVA) confirmed a main effect of time-on-task on sleepiness rating [$F(1, 24) = 12.91$, $p = 0.001$], no significant main effect of group [$F(1, 24) = 0.34$, $p = 0.72$] and no interaction between group and time-on-task: [$F(2, 30) = 0.52$, $p = 0.6$].

2.2.2. Subjective midpoint shifts

In Fig. 3A, individually fitted mean PSE values (% of absolute line length re veridical) and the corresponding 95% confidence intervals are plotted as a function of block rank 1–8 for all 3 experimental groups. In line with previous studies of pseudo-neglect, mean PSE in the left bias (LB) Group at the beginning of the experiment was displaced to the left of veridical centre by -1.47% of absolute line length (block 1, Fig. 3A) significantly deviating from zero/centre (see 95% confidence bar clearly differing from zero). Across the experimental session, a clear systematic shift in subjective midpoint is apparent in the LB group (with 95% confidence bars approaching zero), so that in the final block after extended performance (block 8, Fig. 3A), mean PSE was displaced to the left by -0.59% . This indicates a rightward shift of $+0.88\%$ of absolute line length in subjective midpoint with time on task of 70–80 min. In the no bias (NB) group, mean PSE was slightly to the right of veridical centre ($+0.06\%$) in block 1 (block 1, Fig. 3A). The mean PSE remained relatively stable around veridical centre throughout the experimental session in this group (with 95% confidence bars crossing the zero line in all blocks), so that mean PSE in the final block 8 was to the left of veridical centre by -0.13% . This indicates a slight leftward shift of -0.19% in subjective midpoint with time on task. In the right bias (RB) group, mean PSE was $+0.85\%$ to the right of veridical centre in block 1 (block 1, Fig. 3A), significantly deviating from zero/centre (see 95% confidence bar clearly differing from zero). As in the LB group, a shift in subjective midpoint across the experimental session is apparent in the RB group (the 95% confidence bars progressively approached zero to finally cross the zero line), though in the opposite direction. In the RB group, mean PSE in the final block 8 was to the right of veridical centre by $+0.34\%$ which indicates a leftward shift of -0.51% in subjective midpoint with time on task (block 8, Fig. 3A).

A 3 (Group: LB vs NB vs RB) \times 2 (time-on-task: block 1 vs block 8) Factorial ANOVA on the individually fitted PSE values showed a main effect of group [$F(1, 25) = 14.44$, $p < 0.001$], no significant main effect of time-on-task (block 1 vs block 8) [$F(1, 25) = 0.068$, $p = 0.80$] but a significant time-on-task \times group interaction [$F(1, 25) = 4.72$, $p = 0.02$]. Analysis of simple main effects for exploring the interaction term (paired-sample t -tests performed on PSE values between block 1 and block 8 separately for each group) revealed a statistically significant difference between block 1 and block 8 in the LB Group, characterised by a shift to the right in mean subjective midpoint [$t(16) = -3.187$, $p = 0.01$] indicating a time-on-task effect for those who started with a left bias. In contrast, no statistically significant difference was observed from

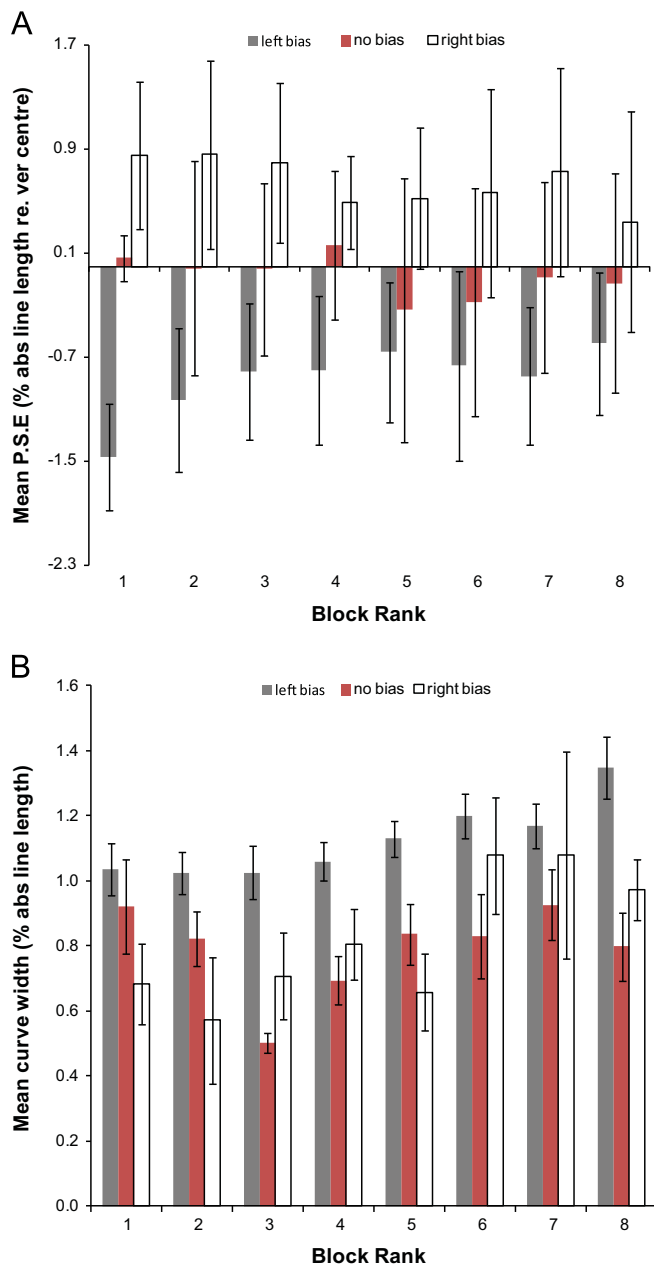


Fig. 3. (A) **Experiment 1:** group averaged PSE values (+ corresponding 95% confidence interval bars) for each block of the experimental session. Grey filled bars represent the initial left bias group, red filled bars represent the no initial bias group and white filled bars represent the initial right bias group. (B) Group averaged curve widths (± 1 S.E.) for each block of the experimental session in each group.

block 1 to block 8 in either the NB group [$t(5)=0.58$, $p=0.59$] or the RB group [$t(4)=1.35$, $p=0.25$].

Linear regression analysis performed exclusively on extended performance (block 1–8) within each group revealed statistically significant linear relationships between block rank and PSE in the LB Group [$r^2=0.61$ [$F(1, 7)=9.23$, $p=0.023$]] and the RB group [$r^2=0.56$ [$F(1, 7)=7.8$, $p=0.032$]] but no statistically significant relationship between the two variables in the NB Group [$r^2=-0.27$ [$F(1, 7)=2.19$, $p=0.19$]].

A possible concern might be that the observed shifts in PSE over the course of the experimental session do not represent true shifts in perceptual bias, but may rather be explained by non-stationary observer response behaviour, perhaps due to learning or an increase in the observers' lapse rate with time-on-task

(Fründ, Valentin Haanel, and Wichmann, 2011). In order to address these issues, we also analysed the widths of the individually fitted PFs and how they evolved over the course of the experimental session. The curve width represents the region of the sigmoid function between the lower and upper asymptotes: the region where changes in stimulus intensity lead to behavioural changes. This provides a measure of how easily the observer was able to correctly discern between the different transector locations per block. Fig. 3B plots the mean width of the PFs (% absolute line length ± 1 SE) for each block of the experimental session for all 3 experimental groups.

A 3 (Group: LB vs NB vs RB) \times 2 (time-on-task: block 1 vs block 8) Factorial ANOVA showed no main effect of time-on-task on curve width [$F(1, 25)=1.71$, $p=0.2$], no main effect of group [$F(1, 25)=2.14$, $p=0.14$] and no interaction between time-on-task and group [$F(1, 25)=1.39$, $p=0.27$]. If there were learning effects we would have expected the curve widths to reduce over time, or conversely to increase with noisier performance. This was not the case. Nonetheless, for the left and right bias groups only, we also correlated the degree of absolute shift in PSE (% of absolute line length from blocks 1–8 regardless of shift direction) with the shift in curve width (% of absolute line length from blocks 1–8) over the course of the experimental session. This analysis revealed no statistically significant relationship between the degree of PSE shift and the degree of curve width shift [Pearson's $r=-0.01$, $p=0.96$]: further evidence that an increase in noise in the psychometric function is unlikely to account for the observed shifts in PSE with time-on-task.

2.3. Interim discussion

In line with the large majority of previous studies (see McCourt (2001) and Jewell & McCourt (2000) for reviews), a majority of the participants in Experiment 1 demonstrated an initial left bias during landmark task performance. Nonetheless different initial biases showed distinct changes over time with initial left biases showing a significant rightward shift (confirmed by both regression and ANOVA analyses) and participants with an initial right bias shifting leftwards. This latter leftward shift in the initial right bias group failed to reach significance in the ANOVA (likely due to the small number of participants showing an initial right bias), but the linear regression revealed a statistically significant relationship between block rank and PSE.

Moreover curve width did not change over time, nor were there curve width differences between the groups, indicating that both groups showed reliable performance over time, and hence practice effects or increased noise in the psychometric function are unlikely to account for the observed shifts in midpoint estimation.

However, one limitation of Experiment 1 is that eye-movements were unrestricted (free-viewing, no fixation cross). Previous research suggests that the possibility of executing eye-movements (free-viewing) during bisection judgments, can influence both the magnitude of the initial bias (Bradshaw et al., 1986, 1987: free-viewing decisions yield smaller biases than instructing participants to fixate centrally), as well as the subsequent magnitude of bias shift with time-on-task (Manly et al., 2005; Dufour et al., 2007). In Experiment 1, participants were instructed to attend to the white line throughout each trial, yet eye-movements were possible in principle, as we had no measure of compliance with this instruction, something of potential importance due to the short presentation time of the transected line (35 ms). In order to control for this possible confound, and to increase statistical power with a larger sample, in the next Experiment 2, we asked 40 participants to perform the landmark task while fixating centrally. Moreover, in line with previous studies of landmark task performance (McCourt, 2001; Foxe, McCourt, and Javitt, 2003) and the

time-on-task effect (Benwell et al., 2013), stimulus presentation time was 150 ms and without the initial appearance of the time-varying plain white line. Finally we varied viewing distance within this experiment, as this manipulation has also been suggested to influence the magnitude and direction of line bisection bias (McCourt and Garlinghouse, 2000; Bjoertomt, Cowey, and Walsh, 2002; Longo and Lourenco, 2006) but its influence on the time-on-task effect has not yet been investigated.

3. Experiment 2

3.1. Methods

3.1.1. Participants

Forty right-handed participants (13 male, 27 female, mean age=22.64 years; SD=3.67, max=39, min=17) took part in the experiment. However, due to poor behavioural performance on the landmark task (see Section 3.1.5: Analyses), 1 participant was excluded from the final analysis. Written informed consent was obtained from each participant. All participants were volunteers naive to the experimental hypothesis being tested. All participants had normal or corrected-to-normal vision and no history of neurological disorder. The experiment was carried out within the Institute of Neuroscience & Psychology at the University of Glasgow and was approved by the local ethics committee.

3.1.2. Instrumentation and stimuli

Stimuli were presented using the E-Prime software package (Schneider et al., 2002) on a CRT monitor with a 1280×1024 pixel resolution and 85 Hz refresh rate, with stimuli and procedure differing slightly from Experiment 1. Again, transected black and white lines of 100% Michelson contrast were presented on a grey background (luminance=179, hue=179), however the transected lines appeared immediately after the fixation cross (no plain white line) and this time remained on the screen for 150 ms (see Fig. 4 for a schematic representation of the trial procedure). 20 participants performed the task at a viewing distance (VD) of 70 cm and 20 participants at a viewing distance of 90 cm. Lines measured 24.3 cm in length by 0.5 cm in height and at a viewing distance of 70 cm subtended 19.67° (width) by $.40^\circ$ (height) of visual angle, whilst at a viewing distance of 90 cm subtended 15.377° (width) by 0.32° (height) of visual angle. Lines were transected at 1 of 17 points ranging symmetrically from $\pm 4\%$ of absolute line length relative to veridical centre (see Fig. 1 for example stimuli). This represented ranges of -0.8° to 0.8° (VD=70 cm) and -0.62° to 0.62° (VD=90 cm) of visual angle relative to veridical centre.

3.1.3. Procedure

At the beginning and end of the experimental session, all participants estimated their subjective alertness on a scale ranging from 100 (fully alert) to 0 (almost asleep). Participants were then seated and their midsagittal plane aligned with the display monitor. Viewing distance was kept constant using a chin rest. Each experimental block consisted of 136 trials (8 judgments at each of the 17 transector locations). Fig. 4 depicts a schematic representation of the trial procedure. Each trial began with presentation of a fixation cross (70cm VD= 0.40° (height) \times 0.40° (width) of visual angle, 90 cm VD= 0.32° (height) \times 0.32° (width)) for 1 s followed by presentation of a transected line for 150 ms. The transection mark was always aligned with the fixation cross (i.e. the eccentricity of the line endpoints varied across trials while the transection point always appeared at the same central position), therefore preventing use of the fixation cross as a reference point for bisection judgments. The fixation cross then reappeared for the duration of the response period, during which participants indicated which end of the line the transection mark had appeared closest to, by pressing either the left or right response key. Participants always responded using their dominant right hand (right index and middle finger respectively) and were instructed to keep their gaze on the fixation cross throughout each trial. The subsequent trial began as soon as the response was made. Trials lasted approximately 2 s with each block lasting 3–4 min. Trial type (location of transector in line) was selected at random. A block of 9 practice trials was performed immediately prior to the beginning of the experimental blocks.

Each participant performed 10 blocks of the landmark task. Participants were allowed to take short breaks between blocks. The entire experiment lasted approximately 40–50 min.

3.1.4. Experimental groups

Group assignment was identical to that of Experiment 1. Participants were split into three experimental groups: an initial left bias group (LB Group: 7 male, 12 female, mean age=23.44 years (max=39, min=17)), a group showing no initial bias (NB Group: 3 male, 10 female, mean age=22.3 years (max=26, min=19)) and an initial right bias group (RB Group: 3 male, 5 female, mean age=21.38 years

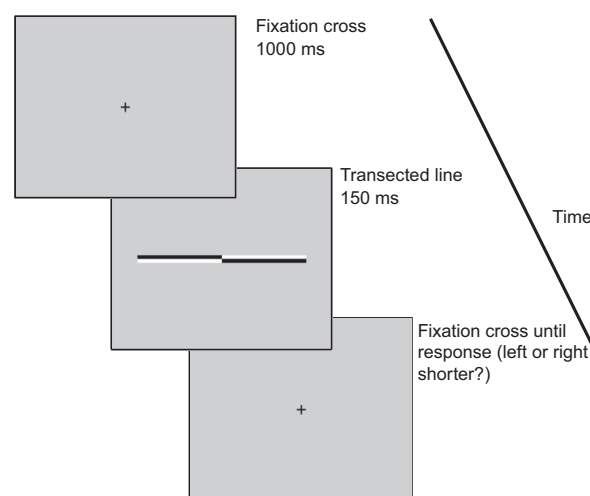


Fig. 4. A schematic representation of the trial procedure of Experiment 2. Following 1000 ms presentation of a fixation cross, transected lines were presented for 150 ms before reappearance of the fixation cross on the screen until the subject responded, by pressing either the left or right (shorter) response key. The subsequent trial began as soon as the response was made.

(max=28, min=19)). As in Experiment 1, group assignment was based on the individually fitted psychometric functions of the 1st block (see (Section 2.1.4: Experimental groups) and (2.1.5: Analyses) above).

3.1.5. Analyses

As in Experiment 1, inferential statistical analyses were performed on the individually fitted psychometric function PSE values and estimated widths, as well as the Sleepiness Scale ratings (see Section 2.1.5: Analyses). On the basis of extreme psychometric curve width values (flagged as outliers by application of the Median Absolute Deviation (MAD) rule for outlier detection), 1 participant was excluded from further analysis.

3.2. Results

3.2.1. Subjective alertness

Sleepiness scale ratings again confirmed a reduction in subjective alertness over the course of the experimental session, with the overall mean score on the sleepiness scale decreasing from 74.37 (SD=18.64) to 58.62 (SD=16.76). A 2 (pre vs post experiment) \times 3 (group) factorial analysis of variance (ANOVA) confirmed a main effect of time-on-task on sleepiness rating [$F(1, 37)=25.868$, $p < 0.001$], no significant main effect of group [$F(1, 37)=0.39$, $p=0.68$] and no interaction between group and time-on-task: [$F(2, 37)=1.42$, $p=0.26$].

3.2.2. Subjective midpoint shifts

In Fig. 5A, individually fitted mean PSE values (% of absolute line length re veridical) and the corresponding 95% confidence intervals are plotted as a function of block rank 1–10 for all 3 experimental groups (collapsed across viewing distances). The mean PSE in the left bias (LB) Group at the beginning of the experiment was displaced to the left of veridical centre by -0.91% of absolute line length (block 1, Fig. 5A), significantly deviating from zero/centre (see 95% confidence bars clearly differing from zero). As in Experiment 1, a clear systematic shift in subjective midpoint is apparent in the LB group across the experimental session (95% confidence bars progressively approaching zero), so that in the final block after extended performance (block 10, Fig. 5A), mean PSE in this group was displaced to the left by -0.53% . This indicates a rightward shift of $+0.38\%$ of absolute line length in subjective midpoint with time on task of 50–60 min, similar to that observed in the LB group of Experiment 1. In the no

bias (NB) group, mean PSE was slightly to the left of veridical centre (-0.17%) in block 1 (block 1, Fig. 5A). The mean PSE shifted slightly to the left across the experimental session in this group, so that mean PSE in the final block 10 was to the left of veridical centre by -0.38% (block 10, Fig. 5A). This indicates a leftward shift of -0.17% in subjective midpoint with time on task. In the right bias (RB) group, mean PSE was $+0.56\%$ to the right of veridical centre in block 1 (block 1, Fig. 5A, significantly deviating from zero/centre, see 95% confidence bars), whereas mean PSE in the final block 10 was to the right of veridical centre by $+0.18\%$ (with the 95% confidence bars crossing the zero line) which indicates a leftward shift of -0.38% in subjective midpoint with time on task (block 10, Fig. 5A), slightly larger than the leftward shift in Experiment 1.

A 2 (VD: 70 cm vs 90 cm) \times 3 (Group: LB vs NB vs RB) \times 2 (time-on-task: block 1 vs block 10) Factorial ANOVA on the individually fitted PSE values showed no significant main effect of viewing distance [$F(1, 33)=0.013$, $p=0.910$], a main effect of group [$F(1, 33)=21.17$, $p<0.001$], no significant VD \times group interaction [$F(1, 33)=0.105$, $p=0.901$], no significant main effect of time-on-task (block 1 vs block 10) [$F(1, 33)=0.433$, $p=0.51$], no significant VD \times time-on-task interaction [$F(1, 33)=0.242$, $p=0.626$], a significant time-on-task \times group interaction [$F(1, 33)=3.94$, $p=0.029$] (as in Experiment 1), and no VD \times time-on-task \times group interaction [$F(1, 33)=0.505$, $p=0.608$]. Analysis of simple main effects for exploring the time-on-task \times group interaction term (paired-sample t -tests performed on PSE values between block 1 and block 10 separately for each group collapsed across viewing distances) revealed a statistically significant difference between block 1 and block 10 in the LB Group, characterised by a shift to the right in mean subjective midpoint [$t(18)=-2.6$, $p=0.018$] indicating a time-on-task effect for those who started with a left bias. In the RB group, a trend towards a difference between block 1 and block 10 was observed [$t(6)=2.186$, $p=0.072$] whereas no statistically significant difference was observed from block 1 to block 10 in the NB group [$t(12)=0.95$, $p=0.36$].

As there was no effect of viewing distance on either the initial bias or the time-on-task effect, the data were collapsed across viewing distances for the remainder of the analyses. [It is likely that the relatively small differences between, and absolute magnitudes of, the viewing distances employed in Experiment 2 (70 cm and 90 cm) and Experiment 1 (100 cm), were not large enough to substantially modulate bisection behaviour as observed in previous studies (Bjoertomt et al., 2002; Longo and Lourenco, 2006) nor subsequent changes in behaviour with time-on-task.]

Linear regression analysis performed exclusively on extended performance (block 1–10) within each group revealed, as in Experiment 1, a statistically significant linear relationship between block rank and PSE in the LB Group [$r^2=0.67$ [$F(1, 9)=16.46$, $p=0.004$]] but, contrary to Experiment 1, no statistically significant relationship between the two variables in the RB group [$r^2=0.11$ [$F(1, 9)=0.97$, $p=0.353$]] nor (again as in Experiment 1) in the NB Group [$r^2=0.27$ [$F(1, 9)=2.99$, $p=1.22$]].

Fig. 5B plots the mean width of the PFs (% absolute line length ± 1 SE) for each block of the experimental session for all 3 experimental groups. A 3 (Group: LB vs NB vs RB) \times 2 (time-on-task: block 1 vs block 10) Factorial ANOVA showed a significant main effect of time-on-task on curve width [$F(1, 36)=17.07$, $p<0.001$], no significant main effect of group [$F(1, 36)=2.53$, $p=0.094$] and no interaction between time-on-task and group [$F(1, 36)=0.623$, $p=0.542$]. Regardless of initial bias direction, mean curve width significantly increased over the course of the experimental session. Mean curve width also increased over the course of Experiment 1, although for Experiment 1 the difference did not reach significance (see Section 2.2.2: Subjective midpoint shifts). The increase

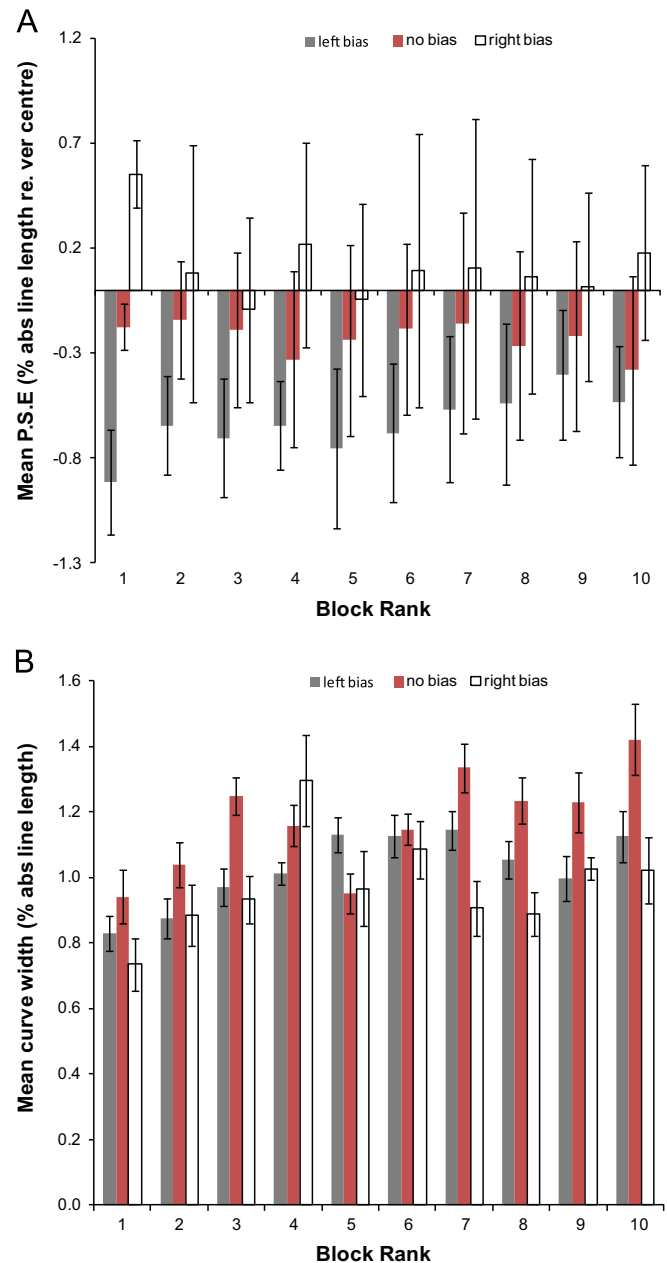


Fig. 5. (A) Experiment 2: group averaged PSE values (\pm corresponding 95% confidence interval bars) for each block of the experimental session. Grey filled bars represent the initial left bias group, red filled bars represent the no initial bias group and white filled bars represent the initial right bias group. (B) Group averaged curve widths (± 1 S.E.) for each block of the experimental session in each group.

in curve width probably represents noisier performance due to an increase in the observers' lapse rate with time-on-task (Fründ et al., 2011). In order to investigate whether any relationship exists between the increase in curve widths and the shifts in PSE in Experiment 1, for the right and left bias groups only, we again correlated the shift in curve width (% of absolute line length from blocks 1–10) with the degree of absolute shift in PSE (% of absolute line length from blocks 1–10 regardless of shift direction) over the course of the experimental session. As in Experiment 1, this analysis revealed no statistically significant relationship between the degree of PSE shift and the degree of curve width shift [Pearson's $r=0.085$, $p=0.68$].

It is possible that increased task demand of the procedure in [Experiment 1](#) compared to [Experiment 2](#) (shorter stimulus presentation time: 35 ms vs 150 ms) and the need to sustain attention on the line throughout variable inter-trial intervals led to an increased need to maintain focus more carefully on the task throughout the experiment. However, since neither experiment revealed any correlation between curve width shift and PSE shift (despite differences in the extent and consistency of curve width shift between the experiments) we would argue that it is unlikely that an increase in noise in the psychometric function can account for the observed shifts in PSE with time-on-task.

4. Further analysis

4.1. Analysis combining Experiments 1 and 2

Both [Experiments 1](#) and [2](#) revealed differential time-on-task effects dependent on initial bias direction. We found a left-to-right shift displayed over the course of the experimental session in those observers who began with a leftward bias to be robust and replicable, in line with previous time-on-task studies of spatial bias ([Manly et al., 2005](#); [Dufour et al., 2007](#); [Benwell et al., 2013](#); [Newman et al., 2013](#)), but we also show that this rightward shift does not occur in observers who begin with either no bias (no shift in either experiment) or a right bias (weak leftward shift in both experiments).

Yet, it could be argued that the post hoc group assignment employed for both experiments may be problematic for interpretation of the results. Due to the predominance of leftward biased individuals in the population ([McCourt, 2001](#)), group assignment based on the bias displayed in the first block, inevitably leads to uneven sample sizes (in favour of left bias) and thus a possible lack of statistical power in the no bias and right bias groups. In order to overcome this, we decided to combine the data from [Experiments 1](#) and [2](#) in a further analysis: due to differences in the total number of blocks (8 in [Experiment 1](#) vs 10 in [Experiment 2](#)) and overall task length (70–80 min in [Experiment 1](#) vs 50–60 min in [Experiment 2](#)) between experiments, we decided not to simply collapse the two datasets together for ANOVA analysis. Instead, we calculated the spearman rho value (block rank v PSE) individually for each participant from Experiments 1 and 2 ($N=67$) as an index of shift direction/strength. We then plotted the bias shift (Spearman rho) values as a function of initial bias value (block 1 PSE) (see [Fig. 6](#)) and performed robust correlation analyses between the two (Spearman rho and Pearson r with bootstrapped 95% confidence intervals (CI) (number of iterations=20,000)).

The analysis revealed a significant negative correlation between the initial bias direction/magnitude and the direction/magnitude of the shift in the bias over the course of the experimental session (Pearson $r = -0.46$, bootstrapped 95% CI = $[-0.63, -0.23]$, $p < 0.001$, Spearman $\rho = -0.48$, bootstrapped 95% CI = $[-0.65, -0.24]$, $p < 0.001$). The stronger the initial bias, the stronger the shift in bias over time in the opposite direction i.e. left biases shifted to the right and right biases shifted to the left. This analysis highlights the differential effects of time-on-task on spatial bias, dependent on initial bias whilst avoiding the potential pitfalls of post hoc group assignment.

5. Testing for reliability of the baseline bias (Experiment 3)

A crucial assumption of the current study is that the initial bias direction occurs as a result of a stable trait of participant (observer sub-type) and that therefore the group assignments do not simply result from a random sampling from a common distribution that

may differ on any given day or testing session. Spatial attention bias has indeed previously been suggested to represent a stable trait within participants ([Newman et al., 2012](#); [Tomer, 2008](#); [Pierce, Jewell, and Mennemeier, 2003](#); [Thiebaut de Schotten et al., 2011](#)). To further validate this assumption, we invited twenty of the participants from [Experiment 2](#) back for two subsequent experimental sessions, in order to test the reliability of baseline bias direction/magnitude across different days. The stimuli and procedure were identical to [Experiment 2](#) except that 1 block of the task was performed per session only. The results of the correlation analysis are displayed in [Fig. 7A–C](#).

We found that, within the participants, baseline bias direction/magnitude was highly consistent across days. Strong positive correlations were found between the baseline biases displayed on days 1 and 2 ([Fig. 7A](#): Pearson $r = 0.75$, bootstrapped 95% CI = $[0.53, 0.93]$, $p < 0.001$, Spearman $\rho = 0.83$, bootstrapped 95% CI = $[0.59, 0.92]$, $p < 0.001$), days 2 and 3 ([Fig. 7B](#): Pearson $r = 0.79$, bootstrapped 95% CI = $[0.56, .90]$, $p < 0.001$, Spearman $\rho = 0.71$, bootstrapped 95% CI = $[0.34, 0.90]$, $p < 0.001$) and days 1 and 3 ([Fig. 7C](#): Pearson $r = 0.77$, bootstrapped 95% CI = $[0.54, 0.91]$, $p < 0.001$, Spearman $\rho = 0.80$, bootstrapped 95% CI = $[0.48, .94]$, $p < 0.001$). The results strongly support the notion that baseline spatial bias represents a stable trait ([Newman et al., 2012](#); [Tomer, 2008](#)) and that group assignment based on initial bias displayed within an experimental session indexes meaningful observer sub-types rather than representing a random split of the data according to one-off values from a common distribution.

6. Discussion

We have argued in the introduction that there may be genuine performance differences in the general population in spatial attention tasks, possibly driven by differences in brain organisation, lateralization and/or function ([Thiebaut de Schotten et al., 2011](#); [Newman et al., 2012](#); [Bellgrove et al., 2007](#); [Greene et al., 2010](#); [Cai et al., 2013](#)). The results of the current study further support this notion by confirming that the baseline spatial bias found in our healthy participants represents a stable trait that

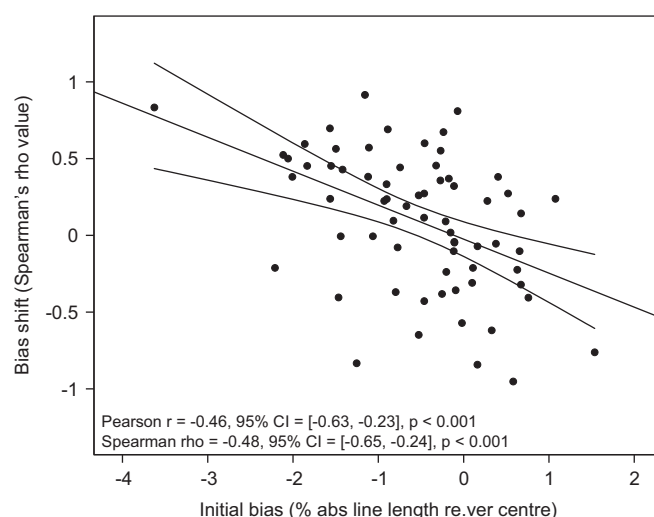


Fig. 6. Scatterplot of the relationship between initial bias displayed on the landmark task and the subsequent direction and magnitude of shift in bias over time (indexed by Spearman's rank correlation between block rank and bias value) for all participants from experiments 1 and 2 ($N=67$). Note the correlation is significant for both Pearson and Spearman analyses, indicating that the stronger the initial bias, the stronger the shift in bias over time in the opposite direction i.e. left biases shifted to the right and right biases shifted to the left.

remained consistent over different days/testing sessions. Our study further revealed that this trait determines the effect of time-on-task on spatial bias. In line with the large majority of previous studies (see McCourt (2001) and Jewell & McCourt (2000) for reviews) we found that most of our participants demonstrated an initial left bias in our landmark judgement task. Nonetheless a significant fraction (18% across both experiments) showed an initial right bias. This result is consistent with previous reports of right biases ranging from a minimum of 5% over 10% (cited in McCourt, 2001) up to 30–50% (Cowie and Hamil, 1998; Braun & Kirk, 1999; Dellatolas et al., 1996; Manning et al., 1990). As McCourt (2001) argues, some of these variations will be due to slightly varying methodologies and differences in participants' ages, yet in our previous study (Benwell et al., 2013), which employed a virtually identical design with participants of the same age and handedness, we found a very similar percentage of initial right bias (15%). As in the present study, the initial right bias was present despite subjective alertness levels being the same compared to the participants that showed initial left biases.

Interestingly these different initial biases showed distinct changes over time, with initial left biases showing a significant rightward shift (confirmed by both regression and ANOVA analyses), and participants with initial right bias shifting leftwards. This latter leftward shift in the initial right bias group failed to reach significance in the ANOVA analyses of Experiments 1 and 2 (probably due to the small number of participants showing an initial right bias), but a combined analysis (both experiments) investigating the relationship between initial bias direction/magnitude and subsequent bias shift direction/magnitude showed a significant negative correlation. We found that the stronger the initial bias, the stronger the shift in bias over time in the opposite direction, i.e. left biases shifted to the right and right biases shifted to the left.

The differential shifts in biases were robust over varying viewing distances and persisted in the absence of potential eye-movements (Experiment 2). Moreover, practice effects or increased noise in the psychometric function with time-on-task are unlikely to account for the observed shifts in midpoint estimation, as no relationship was found between fluctuations in curve width and shifts in bias over time (across participants in either experiment).

6.1. Time-on task effect (general vigilance/arousal)

Right hemisphere dominance for spatial attention is seen as an important factor contributing to the general left bias of pseudoneglect (e.g. Reuter-Lorenz, Kinsbourne, and Moscovitch, 1990; Foxe et al., 2003; Thiebaut de Schotten et al., 2005; Bultitude and Aimola-Davies, 2006; Siman-Tov et al., 2007) and it has been argued that this advantage is facilitated in states of high alertness by interactions between alerting and orienting networks in this hemisphere (Sturm and Willmes, 2001; Corbetta and Shulman, 2002; Sturm et al., 2004). It follows that with increasing fatigue, this advantage may reduce and even reverse, thereby explaining the rightward shift in attentional bias observed with temporary and chronic reduced arousal (Bellgrove et al., 2004; Manly et al., 2005; Fimm et al., 2006; Dufour et al., 2007; Robertson and Manly, 1999; Lazar et al., 2002; Matthias et al., 2009; De Gutis and Van Vleet, 2010; Chica et al., 2012).

What we argue here is that this interpretation does not hold entirely for the time-on-task effect in pseudoneglect. Participants with an initial right bias shifted leftwards, when according to the general vigilance/arousal hypothesis, if anything they should shift rightwards over time. Moreover, in our previous study (Benwell et al., 2013), we found the time-on-task effect to be dependent on the stimulus factor of line length: time-on-task only induced a rightward shift over the course of the experimental session with

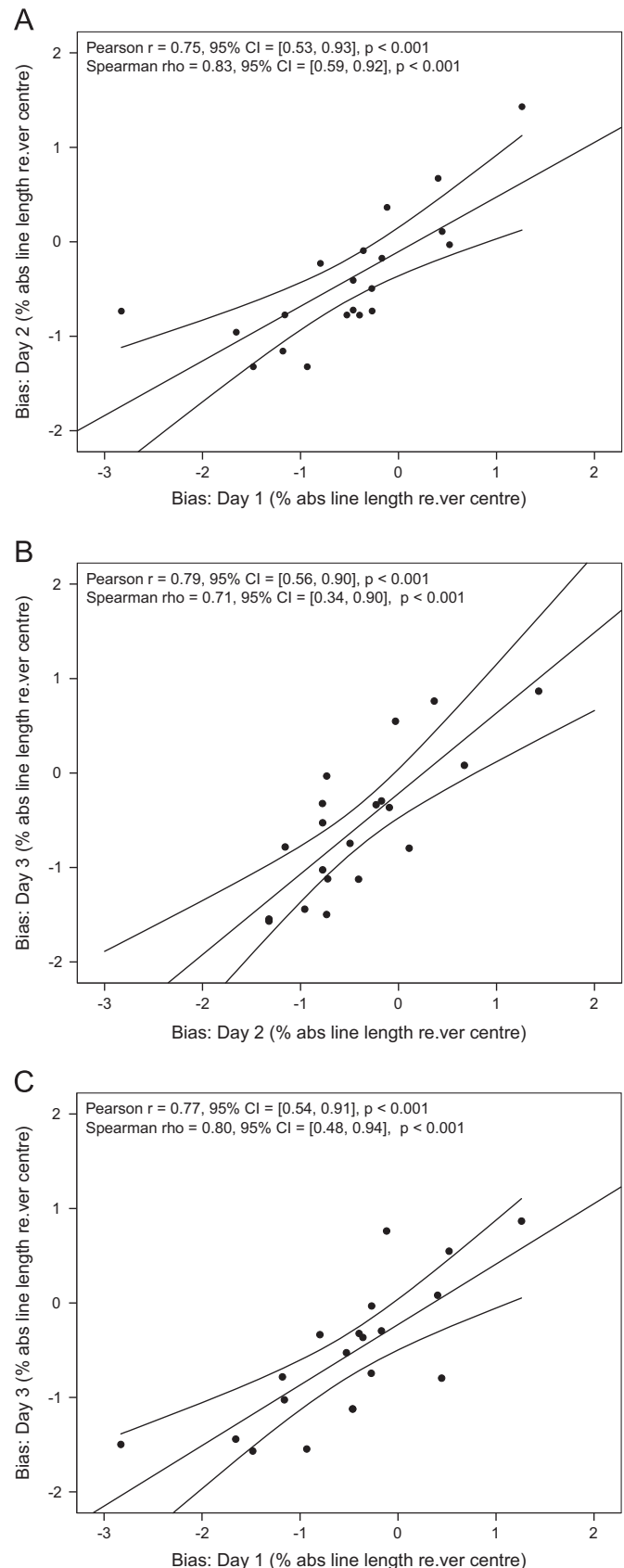


Fig. 7. Scatterplots of the relationships between landmark task bias scores within participants between three separate testing sessions (split apart by at least 24 h). All correlations proved significant for both Pearson and Spearman analyses, indicating that baseline bias represents a stable trait within participants. (A) plots the correlation between bias displayed on days 1 and 2, (B) between days 2 and 3 and (C) between days 1 and 3.

prolonged performance on long lines (not short lines) despite a similar decrease in subjective alertness ratings regardless of line length. This is in accordance with a recent study by Schmitz, Deliens, Mary, Urbain, and Peigneux (2011), who found that sleep deprivation under controlled conditions did not induce any consistent shift in landmark task midpoint estimation within participants, also suggesting that it is not simply a reduction in general arousal that underlies the time-on-task effect.

6.2. Time-on task effect (neural fatigue, anatomical asymmetry)

We propose that the time-on-task effect is better explained by a neuronal fatigue account (as opposed to a purely general vigilance account), in which the neuronal resources for line bisection (likely engaging more the right hemisphere than the left hemisphere in participants with an initial left bias) become differentially depleted as a function of initial bias. In participants with an initial left bias, and possibly as shown by Thiebaut de Schotten et al. (2011) with a larger right than left SLF II, this neural fatigue may be greater in the right hemisphere thus causing a rightward shift. In contrast, in participants with an initial right bias, and possibly as shown by Thiebaut de Schotten et al. (2011) symmetrical or larger left SLF II, this neural fatigue may be greater in the left hemisphere (or bilaterally distributed) thus causing a leftward shift (or no shift). It is noteworthy that in both current experiments the initial average left bias was larger than the initial average right bias, and the right to leftward shifts in the right bias groups were weaker than the left to rightward shifts in the left bias groups. This is in accordance with Thiebaut de Schotten et al. (2011) who also reported a weaker baseline right bias. This similarity could be due to the lack of power due to the smaller subject numbers in both studies, yet it could also be driven by differences in functional and anatomical asymmetries between the right and left hemispheres. The SLF II has been postulated to represent a direct connection between dorsal frontoparietal networks subserving the allocation of spatial attention across the visual field and ventral frontoparietal networks subserving the re-orienting of attention to salient/unexpected stimuli and implicated in the maintenance of arousal/vigilance (Corbetta and Shulman, 2011, Thiebaut de Schotten et al., 2011). In terms of the above mentioned functions, the ventral frontoparietal network is highly right lateralized (Corbetta and Shulman, 2002, Shulman et al., 2010; Sturm et al., 2004), and these functions may contribute to a stronger bias in those individuals with a right lateralized SLF II, as well as a more pronounced depletion of neuronal resources for the task over time.

It is also noteworthy that mirror symmetric shifts in pseudoneglect direction (left or rightward) depending on initial pseudoneglect bias (right or left) as observed here would support models of dual processors of spatial attention in both hemispheres (Kinsbourne, 1970; Szczepanski and Kastner, 2013), i.e. one processor compensating for neuronal fatigue of the other, in particular in cases of crossover of spatial bias over the midline (as observed for example in Manly et al. (2005) and Benwell et al. (2013)), and in line with dynamic models of spatial attention.

We conclude that differences in attentional biases reveal genuine observer subtypes, possibly driven by varying anatomical and/or functional asymmetries, leading to different behavioural patterns for time-on task and possibly other space and stimulus driven behaviours that have not yet been investigated.

Acknowledgements

We wish to thank those who participated in the study. This work was supported by the Economic and Social Research Council [Grant no. ES/I02395X/1].

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