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Research report

Perceptual asymmetries in greyscales: Object-based versus space-based influences

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ABSTRACT

Neurologically normal individuals exhibit leftward spatial biases, resulting from object- and space-based biases; however their relative contributions to the overall bias remain unknown. Relative position within the display has not often been considered, with similar spatial conditions being collapsed across. Study 1 used the greyscales task to investigate the influence of relative position and object- and space-based contributions. One image in each greyscale pair was shifted towards the left or the right. A leftward object-based bias moderated by a bias to the centre was expected. Results confirmed this as a left object-based bias occurred in the right visual field, where the left side of the greyscale pairs was located in the centre visual field. Further, only lower visual field images exhibited a significant left bias in the left visual field. The left bias was also stronger when images were partially overlapping in the right visual field, demonstrating the importance of examining proximity. The second study examined whether object-based biases were stronger when actual objects, with directional lighting biases, were used. Direction of luminosity was congruent or incongruent with spatial location. A stronger object-based bias emerged overall; however a leftward bias was seen in congruent conditions and a rightward bias was seen in incongruent conditions. In conditions with significant biases, the lower visual field image was chosen most often. Results show that object- and space-based biases both contribute; however stimulus type allows either space- or object-based biases to be stronger. A lower visual field bias also interacts with these biases, leading the left bias to be eliminated under certain conditions. The complex interaction occurring between frame of reference and visual field makes spatial location extremely important in determining the strength of the leftward bias.

1. Introduction

Hemispatial neglect most typically occurs following right hemisphere damage, leading to a rightward spatial bias, which is believed to be the result of the right hemisphere's role in spatial attention (Heilman et al., 2003). Interestingly, left and right are only meaningfully defined with respect to a particular frame of reference (Subbiah and Caramazza, 2000). When referring to left and right, their actual locations will differ depending on whether one is referencing their own body, or an object or a location in space. A distinction has been made between retinocentric (Hillis and Caramazza, 1995), body-centred (Heilman et al., 1983), space-based (Halligan et al., 2003), and object-centred (Driver and Halligan, 1991; Hillis

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and Caramazza, 1995) hemispatial neglect. This illustrates the different frames of reference that are relied upon when discussing location and also how a disorder of one frame of reference does not necessarily indicate all will be affected in the same way.

Hemispatial neglect can also occur following left brain damage, although it is reported less frequently (Kleinman et al., 2007). It may be the case that right hemispatial neglect is under-diagnosed or misdiagnosed, leading it to be studied less and to remain poorly understood. Due to a lack of accurate data regarding the occurrence of right hemispatial neglect, Kleinman et al. (2007) examined 47 patients following left hemisphere stroke. They found that 19% of patients presented with right hemispatial neglect and that neglect was better detected when several testing measures were used. This illustrates that although neglect can be seen following left hemisphere stroke, it occurs less frequently than after right hemisphere damage.

Object-based neglect has been examined by presenting patients with either an array of objects or a single stimulus and having them copy it (Gainotti et al., 1972). Object-based neglect is seen when the left side of an object is neglected, regardless of where it is located or whether the image is presented in any particular orientation (Caramazza and Hillis, 1990; Driver and Halligan, 1991; Driver et al., 1992; Niemeier and Karnath, 2002). The central axis of the stimulus defines the left and right sides, which leads patients to neglect the left half of a specific object, but not that side of space more generally (Driver et al., 1994; Driver and Halligan, 1991). As seen in Fig. 1a, when stimuli are presented in their upright orientation, object- and space-based coordinates are congruent and it is impossible to dissociate the two. When the object is rotated by 45° (see Fig. 1b and c), space- and object-based coordinates can now be dissociated from one another, making it possible to demonstrate which of the two contributes more to the bias.

Driver and Halligan (1991) showed patient PP two nearly identical nonsense objects with obvious midlines, one directly above the other. The patient was asked to detect the difference between the two images in both an upright presentation and after 45° rotation. Object-centred neglect was revealed as the principal axis of the shape, and not its spatial location, determined which portion would be neglected (Driver and Halligan, 1991). Object-based biases have been shown using similar tasks (Driver et al., 1994; Hillis et al., 1998) as well as reading tasks, where a portion of each individual word is neglected (Caramazza and Hillis, 1990; Hillis and Caramazza, 1995). In contrast to this, space-based neglect occurs when patients fail to orient towards or attend to the contralesional side of space (typically the left; see Heilman et al., 2003 for a review), regardless of individual objects.

Hemispatial neglect has been reliably identified using the greyscales task (Mattingley et al., 2004; see Fig. 1a). In choosing which image appears to be darker (or brighter), the image with the salient feature on the right is chosen the majority of the time, despite the images being equiluminant (Mattingley et al., 2004). This task has also been used to examine perceptual asymmetries in neurologically normal individuals, who tend to select the image with the salient feature on the left (Nicholls et al., 1999). Similarly, participants typically bisect lines to the left of centre in manual (Barrett et al., 2000; Luh, 1995) and computerized line bisection (McCourt and Jewell, 1999), and most often falsely indicate that the left end of a line is longer on the landmark task (Dufour et al., 2007). It has been suggested that the leftward bias exhibited by neurologically normal individuals, and referred to as pseudoneglect (Bowers and Heilman, 1980; Jewell and McCourt, 2000), results from the same neural mechanisms as the rightward bias in hemispatial neglect (Loftus et al., 2009; McCourt and Jewell, 1999).

Numerous explanations have been put forth to account for spatial biases, such as pre-motor/intentional biases (Brodie and Pettigrew, 1996; Heilman and Valenstein, 1979) or scanning and reading habits (Chokron et al., 1998; Manning et al., 1990). These explanations are not adequate as a left bias is also seen among right-to-left readers and when using bimanual responding (Nicholls and Roberts, 2002). An underlying asymmetry of spatial attention, resulting from right hemisphere dominance, could account for the leftward bias observed among neurologically normal participants as well as the rightward error exhibited by hemispatial neglect patients. The posterior parietal area in the right hemisphere is primarily responsible for spatial attention (e.g., Corbetta et al., 1995; Posner and Petersen, 1990; Posner and Rothbart, 2007), implying that attention is preferentially directed to the left side. This suggestion has been supported with neuroimaging evidence showing that information in the left visual field activates proposed visuospatial attention networks more strongly than information in the right visual field (Siman-Tov et al., 2007). Further, the right hemisphere is more active during line bisection and landmark tasks (Çiçek et al., 2009; Fink et al., 2000, 2001; Foxe et al., 2003), suggesting an attentional bias underlies pseudoneglect.

If the same neural mechanisms are responsible for both phenomena, the body-centred, object-based and space-based biases described in clinical neglect likely also contribute to the spatial biases observed among neurologically normal individuals. Prior research has examined each of these spatial frames of reference in neurologically normal individuals; however their contributions to the left bias are unclear, as no consistent pattern of findings has emerged. This indicates the importance of further considering the influence of each frame of reference on the strength of the left bias.

Nicholls et al. (2003) manipulated object-, trunk- and head-centred coordinates to determine their contributions to lateral biases. They found a leftward bias in all conditions with no effect of either trunk- or head-centred coordinates. The authors concluded that either object-based or space-based coordinates could be responsible for the left bias as only object-based coordinates were examined and the potential influence of space-based biases could not be excluded.

A bias towards the upper features of vertical stimuli has been observed on line bisection (Bradshaw et al., 1985; Drain and Reuter-Lorenz, 1996; McCourt and Olafson, 1997). Both leftward and upward biases have been explained in relation to object-centred biases as the most significant features are attended to, with the left side being significant due to Western reading and scanning habits and upper features carrying more information than the lower ones (Jeerakathil and Kirk, 1994). This has been demonstrated by showing a bias towards the