

Stable individual differences predict eye movements to the left, but not handedness or line bisection

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Abstract

When observers view an image, their initial eye movements are not equally distributed but instead are often biased to the left of the picture. This pattern has been linked to pseudoneglect, the spatial bias to the left that is observed in line bisection and a range of other perceptual and attentional tasks. Pseudoneglect is often explained according to the dominance of the right-hemisphere in the neural control of attention, a view bolstered by differences between left- and right-handed participants in both line bisection and eye movements. We re-examined this observation in eighty participants (half of whom reported being left handed) who completed a computerised line bisection task and viewed a series of images. We failed to replicate the previously-reported effect of handedness on eye movements in image viewing, with both groups showing a large average bias to the left on the first saccade. While there was a modest effect of handedness on line bisection, there was no correlation between the two tasks. Stable individual differences, as well as a shorter latency on the initial saccade, were robust predictors of an initial saccade to the left. Therefore, while there seems to be a reflexive and idiosyncratic drive to look to the left, it is not well accounted for by handedness and may have different mechanisms from other forms of pseudoneglect.

Introduction

Human vision in natural circumstances is gated by saccadic eye movements. These movements are made frequently, executed with speed and precision, and planned on the basis of both the features in the scene and the information that a participant requires for their current task (see Foulsham, 2015, for a review). However, they are also subject to a number of systematic biases which may make determining the role of bottom-up and top-down factors more difficult. For example, there appears to be a strong tendency for participants to fixate the centre of a picture, a bias which occurs regardless of the features in the image or the task being completed (Tatler, 2007). Modelling both general spatial biases and their effects on sequences of saccades has proven fruitful for those trying to predict where people will look in images (Tatler & Vincent, 2008; Clarke et al., 2017).

A number of recent reports have highlighted a separate, pervasive, tendency for participants to initially orient to the left of a scene. Dickinson and Intraub (2009), Foulsham et al., (2013), Nuthmann and Matthias (2014) and Ossandon et al., (2014) all measured saccades while participants viewed a series of images, in a range of free-viewing and memorisation tasks. The results consistently show that about 60-70% of first saccades are made towards the left side of an image. In theory, such a bias could reflect a non-uniform distribution of features or objects of interest in images. However, the bias remained when these studies controlled for this distribution by mirroring images or using randomized patterns. Even when participants are asked to search for a target, and that target appears on the right of the image, there is an early bias to look to the left

(Nuthmann & Matthias, 2014). All things being equal, the first saccade is more likely to move leftward, and thus the initial fixations during viewing are more likely to be on the left. After the first 1-2 seconds of viewing this bias is no longer evident (Foulsham et al., 2013; Ossandon et al., 2014; Nuthmann & Matthias, 2014). Indeed, in some cases participants compensate by spending more time on the right of the image later in viewing, or by making back-and-forth saccades which leads, on average, to approximately 50% of the fixations in each half of the image. Of course, eye movement direction will also be influenced by the spatial position of the preceding fixation. If a fixation is on the left of the image, observers may not need or be able to saccade even further left, promoting an oscillating strategy from left to right. For this reason, the fairest way to examine a systematic bias is to look at the first saccade, whose starting position can be controlled.

In some sense, it is not surprising that there should be a leftward bias in saccades during image viewing because there are many other examples of a bias in this direction in perceptual and cognitive tasks. For example, humans tend to see ambiguous motion as leftward (Morikowa & McBeath, 1992) and they start search and cancellation tasks by checking items on the left side first (Zelinsky, 1996; Nicholls et al., 2017; Gigliotta et al., 2017). Leftward asymmetries are also observed in the information processed during face perception (Butler et al., 2005; Coutrot et al., 2016; Williams et al., 2016). Coutrot et al. find a strong tendency to look at the left eye in a face, particularly early in viewing, and one that is more pronounced in females looking at female faces. Left biases may therefore enable classification of gender or other individual differences on the basis of eye movements. One of the most investigated biases occurs in the line bisection task, where participants show a small but robust tendency to make more errors towards the left

(Jewel & McCourt, 2000). This behaviour, which is in the opposite direction to that observed in patients with right-hemisphere damage and hemispatial neglect, was labelled pseudoneglect by Bowers and Heilman (1980), a term which has also come to be used for other leftward biases.

Although a number of different explanations have been advanced for pseudoneglect in line bisection, perhaps the most common is that leftward asymmetries reflect attentional control mechanisms that are lateralised to the right hemisphere of the brain. A range of evidence from neuropsychology (i.e., the damage and performance associated with neglect) and neuroimaging has implicated the right parietal cortex in the guidance of attention during such tasks (Corbetta & Shulman, 2002; Mesulam, 1981; Mevorach et al, 2006). It has therefore been proposed that activation of this system in typical observers leads to increased salience in the contralateral (left) hemifield and thus an increased likelihood that attention will move in this direction. Recent neuroscientific research has outlined the frontal-parietal networks involved in attention with increasing sophistication (Corbetta & Shulman, 2011; Gigliotta et al., 2017). Connectivity in these networks has been implicated in the line bisection task by Thiebaut de Schotten et al., (2011), who report a relationship between behaviour and the volume of the white matter tracts connecting the frontal and parietal lobes. Participants with a greater volume of these connections in the right hemisphere showed a larger leftward bisection deviation. Inter-hemispheric connectivity may also be asymmetric, with communication more dominant from the right to the left than vice versa (Marzi, 2010).

The presence of lateralized networks in the brain has also led researchers to examine left- and right-handed participants for differences in pseudoneglect, based on

known differences in lateralisation between sinistral and dextral brains. In the line bisection task, an effect of handedness has been shown quite frequently (Jewel & McCourt, 2000; Luh, 1995; Brodie & Dunn, 2005), with left-handers showing less of a leftward deviation than right-handers. However, this difference has not always been observed (e.g., in the tactile bisection task used by Levander et al., 1993), and both groups show pseudoneglect (Jewel and McCourt, 2000, report effect sizes of approximately -0.6 and -0.5 for deviation from zero in right- and left handers, respectively). The greater mean leftward bias reported in dextrals by Brodie and Dunn (2005) indicates an effect size of 0.67 for the difference between groups.

Only one study, to our knowledge, has examined differences in eye movement scanning on the basis of handedness. In their Experiment 2, Ossandon et al. (2014) compared the timecourse of fixations in 31 right-handed and 17 left-handed participants viewing natural and urban scenes (as well as low- and high-pass filtered versions). The results showed that, while right-handed participants showed significant pseudoneglect during the first 1-1.5s of viewing, left-handers did not. 62% of first fixations were on the left in right-handers, but only 50.9% were on the left in left-handers – a bias that was almost completely absent.

The first aim of the present study was to replicate this difference between left- and right-handers' eye movements. Given the somewhat mixed results from the line bisection task, as well as concerns over the utility of handedness as a proxy for brain lateralisation (see Willems et al., 2014; Badzakova-Trajkov et al., 2010), this is an important finding to replicate. Even in language, where lateralisation is very well understood, only about 25% of left handers show reversed cerebral organisation (e.g., Knecht et al., 2000), and so

large effects of handedness on a complex task such as scene viewing might be seen as surprising.

Our second aim was to compare pseudoneglect in image viewing with the line bisection task. We use a computer-based, manual line bisection task with three line lengths and a randomly jittered position on the screen. Line length may modulate pseudoneglect, with leftward errors increasing in longer lines (McCourt & Jewell, 1999), but it is not yet known whether this interacts with handedness. Previous research has drawn useful conclusions by investigating the correlations between multiple spatial tasks such as line bisection, the landmark test and chimeric face recognition (Luh, 1995; Nichols et al, 1999). However, although such comparisons have shown that individual differences are reliable within a task, correlations between tasks have proven more elusive. Learmonth et al., (2015) compared the performance of 50 right-handers across five different tasks, including manual and landmark versions of a bisection task and a sustained attention task in which participants had to detect small targets appearing on the left or right. On average, pseudoneglect was observed on the manual line bisection and landmark tests, although other tests did not show a robust leftward bias. Importantly, none of the correlations between tasks were reliable, despite being apparently robust measures of individual spatial bias (reliable across two testing sessions on different days). A follow-up principal components analysis indicated that while some tasks were weakly related, pseudoneglect probably reflects a number of different component biases and thus researchers should not assume that all measures are capturing the same thing.

In Foulsham et al., (2013; Experiment 2), we used both a line bisection task and a gaze-contingent image-viewing task and found only limited carry-over between tasks.

However, that study was not designed to examine individual differences and did not consider handedness. To our knowledge, no other studies have compared pseudoneglect in line bisection to “pseudoneglect” in a saccade task. Schütz (2014) described a range of novel decision tasks, where participants had to choose one of two opposing directions on a circle (by saccading, following a pursuit target, making a thumb movement, or identifying an ambiguous moving stimulus). The results showed consistent idiosyncrasies, and the most notable bias in the saccade target was to the upper left (when in competition with the lower right). However, there were again only limited correlations between tasks, indicating that someone’s tendency to choose a saccade in a particular direction was not generally related to their preference for a particular direction in thumb-movement or ambiguous motion tasks.

In this paper we address the question of whether pseudoneglect in images is reliable within participants (i.e., idiosyncratic), and whether it is associated with handedness and performance in a manual bisection task. If individual differences in asymmetries in both tasks are caused by lateralisation we should expect a correlation between tasks and an effect of handedness.

Method

Participants

We aimed to recruit a larger sample of left- and right-handed participants than tested in previous studies (Ossandon et al., 2014; Brodie & Dunn, 2005) in order to achieve

greater statistical confidence for detecting a difference between groups. Eighty student participants (55 female) took part, in exchange for payment or course credit. Forty participants self-identified as being right-handed, while the remaining forty participants self-identified as being left-handed. All participants had normal or corrected-to-normal vision and were healthy adults between the ages of 19 and 53.

Design, Stimuli and Apparatus

All participants took part in both tasks (image viewing and line bisection), and the order of these tasks was counterbalanced. After finishing both tasks, participants completed the Edinburgh Handedness Inventory (EHI; Oldfield, 1971) which measures hand preference by asking participants to choose which hand(s) they use for a range of everyday tasks. Participants gave their informed consent and all work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

In the image-viewing task, participants viewed a series of coloured images, one at a time. All images were displayed at a resolution of 1024 x 768 pixels, filling the screen and subtending about 30° horizontally (at a fixed viewing distance of 70 cm). The stimuli consisted of 20 photographs of everyday scenes, a mixture of interiors and landscapes taken from a commercially available collection, and 20 computer generated fractal patterns. The fractal images were sourced from an online collection (the Spanky fractal database) and are designed to have similar power spectra to natural images but with no semantic meaning. In order to control for possible non-random variations in the horizontal position of objects or features, each stimulus was also presented mirror-reversed to half of the participants. Each participant saw one of two counterbalanced sets

containing half of the original scenes and half of the mirror-reversed scenes (and equivalently for the fractals). Thus, across the study, all stimuli were viewed equally often in their original and mirrored versions but participants only saw each image once.

In the computerized line bisection task, participants saw a series of short (200 pixels, 5.9°), medium (400 pixels, 11.8°) and long (600 pixels, 17.6°) lines. Line width was scaled according to line length and lines were presented in black on a white screen. In order to remove cues from the monitor frame and increase variability, lines were centred on a random location within a 10° square of the centre of the screen. Each line length was repeated 20 times for a total of 60 line bisection trials.

Eye movements were recorded monocularly at 1000 Hz during the image-viewing task using an EyeLink 1000 video-based eyetracker (SR Research). By default, recordings were taken using the right eye, but in a minority of cases the left eye was used where accuracy was insufficient from the right eye. Participants viewed the screen on a chinrest which restricted head movements, and calibration accuracy was checked and maintained throughout the task (average error <0.5°). For analysis of saccades and fixations, eye position samples were parsed using the default EyeLink algorithm and velocity and acceleration thresholds of 30°/s and 8000°/s², respectively.

Procedure

Following a 9-point calibration, the image-viewing task proceeded by displaying the series of images, one at a time, in a random order. Each trial began with a central fixation marker, at which point the experimenter confirmed that fixation was stable and in the centre of the screen. The image was then displayed for 4 seconds, and participants were

instructed to view each image in order to answer a subsequent true/false question. After each image a short, written statement about the presence, absence or location of an object (in scenes) or a visual feature (in fractals) appeared on the screen, at which point participants clicked one of two mouse buttons to verify the statement. This task encouraged participants to explore the images. Responses on this task were quite accurate (M accuracy = 80%, SD = 14%). Since we did not control the difficulty of the sentence verification or the location of the object referred to we did not investigate the accuracy of responses further.

In the line bisection task, each trial consisted of a single line presented on the screen. Participants were instructed to move a crosshair mouse cursor and click to mark the centre of the line. The mouse location began in the centre of the screen in each trial. All 60 line trials were presented in a random order.

Results

Handedness scores

EHI scores were calculated for each participant, resulting in a score with a magnitude of 0-100, where a negative score indicates a tendency to left-handedness, and a positive score indicates right-handedness. Descriptive statistics showed that the mean (*SD*) score was 65.7 (22.8) for right-handed participants and -40.0 (39.1) for left-handed participants. There was a significant difference between the two groups, with a very large effect size, $t(78) = 14.7, p < .001, d = 3.4$. Self-declared left-handers were less strongly biased and more variable than right-handers.

We first considered each task separately, examining possible differences between left- and right- handers and within-subject reliability across trials. We then asked whether performance on the two tasks was related.

Image-viewing task

The eyetracking results of one participant from the left-handed group were excluded from this task only, due to excessive data loss. Participants made an average of 13.4 saccades per trial (*SD* = 1.9) while viewing natural scenes, and 12.0 saccades per trial (*SD* = 2.0) while viewing fractal patterns. A paired *t* test confirmed that participants made significantly more eye movements while viewing scenes than fractals, $t(78) = 11.8, p < .001, dz = 1.3$.

In order to measure participants' initial orienting, we computed the direction of the first saccade in each trial that was greater than 1°. The radial plots in Figure 1 show

the frequency of first saccades in each direction, across all participants in the two groups. In both cases there is a very strong bias to move the eyes to the left. Dichotomising saccades into left ($\pm 90^\circ$) and right, the mean proportion of trials in which participants made an initial saccade towards the left was 0.76 ($SD = 0.16$) and 0.72 ($SD = 0.21$), for left- and right-handers, respectively. A two-way, mixed design ANOVA revealed no significant effect of handedness ($F(1, 77) = 1.1, p = .30, \eta_p^2 = .01$). However there was a reliable effect of image type ($F(1, 77) = 10.8, p = .001, \eta_p^2 = .12$), with more initial saccades to the left in fractal patterns ($M = 0.77, SD = 0.20$) than in real-world scenes ($M = 0.71, SD = 0.19$). There was no statistically significant interaction between handedness and image type ($F(1,77) < 1$).

[FIGURE 1 HERE]

Next, we computed correlations between each participant's proportion of initial leftward saccades in scenes and fractals, and their EHI score. The correlation between image types gives a measure of split-half reliability, and a reliable correlation would indicate that people who tended to saccade to the left in scene trials also tended to do so in fractal trials. A relationship with EHI might reveal a more nuanced effect of handedness than any overall difference between groups. Table 1 shows that while making saccades to the left is a reliable aspect of participants' behaviour, it is not related to EHI scores.

[TABLE 1 HERE]

Although measuring the proportion of first saccades to the left is a straightforward way to demonstrate pseudoneglect in images, Ossandon et al., (2014) also calculate a range of other values based on fixation position over time. To ensure that our failure to replicate a difference between left- and right-handers is not due to the specific metrics involved, we followed the same procedures as Ossandon et al., (2014) with the present data.

First, we computed spatiotemporal maps of fixation position separately for each handedness group. These maps show horizontal eye position over time, and they are generated for each image and its mirrored version (smoothed with a Gaussian of full width at half maximum of 2° in x and 20ms in time, and normalized to a fixed range of 0-1). If viewing is entirely driven by scene content, then the original and mirrored spatiotemporal maps will be reflections of one another. Systematic differences from this prediction indicate a spatial bias. A difference map is therefore calculated from the difference between the original map and the (mirror reverse of) the mirrored map. Figure 2 shows the average difference map, taken across all images, and for left- and right-handers separately. Because of the fixed scaling of the fixation maps, the values shown in the *difference* heatmaps fall on a scale from -1 to +1. If all fixations were on the left in both the original and the mirrored versions, then (because the mirrored map is flipped again before subtraction) the difference map values on the left will be positive. If all fixations were on the left in the original but on the right in the mirrored version (i.e., if participants were following the content of the image) then the difference map values will be zero. Like Ossandon et al., (2014), we find a surplus of fixations to the left within the first second of viewing (and a corresponding reduction in fixations to the right), relative

to what we would expect from the mirrored version. This pattern is clearly present in both handedness groups.

[FIGURE 2 HERE]

We also computed Ossandon et al's Asymmetry Index (AI), at each point in time and for each group of participants. The AI for a group of participants is defined as

$$(1) \quad \left(\frac{(N_{i,RH} - N_{i',LH})}{(N_{i,RH} + N_{i',LH})} - \frac{(N_{i,LH} - N_{i',RH})}{(N_{i,LH} + N_{i',RH})} \right) / 2$$

where $N_{i,RH}$ is the number of fixations on the *right* hemifield of image i , $N_{i',LH}$ is the number of fixations on the *left* hemifield of i' , the mirrored version of image i , and so on (we thank Jose Ossandon and Peter König for their correspondence regarding this formulation). Like the spatiotemporal difference maps, each half of Equation 1 therefore calculates the difference between the number of fixations on a hemifield and the number of fixations on the contralateral hemifield of the mirrored version, normalized over the total number of fixations. When combined across both hemifields, the AI gives a single index of the proportion of fixations that are spatially biased. This index will be -1 if all of the fixations are on the left hemifield regardless of content, and +1 if all of the fixations are on the right hemifield regardless of content. If gaze is following the features of an image, then each fixation on the original image will be cancelled out by a corresponding fixation on the contralateral side of the mirrored version, producing an AI of 0.

The AI was computed for each time sample and each image, separately for each group. This measure is therefore pooled across participants, which allows us to take advantage of the design whereby each version of each image was seen by half the participants. Figure 3 shows the average across all images (with 95% confidence intervals from 1000 bootstrapped resamples of the 40 image pairs). There was a strong deviation from zero in the first 1-1.5 seconds, confirming that participants' fixations were spatially biased to the left in this period. Unlike in Ossandon et al., (2014), there is no clear difference in the pattern of AI over time between left and right handers. Pooling across the first 1.5 seconds, the mean bias across images was -0.33 ($SD = 0.11$) for left handers and -0.27 ($SD = 0.12$) for right handers. Thus, in fact, left handers showed a higher proportion of spatially biased fixations to the left hemifield, a difference which was statistically significant ($t(39) = 3.48, p = .001$). Because the AI and the spatiotemporal difference maps are computed based on all fixations in the trial they provide an indication of spatial bias throughout viewing, and not just on the first saccade. However, we find no evidence that left handers are less likely to look towards the left than right handers.

[FIGURE 3 HERE]

Line bisection task

The errors made in the bisection task were small and distributed around the veridical midpoint. We compared the shift in this distribution as a function of line length and handedness (see Figure 4). In general, longer lines led to a more leftward bias (i.e.,

pseudoneglect). For each participant, we calculated two measures of bisection performance: the mean offset (normalized by line length) and the proportion of errors which were to the left of centre. A small number of trials (1.2% of the total number) were excluded when the selected point was too far above or below the line, or when the horizontal offset was more than 25% of the line length.

Participant means from the two dependent measures were entered into separate mixed ANOVAs. The mean offset showed a significant effect of line length ($F(2,156) = 5.4, p = .005, \eta_p^2 = .07$) and a linear trend for more leftward errors in longer lines. Although the between-subjects effect of handedness was not statistically reliable ($F(1,78) = 1.59, p = .21, \eta_p^2 = .02$), this was qualified by a significant interaction between length and handedness ($F(2,156) = 6.8, p = .01, \eta_p^2 = .08$). On average, right-handed participants had a more negative (leftward) mean offset than left-handed participants. However, this was only statistically significant in the shortest lines ($t(78) = 2.3, p = .027, d = 0.51$) and not in the medium ($t(78) < 1, p = .37, d = 0.20$) or long ($t(78) < 1, p = .82, d = 0.05$) condition.

[FIGURE 4 HERE]

A similar pattern of results was evident when errors were dichotomized into either left or right of the centre (see percentages in Figure 4). On average, 57% of errors made by right-handers were to the left, compared to 50% of those of left-handers. However, there was again an effect of line length ($F(2,156) = 8.0, p = .001, \eta_p^2 = .09$) with more errors to the left in longer lines (and a “crossover effect” in left-handers in the short lines;

Halligan & Marshal, 1988). In this measure there was also no significant effect of handedness ($F(1,78) = 1.5, p = .22, \eta_p^2 = .02$), but a reliable interaction ($F(2,156) = 4.0, p = .02, \eta_p^2 = .05$). Again, the difference between groups was only significant in the short lines ($t(78) = 2.2, p = .032, d = 0.49$) and not in the medium ($t(78) = 1.1, p = .27, d = 0.25$) or long ($t(78) < 1, p = .85, d = 0.04$) conditions. Collapsing across line lengths, the estimated effect size for the difference between groups (d) was 0.27 (small to medium in magnitude).

Although there were only modest effects of handedness on bisection performance, individuals varied in the amount of bias shown. The largest errors were shown in the longer lines, and here an average of 59% of errors were made to the left, but this varied considerably amongst individuals (min = 0%; max = 100%; SD = 28%). As with the scene viewing task, we can therefore ask whether a tendency to err to the left was reliable within participants. Table 2 shows the correlations between the proportion of errors each person made to the left in the three line length conditions, as well as the relationship with handedness scores. Behaviour in the three line conditions was significantly correlated, with particularly strong, positive relationships between short and medium and medium and long conditions. Participants who made more errors to the left in one type of line also made more errors to the left in other line lengths. As expected from the modest difference between left- and right-handed groups, the correlation with the EHI is stronger in shorter lines, but in all cases the association is weak and not statistically significant.

[TABLE 2 HERE]

There was evidence for a leftward bias (pseudoneglect) in both tasks, but there were also considerable individual differences. If differences in performing the two tasks are linked then this would be evidence for a shared mechanism. We collapsed across conditions to create a measure of laterality in each task: the proportion of first saccades and the proportion of bisection errors that went leftwards. Figure 5 shows the correlation between the two measures. In neither group was there any evidence for a relationship between performance on the two tasks, and all correlations were negative, weak and non-significant (Left handers only: $r = -.16$, $N = 39$, $p = .34$; Right handers only: $r = -.11$, $N = 40$, $p = .48$; Combined across groups, $r = -.15$, $N = 79$, $p = .20$).

[FIGURE 5 HERE]

Predicting an initial leftward saccade

A number of models are available which seek to predict the target of saccades in a particular image. In order to determine the predictive strengths of individual differences and handedness on the direction of the first saccade, we adopted a generalized linear mixed model approach, attempting to predict the binary outcome of whether each saccade was made to the left or not. This has the advantage of using all the data ($N = 3125$ saccades). Model fitting was performed in R using the lme4 package (Bates et al., 2015) and a binomial link function, and we followed a model building approach, testing nested models using likelihood ratio tests.

First, we assessed the influence of individual differences, by evaluating the random effect of participant in comparison to the random effect of image. Adding the

random effect of participant led to an improved model fit over an intercept-only model ($\chi^2(1) = 405.2, p < .001; AIC = 3193$), as did adding the random effect of image ($\chi^2(1) = 95.7, p < .001; AIC = 3503$). However, comparison of the reduction in AIC values indicated that the random effect of participant is more important for predicting leftward saccades than the random effect of the image. In a model with both random effects, the estimated among-participant variation ($SD = 1.24$) was much greater than that associated with the image ($SD = 0.70$). In terms of classification accuracy, a null model for this data predicts 74% of the saccade directions correctly (this is the overall proportion of leftward saccades across the whole dataset). Adding random effects of the participant and image increases this to 81% of correctly predicted saccades.

Next, we tested the effect of handedness by adding fixed effects. Model comparison with likelihood ratio tests showed that neither a categorical factor of handedness group nor a continuous effect of EHI led to an improved model fit (both $\chi^2(1) \leq 1.0, p > .30$). As expected from the non-significant relationships already discussed, information on participants' hand preference did not produce a better prediction of the direction of the first saccade. Adding a continuous fixed effect of each participant's bisection performance (proportion of errors made to the left) also showed no improvement in model fit ($\chi^2(1) = 0.97, p = .33$).

Finally, we added information on the latency of the saccade, which has been shown to correlate with direction at the aggregate level (Ossandon et al., 2014). Latency was defined as the time from the onset of the image to the start of the first saccade, and this was centred and added as a continuous fixed effect to the random effects of participant and image. In addition, we included the random slope of latency by

participant, (to keep a maximal effects structure; Barr et al., 2013), which allows for the possibility that the effect of latency will vary according to the individual observer. This model improved the fit further ($\chi^2(3) = 39.1, p < .001$), yielding a classification accuracy of 82%. Coefficients show a reliable effect of latency, such that slower saccades were less likely to move to the left ($\beta = -0.31, SE = 0.10, z = -3.02, p < .005$). The (exponentiated) odds ratio for the effect of latency indicates that an initial saccade with a latency one standard deviation greater than the mean has about 27% lower odds of landing on the left. In the empirical data (see Figure 6), the latency of leftward saccades ($M = 265\text{ms}, SD = 153$) was lower than that of rightward saccades ($M = 289, SD = 183$). Inspection of the estimated slopes for each participant revealed individual differences ($SD = 0.46$), but 60 of the 79 participants had negative coefficients.

[FIGURE 6 HERE]

Discussion

Saccades are not uniformly distributed in direction or landing position. Even when content is controlled by mirroring (Ossandon et al., 2014; Foulsham et al., 2013) or by predefining a target (Nuthmann & Matthias, 2014), or measured by examining the distribution of features (Tatler, 2007), some saccades are more likely than others. Participants make more horizontal saccades than vertical or oblique saccades, even in square images, although this is modified by rotating the picture (Foulsham et al., 2008). A similar bias has recently been shown in infants (Van Renswoude et al., 2016). In the

present study, we confirmed that not only is the initial saccade most likely to be horizontal, it is more likely to move to the left. This pattern of pseudoneglect was present in most participants (see Figure 5) and was concentrated in a predominance of saccades in a direction near the left horizontal (see Figure 1).

As in previous studies, we can rule out the possibility that this is due to non-uniform distribution of features or objects since all image content was mirrored in half of the trials, and since analyses which directly compared fixations on original and mirrored images also show a leftward bias (Ossandon et al., 2014). An even greater leftward bias was observed in meaningless fractal images, which are unlikely to have any asymmetrical content. All participants began viewing in the centre of the scene, which probably promotes a general central bias (Tatler, 2007; Rothkegel et al., 2016), and begins the trial with an equal amount of information in each hemifield, on average. We did not find a bias to the upper left, although the predominance of saccades around the horizontal may have been encouraged by the fact that all the images were landscape in orientation.

We failed to replicate the effect of handedness reported by Ossandon et al., (2014). Both left- and right-handed participants showed a strong tendency to look to the left on the original saccade (and in some analyses sinistrals actually showed a greater bias in this direction). In a close replication of the analyses conducted by Ossandon et al., (2014), there was no difference in the spatiotemporal profile of fixations between the two groups. Given that we had almost twice the number of participants as that study, our failure to detect a difference is unlikely to be due to statistical power. Instead, we suggest that the role of brain lateralization in the observed saccade bias has been overstated. We discuss this in more detail after comparing the results with the line bisection task.

The line bisection task showed a small but robust pseudoneglect effect, with a similar effect size to those studied previously (Jewell & McCourt, 2000). Although errors were small, people were more likely to err to the left, particularly in longer lines (an effect of line length that has previously been observed in healthy observers and, reversed, in neglect patients; Halligan & Marshal, 1988; McCourt & Jewell, 1999). We also found a modest effect of handedness in short lines, with fewer and smaller errors to the left in left-handed participants. The size and magnitude of our handedness effect is similar to previous reports, but our results also show an interaction with line length such that any difference between groups disappeared in longer lines. The reasons for this are not clear, and given that neither length nor handedness effects have been universally observed (see Jewell & McCourt, 2000) we are cautious in interpreting this pattern of results. Previous research has identified a cross-over effect, in both normal observers and neglect patients, whereby biases are different in very short lines (e.g., Rueckert et al., 2002). It may be that in the short lines, where dextrals showed very little error, sinistrals are biased to pay attention to the right, leading to more rightward errors. Whatever causes this, it is obviously over-ridden by the more standard pseudoneglect in long lines, where both left- and right-handed participants behaved the same way.

Both tasks were reliable within individuals, meaning that participants who frequently looked to the left in scenes were also likely to look to the left in fractals. Further research could test whether this is reliable across testing sessions, and there is precedent for stable individual differences in eye movement measures across tasks and over time (Schütz, 2014; Rayner et al., 2007). Coutrot et al., (2016) show that fixation patterns in face viewing, including a leftward bias, can predict the gender of an observer.

While this finding may be rather specific to faces, it reflects a growing interest in models of active vision which take into account individual differences (Arizpe et al., 2017; Bargary et al., 2017).

Observers who made more errors to the left when bisecting short lines were similarly more likely to err to the left in medium and long lines. Pseudoneglect in both tasks was variable but consistent within a person, and explaining the roots of this idiosyncrasy, whether neural, physiological or motivational, remains a challenge for future research. Handedness does not seem to underlie the differences between people's behaviour in these tasks, and particularly in eye movements during scene viewing. Even within handedness groups there are consistent individual differences, and in no cases were behavioural biases predicted by variation in handedness as measured by the EHI. Of course, such measurements are imperfect estimates and self-identified left-handers, in particular, are not a homogenous group (Willems et al., 2014). Critically, there was no relationship between individual biases in the two tasks. In a similar way to previous investigators who have compared different tasks, we therefore conclude that it is unlikely that the two tasks are dependent on the same mechanisms. Even within the manual line bisection task, there are probably several reasons why a particular bias emerges (Dellatolas et al., 1996), and these may have a different influence depending on the line length (which would explain the pattern of correlations between individual bias in short, medium and long lines; see Learmonth et al., 2015, for further discussion of potential components in such tasks).

Why did we fail to find an effect of handedness in the scene viewing task? This effect was observed by Ossandon et al., (2014), and would appear consistent with the

suggestion that fronto-parietal attentional networks are lateralized to the right hemisphere (in dextrals, but less so in sinistral participants). There are potentially two reasons why this conclusion is not borne out in the present study. First, self-reported handedness is unlikely to be a good proxy for cerebral lateralization. In language research, it has been acknowledged that while a small proportion of left-handed participants show reversed brain organization, most show the same activation as right-handers (Willems et al., 2014). The average behaviour of even a large sample of self-declared left-handers is therefore not going to reveal major differences from right handers. There is limited evidence about how the lateralization of attention differs according to handedness, but existing studies suggest that there is not a simple relationship (Liu et al., 2009; Whitehouse & Bishop, 2009).

A second reason is that the leftward saccade bias is caused by other factors, instead of or in addition to cerebral asymmetries. For instance, initial orienting to the left could be a habit related to reading direction, with participants typically being left-to-right readers who might have learned to initiate inspection at the (top) left of a display. A number of studies have shown reduced or absent pseudoneglect in readers of Hebrew and other right-to-left languages (Chokron & Imbert, 1993). In one of the few studies to examine the effect of reading direction on eye movements, Afsari et al., (2016) asked participants familiar with different writing systems to view images after first reading text primes. The results showed that right-to-left readers had a reduced leftward bias after reading a left-to-right script and that this pattern reversed when they read their native language (in which case they were more likely to move to the right of the picture). Interestingly, in a follow-up experiment, these authors showed that the same modulation

of the leftward bias was not achieved after a moving dot prime task which encouraged eye movements in one direction. It therefore seems that the long-term habit of initiating reading from one direction has an influence, as well as recent experience with a particular script. We have previously shown that horizontal and leftward biases can be manipulated with a gaze-contingent window (Foulsham et al., 2013). It is clear, therefore, that any effects of cerebral asymmetries can be counteracted by other influences.

Our novel final analysis revealed that the tendency of each individual to saccade to the left (i.e., the random intercept associated with each participant) was useful for predicting individual eye movements. Indeed, knowing which observer was involved was more important than knowing which image was being looked at when making this prediction. This reinforces the conclusion that the variations in pseudoneglect during image viewing are not based on the visual features involved but on a truly top-down factor that varies amongst individuals. The variance amongst participants was much greater than the effect of handedness or any other predictor, and thus the range of individuals was large (relative to the magnitude of any handedness or latency predictors).

Interestingly, we also found a strong association with the latency of the initial saccade, at the level of the individual trial. Ossandon et al., (2014) report that participants with longer latency saccades, on average, show less of a leftward bias. We can add to this by demonstrating that even within an observer, short latency saccades are more likely to move to the left than those that are executed later. In previous research it has been proposed that short-latency saccades are more driven by bottom-up saliency, perhaps because top-down control takes longer to be exerted over eye movements (van Zoest & Donk, 2005). The early leftward saccades in the present experiment cannot be attributed

to bottom-up features (which were controlled in our stimuli and analysis), but it does seem that an early drive to fixate the left is counteracted in delayed saccades. Variation in latency cannot explain the differences between participants, and neither can a simple effect of handedness or a general pseudoneglect as indexed by manual line bisection. Individual differences in cognitive control for overriding the early leftward bias is one potential source of variation which could be explored in future research.

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	Proportion first saccades to the left		EHI
	Scenes	Patterns	
Scenes	-	.714**	-.047
Patterns	-	-	-.008
EHI	-	-	-

Table 1. Correlation coefficients between eye movement behaviour and each participant's score on the Edinburgh Handedness Inventory (EHI). (** $p < .001$; all $Ns = 79$).

	Proportion line bisection errors made to the left			EHI
	Short	Medium	Long	
Short	-	.692**	.399**	.120
Medium	-	-	.753**	.116
Long	-	-	-	-.001
EHI	-	-	-	-

Table 2. Correlation coefficients between line bisection behaviour and the EHI. (** $p < .001$; all $Ns = 80$).

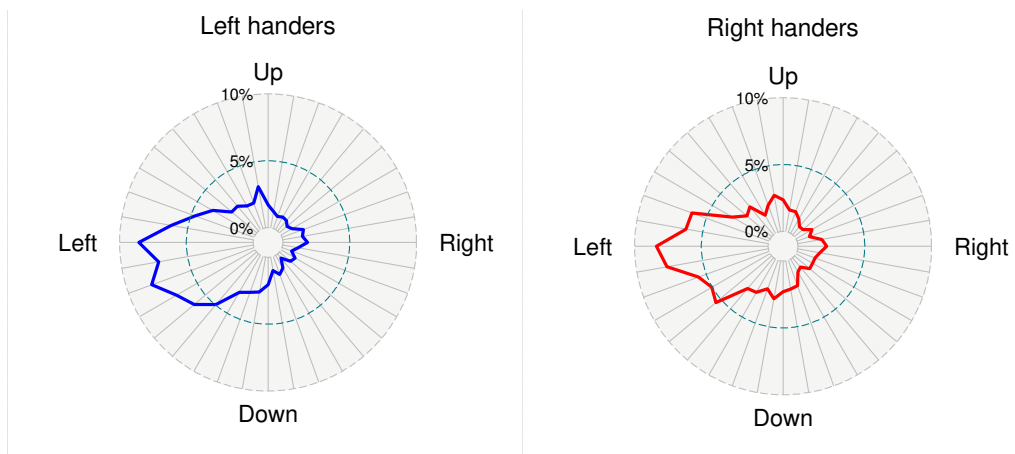


Figure 1. The relative frequency of first saccades in each direction, plotted separately for left- and right-handed participants. Extent of the plot in each direction shows the proportion of saccades, in bins 10° wide.

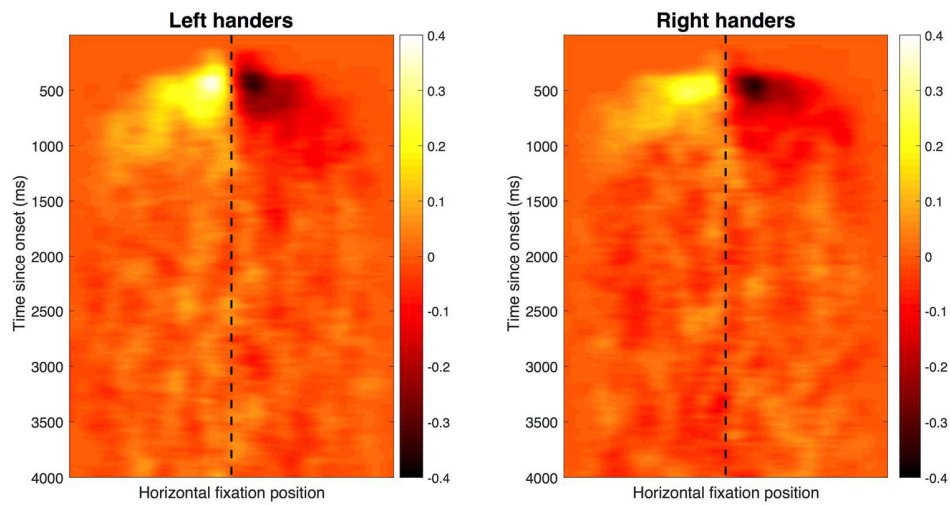


Figure 2. Spatiotemporal difference maps representing the average difference in fixation density between the original image and the same content when mirror-reversed. Image onset is at the top and the dashed line indicates the centre of the screen (where viewing started). Positive values (warmer colours) represent more fixations relative to the mirrored version. Both maps indicate an over-occurrence of fixations on the left during the first second of viewing.

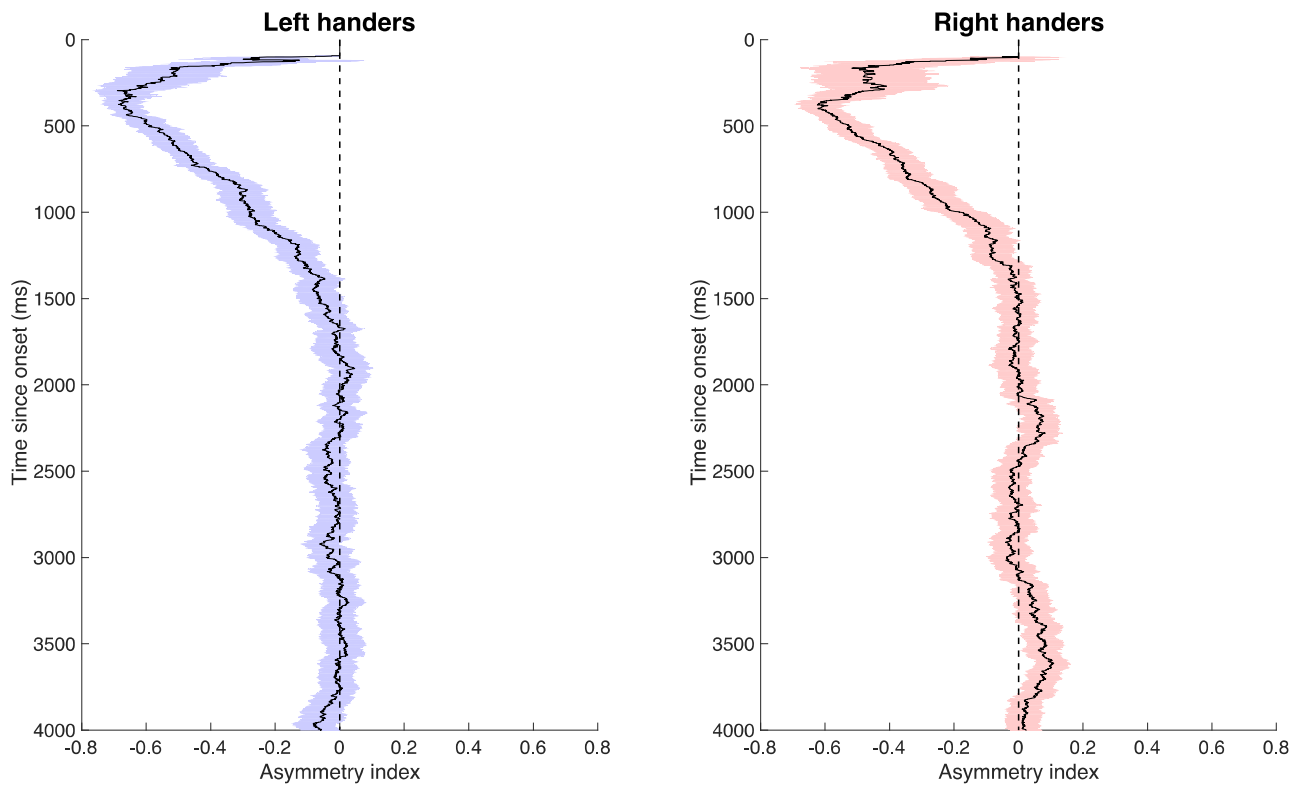


Figure 3. The asymmetry index (AI; see text) for each group of participants. Line shows the average across all images, with the bootstrapped 95% confidence intervals shaded. Equivalent fixations on the original and the mirrored image, corresponding to no spatial bias, would produce an AI of zero (dotted line).

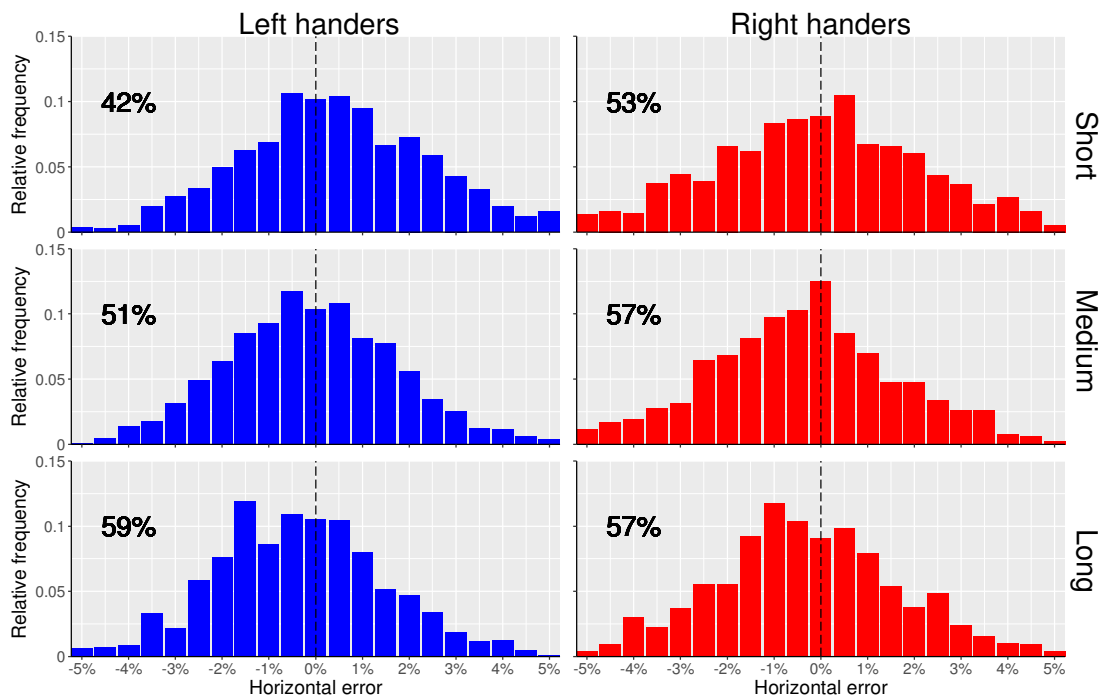


Figure 4. The distribution of errors during the line bisection task, plotted separately for left-handed and right-handed participants. Each plot shows the relative frequency of responses within each line length (short, medium and long, in rows), in fixed-width bins relative to the length of the line. Dashed lines show the true centre and grey bars the median offset. Inset labels show the percentage of all errors made to the left of the centre.

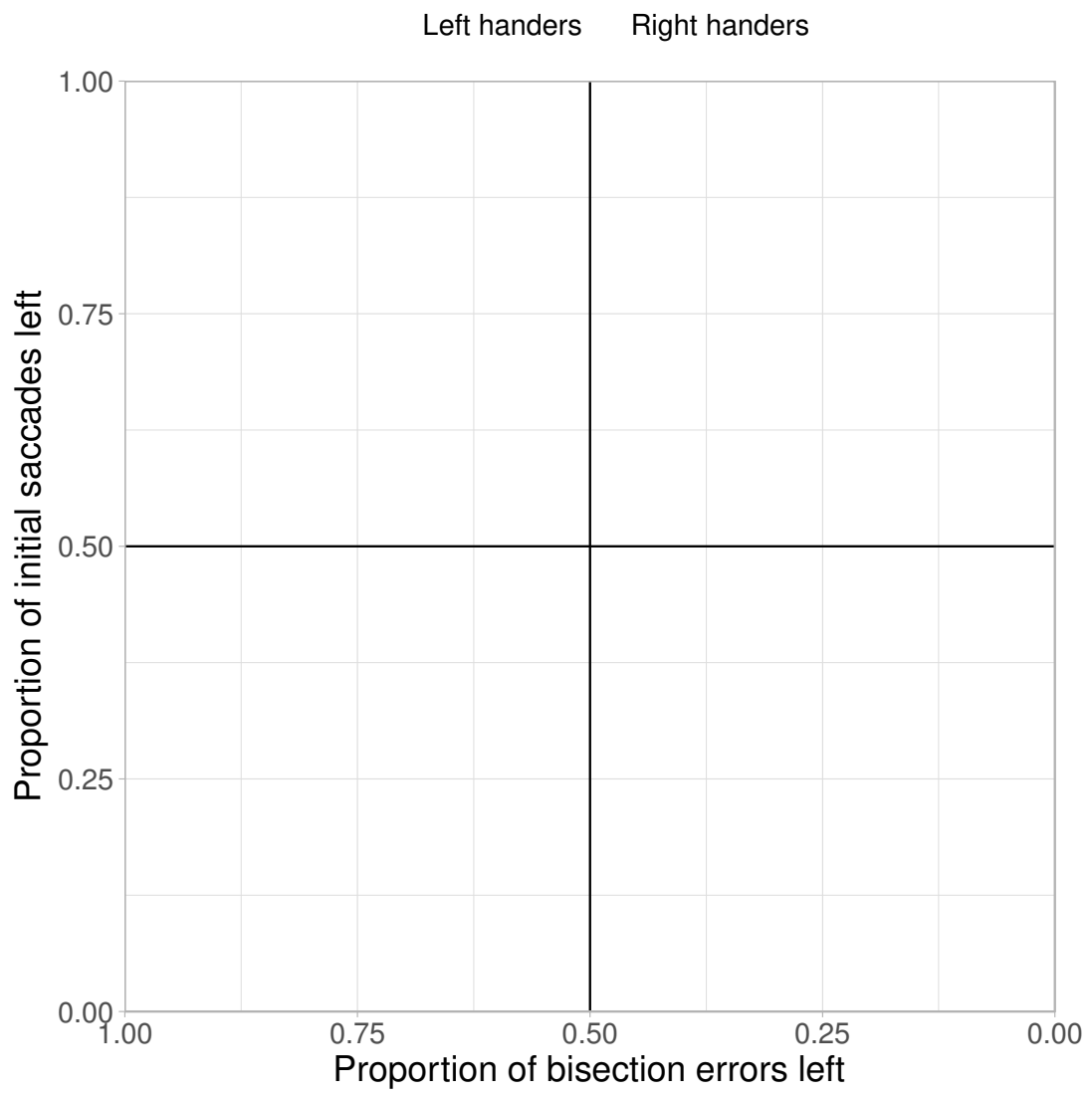


Figure 5. The (negligible) relationship between asymmetries in the two tasks.

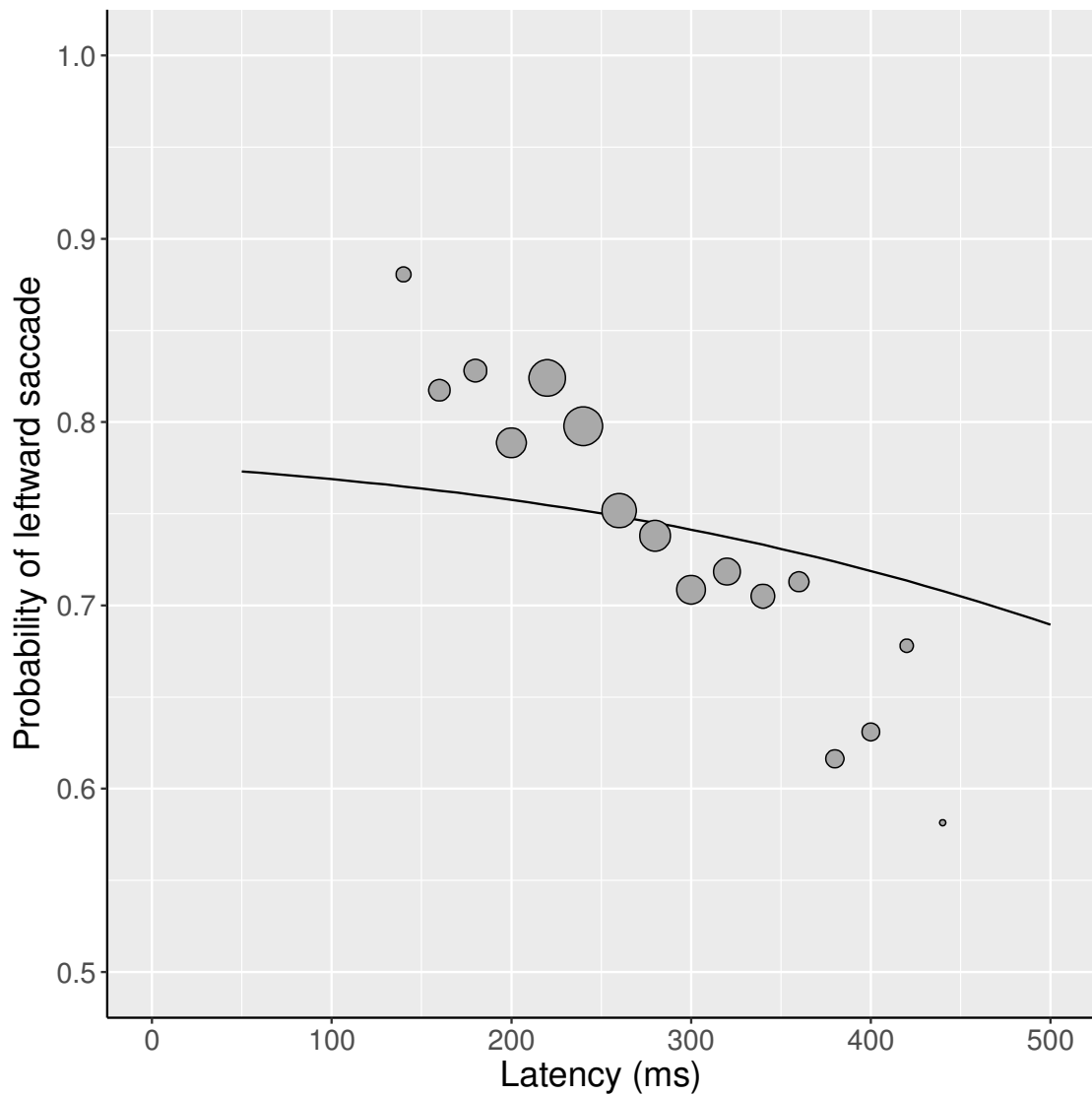


Figure 6. The relationship between the latency of the first saccade and the likelihood that it will move to the left. Circles show empirical data, across all participants and in bins of 20ms, with circle size proportional to the number of saccades (from a minimum of $N = 40$; bins with fewer saccades are not included). The line shows the average marginal probabilities, as estimated by the GLMM with random effects, with upper and lower quartiles shaded.