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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.

1. 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, 2009; Clarke, Stainer, Tatler, & Hunt, 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, Gray, Nasiopoulos, and Kingstone (2013); Nuthmann and Matthias (2014) and Ossandon, Onat, and König (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 s of viewing this bias is no longer evident (Nuthmann & Matthias, 2014; Foulsham et al., 2013; Ossandon et al., 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

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examples of a bias in this direction in perceptual and cognitive tasks. For example, humans tend to see ambiguous motion as leftward (Morikawa and McBeath, 1992) and they start search and cancellation tasks by checking items on the left side first (Gigliotta, Malkinson, Miglino, & Bartolomeo, 2017; Nicholls, Hobson, Petty, Churches, & Thomas, 2017; Zelinsky, 1996). Leftward asymmetries are also observed in the information processed during face perception (Butler et al., 2005; Coutrot, Binetti, Harrison, Mareschal, & Johnston, 2016; Williams, Grealy, Kelly, Henderson, & Butler, 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 (Jewell & 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, Humphreys, & Shalev, 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 (Jewell & McCourt, 2000; Brodie & Dunn, 2005; Luh, 1995), 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, Tegnér, & Caneman, 1993), and both groups show pseudoneglect (Jewell & 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 1–1.5 s 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 Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Willems, Van der Haegen, Fisher, & Francks, 2014), 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; Nicholls 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, Gallagher, Gibson, Thut, and Harvey (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.

2. Method

2.1. Participants

We aimed to recruit a larger sample of left- and right-handed participants than tested in previous studies (Brodie & Dunn, 2005; Ossandon et al., 2014) in order to achieve greater statistical confidence for detecting a difference between groups. Eighty student participants

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