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Representational pseudoneglect: Lateralised biases in attentional orienting in the absence of vision in healthy ageing participants.

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Declaration

I confirm that this thesis submitted to the University of Edinburgh is entirely my own work and has not been submitted for any other degree or professional qualification.

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For my husband x

Abstract

Pseudoneglect is the tendency to be biased towards the left side of space in tasks of a spatial nature. A non-visual form of the bias referred to as ‘representational pseudoneglect’ has been observed when people generate a mental representation of a stimulus in the complete absence of visual input - participants pay more attention to the left-hand side of the mental representation. The aim of this thesis was to advance our understanding of representational pseudoneglect by exploring the bias across lifespan using different modes of non-visual presentation (touch vs. audition vs. visual imagery). In Experiments 1 and 2 healthy participants aged 3 to 96 years used touch alone without vision to bisect wooden rods at the perceived centre. All participants (with the exception of some adolescents) showed leftward biases on tactile rod bisection and significant gender and age effects were found. In Experiments 3 to 10 healthy young adults listened to aural-verbal descriptions of abstract patterns or real-world scenes without vision and formed a mental representation of the spatial layout that was described. A leftward bias was consistently found for a relative judgement task along with a significant effect of monaural presentation and start side, but no lateralised bias for memory recall regardless of ‘mental mapping’ ability or method of response. In Experiment 11 participants eye movements were recorded while they visually processed and then memorised natural real-world scenes; again there was no lateralised memory or eye movement bias. Experiment 12 showed that a secondary task increased the magnitude of visuo-spatial pseudoneglect for children and adults under certain conditions. This thesis argues that purely *representational* forms of *pseudoneglect* clearly exist in healthy participants and that: 1) the results can be explained in terms of contralateral attentional orienting by the right hemisphere, 2) extraneous variables (gender; physical or imagined starting position) can mediate representational pseudoneglect, and 3) current models of cognitive ageing need to provide for a cognitive bias that can be enhanced by age.

Contents

****

Chapter 1

Chapter 2

Tables

****

Chapter 5

Figures

****

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Chapter 1

Literature Review

1.1. Introduction to visuo-spatial line bisection

When healthy participants are asked to centrally bisect a visually presented horizontal line they show a tendency to bisect the line towards the left-hand side of true centre. This phenomenon has been referred to as ‘pseudoneglect’ (Bowers & Heilman, 1980) by analogy to the performance of right-hemisphere impaired patients with left unilateral neglect who bisect visually presented lines towards the right hand-side of true centre (Heilman & Valenstein, 1993; Robertson & Marshall, 1993). Patients with unilateral left neglect also show a general deficit in orienting attention towards contralesional left space (Robertson, Halligan, & Bergego et al., 1994) and may bump into objects and people located to their left, fail to groom the left side of their bodies, or fail to notice the position of their left limbs (Halligan, Fink, Marshall, & Vallar, 2003). The presence of neglect following right hemisphere impairment is generally assessed using a comprehensive battery of standardised neuropsychological tests which include *perceptual* tests like visuo-spatial line bisection and also *representational* tasks like drawing objects or scenes from memory (Halligan & Marshall, 1989a; Halligan, Marshall, & Wade, 1989; Ferber & Karnath, 2001). In a recent review of neglect across difference modalities Gainotti (2010) reported that although left neglect is readily demonstrated in the visual, auditory and tactile domains, the severity of neglect is greater for the visual then for non-visual domain (see also Bartolomeo, Derme, & Gainotti, 1994). The observation of right unilateral neglect following impairment to the left hemisphere is much rarer and comparatively less studied but has been observed (Bartolomeo, Chokron, & Gainotti, 2001; Caramazza & Hillis, 1990; Van Dijck, Gevers, Lafosse, Doricchi, & Fias, 2011). Neglect can be a severe and disrupting attentional disorder but does respond to rehabilitation that includes ‘retraining’ limbs on the neglected side of the body or spatial cueing (Robertson, Hogg, & McMillan, 1998; Robertson, North, & Geggie, 1992; Robertson, McMillan, MacLeod, Edgeworth, &

Brock, 2002; Robertson & Murre, 1999; Mattingley, Robertson, & Driver, 2008; Robertson, Tegner, Tham, & Nimmo-Smith, 1995; for review see Luaute, Halligan, Rode, Rossetti, & Boisson, 2006). Pseudoneglect, by comparison, is not as severe as neglect but it is nevertheless a robust and consistent behavioural phenomenon in healthy participants. Taken together, the empirical observations of both pseudoneglect and neglect have furthered our understanding of spatial attention more so than either phenomenon on its own. Visuo-spatial line bisection has remained a key instrument in the field for more than thirty years and traditionally involves marking, with a pen, the perceived centre of a printed line on paper (Figure 1.1). Visuo-spatial line bisection can also take the form of a visually-guided kinaesthetic matching task in which the left and right portions of a stimulus (a metal or wooden rod) are physically adjusted, using vision to guide the judgement, until the two portions are perceived to be equidistance from a central point. Another variation is the Landmark task (Harvey, Milner, & Roberts, 1995; Milner, Harvey, Roberts, & Forster, 1993) in which visually presented horizontal lines are pre-bisected by a ‘landmark’ (i.e., a vertical line that cuts the line into two portions) and the participant’s task is to judge whether the landmark is positioned towards the left or right of true centre or whether the portion to the left or right is longer. New ways of measuring performance on visuo-spatial line bisection are continually being put forward. For example, McIntosh, Schindler, Birchall and Milner (2005) have argued that a more sensitive version of visuo-spatial line bisection is to systemically manipulate the position of the *endpoint of the line* which has been found to significantly mediate the bisection performance of neglect patients. Visuo-spatial bisection is most typically explored for both healthy participants and neglect patients in the horizontal plane but has also been considered in the radial and vertical planes as well. For visually presented lines in the radial plane, below eye level, there is a tendency to bisect the line further away from the true midpoint for both healthy participants and neglect patients (Barrett, Crosson, Crucian, & Heilman, 2002; Geldmacher & Heilman, 1994; Halligan & Marshall, 1995; Heilman, Chatterjee, & Doty, 1995; Shelton, Bowers, & Heilman, 1990).

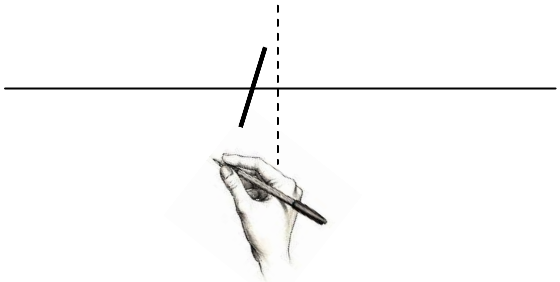

Figure 1.1. A healthy participant bisects a visually presented horizontal line with a pen using the right hand. Performance is biased towards the left-hand side of true centre (represented by the dotted line).

In the vertical plane there is a tendency for healthy participants to bisect lines towards the upper visual field (Bradshaw, Nettleton, Nathan, & Wilson, 1985; Fink, Marshall, Weiss, & Zilles, 2001; Shelton, Bowers, & Heilman, 1990) and horizontal pseudoneglect is greater when lines are presented entirely in the upper versus lower visual field (McCourt & Garlinghouse 2000; McCourt & Jewell, 1999). Previc (1990) postulated that in the upper visual attention is focused for distance-in-depth processing, while in the lower visual field visual attention is focused for tasks like reaching and grasping. The observation of leftward biases for the horizontal plane, distal biases for the radial plane, and upward biases for the vertical plane certainly indicates that spatial attention can be oriented in different ways. This has also been suggested by the fact that visuo-spatial pseudoneglect may be attenuated or reduced when horizontal lines are bisected in extrapersonal space (≥90cm) compared to peripersonal space (≤60cm) though this can depend on the method of bisection – laser pointer versus stick (Gamberini, Seraglia, & Priftis, 2008; Heber, Siebertz, Wolter, Kuhlen, & Fimm, 2010; Longo & Lourenco, 2006; McCourt & Garlinghouse, 2000; Varnava, McCarthy, & Beaumont, 2002).

Interestingly, when participants bisected horizontal lines in a ‘near context’ (lines were superimposed over a photograph showing near placed objects) there was an increased leftward bias, but when participants viewed horizontal lines in a ‘far context’ (lines were superimposed over a photograph showing far placed objects) there was a reversed rightward bias (Nicholls, Forte, Loetscher, Orr, Yates, & Bradshaw, 2011). Rightward biases for neglect patients on horizontal line bisection are also attenuated in extrapersonal space (Halligan & Marshall, 1991; 1995), though it has also been reported that the rightward biases *increase* with distance for neglect patients (Cowey, Small, & Ellis, 1994).

1.1.1. Past Reviews

One the earliest review papers in the pseudoneglect field was presented by Wolfe (1923) who reported a series of studies conducted in the late 1800’s exploring participants’ ability to estimate the middle of horizontal and vertical lines. The emphasis was on *accuracy* and it was reported that when bisecting lines ranging between 50 and 500mm naive participants show approximately one percent of error relative to the total line length. Older children in the ‘eighth grade’ (i.e., probably around 12 years old) were reportedly equivalent in their line bisection performance compared to adults, but younger children showed larger errors. The performance of males and females was similar but women were more variable as a group compared to males. The most recent review and meta-analysis of pseudoneglect in the horizontal plane which focused on *directional* error was conducted by Jewell and McCourt (2000). The meta-analysis included 2191 healthy participants across both visuo-spatial line and tactile rod bisection studies, though the majority were visuo-spatial, as well as pointing tasks where participants simply point towards a given location on the horizontal plane. Leftward biases on line and rod bisection tasks were found to be very robust with an overall moderate-to-strong effect size between -0.37 and -0.44 given the range ±0.2 (small) to ±0.6 (large). With regards to methodology, the meta-analysis noted that forced choice methods (Landmark method) produced larger effect sizes than manual method of adjustment procedures and that while visual line bisection and tactile rod bisection typically elicit leftward biases, kinaesthetic matching tasks often produce rightward biases. The meta-analysis also noted that male participants may show a larger magnitude of pseudoneglect than females; that right-handed participants may show an elevated magnitude of pseudoneglect compared to left-handed participants; and that using the left hand to respond may significantly increase the degree of pseudoneglect compared to using the right hand to respond. The analysis also emphasised that age has a significant effect on pseudoneglect with increasingly rightward errors with increasing age; as well as that starting the task on the left side of space induces greater pseudoneglect compared to starting on the right side of space. Whilst the impact of certain factors on the magnitude of pseudoneglect has since been replicated, the impact of others has not. The notion that directional error becomes more rightward with increasing age, for instance, has since been refuted (i.e., De Agostini, Curt, Tzortzis & Dellatolas, 1999; Varnava & Halligan, 2007) and, in addition, a number of studies in the tactile modality have also since found that *starting right* increases the magnitude of pseudoneglect relative to starting left; these studies will be discussed in due course. Moreover, the meta-analysis by Jewell and McCourt (2000) also concluded that there were no overall clear effects of line length because there is no clear consensus of ‘short’ and ‘long’ but there have been consistent observations that pseudoneglect is observed for most line lengths except very short lines (~2cm) where pseudoneglect may become ‘neglect’ (Chokron & Imbert, 1993; Luh, 1995; McCourt & Jewell, 1999). However, noticeable individual variation with respect to line length between participants has been noted (Manning, Halligan, & Marshall, 1990). This cross-over effect observed in healthy participants (when leftward biases become rightward biases for very short lines) may depend on the type of task; the cross-over effect has been shown to be clearer for Landmark tasks compared to traditional visual line bisection (Rueckert, Deravanesian, Baboorian, Lacalamita, & Repplinger, 2002). The bisection performance of neglect patients is also affected by line length in the same way but in the opposite direction, that is, rightward biases may become leftward biases for very short lines (Bisiach, Bulgarelli, Sterzi, & Vallar, 1983; see also Halligan & Marshall, 1988; 1991; Ishiai, Koyama, Seki, Hayashi, & Izumi, 2006). Indeed, bias may be proportional to stimulus length following the assumptions of a 'Weber's law' of visuo-spatial line bisection (Manning, Halligan, & Marshall, 1990) in which stimulus magnitude is proportional to stimulus bias.

It is useful to further unravel the research on visuo-spatial pseudoneglect especially since over the past decade our knowledge of pseudoneglect has particularly increased. Furthermore, there are many parallels between visuo-spatial and *representational* forms of pseudoneglect – pseudoneglect in the complete absence of vision. It is useful to consider both forms of the bias in order to gain a fuller picture of the phenomenon as a whole and the mechanisms that might underlie it.

1.1.2. The activation-orientation hypothesis

It is widely accepted that the two cerebral hemispheres are functionally distinct. The left hemisphere is specialised for language-based tasks while the right hemisphere is specialised for visuo-spatial processing - though this is a very simplified view (Allen, 1983; Galaburda, Lemay, Kemper, & Geschwind, 1978; Gazzaniga, 2000; Kimura, 1973; Todd & Marois, 2004; White, 1969). Kimura (1966) was among the first to formally note that, due to the anatomical connection of the human brain, visual input to the left visual field is preferentially projected to the contralateral right hemisphere whereas visual input to the right visual field is preferentially projected to the contralateral left hemisphere (Figure 1.2). This assertion followed the observation of an advantage (i.e., better accuracy) for identifying letters in the right visual field/left hemisphere (specialised for language-based tasks) but an advantage for identifying non-alphabetic stimuli like dot stimuli in the left visual field/right hemisphere (see also Bryden, 1966; 1970; 1976; Bryden & Rainy, 1963; Heron, 1957). The neurological and cognitive underpinnings of performance on many different types of tasks have since been widely explored using visual field paradigms (e.g., Ellis, Brooks, & Lavidor, 2005).

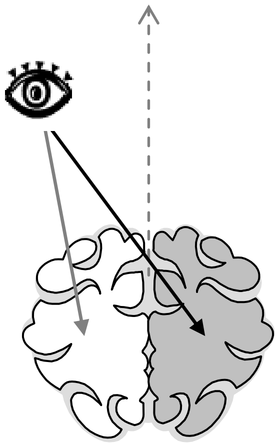

Figure 1.2. The preferential projection of the left visual hemifield to the contralateral right hemisphere. There is still some projection to the ipsilateral hemisphere as indicated by the solid grey line.

Studies with right hemisphere impaired patients have undoubtedly confirmed that the right cerebral hemisphere is involved with preferentially orienting attention towards the left side of space – when damaged it loses this capacity. Although critical lesion sites within the right hemisphere can be difficult to define (Rorden & Karnath, 2004), unilateral left neglect is thought to most commonly follow a lesion to the right parietal lobe (Bartolomeo & Chokron, 2002; Danckert & Ferber, 2006; Halligan, Fink, Marshall, & Vallar, 2003; see also Gottlieb & Snyder, 2010; Mort, Malhotra, & Mannan et al., 2003; Paterson & Zangwill, 1944; Posner, Walker, Friedrich, & Rafal, 1984). Consistently, functional Magnetic Resonance Imaging (fMRI) studies have consistently revealed that regions of the right hemisphere are indeed activated during visuo-spatial line bisection tasks with healthy participants as well. One fMRI study found that when healthy participants judged whether visually presented horizontal lines were prebisected to the left or right-hand side of true midpoint (Landmark task) the right superior posterior and right inferior parietal lobes were particularly activated (Fink, Marshall, & Shah et al. 2000; see also Fink, Marshall, & Weiss et al. 2000). Another fMRI study found that when healthy participants performed a visuo-spatial Landmark task there was significant activation of the right superior and inferior parietal lobes and, for vertical line judgements, of the right parietooccipital cortex (Fink, Marshall, Weiss, & Zilles, 2001). Another fMRI study showed that when healthy participants performed either a visual Landmark task, or a cursor-driven line bisection task (using vision), there was increased activity in the right intra-parietal sulcus and lateral peristriate cortex respectively (Çiçek, Deouell, & Knight, 2009). Consistently, event-related potentials recorded in healthy participants during visual line bisection showed patterns of neural activation over the right temporo-parietal junction, right lateral occipital cortex, and right superior parietal cortex (Foxe, McCourt, & Javitt, 2003). Similar results have been recently shown for general visuo-attentional orienting (Blankenburg, Ruff, & Bestmann et al. 2010). Further evidence comes from ‘knocking out’ these critical right hemisphere regions using Transcranial Magnetic Stimulation (TMS); pseudoneglect became ‘neglect’ in near and far space following TMS over the right posterior parietal cortex and right ventral occipital lobe respectively (Bjoertomt, Cowey, & Walsh, 2002).

One early postulation from Kinsbourne (1970) was that attention is directed to contralateral space by the most activated hemisphere; the potential for attentional control is distributed between the two hemispheres but weighted towards the hemisphere most specialised for a given task such as visuo-spatial processing (e.g., right hemisphere). Leftward biases on visuo-spatial line bisection are sometimes observed under conditions that favour the *left hemisphere*, when a stimulus is presented fully in right hemispace, which suggests that the right hemisphere can also orient attention both contralaterally and *ipsilaterally* while the left hemisphere is only involved with contralateral attentional orienting (Heilman & Van Den Abell, 1979). The central presentation of a horizontal line means one portion of the line extends into the left visual field and one portion extends into the right visual field which would therefore activate each hemisphere in parallel. However, given the visuo-spatial nature of a line bisection task the right hemisphere would have an 'activational advantage' and preferentially direct attention leftward. Reuter-Lorenz, Kinsbourne and Moscovitch (1990) observed that left visual field presentation of lines induced pseudoneglect while the right visual field presentation of lines attenuated or reversed this bias. The results suggested that the biases were a product of contralateral attentional orienting which originated from the most activated hemisphere. The 'activation-orientation hypothesis' (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990) states that contralateral attentional orienting by the right hemisphere leads to directional error because the distribution of attention towards the left portion of a stimulus results in that portion being perceived as longer than the right portion. The right hemisphere orients attention preferentially towards the left because of the superior role it plays in visuo-spatial processing. This critical assumption has been directly tested and will be reviewed in depth in the following section.

In line with the activation-orientation hypothesis is the fact that many studies have found an enhancement of pseudoneglect under conditions that favour the activation of the right cerebral hemisphere. The magnitude of visuo-spatial pseudoneglect is enhanced when a line stimulus is viewed entirely in the left visual field/right hemisphere (Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Luh, 1995; McCourt & Jewell, 1999). The degree of pseudoneglect is also increased when participants are asked to fixate on the left end of a visually presented line (Nielsen, Intriligator, & Barton, 1999) or when participants centrally fixate compared to free viewing (Bradshaw, Nathan, Nettleton, Wilson, & Pierson, 1987; Bradshaw, Nettleton, Nathan, & Wilson, 1985). Fixating leftward directly engages the right hemisphere whereas fixating centrally suppresses the activation of the left hemisphere (because the eyes are kept still). Pseudoneglect has been found to be significantly greater when lines are viewed monocularly through the *left eye* compared to binocularly or with the right eye (McCourt, Garlinghouse, & Butler, 2000); following the aforementioned anatomical connection of the visual system this preferentially activates the right hemisphere. In line with this, Reinhart, Keller and Kerkhoff (2010) recently reported that when patients with neglect dyslexia (manifested as a tendency to miss or misread words embedded within the left side of text) rotated their heads towards the left hand-side when reading a paragraph of text the number of missed stimuli on the left was significantly reduced. A similar finding was noted by Beschin, Cubelli, Della Sala and Spinazzola (1997) who found that when words were placed in right hemispace performance on a reading task improved for neglect patients. Also, Reinhart, Schindler and Kerkhoff (2011) very recently found that leftward ‘optokinetic stimulation’ - physical movement of visually presented stimuli in a right-to-left direction - also reduced the number of missed stimuli on the left hand-side space in neglect dyslexia patients. These two studies also show that external manipulations can mediate the degree to which attention is oriented contralaterally. Pseudoneglect is also enhanced when there is lower contrast on the left portion of the line compared to the right (Bradshaw, Nathan, Nettleton, Wilson, & Pierson, 1987; McCourt & Jewell, 1999) and when asked to choose between two mirror-reversed rectangles that are identical in brightness, there is a tendency for healthy participants to judge the stimulus with the lowest contrast on the left hand-side as darker; the opposite pattern is observed for neglect patients (Mattingley, Berberovic, & Corben et al. 2004). Lower contrast is thought to increase visuo-spatial attentional processing demands in general so when attentional demands are increased for the already preferentially activated right hemisphere, this leads to further right hemisphere excitation and greater pseudoneglect. It has also been widely documented that pseudoneglect on visuo-spatial line bisection is enhanced for left hand responses when compared to right hand responses (Bradshaw, Bradshaw, Nathan, Nettleton, & Wilson, 1986; Brodie & Pettigrew, 1996; Brodie, 2010; MacLeod & Turnbull, 1999; McCourt, Freeman, Tahmahkera-Stevens, & Chaussee, 2001) or bimanual responses (Failla, Sheppard, & Bradshaw, 2003). The left hand effect is reportedly stronger for males (Hausmann, Ergun, Yazgan, & Güntürkün, 2002). This is entirely in keeping with the attentional-orientation hypothesis since motor responses made with the left hand are thought to boost the activation of the contralateral right hemisphere while responses made with the right hand are thought to boost the activation of the contralateral left hemisphere (Brodie, 2010). For neglect patients, consistently, the magnitude of rightward bias on visual line bisection is *attenuated* when the left hand is used (Halligan & Marshall, 1989b; see also Mattingley, Robertson, & Driver, 1998). The left hand attenuation of neglect can be mediated, however, by the left hand starting the bisection from the right hand-side (Halligan, Manning, & Marshall, 1991) or when the right hand is activated at the same time (Robertson & North, 1994); this suggests that competitively engaging the left hemisphere in parallel to the right hemisphere (through stimulating the right visual field or using the right hand) can attenuate the degree of leftward attentional orienting by the right hemisphere.

The activation-orientation hypothesis seems to be the best account of the data as suggested by the fact that presentation modes and response conditions that preferentially engage the right cerebral hemisphere consistently lead to greater visuo-spatial pseudoneglect. It is important to consider the activation-orientation hypothesis in further detail, however, since the same hypothesis will later be scrutinised for its ability to account for *representational* forms of pseudoneglect – pseudoneglect in the absence of vision.

1.1.3. The activation-orientation hypothesis: critical evaluation

With regards to visuo-spatial line bisection, the activation-orientation hypothesis states that contralateral attentional orienting by the right hemisphere leads to leftward bias because the distribution of attention towards the left portion of the line results in that portion being perceived as longer than the right portion – this is a critical assumption. Bultitude and Davies (2006) explored this critical assumption when visual viewing conditions (e.g., eye movements, scanning time) were tightly controlled. In a modified Landmark task participants judged whether pre-bisected lines were bisected to the left or right of true centre. Horizontal lines were presented in the left or right visual fields following a cue which was presented at either the location of the endpoint of the line (invalid cue), or at the location of the centre of the line (valid cue) as illustrated in Figure 1.3. The authors found that response times were faster when the cue was presented at the location of the centre of the line; in this case attention was distributed from the centre of the line outward and thus resulted in a faster response as the positional judgement of the landmark was made relative to the perceived centre. The authors also found that bisection performance was biased leftward in left hemispace but shifted rightward in right hemispace, in line with the general assumptions of attentional orienting. The critical finding was that a left cue, in the location of the left end-point, led to leftward shifts in the perceived midpoint. But right cues, in the location of the right end-point, led to rightward shifts in the perceived midpoint. As the preceding cue biased attention towards one portion of the line which resulted in that portion being perceived as longer the activation-orientation hypothesis is supported. Importantly, in this case the cue preceding the presentation of the line stimulus was very briefly presented (100ms), there was a mask between the cue and the line stimulus (~50ms), fixation was central, and stimuli were also very briefly presented (150ms) which rules out any confounding factors of stimulus presentation or viewing condition. In line with this finding, Bartolomeo and Chokron (2001) asked patients with left neglect to perform a visual line bisection task presented in left or right hemispace and found the presence of a central stimulus presented at the same time as the line (a geometric shape) that had to be identified before bisection improved performance in healthy control participants and patients without neglect (for neglect patients performance worsened with greater neglect under these conditions).

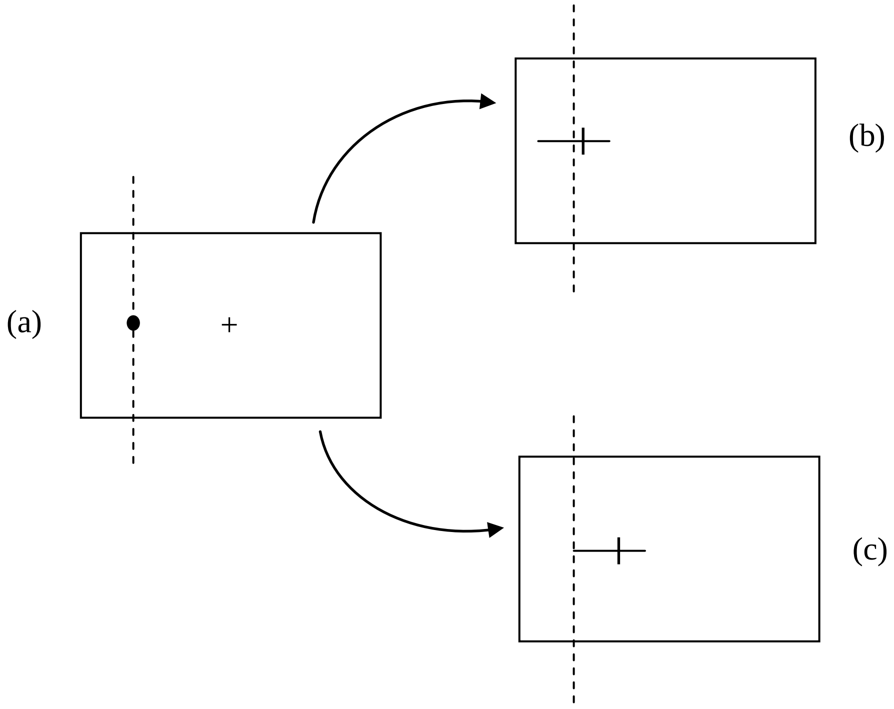

Figure 1.3. An example of the stimuli used in Bultitude and Davies's (2006) experiment (*redrawn from Fig.2. Bultitude & Davies, 2006*). The three boxes represent a computer screen. In (a) a cue - black dot - is shown in the left visual field. Once this cue is removed a horizontal pre-bisected line is presented with its centre aligned with the cue (b) or with its left end-point aligned with the cue (c).

A very recent study by Toba, Cavanagh and Bartolomeo (2011) also supports the critical assumption of the activation-orientation hypothesis. The authors conducted a series of three experiments in which healthy participants were visually presented with pre-bisected lines and were asked to judge whether the transector was to the left or right of midline and also whether the portion on the left or right of the transector was longer. There was a briefly presented preceding cue (a dot) to the left or right endpoint of the horizontally centrally presented line. This experiment differed slightly from Bultitude and Davies's (2006) since the authors plotted psychophysical functions for 'seen at right' and there was an exogenous cue presented entirely in the left or right visual hemifield. The results showed that visuo-spatial attention was biased by the presence of a lateralised cue on either side of space. The point of subjective equality (the point at which participants thought each portion of the line was equal in length) was displaced to the left of midline for left-sided cues – this means the true midpoint was actually to the right - consistent with the left portion of the line being perceived as longer. Consistently, the point of subjective equality was displaced to the right of true midline for right-sided cues - this means the true midpoint was actually to the left - consistent with the right portion of the line being perceived as longer.

A number of other studies have demonstrated that attention can be readily cued to one side of space and, as a result, mediate directional error in that direction. These studies, however, do not necessarily confirm the main assumption of the activation-orientation hypothesis. The most common demonstration of attentional cueing in line bisection has been the placement of a flanker, such as a number, letter, or shape, at one end of the line to be bisected. In an early study by Nichelli, Rinaldi and Cubelli (1989) healthy control subjects showed significant biases toward the side of cueing on visual line bisection; Milner, Brechmann & Pagliarini (1992) found across three experiments that visual line bisection performance was strongly mediated in a leftward or rightward direction by a letter cue at the left or right end of the line respectively[1]. Fischer and Stumpp (2001) found a similar effect with visually presented horizontal lines in college-aged participants whereby flankers presented to the left or right hand side of the line drew attention in that direction and resulted in bisections that were biased towards the side that was flanked. Fischer (1996) presented horizontal lines in isolation or with word flankers that were either three or six letters in length and found word length significantly influenced bisection performance in the direction of the longer word. Likewise, Garza, Eslinger and Barrett (2008) found under normal viewing conditions that visual line bisection performance was significantly biased by the presence of the experimenter standing to the left or right hand-side of space. McCourt, Garlinghouse and Reuter-Lorenz (2005) showed that several factors, like physical cues and stimulus geometry, can combine to produce cueing effects (i.e., like leftward or rightward pointing wedges combined with lateralised cues). In the cases of attentional flankers, however, it is highly possible that the Gestalt principle of perceptual grouping (see Rock & Palmer, 1990) was the driving force behind the bias with the line simply being *merged* into the flanker and thus being perceived as longer; though this is more difficult to argue in certain cases like Garza et al. (2008). The issue is presenting a cue and a stimulus at the same time, or within a time-frame that may allow a retinal trace of the cue to combine with the line stimulus. But how can the perceptual grouping of a flanker with the line lead to pseudoneglect? Morgan, Hole and Glennerster (1990) asked participants to compare the horizontal distance between a pair of target dots each surrounded by a cluster of dots and found that participants extracted the distance between the *dot clusters* instead of the distance between the targets. If a flanker is presented on the left-hand side of a horizontal line and is subsequently merged into the line then the left extent may appear longer; if the centre is extracted from that line it may be biased towards the left-hand side. Porac,

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[1] Around the same time Riddoch and Humphreys (1993) demonstrated that cueing with letter flankers could also reduce neglect by drawing attention to the neglected field.

Searleman and Karagiannakis (2006) asked healthy participants to bisect visually viewed lines with a non-target dot near one or both ends of the line either occluding the line or with a gap between the dot and the line (Figure 1.4). When the dots were strategically placed with one dot to elongate the left portion of the line (dot placed on far left extent with a gap between the line and the dot) and, at the same time, to perceptually shorten the right side of the line (dot placed towards the far right of the line occluding the line) the perceived centre was shifted leftward and the maximum leftward bias was observed. This was relative to elongating the left portion or shortening the right portion in isolation or when the dots were strategically placed to elongate the right portion and shorten the left portion in a combined condition. These results are more in line with the theory of centroid extraction than attentional orienting (Porac et al. 2006).

Figure 1.4. An example of the stimulus in Porac et al. (2006) (*redrawn from Fig.2. Porac et al., 2006*). Here, the left portion of the line is elongated relative to the right which would bias the bisection towards the left.

Mattingley, Pierson, Bradshaw, Phillips and Bradshaw (1993) asked participants to mark with a pen on a visually presented horizontal line on paper, a small vertical line on the left end-point, a small vertical line on the right end-point, or a small vertical line on both endpoints before bisecting the line at the perceived centre. In a separate condition participants were asked to make the physical motion of drawing the vertical mark but without actually leaving a pen mark - the ‘invisible’ cue condition. Interestingly, the authors found no influence on bisection performance in either condition for healthy participants. It would thus seem that the mere act of drawing attention to either end of the line is not enough to mediate pseudoneglect. Harvey, Pool, Roberson and Olk (2000) demonstrated that when similar 'invisible cues' were placed at the left or right end point by the experimenter this *did* bias healthy participants' bisection performance in the direction of the cue perhaps indicating an important difference between 'direct' and 'indirect' attentional cueing. Even so-called invisible cues may, however, leave a retinal trace given the length of time that would be involved with marking the invisible cue; so even when the cue has 'disappeared' this could still promote perceptual grouping (i.e., the line could be perceptually grouped with the retinal trace of the mark).

The activation-orientation account certainly seems to account for the data and holds up under close scrutiny. It has also managed to provide a better fit to the data compared to alternative theories of pseudoneglect. One earlier theory, for example, was that a relative over-activation or under-activation of motor systems in the right hemisphere leads to leftward or rightward bisection errors for healthy participants or neglect patients respectively (Heilman & Valenstein, 1979). However, as we shall shortly see, a large number of studies have since emerged which show that pseudoneglect can occur in the absence of a physical motor response. Another contender was Halligan, Manning and Marshall's (1991) interpretation that the hand's initial position and subsequent *visuo-motor-scanning* direction are most important for spatial biases. These two factors together may drive an 'attentional spotlight' resulting in a 'just noticeable difference' slightly weighted in the direction of starting position (left vs. right) regardless of which hand is used. This account is theoretically similar to that of Anderson (1996) who put forward a mathematical model proposing that participants bisect lines at the point where they perceive the 'salience' of the two line segments to be equal. However, a number of studies, as shall soon be demonstrated, has shown forms of pseudoneglect where no physical starting position is required. Moreover, a classic study from Reuter-Lorenz and Posner (1990) with neglect patients who performed a traditional visuo-spatial line bisection scanning from left-to-right or vice versa or watched an experimenter scan the line with a pen (from left-to-right or vice versa), showed that neglect patients demonstrated significant rightward biases (except when watching the experimenter scan left-to-right). Ishiai, Koyama, Seki, Hayashi and Izumi (2006) recorded eye movements during visuo-spatial line bisection in neglect patients and found that the far extents of leftward portions of a line were often not explored - this would be inconsistent with a *visuo-spatial scanning* hypothesis. A good comparison of the contribution of motor, scanning, and attentional factors was also provided by Nicholls and Roberts (2002). In order to control for scanning behaviour the authors asked both English readers (direction of reading left to right) and Hebrew readers (direction of reading right to left) to perform a version of the Greyscales task (Mattingley, Berberovic, & Corben et al. 2004) which involved making relative brightness judgements for left/right mirror-reversed greyscale stimuli - bimanually in order to control for motor-activation. Participants also performed a visuo-spatial line bisection task by watching a cursor physically move along a line from one direction to the other, left-to-right or right-to-left, and were asked to stop the cursor when it reached the perceived middle; this task was mainly designed to control for scanning speed. For all participants leftward biases were observed on both tasks. A follow-up study with English readers involved lateralised left versus right visuo-spatial cues preceding the presentation of the Greyscale stimuli (with bimanual response) which showed that leftward biases were reduced by right lateralised cues. The results are, therefore, more in line with the activation-orientation account than the scanning or motor activation account. The fact that visuo-spatial pseudoneglect so readily occurs for tasks other than line bisection also supports the activation-orientation hypothesis. Pseudoneglect has been previously reported on tasks such as target cancellation (Vingiano, 1991). Nicholls, Wolfgang, Clode and Lindell (2002), for example, found that models with their faces slightly turned to show the left hemiface were rated as more emotionally expressive compared to right hemiface models even when the images were mirror-reversed. Coolican, Eskes, McMullen and Lecky (2008) also found a significant leftward perceptual bias for a facial emotional judgement task in young and older participants but a rightward bias for right hemisphere impaired patients. Charles, Sahraie and McGeorge (2007) simultaneously presented a circle and an ellipse in either hemifield and asked participants to make a judgement about which stimulus was larger; the results showed that participants underestimated the width of objects in left hemispace, that is, the objects of the left-hand side were perceived to be larger than they actually were. Fischer (2008) conducted a study with 445 adults and found that, in general, participants started counting with the fingers on their left hand independently of handedness. Arduino, Previtali and Girelli (2010) recently found pseudoneglect for the bisection of words containing five or more letters, but not for words containing less than five letters where, instead, rightward biases were observed (see also Fisher, 2004). That is not to say that scanning (or motor activation) is irrelevant to pseudoneglect; but rather that scanning (or motor activation) alone cannot fully account for the data whereas activation-orientation hypothesis can.

1.1.4. Summary

Taken together, the research on visuo-spatial pseudoneglect has indicated that it is a robust phenomenon which occurs under a wide variety of conditions. Visuo-spatial pseudoneglect seems to be best accounted for by right hemisphere attentional orienting and the activational-orientation account (Reuter-Lorenz et al., 1990). The activational-orientation account of pseudoneglect, however, has so far been reviewed for visuo-spatial line bisection as well as other visually-driven tasks; but there are numerous hints in existing literature that suggest a *representational* form of pseudoneglect exists as well. In other words, a form of pseudoneglect that emerges in the complete absence of direct visuo-spatial processing when participants are asked to create a spatial representation in the mind's eye.

1.2. Representational pseudoneglect

1.2.1 Hints from mental representation

The notion of a representational form of pseudoneglect first arose from early studies hinting at a representational form of *neglect*. One early example comes from Bisiach and Luzzatti (1978) who asked neglect patients with right hemisphere impairment to imagine a highly familiar scene, the Piazza del Duomo in Milan, and to describe the landmarks (buildings) on each side from two opposite imagined viewing perspectives (at either end of the Piazza). The majority of landmarks recalled were positioned rightward of the imagined viewpoint, suggesting that the mental representation was better accessed or explored on the right hand-side compared to the left. The authors noted, however, that some of the landmarks could not be physically seen from the imagined viewing position though they did exist. This poses the question of whether patients were actually imagining themselves from the instructed viewing perspective or whether they had temporarily activated a depiction of the scene from another point of view. It is possible that landmarks recalled as being on the right may actually have been positioned more towards the left-hand side. Previously, Paterson and Zangwill (1944) had attempted a similar exploration with a neglect patient who was asked to imagine a highly familiar scene, Princes Street in Edinburgh, and report landmarks from either side of that street - but the authors did not ask the patient to report landmarks from different imagined viewpoints which means that any observations may have been inherently biased towards the most salient landmarks like Edinburgh Castle. Prior to this, Brain (1941) had observed that a patient with right hemisphere impairment correctly recalled landmarks from highly familiar spatial routes but failed to say ‘turn left’ at the appropriate time and replaced the phrase with ‘turn right’ (this was later replicated by Bisiach, Brouchon, Poncet, & Rusconi, 1993). Bisiach, Luzzatti and Perani (1979) also found that right hemisphere impaired patients with neglect also showed deficits on the left hand-side in a ‘spot the difference’ task with patterns after they were moved out of view: here viewing perspective was fully controlled which indicates that the *mental representation* of immediately seen material was indeed subject to neglect. Likewise, Rode, Perenin and Boisson (1995) asked right hemisphere impaired patients with left neglect to mentally represent a map of their home country, France, and recall as many towns/cities as possible on each side whilst imagining the map from North to South or vice versa; the authors found a similar result to Bisiach and Luzzatti (1978) with more items recalled for the right hand-side. Perhaps the clearest demonstration of a *purely* representational form of neglect was provided by Guariglia, Padovani, Pantano and Pizzamiglio (1993) who found that a right hemisphere impaired patient showed no typical neglect on visuo-spatial line bisection, target cancellation, personal neglect tasks, or sentence reading, but when asked to report details from imagined highly familiar scenes (e.g., a Piazza) the same patient demonstrated left neglect (reported few or no details from the left hand side) regardless of imagined perspective. The patient’s performance was the same when tested again one month later and also two months later. On a further task the patient was asked to memorise objects in a completely novel room and was asked to describe the room from two perspectives: the results were similar as when details were reported from a highly familiar imagined scene. Interestingly, the same patient was able to identity which objects existed in the room when provided with multiple choices, indicating that a purely representational form of neglect without a corresponding perceptual form of neglect exists. Similarly, Beschin, Cocchini, Della Sala and Logie (1997) found that one right hemisphere impaired patient was able to report the names of objects visually presented in a spatial array but showed a leftward deficit when reporting objects from a mental representation of a similar scene held in visuo-spatial working memory, indicating again a purely *representational* form of neglect. Beschin, Basso and Della Sala (2000) also found *left neglect* when drawing from memory. Denis, Beschin, Logie and Della Sala (2002) conducted a study with right hemisphere impaired patients with and without neglect and healthy controls; participants were asked to report the name and spatial location of objects visually presented in a square layout. The objects were then removed and the task was to again report the name and spatial location of the objects based on the visuo-spatial mental representation of the scene and, in a variation of this task, the authors also aural-verbally described the objects and asked the participants to perform the same task. The patients with neglect showed a severe deficit in reporting objects from the left-hand side in all conditions (visual, visuo-spatial memory, and aural-verbal memory) whereas non-neglect patients and healthy controls showed no bias. The results indicate different forms of neglect - both representational and visual. Della Sala, Logie, Beschin and Denis (2004) conducted a similar task but asked the patients to report the objects from the original presentation layout and also when the layout had been mentally rotated so that the objects that were originally on the left were imagined on the right and vice versa for objects that were originally on the right (mentally rotated to the left). The results showed that the patients were able to mentally rotate the objects (i.e., objects were still reported in the mentally rotated conditions) but that items that were initially presented on the right hand side were lost when mentally rotated to the imagined left. Items presented on the left transferred to the right were recalled similarly. So whatever information was already available on the neglected left side *remained available* even after mental rotation from left to right. Logie, Della Sala, Beschin and Denis (2005) again conducted a similar study with two patients with right hemisphere impairments one of whom had representational and perceptual neglect (BG) and one of whom had only representational neglect (PT) as well as healthy controls. Participants were asked to report the name of an object and its spatial position when an object array was visually present or when it was aural-verbally described. In the visual conditions (when the objects were in view) PT reported the objects and BG showed left neglect (omitted objects on the left side of the array). For the aural-verbal condition, however, both BG and PT showed left neglect (healthy participants showed no lateralised bias). As verbal memory capacity was taken into account the only adequate explanation for the data is that the bias occurred during the *mental representation* of the stimuli. The same patients were also asked to imagine mentally rotating the objects and both patients were still able to recall information in the mentally rotated condition indicating that the control of attention was intact; while the recall of information for objects initially presented on the left but mentally rotated to the right hand side was unimpaired relative to the non-rotated condition the recall of information for objects initially presented on the right but mentally rotated to the left hand side was impaired. As in the aforementioned study, the patients did not experience problems with executive control of attention as they were able to mentally rotate the scenes - general attention may be intact but the maintenance of material attended to may be impoverished. One interpretation, therefore, is that representational neglect arises from impairment to visuo-spatial working memory (Logie et al., 2005).

Taken together, these studies indicate that there are different forms of neglect, perceptual and representational, and that the same patients can display one or both forms of the bias. Most importantly, these studies have highlighted a critical point: if there is a representational form of neglect it follows that there may be a representational form of pseudoneglect. One of the best demonstrations of a representational form of *pseudoneglect* was provided by McGeorge, Beschin, Colnaghi, Rusconi and Della Sala (2007) who conducted the same task as Bisiach and Luzzatti (1978) but with healthy participants aged 20 to 86 years old who were also asked to visually image the highly familiar scene of the Piazza del Duomo in Milan, and to describe the landmarks on each side from two viewing perspectives. The majority of landmarks recalled that could actually be seen from the imagined viewpoint were towards the left hand side and this bias increased in a negative direction as age increased (the older the participant the greater the leftward bias). Given that the bias was based on a visuo-spatial mental representation, this suggests a *representational* form of pseudoneglect. The authors noted that visual imagery may have engaged visuo-spatial processing mechanisms in the right hemisphere due to the spatial nature of the task and, because of this activation, the right hemisphere directed attention leftward. The results, therefore, are wholly in line with an activation-orientation account of pseudoneglect. Likewise, Bourlon, Duret and Pradat-Diehl et al. (2010) found in 12 healthy control participants (mean age 69 years) who described from memory geographical landmarks in France a slight tendency to report more landmarks from the left-hand side - though this was not significant. Della Sala, Darling and Logie (2010) also found that lateralised memory biases can occur for completely *novel* visually processed stimuli. Participants were asked to view artificial spatial arrays containing objects of different shape and colour and once the array was removed participants were asked to recall the characteristics of the previously seen objects by choosing the relevant characteristics from a subsequently presented array (i.e., six possible colours and six possible shapes). The authors found that there were significantly more errors for recalling the characteristics of objects on the right side of the array. A related study from Cocchini, Watling, Della Sala and Jansari (2007) asked healthy participants to imagine the virtual trajectory of a ball which rotated in a 360 degree circle around them (they imagined themselves at the centre) and judged, while fixating centrally, the time at which the ball would align with the middle of their backs. When the ball moved in a clockwise direction (around the right-hand side of their bodies) participants underestimated the time and signalled too early that the ball had reached their back midline; but when the ball moved in an anticlockwise direction (around the left-hand side of their bodies) participants were relatively unbiased.

These studies indicate that spatial biases can occur within a range of task that involve the mental representation of spatial layout. These observations are important since they clearly demonstrate that pseudoneglect is not simply a function of visuo-spatial processing.

1.2.2. Hints from tactile rod bisection

There is also another main line of evidence that can be considered to be indicative of representational pseudoneglect in the absence of direct visuo-spatial processing – performance on tactile rod bisection. It is important to note that some studies defined as 'tactile rod bisection' have involved the visual guiding of a physical cursor or the physical matching of two portions of a rod. While these studies are indeed tactile in nature, if the task is conducted with direct visual processing they are essentially visuo-spatial tasks. Tactile rod bisection conducted in the complete absence of direct visual processing can be referred to as a *representational* task where the representation of spatial layout is driven through touch (Figure 1.5). Tactile rod bisection is typically conducted in the horizontal plane, but in the radial plane a proximal bias has been reported (Chewning, Adair, Heilman, & Heilman, 1998).

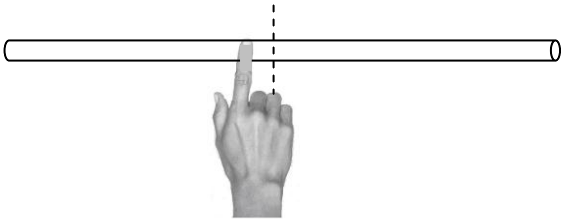

Figure 1.5. A healthy participant bisects a wooden rod with the right index finger. The participant is biased towards the left-hand side of centre (represented by the dotted line).

Bowers and Heilman (1980), who coined the term pseudoneglect, demonstrated that college-aged participants bisected centrally presented wooden rods of different lengths - in the absence of vision - with the index finger of both the left and right hand, significantly towards the left hand-side of true centre. The same leftward pattern was seen when the participants were presented with the rods in right hemispace but in left hemispace bisection was slightly biased towards the right hand-side. Performance at midline and also right hemispace can be explained by the preferential involvement of the right hemisphere in line with the activation-orientation hypothesis - if the right hemisphere also orients attention to both left and right space (e.g., Heilman & Van Den Abell, 1979). But left hemispace performance is not consistent with the hypothesis. It is possible that the left hemispace results were simply a result of a number of variables that interacted in that particular condition (rod length, response hand, starting position) not obviously untangled under statistical scrutiny. Interestingly, pseudoneglect was also greatest when starting the exploration from the right hand side of the rod which at first glance may also seem inconsistent with the hypothesis; however, in this study participants were allowed to scan the rod as many times as preferred so the starting position for exploration did not necessarily equate to the direction that the bisection was made from. Sampaio and Philip (1991) conducted a tactile rod bisection task in the same way as Bowers and Heilman (1980), presenting rods of length 14 to 32cm to right handed participants in left hemispace, at midline, and in right hemispace. Participants were asked - in the absence of vision - to use their index finger to trace the wooden rod from a start left or start right position an unlimited number of times before bisection, or to use an aluminium cursor instead of the index finger to conduct the exploration and bisection (with aluminium bars). Results showed a striking contrast between the two scanning conditions: significant leftward biases at all spatial positions when using the index finger in the direct sensory condition but ‘reversed pseudoneglect’ or rightward biases for all spatial positions when using the cursor in the indirect motor condition. There was no effect of starting point. Sampaio and Chokron (1992) later found leftward biases on a range of ten rods (14 to 32cm) presented only at midline in the absence of vision when the index finger was used to bisect the rod for both left and right handed participants. There was an increase in the bias as a function of rod length for right handed participants only - this is similar to visuo-spatial line bisection (Arduino, Previtali, & Girelli, 2010; Luh, 1995; McCourt & Jewell, 1999) - but when a cursor was used for bisection the directional error was contralateral to response hand and there was no effect of rod length. In this study participants reported that directly using their index finger prompted them to imagine the stimulus as a whole prior to bisecting, but using the cursor induced perceived duration movement to be transferred into a length estimate. The former sensory strategy is perhaps more consistent with visuo-spatial line bisection in which the whole stimulus is perceived all at once. The latter strategy could be interpreted as a temporal order strategy and could potentially be consistent with participants overestimating the duration of movement. Laeng, Buchtel and Butter (1996) also found, in the absence of vision, leftward biases for rods of different lengths (24, 28, 30, 35, and 40cm) except for the smallest rod (20cm) which induced a rightward bias and that the bias increased with rod length. The magnitude of the leftward bias was significantly enhanced by factors that favoured the activation of each hemisphere: when the left hand was used and when rods were presented in left hemispace (see also Hatta & Yamamoyto, 1986) which is entirely consistent with the activation-orientation hypothesis and the visuo-spatial line bisection literature. The authors also found that a secondary verbal task, designed to boost activation of the left hemisphere, had no influence on bisection performance. Importantly, this undermines the likelihood that a temporal order strategy such as counting was automatically used during tactile rod bisection; counting would arguably be a verbal strategy and should therefore be disrupted by a secondary task of the same verbal nature. The authors also found no significant effect of starting position but again asked participants to use a metal pointer to make the bisection judgment after exploring the rod with the index finger; bisecting the rod in the absence of direct sensory input seems to introduce additional ‘noise’ which may explain why no effect of starting position was found. Philip and Hatwell (1998) reported an ‘overshooting’ error in tactile rod bisection with the direction of error being pulled towards the contralateral end to the starting point. The first comprehensive evaluation of scanning direction, starting position, the direction the bisection was made from, and the number of scans was conducted by Baek, Lee and Kwon et al. (2002) who found that when participants tactilely scanned horizontal rods once (left-right, right-left) before bisecting ‘on the way back’ there was a bias in the direction of the current movement - referred to by the authors as the ‘overshoot’ phenomenon. At first glance, this would appear to be in line with a scanning theory of pseudoneglect; but bisecting from the right hand-side induced greater overshooting than bisecting from the left. A similar pattern of results was seen for multiple scans of the rod and, for both conditions, bias did not scale with rod length. It has been previously noted that starting position, in tactile rod bisection, could be perceived as a spatial cue (Levander, Tegner, & Caneman, 1993). Urbanski and Bartolomeo (2008) asked both neglect patients and healthy participants to first mark the left endpoint of a visual or imaginary line, then the midpoint, and then the right endpoint of the line (or vice versa from the right to the left) using the right hand – synonymous with the task of Baek, Lee and Kwon et al. (2002) but allowing a comparison between visual-physical and visual-imagery conditions. Marking the left endpoint first relative to the right endpoint first significantly reduced neglect patients’ rightward bias (with the right hand). Importantly, control participants showed small leftward biases in all conditions regardless of hand or starting side.

One of the strongest lines of evidence for a representational form of pseudoneglect on tactile rod bisection perhaps comes from the finding that blind participants have also been found to display the same leftward biases when bisecting rods; for congenitally blind participants it is impossible that visuo-spatial processing contributed in any way to the bias (Cattaneo, Fantino, & Tinti et al. 2011). This is of particular interest since early blind and later blind participants have been found to have superior tactile acuity skills relative to healthy sighted participants (Norman & Bartholomew, 2011; Wong, Gnanakumaran, & Goldreich, 2011) – yet they are still biased. However, it has also been noted that participants who were blind from birth showed strong rightward biases on tactile rod bisection whereas participants who were blind from an early age but experienced some early vision showed comparably less bias but still slightly rightward; sighted participants in the same study showed leftward biases (Bradshaw, Nettleton, Nathan, & Wilson, 1986).

Additional observations can be gleaned from examining the performance of healthy participants acting as controls for neglect patients. Beschin, Cazzani, Cubelli, Della Sala and Spinazzola (1996) conducted a study with right hemisphere impaired patients and healthy control participants (mean age 45 years) who were asked to find a marble in a tactile maze in the absence of visual input. Control participants were significantly faster at finding the marble when it was placed in near space but showed no lateralised bias; a case-by-case analysis of the patients showed that only a few patients demonstrated tactile left neglect and neglect for far space. However, Beschin, Cubelli, Della Sala and Spinazzola (1997) report that while neglect patients were faster when searching on the right-hand side of a tactile maze for a marble (when blindfolded), there were hints in the data that control participants were faster when searching on the *left*.

1.2.3. Hints from the mental representation of numbers

Research has also shown that people tend to mentally represent smaller numbers on the left side of space and larger numbers on the right side of space in a mental number line. An early understanding of how numbers are represented in the mind's eye came from Galton (1880) who once said: "Persons who are imaginative almost invariably think of numerals in visual imagery. If the idea of six occurs to them, the word "six", does not sound in their mental ear, but the figure '6' in a written or printed form rises before their mental eye" (pg. 86). The observation that participants typically respond faster to smaller numbers with the left hand but faster to larger numbers with the right hand was noted by Dehaene, Bossini and Giraux (1993) who coined the term Spatial Numerical Association of Response Codes (SNARC) to describe this observed relationship (for review see Hubbard, Piazza, Pinel, & Dehaene, 2005). Dehaene and Akhavein (1995) then showed the influential 'distance effect' when participants were asked to judge whether or not two numbers matched in physical terms (e.g., '3-three' does not match in physical terms but matches in numerical terms); a smaller numerical distance ('3-four') slowed judgements compared to a larger numerical distance ('3-nine') which suggests that even when participants focused on the physical nature of the stimulus additional number-based information was subconsciously extracted. To this end, several studies have shown that neglect patients respond more slowly to smaller 'leftward' numbers on the mental number line whereas healthy controls respond faster (Hoeckner, Moeller, & Zauner et al., 2008; Vuilleumier, Ortigue, & Brugger, 2004) regardless of whether the response is manual (parity task) or aural-verbal (Gevers, Santens, & Dhooge et al., 2010). These results present strong evidence that smaller numbers are mentally represented on the left-hand side of space and larger numbers on the right. Empirical observations have also indicated that attention can be preferentially oriented internally *along* a mentally represented number line. Zorzi, Priftis and Umiltà (2002) asked neglect patients to report the midpoint between two verbally presented numbers and found midpoints were typically reported in the direction of the larger number consistent with a rightward bias that also increased with numerical distance but was, paradoxically, reversed leftward for very small numerical intervals similar to the line length effect in visuo-spatial line bisection (see also Umiltà, Priftis, & Zorzi, 2009; Zorzi, Priftis, & Meneghello et al., 2006). While neglect patients show rightward biases on the mental number line with estimates of numerical midpoint biased towards larger numbers, healthy participants show the opposite bias towards smaller numbers. Loftus, Nicholls, Mattingley, Chapman and Bradshaw (2008) asked participants to decide which flanker number was further away from the middle number in a triplet (15_22_47). Regardless of how the numbers were presented (i.e., in a horizontal line or sequentially with the smaller vs. larger number first) there was a bias in the direction of the lower numerical flanker - a leftward bias on the mental number line and this bias increased with numerical distance between the flankers. A similar experiment showed the same pattern of results for negative numbers; when the task was amended so that participants judged whether the middle number was, in fact, the true midpoint between the flankers the bias still remained; and when three patients with right hemisphere impairment to the parietal region were asked to perform this task there was a rightward bias. Loftus, Nicholls, Mattingley and Bradshaw (2008) also found leftward biases in number triplet bisection in another task of this nature. Nicholls and Loftus (2007) had previously shown a similar effect for the mental representation of alphabet triplets (A_D_P) when participants were asked to judge which flanker, left or right, was furthest away from the middle letter regardless of whether the alphabet stimuli were presented visually or sequentially; in addition, a group of three neglect patients showed the opposite rightward bias, consistent with the results of visuo-spatial line bisection. Despite the fact that number stimuli may be initially presented in visual form the bias is representational in nature because the actual task of bisection occurs in the *mind's eye*. Calabria and Rossetti (2005) showed that when healthy participants were asked to bisect lines of words that represented smaller numbers (i.e., 'four') there was a tendency to bisect towards the left but for lines of words that represented larger numbers (i.e., 'nine') the bias was significantly reduced. Loetscher, Nicholls, Towse, Bradshaw and Brugger (2010) found that when asked to choose a number between 1000 and 10,000 healthy participants and neglect patients performed similarly, showing a leftward bias. One of the strongest lines of evidence for a representational form of pseudoneglect on the mental number line comes from the finding that blind participants have also been found to display the same leftward biases when bisecting the mental number line; for congenially blind participants it is impossible that early visuo-spatial processing contributed to the bias (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011).

1.2.4. Evaluation of representational forms of pseudoneglect

The main message from these studies is that representational forms of pseudoneglect can be readily observed for healthy participants. This indicates that spatial biases *can* and *do* occur in different forms and cannot merely be explained by direct visuo-spatial processing. There are also other studies that worth mentioning that fall under same *representational* umbrella. Mohr, Brugger, Bracha, Landis and Viaud-Delmon (2003) found in healthy participants a spontaneous bias in turning with a greater number of 360 degree turns made to the left hand side. Lewald (2002) asked congenitally or early blind subjects as well as healthy sighted controls in the absence of vision to locate the direction of sounds presented in the testing environment by moving their head (i.e., direction measured using a potentiometer), as well as a dichotic listening test to assess whether or not the position of the head affected the lateralisation of dichotic listening. In the first task, healthy subjects underestimated the direction of sounds, whereas blind participants showed a tendency to overestimate the position of sounds. The second dichotic listening experiment showed for healthy participants that location was biased in the direction of the head position, left or right, with a tendency to be more biased towards the left; but blind participants performed in the opposite direction with a bias towards the right (see also Lessard, Pare, Lepore, & Lassonde, 1998).

The activation-orientation hypothesis can readily hold for representational pseudoneglect with the right hemisphere orienting attention leftward within a mental representation of spatial layout. Of course, one main evidence for this has already been discussed and relates to representational forms of *neglect* from right hemisphere impairment. Gobel, Calabria, Farne and Rossetti (2006) found in participants aged between 19 and 41 years that repetitive Transcranial Magnetic Stimulation (TMS) applied over right parietal regions but not occipital regions during mental number line bisection induced performance consistent with neglect - a bias towards larger numbers with the perceived numerical midpoint shifted rightward. This is entirely consistent with the results of visuo-spatial line bisection in the same field. Cattaneo, Silvanto, Pascual-Leone and Battelli (2009) also found that TMS over the right angular gyrus, but not the left, disrupted the priming of attention towards smaller numbers on the left side of the mental number line. Kadosh, Muggleton, Silvanto and Walsh (2010) used TMS over the left and right intraparietal sulcus while participants performed a same-different task with visually presented digits (‘5’) or numbers (“five”); TMS over the right parietal lobe disrupted the processing of digits but not verbal numbers. The activation-orientation hypothesis states that contralateral attentional orienting by the right hemisphere leads to the left portion of a stimulus being perceived as longer than the right portion. For visuo-spatial line bisection we saw two clear examples of this demonstrated by Bultitude and Davies (2006) and also by Toba et al. (2011). But can this critical assumption really hold for representational pseudoneglect? Nicholls and McIlroy (2010) asked college-aged participants to bisect number triplets that were presented sequentially in ascending or descending order with or without a lateralised cue (geometric shape) to the left or right-hand side. The results showed that the leftward bias for mental number line bisection task was not influenced by a left lateralised cue or lateralised cues, but was attenuated for right lateralised cues. Although the cue was visual in nature the mental number line bisection was conducted in the mind's eye and any argument of perceptual grouping does not hold since there is no 'stimulus' with which the cue could be grouped. There is no doubt, however, that direct and convincing evidence for this critical assumption in the absence of vision is lacking especially when compared to visuo-spatial line bisection. But how can this issue be resolved?

Our comprehensive understanding of visual-perceptual pseudoneglect has stemmed from the fact that there have been hundreds of studies of this phenomenon. Taken together, these studies have allowed us to make important inferences about the suitability of various hypotheses, like activation-orientation, for explaining the bias. Representational pseudoneglect deserves the same level of scrutiny; our understanding of pseudoneglect as a whole cannot be complete without it. The activation-orientation hypothesis of pseudoneglect has not been formally updated since its creation and, as mentioned, still mainly accounts for visuo-spatial pseudoneglect. The aim of the research reported here is to build our understanding of representational pseudoneglect by exploring some core but as yet unanswered questions in the field.

1.3. Representational pseudoneglect across lifespan

The first unanswered question is how are representational forms of pseudoneglect influenced by age? The empirical observation of representational pseudoneglect across the entire lifespan, from a very young to a very old age, would be important as this would indicate an early and persisting role for the mechanisms in the right hemisphere that orient attention in the absence of vision. This observation would allow us to make important inferences about the early, middle, and late developmental trajectory of attentional orienting - without vision. To date, there is no study demonstrating representational pseudoneglect across the entire human lifespan in the complete absence of vision. Changes to numbers have been shown to elicit activity in right parietal and prefrontal cortex of three month old infants (Izard, Dehaene-Lambertz, & Dehaene, 2008) and pre-schoolers have been found to search an array of boxes in a horizontal line (i.e., ‘rooms’) faster and more accurately when labelled in ascending numerical order (Opfer & Furlong, 2011; see also Opfer, Thompson, & Furlong, 2010). Likewise, Berch, Foley, Hill and Ryan (1999) found children as young as nine years of age readily demonstrated the SNARC effect. On one hand, this may demonstrate a very early and automatic association between numbers and space. However, the mental number line is difficult to assess across the entire lifespan because familiarity with numbers strongly influences how they are mentally represented. Adults are thought to have a linear representation of the number line whereas children may have a logarithmic representation or two linear representations – one for double digits and one for single digits (Berteletti, Lucangeli, Piazza, Dehaene, & Zorzi, 2010; Ebersbach, Luwel, Frick, Onghena, & Verschaffel, 2008; Moeller, Pixner, Kaufmann, & Nuerk, 2009; Nuerk, Kaufmann, Zoppoth, & Willmes, 2004). Moreover, reading direction may also have an influence on mental number representation tasks (Kazandjian, Cavézian, Zivotofsky, & Chokron, 2010) - this has also been demonstrated for visuo-spatial line bisection (Chokron & De Agostini, 1995; Chokron & Imbert, 1993; Zivotofsky, 2004). Reading is a learned behaviour and as children become more familiar with reading from one direction this may thus have a developmental influence on number-space associations. To this end, dyslexic children show *rightward biases* on visuo-spatial line bisection (Michel, Bidot, Bonnetblanc, & Quercia, 2011). Another issue in the context of the mental number line is that working memory function may decline with increasing age (Hartman & Warren, 2005; Johnson, Logie, & Brockmole, 2010; Park, Lautenschlager & Hedden et al. 2002). It could be argued that working memory is highly involved with mental number line bisection since the participants is required to hold numbers in mind while deciding on and reporting the midpoint; this means that any interesting differences in performance for older compared to younger adults found on mental number line tasks may actually be reflective of unreliable working memory rather than representational pseudoneglect or attentional orienting. Indeed, Van Dijck, Gevers, Lafosse, Doricchi and Fias (2011) showed for healthy controls aged 52 to 58 years no clear bias on mental number line bisection. For similar reasons, it would be difficult to assess lateralised working memory biases across the entire lifespan. However, there have been many studies exploring pseudoneglect on *visuo-spatial line bisection* across the entire lifespan which *can* provide useful and interesting hints for the current research question. De Agostini, Curt, Tzortzis and Dellatolas (1999) compared visual line bisection in participants aged 5 to 6 years, adults aged 20 to 45 years, and older adults 60 to 94 years and found leftward bisection error regardless of age, gender, or response hand. Varnava and Halligan (2007) explored the influence of age and sex on visual line bisection with participants aged 14-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80 years. Across all age groups participants showed leftward biases and there was no significant interaction between line length, age group or sex; no interaction between age cohort and sex; no main effect of sex; and no main effect of age cohort for the percentage deviation scores. There are also a very large number of studies to draw upon that have tested age-matched controls for neglect patients. Age matched controls aged 66 years showed leftward errors on visual line bisection and a Landmark judgement task (Harvey et al., 1995); age-matched controls aged 76 years (on average) showed leftward biases on an emotional judgement chimeric faces task in line with younger participants (Coolican, Eskes, McMullen, & Lecky, 2008). There was also leftward bias for older controls aged 75 years on the Greyscales task (Mattingley et al., 2008). Interestingly, this pattern of performance on visuo-spatial line bisection pseudoneglect across lifespan is not consistent with current models of cognitive ageing.

1.3.1. Hemispheric asymmetry reduction and cognitive ageing

The Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model (Cabeza, 2002) is one of the most widely accepted model of cognitive ageing (see also Salthouse, 1988; 1996; 2009) and argues that with increasing age cognitive functioning becomes *less lateralised* at the neural level. The model does not provide for a cognitive bias like pseudoneglect that is retained (or even enhanced) by increasing age. There is an overwhelming amount of behavioural and brain imaging support for HAROLD and it is certainly worth providing some solid examples. Cabeza, Grady and Nyberg et al. (1997) explored using Position Emission Tomography (PET) memory encoding and retrieval in participants of different ages in word-pair experiment where participants were required to provide the second word in a previously seen pair when prompted with the first word. In younger participants (mean age 20 years) there was left lateralisation during the stage at which the words were encoded but right lateralisation during the stage at which the words were recalled; but in older adults (mean age 70 years) there was reduced lateralised activity in general. Another PET study also found that younger participants (mean age 26 years) showed left lateralised activity during encoding and right lateralised activity during retrieval in a word-pair memory experiment, whereas older adults (mean age 70 years) showed more bilateral activation throughout (Cabeza, McIntosh, Tulving, Nyberg, & Grady, 1997). Madden, Turkington and Provenzale et al. (1999) also showed that in a word recognition paradigm younger participants showed lateralised activity whereas older participants showed bilateral activity. In another temporal order memory task using PET older adults also showed less activation in the right prefrontal cortex relative to younger adults but increased activation in other areas like the left prefrontal cortex (Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000). A range of other tasks have shown similar findings. Reuter-Lorenz, Jonides, and Smith et al. (2000) showed that in younger participants' activity was lateralised to the left hemisphere during a verbal working memory task but to the right hemisphere for a spatial task; but in older adults there was bilateral recruitment for both. Another interesting example is provided by Thomsen, Specht and Hammar et al. (2004) who used Magnetic Resonance Image (MRI) to investigate the neural mechanisms underlying attentional orienting in younger (mean age 25 years of age) versus older adults (mean age 58 years of age) as a function of dichotic listening. When asked to attend to both ears or the right ear monaurally there was the usual right ear advantage for both older and younger participants; when asked to attend to the left ear monaurally the right ear advantage was still observed for the older but not the younger participants with consistent fMRI activation patterns. The results suggest that older participant experience a difficulty in controlling attention allowing the *stimulus* to drive processing. Very recently, Przybyla, Haaland, Bagesteiro and Sainburg (2011) found reaching accuracy and precision was dependant on the dominant hand for younger participants (20 to 40 years of age) but not for older adults (60 to 80 years of age) with performance for the dominant and non-dominant hand being overly similar. Vallesi, McIntosh, Kovacavic, Chan and Stuss (2010) also showed that younger adults (mean age 26 years of age) displayed contralateral hemispheric activity relative to the hand performing a target identification task but older adults (mean age 72 years of age) showed symmetrical activity (see also Jimenez-Jimenez, Calleja, & Alonso-Navarro et al. 2011). However, the recruitment of the two hemispheres may be notably asymmetrical during simple motor tasks but there is more bilateral recruitment when the task is more complex in general (Hausmann, Kirck, & Corballis, 2004). Zhu, Guo and

Jin et al. (2011) explored using EEG cortical networks in children aged 0–10 years of age, adults aged 26–38 years of age and 56–80 years of age during relaxed wakefulness; neural network in the right hemisphere developed earlier than those in the left hemisphere and the asymmetry of cortical networks declined with age.

Cabeza and colleagues have explained these results in terms of older adults recruiting both hemispheres in a *compensatory* strategy for general lessening of lateralisation or a difficulty with accessing lateralised functions. It is indeed possible that the less lateralised performance of older participants is due to the fact that older brains ‘compensate’ for general cognitive decline by employing additional activation from different areas and therefore recruit a greater number of regions in this ‘compensatory strategy’ (Cabeza et al. 1997). This account is consistent with the fact that rehabilitation following unilateral brain damage is associated with the recruitment of the healthy unimpaired hemisphere (Silvestrini, Cupini, Placidi, Diomedi, & Bernardi, 1998) and following stroke in the left hemisphere, bilateral recruitment is associated with a greater recovery of language function (Cao, Vikingstad, George, Johnson, & Welch, 1999). Evidence from fMRI has shown that motor activation of younger adults (mean age 22 years) in more asymmetrical than older adults (mean age 71 years) who recruit *additional* premotor areas (McGregor, Craggs, Benjamin, Crosson, & White, 2009). Prakash, Erickson and Colcombe et al. (2009) also found using fMRI during a modified Stroop task that younger participants (18 to 35 years of age) demonstrated changes in cortical activation as a function of cognitive demand but older adults (58 to 75 years of age) generally recruited wider hemisphere regions. Likewise, Velanova, Lustig, Jacoby and Buckner (2007) again showed that older adults (74 to 75 years of age) recruited additional frontal regions compared to younger adults (21 to 22 years of age) when more effort was required in a memory retrieval task. It is possible that the human brain gradually becomes more lateralised from birth to early adulthood and then starts to decline again in older age due to a general difficulty in engaging lateralised functions; as noted by Dolcos, Rice and Cabeza (2002) “a process of functional differentiation during childhood is reversed during aging by a process of functional dedifferentiation” (pg. 822). Cabeza, Anderson, Locantore and McIntosh (2002) found using PET that the prefrontal cortex was indeed more asymmetrically active in younger versus older adults but that this was related to the level of performance; low-performing older adults and young adults both engaged similar networks whereas high-performing older adults activated additional networks.

One pattern of performance that has also emerged in the visuo-spatial line bisection literature to support HAROLD is ‘symmetrical pseudoneglect’ (Figure 1.6) - a leftward bias when responding with the left hand but a rightward bias when responding with the right hand.

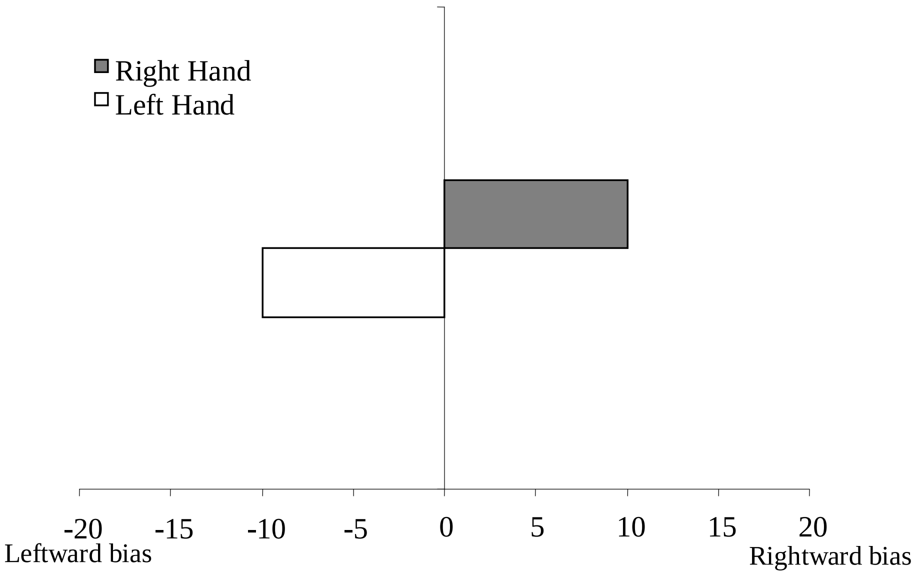

Figure 1.6. A graphical illustration of symmetrical biases in a visuo-spatial line bisection task. The values are made-up and do not represent real magnitude of bias. Positive values are illustrative of rightward biases; negative values are illustrative of leftward biases.

Bradshaw, Nathan, Nettleton, Wilson and Bradshaw (1987) found that left-handed children around or younger than five years of age showed leftward bias with the left hand but rightward bias with the right hand indicating symmetrical pseudoneglect. Dellatolas, Coutin and De Agostini (1996) also found that children aged four to five years demonstrated rightward biases with the right hand but leftward biases with the left hand, but children aged 10 to 12 years demonstrated leftward biases regardless of hand. This is an important observation hinting towards the fact that hemispheric maturation changes the way in which attentional is directed to each side of space, though there is some discrepancy over when this change actually occurs. Hausmann, Waldie and Corballis (2003) explored the influence of hand and line position in participants aged 10 to 12 years, 13 to 15 years, 18 to 21 years, and 24 to 53 years and found that participants aged 10 to 12 years showed a symmetrical visual line bisection bias bisecting towards the left with the left hand but the right with the right hand but participants aged 13-15, 18-21 and 24-53 bisected towards the left with both hands (though more strongly towards the left with the left hand compared to the right hand). Failla, Sheppard and Bradshaw (2003) found that visual line bisection participants aged five to seven years and 60 to 70 also showed evidence of a symmetrical bias whereas participants aged 10 to 12 years and 20 to 30 years showed leftward biases in general with all hand conditions - though the greatest bias was when the left hand was used. The same authors found, on a chimeric faces task, an overall bias towards the left-hand side for all age groups (except those aged 60 to 70 years) with faces being judged as ‘happier’ when the expression of happiness was on the left hand side. For older adults, symmetrical biases on visuo-spatial line bisection are completely in line with HAROLD as there is less lateralisation of cognitive function and hence less attentional orienting by the right hemisphere. Here, symmetrical biases represent more balanced activation of the cerebral hemispheres and a reduction in the increased activation of the right hemisphere relative to the left. In children symmetrical biases may indicate an immature attentional orienting system. One theory is that corpus callous maturation can explain the symmetrical nature of the biases of younger children, with incoming visuo-spatial information not being immediately transferred to the right hemisphere so the preferentially activated left hemisphere retains control of directing attention rightward. Pulsipher, Seidenberg and Hermann (2009) explored corpus callosum volume using MRI in children split into four age groups (8 to 9; 10 to 12; 13 to 15; 16 to 18 years) but found no significant relationship between corpus callosum volume and right hand deviation, left hand deviation, or differences between directional error by hand for any age group.

1.3.2. Ageing of the right hemisphere

The right hemiageing model, in contrast, argues that the two hemispheres age differentially with the right hemisphere ageing faster or more detrimentally than the left hemisphere (Dolcos, Rice, & Cabeza, 2002). The right hemiageing model has support from studies showing good performance on left hemisphere lateralised tasks (language) but poorer performance on right hemisphere lateralised tasks (visuo-spatial). An early example of this comes from Goldstein and Shelly (1981) who found that older participants were more impaired on tasks that are lateralised to the left hemisphere like verbal tasks compared to tasks that are lateralised to the right hemisphere like spatial tasks. Klisz (1978) also reported that the performance of older adults on a neuropsychological test battery resembled that of neglect patients. Prodan, Orbelo and Ross (2007) presented participants aged 20 to 78 with drawings of faces which displayed different emotions on the upper and lower halves of the face; when specifically instructed to pay attention to the upper half of the face older participants aged over 62 years showed a deficit in identifying the facial emotion relative to younger participants and this was especially noticeable in the left visual field (right hemisphere). In line with the right hemiageing model is the finding that as people age, increasingly rightward biases are demonstrated on line bisection. Stam and Bakker (1990) then demonstrated in participants with a mean age of 58 years a slight rightward bisection on visual line bisection; this was replicated in another study by Fujii, Fukatsu and Kimura (1995) who found that older participants bisected lines significantly towards the right relative to middle-aged and younger participants. Schmitz and Peigneuz (2011) explored the effect of age on pseudoneglect by asking participants aged 22 years or 69 years to perform a Landmark task with 100 prebisected lines that were visually presented. The results showed that, while younger participants produced the typical leftward biases, older adults showed a significantly reduced bias which was more in line with the bias shown by neglect patients when compared against the younger participants. However, it is important to note that there is far more empirical support, both behavioural and brain imaging, for HAROLD than the right hemi-aging account of cognitive ageing.

1.3.3. A new paradigm

The effect of cognitive ageing on representational form of pseudoneglect will be explored in this thesis using tactile rod bisection as it is a novel task that can be conducted in the complete absence of vision, does not directly tap into working memory, and is unaffected by familiarity. A tactile based task may also allow us to make some further secondary observations about how sensory information in the absence of vision is processed in children as well as younger and older adults. Previous research has shown that tactile stimulation may be remapped into an external spatial frame of reference relating to the posture of the body (Azañón, Camacho, & Soto-Faraco, 2010; Azañón & Soto-Faraco, 2008). Pagel, Heed and Röder (2009) conducted a study with 5 to 10 years old children who were asked to decide which hand had been tactilely stimulated first when the hands were crossed (when such judgements are generally less accurate) or uncrossed (when such judgements are generally more accurate) and showed that the accuracy of judgements generally increased with age with older but not younger children displaying a crossed hand effect. It may be useful for the current study to draw on such theoretical frameworks given that during a centrally presented tactile rod bisection task the participant's hand must cross the body midline to fully explore the rod (if the rod is horizontal and extends into left and right space). Likewise, it may also be useful to draw upon studies that have shown how age affects internal motor scanning. For instance, Hoyek, Champely, Collet, Fargier, and Guillot (2009) explored how children (aged seven to eight years and 11 to 12 years) physically completed or imagined completing an obstacle course which involved actions like running, rolling, jumping and crawling, and found that the duration of motor imagery was closer to the duration of physical completion for older relative to younger children. Personnier, Kubicki, Laroche and Papaxanthis (2010) asked participants aged 25 years and 71 years to physically or mentally walk though different visible pathways that were either broad, average, or narrow in width at a self-paced speed. For younger adults motor imagery was similar between the physical and imagined condition regardless of path width but for older adults performance was relatively significantly worse - older adults significantly over-estimated walking in the imagery condition relative to physical condition and there was a decrease in a performance as a function of path width (see also Poliakoff, Shore, Lowe, & Spence, 2006). The results from this study may also complement the previous research that has explored how attention is allocated across lifespan in general (e.g., Cowan, Fristoe, Elliot, Brunner, & Saults, 2006; Cowan, Morey, AuBuchon, Zwilling, & Gilchrist, 2010).

Exploring age on visuo-spatial line bisection is not necessarily straightforward, however, as van Vugt, Fransen, Creten and Paquier (2000) found when exploring visuo-spatial line bisection in 650 participants aged seven to 12 years and found for horizontal lines several variables such as gender, handedness, response hand, age and stimulus variables such as orientation, length, as well as position all interacted to modulate the degree and direction of pseudoneglect. Indeed, it has been recently shown that males' performance on visuo-spatial line bisection becomes increasingly rightward with age (e.g., 23 to 93 years) but females' bias does not (Chen, Goedert, & Murray et al., 2011; see also Roig & Cicero, 1994). Furthermore, it is possible that adolescents would produce a very noisy bisection since there are many changes during adolescent at the neural and structural brain level (Sisk & Zehr, 2005; see also Giorgio, Watkins, & Chadwick et al. 2010).

1.4. Representational pseudoneglect for novel spatial layout in the absence of vision

A second unanswered question is as follows: is the mental representation of a completely novel spatial layout built from aural-verbal description in the complete absence of vision subject to representational pseudoneglect? In sighted individuals highly familiar scenes stored in long-term memory (as well as numbers) are arguably encoded in the first instance using direct visual processing. Any biases that are demonstrated during the mental representation of highly familiar information, therefore, may not reflect a purely *representational* form of pseudoneglect but, rather, a perceptual form of the bias activated during mental representation. Furthermore, when the scenes were highly familiar it is not clear to what extent familiarity itself was involved in driving the lateralised bias. Denis, Goncalves and Memmi (1995) suggested that the location of a landmark within a spatial description is not necessarily mentally represented at a specific location but is rather associated with a wide region of space; familiarity with the spatial description results in these regions becoming narrower. If the same lateralised biases occur in healthy participants who have conducted the task in the complete absence of visual processing for completely novel stimuli, this empirical observation would allow us to be sure that the lateralised biases were purely *representational* in nature and remove the question of familiarity.

Visuo-spatial working memory (Baddeley & Hitch, 1974; see also Baddeley, 1981; 1992; 2003; Baddeley & Logie, 1999; Logie, 1995; 2003)[2] is arguably highly involved in building a spatial layout from aural-verbal description and provides the capacity to form a mental representation of what is being described as well as the ability to maintain and retrieve details from the scene. Interestingly, it is possible that if attention is oriented towards the left-hand side of the mental representation this may lead to enhanced recall for left-hand side details. Lepsien, Griffin, Devlin and Nobre (2004) found that attention cued towards a given location facilitated retrieval of information that was earlier presented at that location (see also Griffin & Nobre, 2003; Lepsien & Nobre, 2006). A paradigm is required which involves the aural-verbal description of spatial layout in the complete absence of visual processing so how this could be achieved? Both sighted and blind participants are able to build spatial representations from aural-verbal description (Noordzij, Zuidhoek, & Postma, 2006) and are able to mentally represent spatial locations of landmarks in three-dimensional space - providing complex orientation of the scene is not required (Iachini & Logie (2003). Denis, Pazzaglia, Cornoldi and Bertolo (1999) found that when verbally describing highly familiar locations the distribution of two and three-dimensional landmarks (streets, bridges, squares, churches, monuments) were common across participants. Janzen (2006) found that when participants were asked to learn a route through a virtual environment objects placed at intersections were later recognised faster than objects placed randomly along the route. Della Sala, Gray, Baddeley, Allamano and Wilson (1999) designed the Visual Pattern Test (VPT) to

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[2] Delving into the range of different models of temporary visual memory, or the extent to which working memory has been reviewed, is not relevant here, but it is appropriate to note that interesting discussions within this context exist (Barrouillet, Bernardin, & Camos, 2004; Conway, Jarrold, Kane, Miyake, & Towse, 2007; Logie, 2011a; Logie, 2011b; Logie & D'Esposito, 2007; Osaka, Logie & D'Esposito, 2007).

measure visual memory and involves presenting the participant with a square matrix (2 x 2) containing both filled-in and empty cells (Figure 1.7). The participant views the matrix and then, once removed from sight, copies the pattern within the matrix which gives rise to 'pattern span'. The size of the matrix increases until the participant's performance becomes inaccurate. Similarly, previous to this, Brooks (1968) had devised a task that required participants to remember a sequence of instructions while viewing a blank matrix[3] but this task is more a measure of spatial *imagery*.

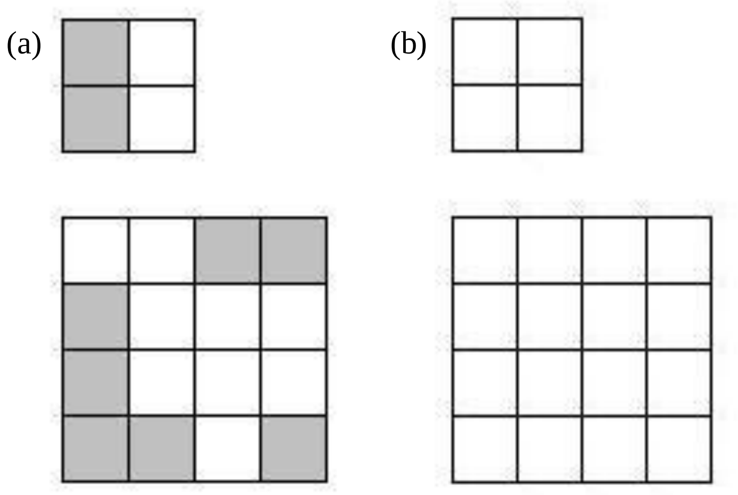

Figure 1.7. An example of the stimuli used in the Visual Patterns Test (Della Sala, Gray, Baddeley, Allamano, &Wilson, 1999). The stimulus is shown (a) and a blank response grid (b).

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[3] In the Brooks (1968) task participants are instructed "in the starting square put a 1; in the next square down put a 2; in the next square to the right put a 3" during which the sequence can be encoded as a pathway through the matrix (typical span is 8 sequences). In another non-spatial condition the instructions may be "in the starting square put a 1; in the next square to the *slow* put a 2; in the next square to the *bad* put a 3" (typical span is 6 sequences).

The Corsi Block Tapping Task (Milner, 1971; Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000) was devised to measure spatial short term memory and involves the experimenter tapping a sequence of nine blocks that are visually presented and the participant then taps the blocks in the same sequence (generating a ‘spatial span’ for the correctly remembered sequence). Lateralised performance has been reported on the Corsi block tapping task with males performing at significantly greater levels of accuracy than females in the left visual field compared to the right visual field (Nalcaci, Cicek, Kalaycioglu, & Yavuzer, 1997).

An aural-verbal version of the VPT (Della Sala, Gray, Baddeley, Allamano, &Wilson, 1999) where the matrix is simply described as having ‘filled-in’ or ‘empty cells’ would allow a comparison between a general lateralised judgement based on the general impression of the mental representation such as “which side of the pattern has the most filled-in cells?” and a more detailed retrieval of information such as “recall the pattern on the side that has the most filled-in cells”. If an aural-verbal version of the VPT is adopted in the way described above it might be possible to tap into ‘categorical’ (relative) versus ‘coordinate’ (fine-grained) spatial processing (Kosslyn, 1987). Kosslyn, Koenig and Barrett et al. (1989) found that participants responded faster to categorical judgements (up/down, left/right) when stimuli were presented to the left hemisphere but faster to coordinate judgements (fine-grained distance judgements) when stimuli were presented to the right hemisphere (see also Kessels, Kappelle, de Haan, & Postma, 2002; Slotnick & Moo, 2006; van Asselen, Kessels, Kappelle, & Postma, 2008; van der Ham & Borst, 2011). It is possible that a similar distinction may be observed with this design - in the complete absence of vision. Indeed, Rinck and Denis (2004) conducted two experiments with healthy participants who were asked to learn the layout of a novel art museum which contained ‘paintings’ in different galleries along different paths. When participants were given a task that involved longer distances (walking down a long path) imagery also took longer; the same effect was observed when participants were asked to move between two rooms versus one room. The results indicate that two different types of spatial processing are used when *imagining* spatial layout - Euclidean distance (fine-grained information about distance) and categorical distance (reference to the number of units). Given that the focus of this thesis it may be useful to later draw on this theoretical framework for the current paradigm.

1.4.1. An auditory hemifield approach

An aural-verbal paradigm of this nature allows elements of the aural-verbal description to be manipulated in a systematic way. It is possible that sensitivity to representational pseudoneglect during aural-verbal description could be maximised by presenting the stimuli in isolation to the right hemisphere; this could be achieved using an auditory hemifield approach. There is plenty of evidence to suggest that monaural presentation induces contralateral hemispheric activity while binaural presentation induces balanced activity between the hemispheres. Schönwiesner, Krumbholz, Rübsamen, Fink and Yves von Cramon (2007) presented pulsed noise to the left and right ears monaurally or binaurally during fMRI and found, in the absence of binaural stimulation, preferential neural activity in the hemisphere contralateral to the stimulated ear. When binaural stimulation was added to the sequences this contralateral pattern of activity disappeared in the right hemisphere. Paiement, Champoux and Bacon et al. (2008) presented a variety of auditory real-world stimuli like human crying, footsteps, and tapping during fMRI to healthy participants and also two hemisperectomised patients. For healthy participants the presentation of auditory sounds binaurally elicited bilateral activity whereas presenting the auditory stimuli monaurally elicited preferential contralateral hemispheric activity; for the patients monaural presentation to the intact hemisphere on the ipsilateral side elicited greater activity whereas presentation contralaterally reduced activity. Hirano, Naito and Okazawa et al. (1997) found increased regional cerebral blood flow for both speech (Japanese) and reversed speech stimulus in the contralateral hemisphere. Likewise, Gilmore, Clementz and Berg (2009) found in an auditory oddball task contralateral activation as a function of ear of stimulation. Lazzouni, Ross, Voss and Lepore (2010) performed a task involving the detection of frequency changes in tones found larger responses in the contralateral hemisphere relative to the stimulated ear. When participants listened to irrelevant sounds (speech utterances or tones) at the same time as processing visual information for later serial-order recall (letters) there was a disadvantage for irrelevant sounds for the *left ear* indicating a specialised role for the right hemisphere in ignoring irrelevant sound (Beaman, Bridges, & Scott, 2007; Hadlington, Bridges, & Darby, 2004; Hadlington, Bridges, & Beaman, 2006). Typical recall recency effects have also been found to be strongest when the presentation of stimuli was to the right ear (Burns & Manning, 1981; Taylor & Heilman, 1982).

Taken together, the research suggests that the right hemisphere can be preferentially activated by the stimulation of the left ear monaurally which could represent a large boost to right hemisphere activity which may subsequently augment attentional orienting. This is essentially in line with the aforementioned visuo-spatial line bisection research that has shown favouring the right hemisphere through left hand response, left visual field presentation, or left eye viewing also augments pseudoneglect.

1.4.2. Visual imagery

There is also room within an experimental design of this nature (aural-verbal description of spatial layout) to consider the issue of visual imagery ability. Denis (2008) found that when participants were asked to create a visual image of a spatial layout and then make mental comparisons of distance within that layout between two landmarks (i.e., harbour - beach), participants with high visuo-spatial performance were more accurate in their comparisons and performed the mental comparisons more quickly compared to participants with low scores on the same task. Likewise, Garden, Cornoldi and Logie (2002) asked participants to follow an experimenter as she walked along the streets of the city of Padua in Italy, following which the participants started from the beginning of the route and retraced their steps; the degree to which a secondary task influenced performance depended on the self-reported spatial ability of the participants. In this case the authors recorded ‘mental mapping’ ability and found that highly spatial participants were more affected by a secondary task that involved spatial-tapping while low spatial participants were more affected by articulatory suppression - indicating that spatial skill may predict strategy usage (visual imagery vs. verbal respectively). Dean and Morris (2003) found that when spatial ability was assessed using spatial test and imagery questionnaires there was an association between participants reported imagery and performance on spatial tasks. It is also interesting to consider the impact of *strategy* in a task designed to explore a representational form of pseudoneglect since this is something that has already been explored for visuo-spatial line bisection. Varnava and Halligan (2009) asked 140 participants to perform a traditional line bisection task with five horizontal lines (18cm) and then report the strategies they used while doing so. Three main strategies arose from participant reports: 1) extracting the centre of the line first, 2) making a comparison between the two portions of the line, 3) using an external frame of reference such as the body, the page, or an imagined stimulus (a piece of wood that needs to be sawed in half). Regardless of the strategy used, however, participants deviated towards the left-hand side. Nicholls, Mattingley and Bradshaw (2005) also conducted a study exploring the strategy that healthy participants used for luminance judgements on the Greyscales task by forcing a ‘comparison strategy’ (i.e., explicitly compare left and right portion of a stimulus with separated left and right portions) versus a 'global strategy' (i.e., view stimulus as a whole not separated). Regardless of strategy leftward biases were observed.

1.4.3. A new paradigm

The extent to which a purely representational form of pseudoneglect arises for completely novel spatial layouts created from aural-verbal description will be explored both for abstract pattern stimuli and real-world scenes, taking into account visual imagery strategy and mental mapping ability. Given the aural-verbal nature of the stimuli there will be monaural presentation of the stimuli to either the left or right ear in a bid to explore how representational pseudoneglect can be boosted under conditions that enhance the activation of the right hemisphere (left ear presentation).

1.5. Psychophysical evidence for representational pseudoneglect

A third unanswered question is do participants' eye movements during mental representation reflect lateralised recall biases, if any? Fixations, almost stationary gazes on one location, are a useful measurement of eye movements - especially the *position* and *duration* of fixations (Henderson, 2003). Fixations precede and follow saccades which are rapid jumps of the eye from one location to another which take a few tenths of a second. A typical fixation duration is usually between 200 and 600ms with an average fixation being around 330ms (Henderson, 2003), but this can be influenced by the scene content and the goals of the task. There are typically longer fixations during the memorisation of visual material compared to the exploration of it (Henderson & Hollingworth, 1999). Fixation itself is not completely stationary - tremors, drifts, and microsaccades are tiny eye movements that prevent a given object from 'fading perceptually' (Martinez-Conde, Macknik, & Hubel, 2004). Eye movements have been used to explore a wide range of cognitive processes like reading and language (Hautala, Hyönä, & Aro, 2011) and mental rotation (Martini, Furtner, & Sachse, 2011). Indeed, eye movements have been assessed in a range of other tasks as well. Butler, Gilchrist and Burt et al. (2005) found that pseudoneglect on a facial recognition task was accompanied by leftward fixations that were longer in duration. Slagter, Davidson and Tomer (2010) found that participants who blink more often show biases towards the right side, not the left side, in visuo-spatial tasks. Loetscher, Bockisch and Brugger (2008) showed that the processing of small numbers elicits leftward eye movements (see also Fischer, Warlop, Hill, & Fias, 2004; Sullivan, Jurhasz, Slatterly, & Barth, 2011). Similarly, Harvey, Gilchrist, Olk and Muir, (2003) found that participants showed a significant tendency to fixate more often on the right but produce significantly longer fixations on the left when free viewing visual images. One eye tracking experiment found that when viewing pictures the very first eye movement was significantly more often towards the left hand side of midline than to the right of midline (Dickinson & Intraub, 2009). Likewise, fixation patterns have been assessed in memory tasks. Loftus (1972) showed that the accuracy of memory for pictures was directly linked to the number of fixations that were made during visual exploration. Tatler, Gilchrist and Land (2005) presented participants with natural real-world scenes as well as computer generated images of these scenes and explored how patterns of fixations were related to the recall of object properties such as shape, colour, or relative distance. These results show that recall for object positional information (i.e., “where was the…”) was related to the total number of fixations on the object in question as well as the duration of fixations; but recall for colour information was not. Very recently, Huebner and Gegenfurtner (2010) explored patterns of fixations and memory for briefly presented series of visual objects shown together and found that the recall of object information was enhanced when the exposure time to the objects was longer (7s compared to 1s or 3s) and, for very short viewing times (1s), when objects were directly fixated. Brandt and Stark (1997) found that when participants viewed, and then memorised, checker-board patterns the sequence of eye movements during memorisation closely matched the sequence of eye movements during exploration. Laeng and Teodorescu (2002) explored the same idea under a variety of different viewing conditions in which participants viewed a checkerboard pattern stimulus while fixating centrally or during free viewing. During imagery, eye movement were surprisingly reflective of the visual processing condition – the participants who had fixated centrally also fixated centrally during imagery and vice versa for those who moved their eyes. In addition, the sequence of fixations was very similar when fixations were made between the two conditions visually processing and imagery.

During mental representation there is no direct visual processing but eye movements can still be made. If there is a lateralised bias towards remembering more information on the left versus right hand side of a mentally represented novel scene would this be reflected in patterns of eye movement at the time of mental representation? This may provide important information about how the mind's eye guides the visual eye in a task in which participants are explicitly instructed to construct a mental representation of novel material.

1.6. The effect of internal attentional orienting on external attentional orienting.

The final question of this thesis is as follows: does internal attentional orienting influence external attentional orienting? There is evidence to suggest that if two tasks performed in conjunction tap into the same cognitive resources then performance on one or both tasks may differ relative to when each task is conducted alone; but that if the same tasks tap into different cognitive resources then performance may be relatively unaffected (Pashler, 1994; McCann & Johnston, 1992). So what would happen if we pair a *representational* pseudoneglect task with a *visual* pseudoneglect task? It is possible that both tasks may engage attentional orienting or one task may engage attentional orienting at the expense of another as one task may 'capture' attention to a higher degree. This idea is not so far removed from the 'cocktail party effect' where highly salient information (a person's name) can capture the person's attention (Cherry, 1953; Conway, Cowan, & Bunting, 2001) – in the same way one task may be more salient than the other. The capacity to perform two tasks at the same time has attracted a lot of attention in those interested in the underlying mechanisms of attentional processing as well as memory. In order to provide an example, one key area has been exploring the limitations of working memory in dual-task conditions in healthy participants (Cowan & Morey, 2007). Also, another key focus has been dual tasking in patients with Alzheimer's disease who show a severe deficit in being able to divide their attention between two tasks (Baddeley, Bressi, Della Sala, Logie, & Spinnler, 1991; Della Sala, Baddeley, Papagno, & Spinnler, 1995; Logie, Cocchini, Della Sala, & Baddeley, 2004; MacPherson, Della Sala, Logie, & Wilcock, 2007). Another important line of enquiry has been dual-tasking in healthy older adults who, by comparison, are quite able to perform two tasks simultaneously providing each task takes into account individual performance on each task and that each task taps into different cognitive functions (Logie, Della Sala, MacPherson, & Cooper, 2007; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005; Salthouse, Fristoe, Lineweaver, & Coon, 1995; Somberg & Salthouse, 1982). In addition, the outcome of dual tasking may depend on the specific demands of the task. Kemper, Schmalzried, Hoffman and Herman (2010) compared the performance of older adults (aged 65 to 85 years) and younger adults (aged 18 to 28 years) when they completed a motor tracking task involving chasing a moving target on a computer screen using a mouse under dual task conditions which involved verbal response; the results showed that the speech of *both* younger and older adults become incoherent and disjointed when the demands of the dual task were high (the tracking speed was fast) compared to when it was moderate. Kemper, Schmalzreid, Herman, Ano and Mohankumar (2009) also previously found that older adults could protect their performance on a similar tracking task if they slowed their speech production.

The current aim is to explore whether or not attentional orienting is additive: a first step towards a more comprehensive dual-task paradigm. The data may provide hints about the mechanisms that underlie different forms of pseudoneglect. Longo and Lourenco (2007) showed that for participants aged between 18 and 35 pseudoneglect observed on the mental number line was greater for participants who also showed larger leftward biases on visual line bisection, suggesting that the mechanisms that underlie each type of bias may be the same or at least related. Longo and Lourenco (2010) compared physical line bisection and mental number line bisection at different distances (60cm to 240cm) and found that mental number line bisection, like physical line bisection, shifted from a leftward bias at near distances (60cm) towards a rightward bias at far distances (240cm) - furthermore there was a correlation between individual participants bias on both tasks. Considering representational and visual forms of pseudoneglect as completely similar entities, however, may be somewhat misleading given the evidence from the aforementioned neglect literature that show the two forms are readily dissociated. Doricchi, Guariglia, Gasparini and Tomaiuolo (2005) showed that in right hemisphere brain damaged patients with neglect physical and numerical line bisection was, overall, unrelated. Chokron, Colliot and Bartolomeo et al. (2002) found healthy control participants showed a non-significant leftward bias on tactile bisection but a significant leftward bias on visual line bisection; neglect patients demonstrated rightward biases only on visuo-spatial bisection. Performance on the three tasks did not correlate for the control participants or the neglect patients and only performance on visual line bisection correlated with the degree of neglect. In another study by Schindler, Clavagnier, Karnath, Derex and Perenin (2006) control participants (age range 50 to 76 years) showed tactile exploration was more biased towards the right in line with neglect patients and visual exploration was only very slightly biased towards the left.

The aim here is to explore this issue in more detail by adopting a paradigm where internal attentional orienting is a form of ‘processing load’ (e.g., Mattys, Brooks, & Cooke, 2009). Similarly, Loftus, Nicholls, Mattingley and Bradshaw (2008) asked healthy participants and neglect participants to perform a variation of the Greyscales task at the sane time report whether an overlaid stimulus was high (the numbers 8 or 9), low (the numbers 1, 2) or neutral (the symbol #). The participants’ task was to respond whether the number was high, low or neutral and then judge the relative luminance of the Greyscale stimulus. For neglect patients, their rightward bias on the Greyscales task was attenuated by processing a low number, but for healthy participants their leftward bias on the Greyscales task was attenuated by processing a high number. Nicholls, Loftus and Gevers (2008) also replicated this finding with a slightly different design using different types of responses (i.e., parity judgement vs. linguistic labels). Lourenco and Longo (2009) recently asked participants to hold in mind small or large numbers in working memory whilst performing the traditional mental number line bisection task (i.e., report the midpoint between a pair of numbers); when participants held small numbers in mind responses were further leftward. Also, de Hevia and Spelke (2009) asked adults (25 years of age) and children (five and seven years of age) to perform a visual line bisection when Arabic numerals such as ‘2’ and ‘9’ were presented on the left versus right side of the line. There was also a condition in which the lines were surrounded by dots – either a two dot array or nine dot array but the arrays occupied the same area. Adult participants were biased in the direction of the larger number or the larger dot array; all children were biased in the direction of the larger dot array (left or right). But the previous research has not assessed how internal attentional orienting *directly impacts external attentional orienting* – that is the aim here.

1.7. Conclusions and summary

Our understanding of visuo-spatial pseudoneglect has greatly increased over the past thirty years - even in the past decade since the last meta-review by Jewell and McCourt (2000) our understanding of how pseudoneglect is mediated, enhanced and attenuated has been hugely augmented by the sheer number of studies conducted in this field. Within this Literature Review the many empirical observations of visuo-spatial pseudoneglect were unravelled to demonstrate that the phenomenon occurs under a wide variety of conditions and presentation modes, across many different empirical settings, and in participants of different ages. The most widely accepted and fitting explanation for visuo-spatial pseudoneglect is the activation-orientation hypothesis put forward by Reuter-Lorenz et al. (1990) which asserts that the right hemisphere orients attention leftward in tasks of a spatial nature. The research presented within this Literature Review has shown that the activation-orientation hypothesis for visuo-spatial pseudoneglect clearly holds under direct scrutiny, but there are outstanding questions about the extent to which it can account for representational forms of pseudoneglect.

To this end, representational forms of pseudoneglect are clearly distinct from visual forms of pseudoneglect, occurring in the complete absence of direct visuo-spatial processing across a range of different tasks. The empirical observations of representational pseudoneglect have also been thoroughly untangled within this Literature Review but our understanding of representational pseudoneglect is more incomplete.

The main aim of the research reported within this thesis is to build our knowledge of representational forms of pseudoneglect in healthy participants by addressing the unanswered questions in the field. Firstly, the effect of cognitive ageing on representational form of pseudoneglect will be explored using tactile rod bisection, a completely novel task that can be conducted in the complete absence of visuo-spatial processing. Secondly, the extent to which a purely representational form of pseudoneglect arises for completely novel spatial layouts created from aural-verbal description will be explored both for abstract pattern stimuli and real-world scenes, taking into account visual imagery strategy and ability. Given the aural-verbal nature of the stimuli there will be monaural presentation of the stimuli to either the left or right ear in a bid to explore how representational pseudoneglect can be boosted under conditions that enhance the activation of the right hemisphere (left ear presentation). Thirdly, eye movements will be tracked while participants are asked to mentally represent a previously viewed scene in order to explore whether participants' eye movements during mental representation reflect both performance on a lateralised memory task as well as eye movements during visual processing. Finally, the interplay between representational and visual forms of pseudoneglect will be explored.

Aims of Current Thesis

1. The first main aim of this thesis (Chapter 2) was to assess representational pseudoneglect across lifespan in the complete absence of visual processing on tactile rod bisection - an unfamiliar and novel task - when:
    a. Physical starting position was fully controlled.
    b. Bisection direction was fully controlled.

2. The second main aim of the thesis (Chapters 3 and 4) was to explore the presence of representational pseudoneglect for completely novel spatial layouts generated from aural-verbal descriptions held in working memory in the form of:
    a. An abstract stimulus.
    b. A highly imageable stimulus.

    And when

    c. Imagined starting position was fully controlled.
    d. When aural-verbal presentation was monaural or binaural.

    And when

    e. A visual imagery strategy was used.
    f. Mental mapping ability was accounted for.

3. The third main aim of the thesis was to explore lateralised memory biases for briefly presented visual scenes (Chapter 5).

4. The final aim of the thesis was to explore how a secondary representation pseudoneglect task (mental number line bisection) influences performance on visuo-spatial line bisection (Chapter 6) in adults and children.

Chapter 2

Tactile rod bisection in the absence of visuo-spatial processing in children, mid-age and older adults.

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Appendix A

2.1. Introduction

Previous research has reported that healthy adults often show biases on visual line bisection, tending to bisect horizontal visually presented lines towards the left-hand side of true centre (*for review see* Jewell & McCourt, 2000). This phenomenon is known as ‘pseudoneglect’ (Bowers & Heilman, 1980). One explanation of errors on visual line bisection relates to the theory that each hemisphere orients attention towards contralateral space (Heilman & Van Den Abell, 1979; Kinsbourne, 1970; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990), with the right hemisphere preferentially directing attention leftward. Evidence in support of this theory of pseudoneglect comes from functional Magnetic Resonance Imaging studies with healthy adults that implicate right parietal regions in visual line bisection (Finke, Bublak, & Zihl, 2006; Fink, Marshall, Weiss, & Zilles, 2001). Further evidence comes from the observation that when the right parieto-frontal regions are damaged, patients make *rightward* errors on visual line bisection (Halligan & Robertson, 1999). Moreover, the involvement of the right hemisphere in spatial processing has been well documented (Della Sala, Logie, Beschin, & Denis, 2004; Gobel, Calabria, Farnè, & Rossetti, 2006; Halligan & Marshall, 1989). Recent studies have demonstrated that there is a form of pseudoneglect that is representational in nature, appearing when participants recall characteristics of recently viewed stimuli (Della Sala, Darling, & Logie, 2010) or information from highly familiar scenes (Bourlon, Duret, & Pradat-Diehl et al., 2011; McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzzatti, 1978), and also when participants predicted the position of a moving target which disappeared from view in a virtual reality environment (Cocchini, Watling, Della Sala, & Jansari, 2007). In number based tasks a preference is also observed towards smaller numbers thought to be represented on the left-hand side of the mental number line (Loftus, Nicholls, Mattingly, Chapman, & Bradshaw, 2008; *for review see* Hubbard, Piazza, Pinel, & Dehaene, 2005).

Representational pseudoneglect has also been demonstrated on *tactile-driven* rod bisection (Bowers & Heilman, 1980; Bradshaw, Nettleton, Nathan, & Wilson, 1985; Bradshaw, Nathan, Nettleton, Wilson, & Pierson, 1987; Brodie & Pettigrew, 1995; Sampaio & Chokron, 1992; see also MacLeod & Turnbull, 1999) which is not directly affected by factors such as familiarity, previous experience, or, in some cases, visual processing.

One unanswered question is what happens to representational forms of pseudoneglect across lifespan? The existence of pseudoneglect across lifespan, in general, is an important observation since current models of cognitive ageing have no provision for spatial biases that can be *enhanced* by age. The Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model (Cabeza, 2002) is a widely accepted model of cognitive ageing and argues that, with increasing age, general cognitive functioning becomes less lateralised. There is much support for HAROLD with a plethora of neuroimaging studies showing bilateral activation in older adults but asymmetrical activation in younger participants for similar tasks (Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010; *for review see* Eyler, Sherzai, Kaup, & Jeste, 2011). In contrast, the right hemiageing model argues that the two hemispheres age differentially with the right hemisphere ageing faster or more detrimentally than the left hemisphere (*for review see* Dolcos, Rice, & Cabeza, 2002). The right hemiageing model has support from studies showing good performance on left hemisphere lateralised tasks (i.e., language) but poorer performance on right hemisphere lateralised tasks (i.e., visuo-spatial).

The empirical observation of pseudoneglect *across lifespan* on tactile rod bisection would be of particular importance for several reasons. Firstly, it would indicate that a representational form of pseudoneglect, *independently of vision*, is retained in older age which has implications for current models of cognitive ageing. Secondly, it would indicate that motor-driven lateralised biases are retained in older age which is of interest since lateralised motor responses, in general, are thought to become less lateralised with age (McGregor, Craggs, Benjamin, Crosson, & White, 2009; Przybyla, Haaland, Bagesteiro, & Sainburg, 2011; Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010). Thirdly, it would allow us a more complete understanding of the developmental trajectory of pseudoneglect between modalities which is important for understanding how right hemisphere attentional orienting operates and is modulated as a whole.

Whilst our knowledge of the developmental trajectory of pseudoneglect on mental representational tasks is lacking there are some hints, albeit inconsistent ones, regarding the impact of age on pseudoneglect in the literature on visual line bisection. Visual pseudoneglect has been reported in participants aged 5 to 94 years old (De Agostini, Curt, & Tzortzis, 1999; Varnarva & Halligan, 2007). Other visual line bisection studies have reported symmetrical neglect, that is, when the left hand is used the bias is towards the left-hand side but when the right hand is used the bias is towards the right-hand side. Symmetrical errors on line bisection have been shown in children aged around 5 years of age (Bradshaw, Nettleton, Wilson, & Bradshaw, 1987; Dellatolas, Coutin, & De Agostini, 1996), in children aged 5 to 7 years as well as older adults aged 60 to 70 years (Failla, Sheppard, & Bradshaw, 2003), and also in older children aged 10 to 12 years (Hausmann, Waldie, & Corballis, 2003). In children symmetrical biases are suggestive of an ‘immature’ attentional orienting system (Hausmann, Waldie, & Corballis, 2003) but for older adults symmetrical biases are certainly in line with HAROLD. However, some studies on visual line bisection have reported rightward biases for older adults (Fugii, Fukatsu, Yamadori, & Kimura, 1995; Stam & Bakker, 1990; Schmitz & Peigneux, 2011); this is in line with the view that the right hemisphere may be more sensitive to cognitive ageing than the left.

The influence of age on tactile rod bisection in the context of current models of cognitive ageing is hereby addressed. Following HAROLD, older participants should display less bias on tactile rod bisection compared to younger participants. Following the right hemiageing model, older participants should display reversed pseudoneglect, that is, rightward biases on tactile rod bisection. Alternatively, pseudoneglect may be maintained or enhanced on tactile rod bisection in older age.

In the current study participants were asked to use their index finger to explore wooden rods in the horizontal plane while keeping their eyes closed, and indicate their judgement as to the position of the centre point of the rod. Previous research has demonstrated the importance of starting side on line bisection (Bowers & Heilman, 1980; Brodie & Pettigrew, 1996; Urbanski & Bartolomeo, 2008) but also the importance of the direction in which the bisection is actually made (Baek, Lee, & Kwon et al. 2002). Therefore, a secondary aim was to explore how performance on tactile rod bisection can be mediated by the spatial direction from which the judgement was made in younger, mid-age and older participants. In Experiment 1 the performance was assessed of 549 healthy right-handed participants aged between 3 and 84 years of age who bisected a single horizontal rod with the right index finger in the absence of direct visuo-spatial processing. Experiment 2 assessed the performance of a new group of 72 right handed participants aged between 6 and 96 years of age who bisected three horizontal rods of different length over a larger number of trials with the right index finger in the absence of direct visuo-spatial processing. In Experiment 2 gender was controlled for because there is some suggestion that pseudoneglect in young adults is influenced by gender (Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Laeng, Buchtel, & Butter, 1996; see also van Vugt, Fransen, Creten, & Paquier, 2000).

2.2. Experiment 1

2.2.1. Participants

A total of 549 right-handed native English speaking participants were divided into eight different age groups; the rationale for these age groups was to provide an illustration of bisection performance across lifespan. There were 72 participants between 3 and 6 years of age (*M* = 5.36, *SD* = .76), 108 participants between 7 and 8 years of age (*M* = 7.48, *SD* = .50), 95 participants between 9 and 10 years of age (*M* = 9.49, *SD* = .50) and 59 participants between 11 and 12 years of age (*M* = 11.25, *SD* = .44): all these participants were recruited from primary schools in the United Kingdom and the annual Edinburgh International Science Fair. There were 22 participants between 13 and 20 years of age (*M* = 15.50, *SD* = 2.60) recruited from secondary schools in the United Kingdom and the Edinburgh International Science Fair. There were 86 participants between 22 and 40 years of age (*M* = 34.94, *SD* = 4.72) recruited from universities in Scotland and the Edinburgh International Science Fair; there were 79 participants between 41 and 60 years of age (*M* = 47.08, *SD* = 5.22) recruited from the Edinburgh International Science Fair. Finally, there were 28 participants between 61 and 84 years of age (*M* = 70.82, *SD* = 6.87) recruited from public libraries in Edinburgh and the Edinburgh International Science Fair. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). The calculation of the handedness score was achieved using the formula (R-L/R+L) x 100 with a score of +100 indicating exclusive right handedness and a score of -100 indicating exclusive left handedness. All participants were right-handed, reported normal or corrected-to-normal vision and hearing and did not report a history of dyslexia, spatial disorder, dementia, or memory loss. All participants were naive to the study hypothesis. The younger children were given a pencil for participating. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

2.2.2. Stimuli

A custom-made portable tactile rod bisection task was devised for the purpose of the experiment. There was one wooden dowling rod measuring 32cm in length and 2cm in diameter. A rectangular wooden stopper was firmly attached to the end of each rod to stop the participants overshooting the ends of the rod during tactile exploration. The rod was held in place using a custom-made wooden base. The true centre of the rod was carefully measured and defined by a 0.5mm black line drawn on the side of the rod facing the experimenter, but that was not visible to the participants.

2.2.3. Procedure

Participants were tested in three locations: at a table set aside from the main exhibition area at the Edinburgh Science Festival (a large, annual interactive exhibition of science for the general public); in a quiet area of a classroom within a school; or in a quiet room set aside in a library. In all cases the testing location was similar and the stimuli were set-up in exactly the same way. In each case, the stimulus was positioned on the testing table with the wooden rod centrally aligned with the participants' midsaggital plane. The experimenter was positioned opposite the participant with the wooden rod in-between the participants and the experimenter. Participants were asked to place their right index finger at a central location on the testing table, in line with the participant's body mid-line, which was the starting point of each trial. Participants were asked to keep their non-dominant hand by their side and close their eyes. The experimenter was careful to monitor compliance with this last request: if participants opened their eyes at any time during a trial their data were not included for analysis (this happened for three participants). The reaching distance to the rod was approximately 15cm. The experimenter guided the participant's right index finger from the central location to the extreme left-hand side of the wooden rod or the extreme right-hand side of the wooden rod. The experimenter then let go of the participant's index finger which was the participant's cue to begin moving the index finger along the entire length of the rod either from left to right (i.e., start left condition) or from right to left (i.e., start right condition). Start side was counterbalanced across participants. Participants moved their index finger along the entire length of the rod (i.e., from left to right) and then re-traced this path in the opposite direction for the entire length of the rod (i.e., from right to left) as many times as preferred before moving their index finger back to the perceived middle of each rod. The number of times each participant moved along the rod was not recorded (i.e., in line with the previous line bisection literature). The participant was required to leave their index finger at the perceived middle until directed by the experimenter who recorded the position as belonging in one of three categories: 'left of midpoint' or 'right of midpoint' or 'at midpoint'. The experimenter recorded the measurement on paper. Each participant completed a single trial with start side (start left versus start right) counterbalanced across participants.

2.2.4. Results

Figure 2.1 shows the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint when starting on the left side of the rod (a) or when starting on the right side of the rod (b). For the start right condition there was a clear trend for participants in all age groups to bisect the rod towards the left hand side; there was no significant difference in bisection performance across age group (χ^2(14, N254) = 11.27, *p* = .664), However, for the start left condition the same effect was observed for younger (aged 3 to 10 years) and adult participants (aged 22 to 84 years) but not for adolescence participants (aged 11 to 20 years) who showed a different pattern of performance. Hence, there was a significant difference in bisection performance across age group (χ^2(14, N295) = 28.72, *p* = .011). A further analysis was conducted in order to fully counterbalance – for each age group - the number of participants who started either left or right. There was no significant effect for the start right condition (χ^2(14, N237) = 12.44, *p* = .571) nor start left condition (χ^2(14, N237) = 29.29, *p* = .010).

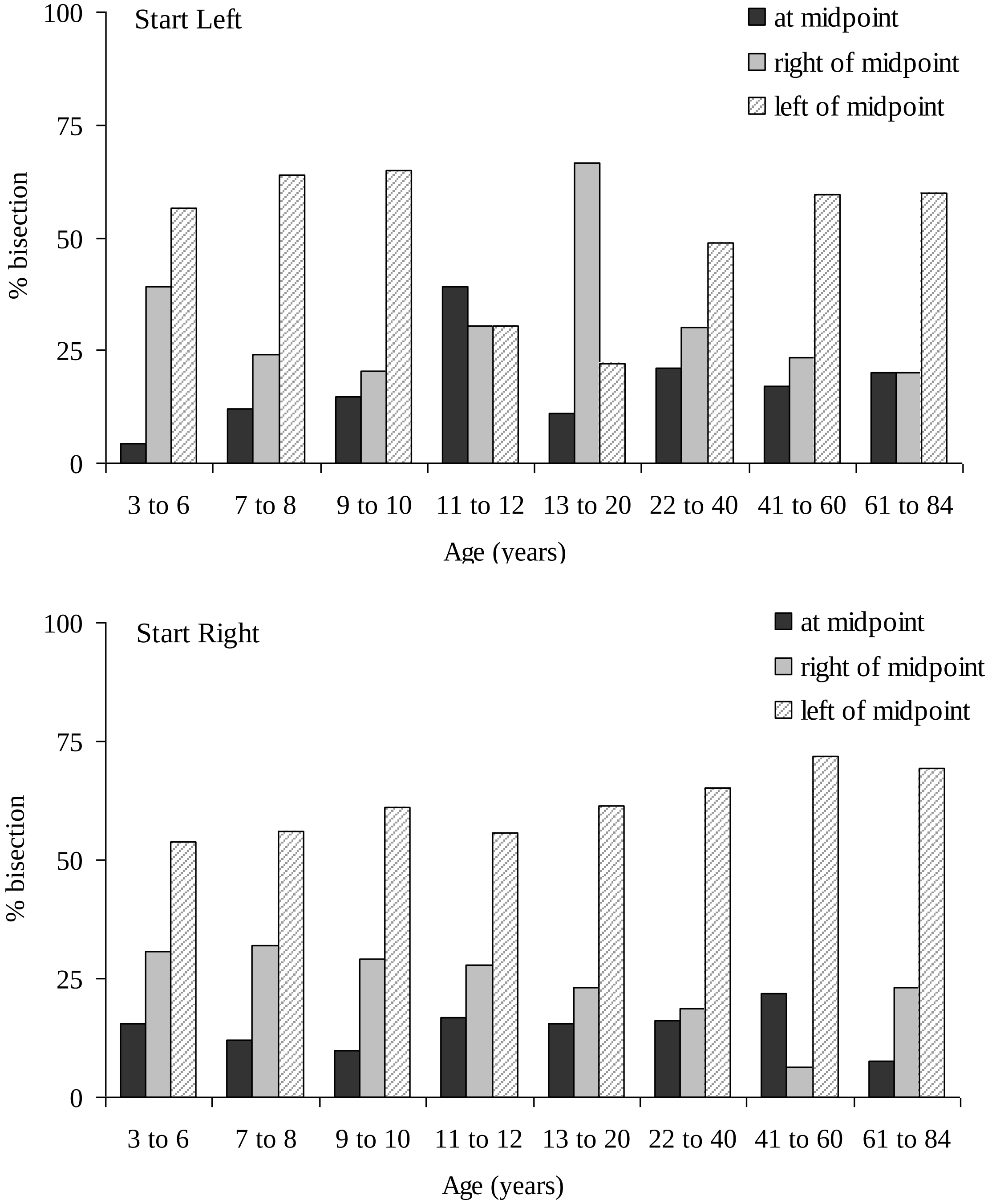

Figure 2.1. The proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint in Experiment 1.

2.2.5. Discussion

The results of Experiment 1 suggest that when bisection starts on the right hand-side the right hemisphere exerts an early capacity to orient attention contralaterally and that this capacity persists in middle and older adulthood. The results of Experiment 1 also demonstrate that the performance of adolescents is different from that of younger children or older adults when starting and bisecting from the left hand-side. Indeed, it is probable that this variability in performance may arise from changes in hormonal levels, or even brain structure, during adolescence which indirectly influence cognitive processes like attentional orienting (Giorgio, Watkins, & Chadwick et al. 2010; *for review see* Sisk & Zehr, 2005). Experiment 2 sought to address two further questions motivated by Experiment 1. Experiment 2 assessed the magnitude of bias over a larger number of trials across lifespan (rather than using the proportion of participants showing a bias that was adopted for Experiment 1) with gender and start side completely counterbalanced. In Experiment 1 tactile scanning of the rod was unrestricted and the direction from which the scan was made was unknown despite starting on the left-hand side or right-hand side. In Experiment 2 tactile scanning was therefore restricted to one complete scan of the rod before the bisection was made from the same direction as the starting position. This means that when the scan started from the left-hand side of the rod the bisection also started from the left-hand side (and vice versa when the scan started from the right-hand side).

2.3. Experiment 2

2.3.1. Participants

A total of 72 right-handed native English speaking participants were divided into three different age groups. None of the participants had taken part in Experiment 1. The rationale for these age groups was to provide an illustration of bisection performance during early development, middle adulthood, and older adulthood; the main concern was exploring early and late attentional biases but included an intermediate age group for comparison. As participants aged 11 to 12 years in Experiment 1 did not preferentially bisect the rod in either direction participants of this age were included in Experiment 2 as bisection performance was explored across a larger number of trials instead of just one single trial. One participant who turned 13 years old on the day of testing was included in Experiment 2 but none other participants aged between 13 and 17 years old were included in order to reduce the suggested variability in bisection performance for the start left condition in Experiment 1. There were 24 participants between 6 and 13 years of age (*M* = 9.42, *SD* = 1.55) recruited from primary schools in the United Kingdom; there were 24 participants between 18 and 55 years of age (*M* = 30.29, *SD* = 12.93) recruited from universities in Scotland; and there were 24 participants between 60 and 96 years of age (*M* = 74.17, *SD* = 11.20) recruited from public libraries in Edinburgh and through personal acquaintance of the experimenter. All participants were right-handed (Edinburgh Handedness Inventory), reported normal or corrected-to-normal vision and hearing and did not report a history of dyslexia, spatial disorder, dementia, or memory loss. All participants were naive to the study hypothesis. The participants aged 6 to 13 years were offered a pencil for participating. All of the adult participants were given a small honorarium. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

2.3.2. Stimuli

A custom-made portable adjustable tactile rod bisection task was devised for the purpose of the experiment (Figure 2.2). There were three wooden dowling rods measuring 24cm, 32cm, and 40cm in length and 2cm in diameter. A rectangular wooden stopper was firmly attached to the end of each rod to stop the participants overshooting the ends of the rod during tactile exploration. Strips of high quality Velcro (i.e., hook-and-loop fasteners) were affixed along the entire underside of each rod and in a horizontal line across a solid wooden base measuring 40cm x 30cm x 1.5cm. These Velcro strips allowed each rod to be held in a sturdy horizontal position during tactile exploration. The true centre of each rod was carefully measured and defined by a 0.5mm black line that was not visible to the participants but visible to the experimenter since the experimenter was seated opposite the participant.

Figure 2.2. The rod stimulus in Experiment 2.

2.3.3.. Procedure

Participants were tested in three locations: at a table in a quiet area of a classroom within a school; in a quiet room set aside in a library; or in a quiet room within the university. In all cases the testing rooms were similar and the stimuli were set-up in exactly the same way. Participants aged 6 to 13 years were tested in pairs but seated on opposite sides of the room (with two experimenters) due to the requirements of one primary school; this design was replicated across all participants in that particular age group for the sake of consistency. Adult participants aged 18 to 96 years were tested alone.

Participants were seated at a table directly in front of the wooden base affixed to the table and centrally aligned with the participant's midsaggital plane. The experimenter was seated opposite the participants on the other side of the table with the wooden rod in-between the experimenter and the participant. Participants were asked to place their right index finger on the wooden base at a central location which was the starting point of each trial. Participants were asked to keep their non-dominant hand on their lap and close their eyes. Participants were not blindfolded due to the requirements of one primary school so this design was replicated across all participants for consistency. All participants were carefully watched by the experimenter throughout the trial in order to ensure the participant did not open their eyes. This happened on a small number of occasions (N5 trials) across older, but not younger participants, and the data for that trial were discarded and the trial was repeated at the end of the block. The experimenter then attached a wooden rod, horizontally, to the strip of Velcro on the wooden base. The reaching distance to the rod was approximately 15cm and the middle of the rod was centrally aligned with the participants' midsaggital plane. The experiment started when the experimenter guided the participant's right index finger from the central baseline position to the extreme left-hand side of the wooden rod or the extreme right-hand side of the wooden rod. The experimenter then let go of the participant's index finger which was the participant's cue to begin moving the index finger along the entire length of the rod either from left to right (i.e., start left condition) or from right to left (i.e., start right condition). Start side was counterbalanced across participants and participants were given a three minute break in between start side conditions (after 15 trials). During this break participants were allowed to open their eyes but the stimuli and testing table were hidden from sight using a large black cloth. Participants were restricted to one complete scan of the rod. This meant that the participants moved their index finger along the entire length of the rod (i.e., from left to right) and then re-traced this path in the opposite direction for the entire length of the rod (i.e., from right to left). Then participants were asked to move their index finger back to the perceived middle of each rod. When the exploration started left, the bisection was also made from the left and when the exploration started right the bisection was also made from the right. The participant was required to leave their index finger at the perceived middle until directed by the experimenter who used a stainless steel half millimetre ruler to measure the position of the subjective midpoint relative to the objective middle. Bisection was recorded ‘at midpoint’ when the index finger was aligned with the objective middle. The experimenter recorded the measurement on paper. The participant then guided the participant’s index finger back to the central location on the wooden base, removed the rod, attached another rod (according to a pre-determined random order) and began the next trial by placing the participant’s right index finger on the extreme (left or right) end of the rod.

Each participant completed 30 trials in total: 15 start left trials and 15 start right trials, with start side blocked across participants and rod length randomised across participants. Importantly, there were an equal number of males and females across the counterbalanced design (i.e., the same number of males and females start left or right first in each age group). Each rod length was repeated five times for each start side condition.

2.3.4. Results

First, for comparative purposes with Experiment 1, the total number of participants in each age group (N24) who bisected at ‘midpoint’, ‘left of midpoint’, and ‘right of midpoint’ for the first trial only (there were missing data for one person in the age group 60 to 96 years), with start side combined, was analysed. Figure 2.3 shows the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint. The results complement Experiment 1 and across age groups there was no significant difference in the proportion of participants who bisected left of midpoint, right of midpoint or at midpoint (χ^2(4, N71) = 1.321, p = .85).

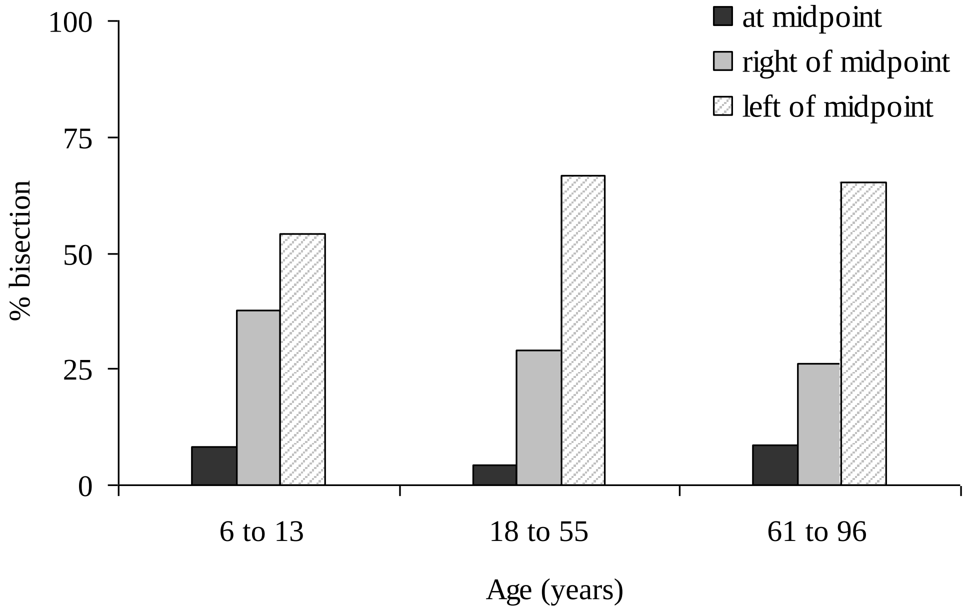

Figure 2.3. The proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint in Experiment 2.

For each age group the directional bias from midpoint was calculated as a percentage of the rod length. This is a standard method of computing line bisection performance (see Fujii et al., 1995; Failla et al., 2003; Hausmann et al., 2002; 2003) and takes into account the magnitude of bias as a function of stimulus (i.e., rod) length. This is important to consider because a bias of 5cm, for example, would be proportionally greater for a 24cm rod compared to a 40cm rod. The resulting score is negative or positive: negative scores indicate a leftward bias while positive values indicate a rightward bias (relative to the true centre). A score of zero reflects no bias. Figure 2.4 displays the mean percent deviation scores for each group.

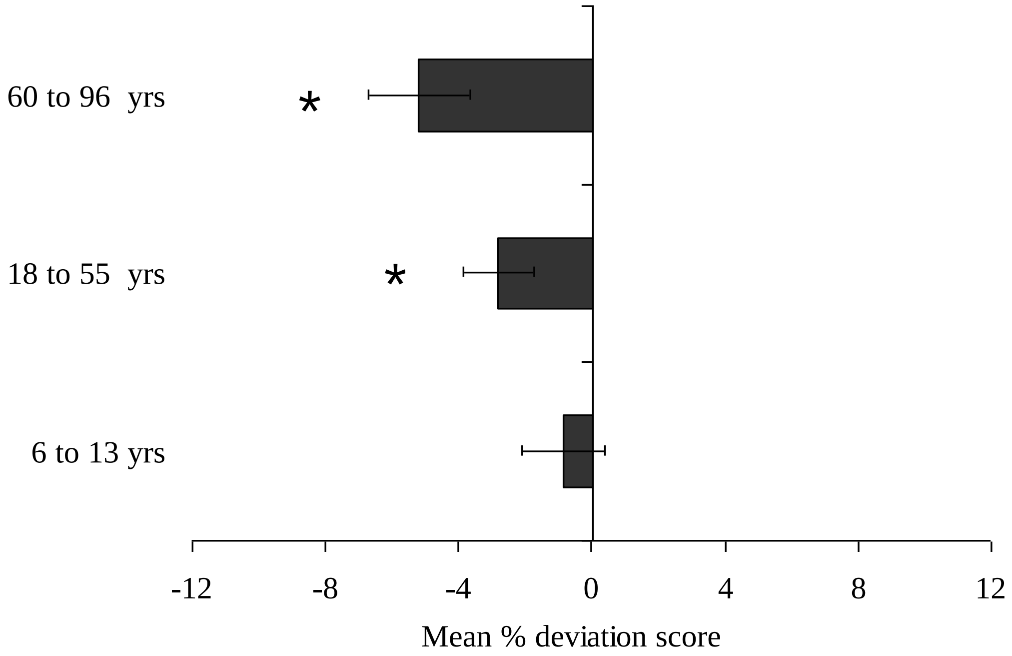

Figure 2.4. The mean percent deviation score for participants in each age group in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias.

For participants aged 6 to 13 years the bias was not significantly different from zero (*t*(23) = -.691, *p* = .496). In order to ensure that there was no indication of a hidden developmental stage in bisection performance participants aged 6 to 13 were further divided into two smaller age groups: aged 6 to 9 years (N13) and aged 10 to 13 years (N11). The overall mean bias for the 6 to 9 year olds (*M* = -1.66, *SD* = 7.38) was not significantly different from zero (*t*(12) = -.811, *p* = .433) and the mean bias for the 10 to 13 year olds (*M* = .09, *SD* = 4.17) was also not significantly different from zero (*t*(10) = .074, *p* = .942). For participants aged 18 to 55 years the bias was significantly different from zero (*t*(23) = -2.657, *p* = .014) and for participants aged 60 to 96 years the bias was highly significantly different from zero (*t*(23) = -3.409, *p* = .002). There was a trend for the bias to increase with age and this difference fell short of significance (*F*(2,71) = 2.840, *p* = .065).

A comparison was also made between the overall bias for males (N12) and females (N12) in each age group. Figure 2.5 displays the mean percent deviation scores for each group split by gender. There was a significant difference between male and female bisection performance for participants aged 6 to 13 years (*F*(1,22) = 5.097, *p* = .034) with females showing a greater leftward bias compared to males who showed a rightward bias but this was not significantly different from zero (*t*(11) = 1.145, *p* = .277). There was no significant difference between male and female bisection performance for participants aged 18 to 55 years (*F*(1,22) = .692, *p* = .414) and neither for participants aged 60 to 96 years (*F*(1,22) = 1.390, *p* = .251), although there was a tendency for males to show larger leftward biases compared to females. A comparison of bisection performance for males and females across age groups confirmed a significant interaction between gender and age group (*F*(2,66) = 3.364, *p* = .041). Post-hoc comparisons were conducted using Tukey HSD. For *males* the bias for participants aged 60 to 96 years was significantly different to that of participants aged 6 to 13 years (*p* = .002) but not to participants aged 18 to 55 years (*p* = .359). The bias for participants aged 6 to 13 years was not significantly different to the bias of participants aged 18 to 55 years (*p* = .069). For *females* the bias for participants aged 60 to 96 years was not significantly different to that of participants aged 6 to 13 years (*p* = 1.000) nor participants aged 18 to 55 years (*p* = .843). The bias for participants aged 6 to 13 years was not significantly different to that of participants aged 18 to 55 years (*p* = .839).

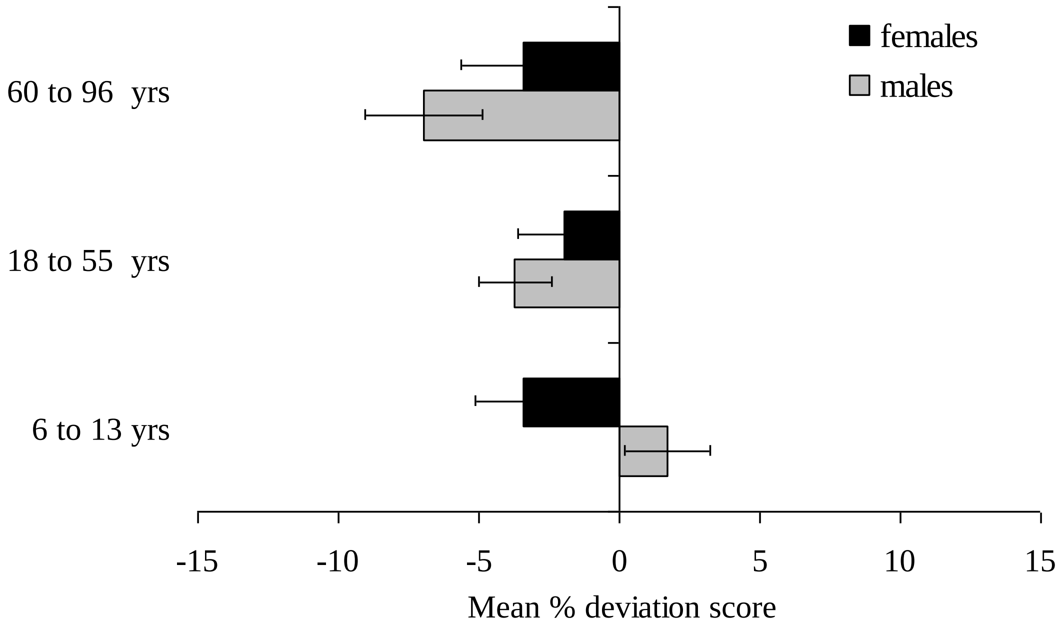

Figure 2.5. The mean percent deviation score for male and female participants in each age group in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias.

The influence of starting side was then explored. Figure 2.6 displays the mean percent deviation scores for each group as a function of start side (start left vs. start right). As shown in Figure 2.6, when participants started right and bisected from the right (and physically moved the index finger towards the left) bisection error was noticeably leftward in all age groups - but particularly so for the participants aged 60 to 96 years. A mixed ANOVA was conducted with rod length (24cm, 32cm, 40cm) and start side (start left vs. start right) as the within-subject variables and age-group as the between-subject variable and gender as a covariate. There was a highly significant main effect of start side (*F*(1,68) = 7.645, *MSE* = 323.39, *p* = .007) and a highly significant interaction between start side and group (*F*(2,68) = 13.919, *p* < .001). There was no significant main effect of rod length (*F*(2,136) = .677, *MSE* = 24.08, *p* = .510), no interaction between rod length and group (*F*(4,136) = .684, *p* = .604) or rod length and start side (*F*(2,136) = .120

, *MSE* = 34.68, *p* = .887), rod length, start side, and group (*F*(4,136) = 1.478, *p* = .212). There was no significant interaction between gender and rod length (*F*(2,136) = .503, *p* = .606) or gender and start side (*F*(1,68) = .815, *p* = .370). Post-hoc comparisons were conducted using Tukey HSD. For the start right condition the leftward bias for the participants aged 60 to 96 years was significantly different to the bias of participants aged 6 to 13 years (*p* < .001) and 18 to 55 years (*p* = .034). The leftward bias for participants aged 6 to 13 years was also significantly different to that for the participants aged 18 to 55 years (*p* = .046). For the start left condition the bias for participants aged 60 to 96 years was significantly different to the bias for participants aged 6 to 13 years (*p* = .017) but not to the bias for participants aged 18 to 55 years (*p* = .392). Likewise, the bias for participants aged 6 to 13 years was not significantly different to the bias for participants aged 18 to 55 years (*p* = .291).

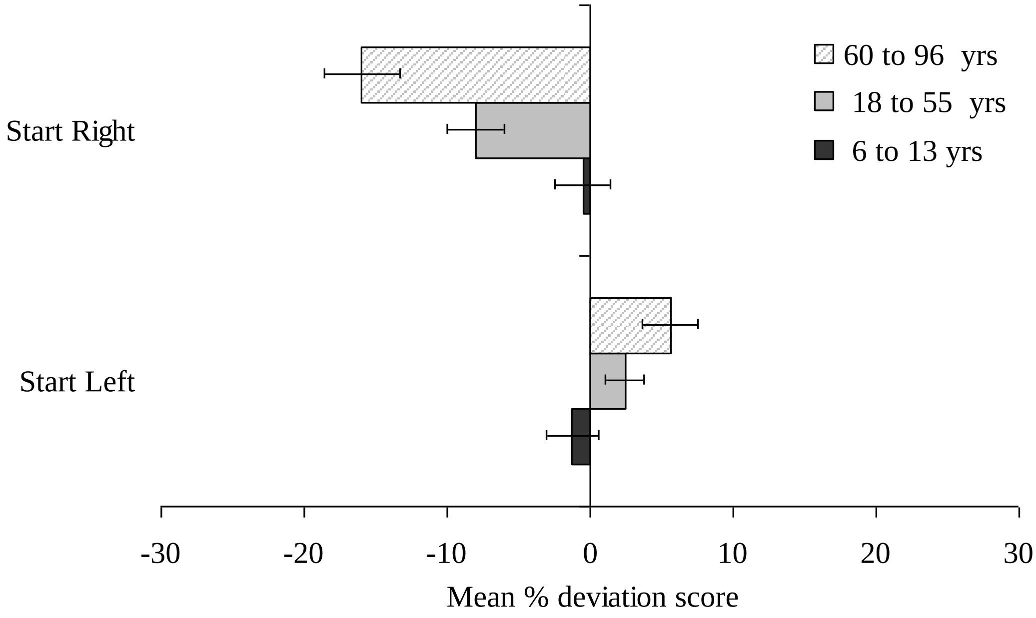

Figure 2.6. The mean percent deviation score for participants in each age group as a function of start side (start left vs. start right) in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias.

2.3.5. Discussion

Experiment 2 showed, for the first time, the presence of pseudoneglect on tactile rod bisection, in the absence of visual input, across the full adult life span and most notably in the oldest participants. This form of representational pseudoneglect was not as clear for the youngest participants who also displayed a gender difference in bisection performance, with greater pseudoneglect for female participants. The results of Experiment 2 suggest that the right hemisphere exerts an early capacity to orient attention contralaterally and that this capacity continues in middle and older adulthood; this empirical observation is at odds with the notion that there is more bilateral recruitment during cognitive tasks in older adults. It is also inconsistent with the argument that the right hemisphere is more sensitive to cognitive ageing than its left hemisphere counterpart. Experiment 2 also showed that side from which the bisection started was crucial for mediating the bias: when participants started and bisected from the right-hand side (consistent with the direction of attentional orienting) the lateralised bias towards the left was significantly enhanced. Again the oldest participants were far more sensitive to this effect compared to the other two groups. However, when participants started and bisected from the left-hand side (inconsistent with the direction of attentional orienting) the bias was not simply reversed in the opposite direction which is evidence that the bias is not simply a product of over-estimation.

2.4. General Discussion

The main aim of the current study was to explore tactile line bisection across lifespan whilst taking into account the influence of starting position and gender. Experiment 1 showed representational pseudoneglect on tactile rod bisection across a large number of younger and older participants, but the results were dependant on starting side with adolescents showing different performance when bisection started on the left-hand side.

In Experiment 2 clear representational pseudoneglect was demonstrated on tactile rod bisection with older participants aged 60 to 96 years showing the largest bias and the youngest participants aged 6 to 13 years being statistically unbiased in their bisection performance overall. However, Experiment 2 also showed that tactile rod bisection performance in male and females was different for participants aged 6 to 13 years but this difference was not as clearly observed for participants aged 18 to 55 years or participants aged 60 to 96 years. Experiment 2 also showed that when participants started from the right to undertake tactile scanning and bisection representational pseudoneglect was significantly increased; again this bias was significantly enhanced by age.

The data from Experiments 1 and 2 provide evidence for a representational form of pseudoneglect for adults not driven by direct visual attention but by the creation and maintenance of a mentally represented spatial layout. Interestingly, there is evidence to suggest that tactile input can be readily mapped onto an external visuo-spatial framework (Azañón, Camacho, & Soto-Faraco, 2010; Pagel, Heed, & Röder, 2009) which poses a question as to whether or not the pseudoneglect observed in the present study was really ‘representational’ in nature. Indeed, if a visuo-spatial framework was activated this may have engaged visuo-spatial mechanisms in the right hemisphere and resulted in preferential right hemisphere attentional orienting from visuo-spatial attention. While this is a possibility, it is unlikely to account for the effect observed. Line length effects have been well documented to have a critical effect on visual line bisection (Jewell & McCourt, 2000) and so, arguably, if the rod was translated into a visual representation, a similar effect may have been expected here. But there was no significant effect of rod length in Experiment 2. Although previous research has documented a significant effect of rod length during tactile line bisection (Laeng, Buchtel, & Butter, 1996; Sampaio & Chokron, 1992) other tactile-driven studies have not directly reported rod length effects

(Baek, Lee, & Kwon et al., 2002; Bowers & Heilman, 1980; Sampaio & Philip, 1991). Also, the spatial position of the rod was not varied (e.g., Laeng, Buchtel, & Butter, 1996) and it is possible that tactile-visual mapping would be more likely to occur when a tactile stimulus is perceived in a more spatially complex orientation. Certainly, body posture has been shown to influence pseudoneglect on both visual and tactile rod bisection (Bradshaw et al., 1985).

The results from Experiment 2 suggest a more symmetrical bias for participants aged 6 to 13 years old, dependant on starting and bisecting direction, which supports the notion that leftward asymmetries in attentional orienting may be the signature of a more mature system. The present study suggests that the mechanisms that underlie representational pseudoneglect may be engaged in older age and that this capacity should be included in current models of cognitive ageing like HAROLD (Cabeza, 2002). Indeed, the fact that pseudoneglect occurs for older adults on a motor-driven task is somewhat surprising; a related finding is that motor responses become less lateralised in older age (McGregor et al., 2009; Przybyla et al., 2011; Vallesi et al., 2010). Our results also indicate that for older participants the process of ‘dedifferentiation’ - reliance on a broader range of cognitive resources – may be selective. The selective nature of age-related dedifferentiation has been reported for other tasks. Johnson, Logie and Brockmole (2010) demonstrated that in older adults individual variation in *verbal* immediate memory capacity is accounted for by task-specific variance whereas individual variation in *visual* immediate memory shares common variance with a range of other working memory tasks. This suggests that while visual immediate memory is modality specific early in adulthood but subject to dedifferentiation with age, verbal memory remains modality-specific in older adults.

Experiment 2 showed significant gender differences in bisection performance for the youngest age group (aged 6 to 13 years) with females showing a significantly greater degree of pseudoneglect compared to males. In line with these results is a study with 650 healthy children suggested that males were more accurate than females on horizontal visual line bisection (van Vugt et al., 2000). Interestingly, our results suggest a trend in the opposite direction for adults; this has also been recently suggested for visual line bisection (Brodie, 2010). However, the degree of pseudoneglect demonstrated by males and females on visual line bisection has been shown to be influenced by the hand used (Hausmann et al., 2002). The effect of hand was not addressed in the current study as our research was motivated by a different question – to explore whether representational pseudoneglect is present across lifespan – but the age at which pseudoneglect on both visual and tactile bisection is first demonstrated in children, when controlling for gender and hand, would benefit from further scrutiny.

Previous research has demonstrated the importance of starting side on line bisection (Bowers & Heilman, 1980; Urbanski & Bartolomeo, 2008) and in Experiment 2 starting side was controlled (start left versus start right) but, in addition, controlled the direction from which the bisection was made. Importantly, the results of Experiment 2 showed the influence of starting side was crucial for the magnitude of pseudoneglect: starting from the right and bisecting from the right enhanced this bias, especially for the oldest adult participants. Arguably, if the direction of bisection is consistent with the direction of attentional orienting (bisecting from the right) the lateralised bias will be enhanced; but if the direction of bisection is inconsistent with the direction of attentional orienting (bisecting from the left) the lateralised bias will be reduced or even observed in the opposite direction. As the bias was not simply symmetrical when start side and bisection was counterbalanced this strongly suggests that the bias is not simply a product of over-estimation, or the ‘overshoot phenomenon’ (Baek, Lee, & Kwon et al. 2002), but rather stems from a ‘weighted’ influence of the left side of the rod. Indeed, this may be increased when the left side of his rod is being anticipated. If anticipation alone was driving the bias then the opposite pattern of results should be observed when starting, and bisecting, from the opposite direction (left towards the right). Again, the bias was not symmetrically reversed. An exploration of why older adults would be more sensitive to this effect is an important question for future research.

There is little doubt that tactile rod bisection involves additional or different processes compared to visual line bisection related to sequential mental scanning (Sampaio & Chokron, 1992) and it is highly likely that these are related to working memory. During tactile rod bisection participants must retain information about the distance that they have travelled along each rod in each direction and then use this information to estimate the middle of the rod; it is likely that working memory mechanisms (Baddeley & Hitch, 1974; Baddeley & Logie, 1999; Logie, 2011a) were involved in the creation and maintenance of this spatial layout. Working memory function is well known to decline with age (Park, Lautenschlager, & Hedden, 2002; Johnson, Logie, & Brockmole, 2010) which means that relatively older adults may be more likely to ‘forget’ about earlier explored portions of the rod leading to an impoverished representation of earlier spatial layout compared with younger adults or children. While working memory mechanisms may play some role in tactile rod bisection, arguably, the role of attentional orienting predominantly drives the bias observed here. If the bias resulted purely from an impoverished representation of earlier spatial layout it would be expected to observe symmetrical biases in each direction when starting and bisecting from each side: this was clearly not the case. Rather, the bias observed for adults is more consistent with an over-representation of the left side of the rod in visuo-spatial working memory (i.e., Della Sala, Darling, & Logie, 2010; Logie, 2011b) driven by attentional mechanisms and perhaps synonymous with the formation of a ‘general impression’ of the stimulus which may be more salient in attentional terms for the left side (Mattingley et al., 2004). A related question is the extent to which visual imagery was used by participants of different ages during the scanning of the rod, as in a motor imagery task elderly adults with a mean age of 71 years performed considerably worse than younger adults with a mean age of 25 years (Personnier, Kubicki, Laroche, & Papaxanthis, 2010).

It would be interesting to explore the strategy that is used during bisection tasks and whether this differs for males compared to females. Varnarva & Halligan (2009) conducted a study to explore the strategy used during visual line bisection and found that the reported strategies including making a direct comparison of the perceived leftward and rightward portions of the line as well as using the body as a reference to find the middle of the line. It is possible that during tactile rod bisection participants employ a strategy of using their body mid-line as an external reference point from which to base judgments about the perceived centre of the rod; critically, this may change with age and be different in males versus females. In addition, given that tactile rod bisection is a temporal-order task it is possible that participants adopted a counting strategy; the strategy may have been to count during movement from one end of the rod to the other and then take the median number as representative of the rod's middle. Needless to say, whichever strategy was used it was arguably unsuccessful. Finally, further psychometric testing of tactile rod bisection would help us assess its validity and reliability as a measure of non-visual pseduoenglect. For example, it would be interesting to ask participants to judge using touch alone whether two portions of a rod are equal in length; the point of subjective equality should in theory be biased towards the left.

In conclusion, the present study has provided evidence that pseudoneglect in non-visual motor-driven tactile rod bisection appears throughout the adult age range but not necessarily in adolescents or younger children. Moreover, the results have illustrated that the phenomenon of representational pseudoneglect is robust and calls for further empirical investigations into tactile rod bisection, in the absence of vision, across lifespan.

Chapter 3

Representational pseudoneglect in an auditory-driven spatial working memory task

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Appendix A

3.1. Introduction

In the previous Chapter, a representational form of pseudoneglect was demonstrated across lifespan in the absence of direct visual processing for a completely novel spatial task. The first aim of the thesis was, therefore, achieved with pleasing results. In the current Chapter the aim was to determine whether a representational form of pseudoneglect could be shown when participants were asked to build an abstract spatial layout from aural-verbal description in the complete absence of visuo-spatial processing. This Chapter follows on from the previous Chapter in terms of further scrutinising representational forms of pseudoneglect in different contexts. Healthy participants often bisect visually presented horizontal lines to the left of the line’s true centre (review in Jewell & McCourt, 2000) and that this phenomenon has been termed ‘pseudoneglect’ (Bowers & Heilman, 1980) by analogy to the performance of right-hemisphere impaired patients who neglect the left side of space and demonstrate rightward biases on line bisection (Halligan & Robertson, 1999). Pseudoneglect on physical line bisection tasks has been explored extensively (Brodie & Pettigrew, 1996; MacLeod & Turnbull, 1999; McCourt, Freeman, Tahmahkera, Stevens, & Chausse, 2001; McCourt & Garlinghouse, 2000; Varnava, McCarthy, & Beaumont, 2002). One recent study (Della Sala, Darling, & Logie, 2010) has demonstrated a related, but different phenomenon in visuo-spatial working memory, with healthy participants having better memory for material on the left of a briefly presented visual array. This leftwards bias in memory could not be explained in terms of any visual encoding bias and appeared to be a specific phenomenon of immediate visuo-perceptual memory - that is referred to here as 'representational pseudoneglect'. This empirical observation raises questions about the characteristics of visuo-perceptual working memory that are not considered in current theoretical developments. However, to be confident that the lateralized bias is not driven by visual perception, it would be crucial to explore the phenomenon in the absence of visual input.

Explored here is whether this bias in visuo-spatial representations arises when these representation are based on auditory descriptions of visual arrays with no visual perceptual input.

There are additional hints in the previous literature of lateralized biases in visual memory. For example, when healthy participants were asked to recall details from a highly familiar imagined scene (the Piazza del Duomo in Milan), they reported significantly more details from the left side of the imagined scene than from the right; this bias was independent of viewpoint (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzzatti, 1978). Arguably, this could be evidence for the existence of a pseudoneglect that is *representational* and not dependent on visual perceptual input. Moreover, given the familiar nature of the stimulus, this suggests that temporary activation of visual information held in long term memory is also subject to the bias. Similarly, when asked to report the midpoint between a pair of mentally represented numbers healthy participants also consistently show a preference towards the smaller number in the pair (Loftus, Nicholls, Mattingly, Chapman, & Bradshaw, 2008). Since numbers are thought to be mentally represented with smaller numbers to the left and larger numbers to the right (for review see Hubbard, Piazza, Pinel & Dehaene, 2005), this is also argued to be indicative of a leftward representational spatial bias. Furthermore, leftward biases have been demonstrated for mental alphabet lines (Nicholls & Loftus, 2007), finger counting habits (Fischer, 2008) and in listing cities of a country from different imagined viewpoints (Bourlon, Duret, & Pradat-Diehl et al., 2011).

While these studies indicate that pseudoneglect can occur in the absence of direct visual input immediately prior to the behavioural response, the experimental paradigms were based on visual information that was highly familiar and stored in long term memory. An unanswered question is whether or not the same phenomenon can be seen with completely novel stimuli generated from an aural verbal description and held in visuo-spatial working memory. Although the asymmetry reported by Della Sala, Darling and Logie (2010) was demonstrated for novel stimuli held in visuo-spatial working memory, the initial input was visual in nature. Moreover, it is unclear how such asymmetries may be maximised or mediated. To address these issues, the current study used aural verbal descriptions of completely novel stimuli. Participants were asked to create a mental visual representation of the stimulus during the aural verbal description and, when the description was complete, retrieve certain details from the left and right side of the stimulus held in visuo-spatial working memory.

The main aim of the current study was to explore the possibility that the left side of the mental representation constructed from an aural verbal description was more salient than the right side of the mental representation and also incorporated greater and more accurate detail due to a leftwards bias in visuo-spatial working memory.

To explore this, participants were asked to imagine a verbally described matrix pattern. As the stimuli were both novel and aurally described this removed any confounding effect of previous visual perceptual processing or prior visual experience. The primary task was to judge which side of the pattern contained the greatest number of filled cells. The rationale for asking participants to make a relative side fuller judgement stems from similar perceptual tasks, such as the greyscales task (Mattingley, Berberovic, & Corben et al. 2004), in which participants typically show a tendency to perceive the left side of a stimulus as darker in terms of light intensity than the right side. In the current task, if the left side of the pattern was represented more saliently this may be manifested as a tendency to judge that the left side was fuller than the right. In this view, over-representation may be driven by attentional mechanisms and is synonymous with the formation of a ‘general impression’ of the stimulus which may be more salient for the left side. Additionally, working memory mechanisms may maintain the left side of the stimulus in more detail.

In order to maximise potential representational pseudoneglect the verbal description started on either the left-hand side of the stimulus or the right-hand side of the stimulus bringing the task in line with previous research that has demonstrated that starting position strongly influences biases on line bisection (Urbanski & Bartolomeo, 2008). Furthermore, given the aural-verbal nature of the task, stimuli were presented either monaurally or binaurally. Indeed, monaural presentation to each ear has been shown to produce asymmetrical performance on certain auditory tasks such as ignoring irrelevant acoustic stimuli (Hadlington, Bridges & Beaman, 2006; Hadlington, Bridges & Darby, 2004). Monaural presentation is known to induce contralateral hemispheric activity while binaural presentation induces bilateral activity (Schönwiesner, Krumbholz, Rübsamen, Fink, & Yves von Cramon, 2007; Paiemont, Champoux, & Bacon et al., 2008). If presentation to the left ear preferentially engages the right hemisphere this may lead to increased sensitivity of encoding or maintaining the left side of the mental representation given the widely documented involvement of the right hemisphere in spatial processing (Della Sala, Logie, Beschin, & Denis, 2004; Finke, Bublak, & Zihl, 2006; Gobel, Calabria, Farnè, & Rossetti, 2006; Halligan & Marshall, 1989).

Experiment 3 and 4 were relative judgement tasks that involved comparing the left and right halves of a verbally described pattern and responding, on a certainty scale, to indicate which side of the pattern was fuller. Experiment 5 and 6 were recall tasks in which participants also physically replicated the side perceived as fuller as accurately as possible.

3.2. Experiments 3 and 4

3.2.1. Participants

There were 112 right-handed native English speaking undergraduate participants from the University of Edinburgh. There were 56 participants in the binaural listening condition (Experiment 3) and a separate 56 participants in the monaural listening condition (Experiment 4). Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), with a score of +100 indicating exclusive right handedness and a score of -100 indicating exclusive left handedness: all participants scored over +65 on the handedness questionnaire. All participants were aged between 18-38 years with normal or corrected-to-normal vision and hearing. Participants were paid a £6 honorarium. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

3.2.2. Stimuli

The stimuli for both experiments were aural verbal descriptions of 36 patterns designed by the experimenters. Each side of the pattern (left and right) consisted of 3 x 3 cells (Figure 3.1). Please see Appendix B for the full stimulus set. Each cell was either “filled” or “empty”. The filled or empty cells on each side were chosen at random. The pattern of filled and empty cells for each stimulus was unique within the stimulus set. Each pattern was verbally described by a pre-recorded female voice, in a snake-like manner, starting either from the top left (‘start left’ description), or the top right corner (‘start right’ description). For instance, a start left verbal description of the pattern in Figure 3.1 would be *“filled empty filled empty filled empty filled empty empty filled empty empty filled empty empty filled empty empty”.* Start side (start left vs. start right) and side fuller (left fuller vs. right fuller) were within-subject variables.

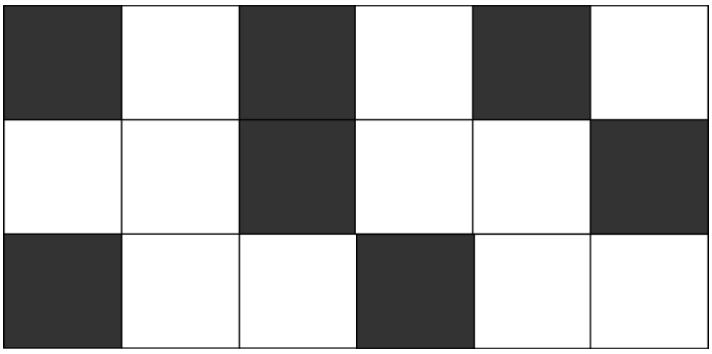

Figure 3.1. Illustration of the pattern stimulus in Experiments 3 and 4. The left side of the pattern (defined within a 3 x 3 matrix) is fuller than the right side (also defined within a 3 x 3 matrix).

Each participant performed two blocks of 18 trials. Two of the trials had four filled cells on each side of the pattern (i.e., neutral trials); these trials were included in order to encourage use of the full certainty scale (including certainty = 0). For the remaining 16 trials, eight had four filled cells on the left side, and either two, three, five or six filled cells on the right, with each combination presented once with a start-left, and once with a start right description. The other eight trials followed the same format except that the four filled cells were on the right. Therefore, within each block, there were eight 'left fuller' and eight 'right fuller' trials. Trial order within each block was randomly shuffled. Listening condition was a between-subjects variable with 56 participants in a binaural condition (Experiment 3) and 56 in a monaural condition (Experiment 4). Within the monaural condition ear of presentation (left, right) was blocked, with one block per ear, and block order counterbalanced across participants. Finally, half of the participants in each listening condition had patterns presented at a relatively slow speed (16 seconds per pattern) and the other half at a faster speed (11 seconds per pattern).

3.2.3.Procedure

Both Experiments had exactly the same procedure. Participants were seated in front of a computer monitor at a comfortable viewing distance of approximately 60cm. The monitor and keyboard were centrally aligned with the participants' body mid-line. Participants were asked to close their eyes and clasp their hands in front of them on their lap or on the table at the beginning of each trial. The experiment started when the spacebar was pressed. After a 1s pause, a pre-recorded verbal pattern description was played over a pair of Sony noise-cancelling headphones at the same volume for each participant binaurally or monaurally. When the description was completed there was a 1s pause and then participants opened their eyes, unclasped their hands and reported which side of the pattern, left or right, contained the most filled cells using a graded scale of certainty [LEFT 4 3 2 1 0 1 2 3 4 RIGHT] presented at the centre of the screen. The scale was physically replicated on the computer keyboard. Participants were to choose zero if they were completely uncertain. If participants thought there were more filled cells on the left side of the stimulus they were to choose a number from 1 (slightly certain) to 4 (absolutely certain) on the left-hand side of the scale, whereas if they judged there to be more filled squares on the right side of the stimulus they were to chose a number from 1 (slightly certain) to 4 (absolutely certain) on the right-hand side of the scale. In order to differentiate between certainty on each side of the response scale, responses on the left side were assigned negative values and responses on the right side were assigned positive values. A randomly selected pattern was used as a practice trial. All participants heard exactly the same stimulus patterns in a random order.

3.2.4. Results

Proportional bias

For the 56 participants in the binaural condition (Experiment 3) and 56 participants in the monaural condition (Experiment 4) the total number of left side fuller responses was subtracted from the total number of right side fuller responses and then divided by the overall number of responses (including the neutral trials), to yield a measure of ‘proportional bias’. A negative proportional bias therefore indicates a tendency to respond left fuller more often than right fuller, whereas a positive value would reflect the opposite tendency. An initial analysis showed that the proportion of left-fuller versus right-fuller responses in both the binaural and monaural listening condition was not significantly affected by the speed of the stimulus description, so the data were therefore collapsed across this factor to simplify subsequent analyses.

Figure 3.2 displays mean proportional bias for participants in the binaural condition and separate monaural condition. All mean values were negative indicating that participants were more likely to respond left-fuller than right-fuller. The proportional bias was significantly different from zero for the left ear ($t(55) = -4.286$, $p < .001$) but not for the right ear ($t(55) = -.394$, $p = .695$). In contrast for the binaural condition, proportional bias was not significant ($t(55) = -1.204$, $p = .234$)[1]. A one-way ANOVA was used to compare the proportional difference between the binaural, monaural left ear and monaural right ear listening conditions. Proportional bias was significantly different across the three listening conditions ($F(2, 165) = 3.825$, $p = .024$).

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[1] The neutral trials were included in the experimental stimulus set purely to encourage full use of the certainty scale; for this reason there were too few trials per participant (i.e., four per participant) to analyse the neutral trials in isolation.

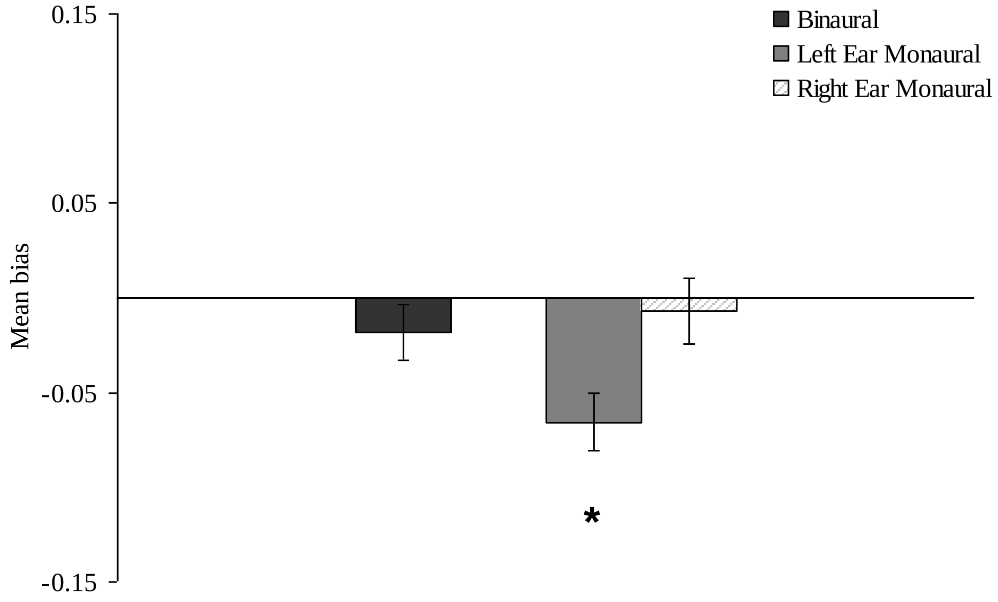

Figure 3.2. Proportional bias is shown for the separate binaural and monaural listening conditions in Experiments 3 and 4. Asterisk indicates significance. Error bars indicate standard error of the mean.

Certainty

Certainty responses were then recoded according to whether certainty related to a correct judgement (e.g. participants responded left fuller when it was in fact left fuller) or an incorrect judgement (e.g. participants responded left fuller when the right side was in fact fuller). Correct judgements were assigned positive values and incorrect judgements negative values (i.e. negative responses reflect certainty in an incorrect response) creating a ‘certainty index’. The certainty analysis was conducted with correct and incorrect trials binned together because a tendency to over-represent the left side of the pattern should occur regardless of whether or not participants were correct or incorrect in their responses. Certainty was compared for left-fuller patterns and right-fuller patterns for 28 participants at both speeds 1 and 2 in the binaural condition and 28 participants at both speed 1 and speed 2 in the monaural condition. An initial analysis showed that certainty for left fuller versus right fuller responses in both the binaural and monaural listening condition was not significantly affected by the speed of the stimulus description, so the data were therefore collapsed across this factor to simplify subsequent analyses.

Figure 3.3 shows mean certainty for 56 participants in the binaural and monaural condition overall[2]. For the monaural condition side fuller was analysed as a function of ear and start side. There was a highly significant main effect of side fuller ($F(1,55) = 27.573$, $MSE = .361$, $p < .001$) with significantly greater certainty for left fuller compared to right fuller stimuli. There was also a significant interaction between start side and side fuller ($F(1,55) = 8.351$, $MSE = .745$, $p = .006$) with a noticeable increase in certainty for left fuller patterns when the description started left. There was also a significant interaction between ear and side fuller ($F(1,55) = 4.098$, $MSE = .488$, $p = .048$) with presentation to the left ear strongly enhancing the tendency to be more certain about left fuller stimuli. The effect of ear alone was not significant ($F(1,55) = .057$, $MSE = .620$, $p = .812$) and neither was start side ($F(1,55) = 2.237$, $MSE = .709$, $p = .140$). Side fuller as a function of start side was then analysed for the binaural condition using a repeated-measures ANOVA. Replicating the monaural condition, there was a significant main effect of side fuller ($F(1,55) = 5.045$, $MSE = .456$, $p = .029$) with certainty being reliably greater for left fuller compared to right fuller stimuli. There was no main effect of start side ($F(1,55) = 3.892$, $MSE = .665$, $p = .054$) and no significant interaction between start side and side fuller ($F(1,55) =1.626$, $MSE = .513$, $p = .208$). A repeated-measures ANOVA with start side and side fuller as the within-subject variables and

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[2] A separate analysis was conducted on correct trials only (i.e., when the left side of the pattern was fuller and participants responded that it was fuller, or when the right side of the pattern was fuller and participants responded that it was fuller). Certainty was greater for left fuller stimuli over right fuller stimuli in each listening condition.

listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted. The interaction between side fuller and listening condition was not significant (*F*(2,165) = 2.692, *MSE* = .435, *p* = .071) and there was no interaction between start side and listening condition (*F*(2,165) = .390, *MSE* = .606, *p* = .678), nor start side, side fuller and listening condition (*F(*2,165) = .689, *MSE* = .554, *p* = .504).

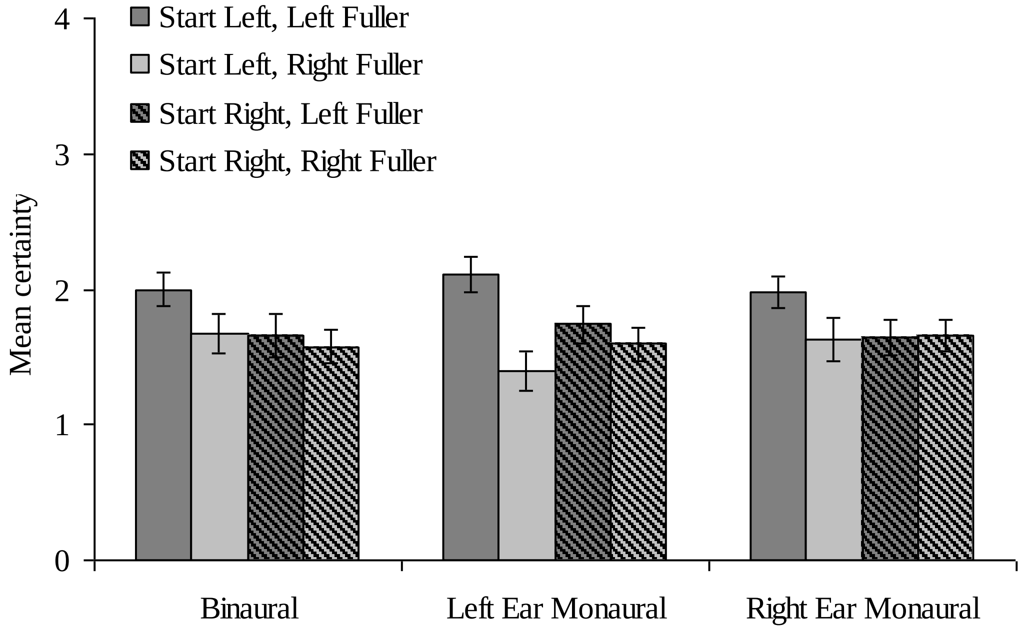

Figure 3.3. Mean certainty response as a function of start side in Experiments 3 and 4. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left fuller and right fuller stimuli. Error bars indicate standard error of the mean.

3.2.5. Discussion

For all listening conditions, when participants made a relative judgement between the two sides of a verbally described pattern, there was a tendency to over-represent the left side of the pattern. This was reflected in the fact that participants responded ‘left fuller’ more often than ‘right fuller’ and also that participants were more certain when judging left fuller patterns. The predictions were therefore supported as it can be argued that there was greater saliency for the left side of the pattern. The certainty results could not have arisen because participants were only using one side of the certainty response scale; if participants were only using one side of the scale (i.e., the left) this would have been reflected as a systematic pattern of certainty across all conditions but this was clearly not the case which suggests that any differences between the ratings of each side arose as a genuine refection of the impression that participants had in their representation of each side.

It is also unlikely that the results were based on merely the last three instructions of “empty” or “filled” on either side because every pattern was unique and, indeed, for some patterns the last three cells were blank. The contents of late presented cells were chosen at random which makes it difficult to conduct a separate analysis on how the contents of late presented cells influenced certainty given that these were not counterbalanced across stimuli. While it is possible that the contents of the late presented cells played some role in certainty responses there was no symmetrical recency effect demonstrated for any listening condition which indicates that certainty judgements were based on a genuine impression of each stimulus side.

The findings from Experiments 3 and 4 therefore appear to support the hypothesis that there is a lateralized bias towards the left in visual mental representations, even if they did not involve visual input. The results were clear, but leave open the question as to whether the bias observed in certainty judgements would also appear in a test of memory for each side of the pattern. The result is also new, and so it is important to demonstrate that it replicates with different participants and with a modified paradigm. However, it is possible that when participants are required to maintain the details of the pattern this changes the general impression of the stimulus and therefore may reduce the likelihood to respond ‘left fuller’ over ‘right fuller’ and lead participants to be less certain about the general impression of the stimulus. Therefore, Experiments 5 & 6 were designed partly to replicate these results and also to explore whether over-representation of the left side resulted in more accurate maintenance and retrieval of the left side of the pattern.

3.3. Experiments 5 and 6

3.3.1. Participants

A total of 56 right-handed native English speaking undergraduate participants were recruited for the experiment. There were 28 participants in a binaural listening condition (Experiment 5) and 28 participants in a separate monaural condition (Experiment 6). Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), with a score of +100 indicating exclusive right handedness and a score of -100 indicating exclusive left handedness: all participants scored over +65 on the handedness questionnaire. All participants were aged between 18-38 years from the University of Edinburgh with normal or corrected-to-normal vision and hearing. Participants were paid a £6 honorarium. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

3.3.2. Stimuli

The stimuli were the same as Experiments 3 and 4.

3.3.3. Procedure

Two separate groups of 28 participants each performed the task in either a binaural (Experiment 5) or a monaural listening condition (Experiment 6) at speed 2, the higher speed (11 seconds per pattern). The Design and Procedure were the same as for Experiments 3 and 4 with the exception of an additional recall response demand. After a pre-recorded aural verbal pattern description was played over a pair of Sony noise-cancelling headphones at the same volume for each participant binaurally or monaurally, there was a 1s pause and then participants opened their eyes, unclasped their hands and reported which side of the pattern contained the most filled cells using the same graded scale of certainty [LEFT 4 3 2 1 0 1 2 3 4 RIGHT] as Experiments 3 and 4. Following their certainty response participants recalled the pattern for the side they perceived fuller using a paper booklet situated between the participant and the keyboard. The booklet consisted of 19 A4 sheets of paper in landscape orientation stapled together at the top centre (1 practise trial plus 18 experimental trials). On each sheet of appear there was an outline of a 6 x 3 cell matrix in black ink printed centrally both horizontally and vertically. The left and right side of the matrix was separated by a thicker black line. If participants perceived the left side of the stimulus to be fuller they recalled the left side of the pattern using the left side of the matrix by making a cross (x) inside the blank cells to designate a filled cell. If participants perceived the right side of the stimulus to be fuller they recalled the right side of the pattern using the right side of the matrix by making a cross (x) inside the blank cells to designate a filled cell. If participants were not sure which side was fuller (and thus had pressed ‘0’ on the response scale) they were not required to recall the pattern. Following recall, participants turned over the page in the booklet, closed their eyes, pressed the spacebar and clasped their hands ready for the next trial.

3.3.4. Results

Proportional bias

The proportional bias was calculated for each of the 28 participants in the binaural (Experiment 5) and monaural listening condition (Experiment 6) across all trials (Figure 3.4). All mean values for the monaural condition were negative indicating that participants were more likely to respond left-fuller than right-fuller. For the binaural listening condition the mean value was positive indicating the opposite trend. The proportional bias for the left ear approached significance (*t*(27) = -1.841, *p* = .077) and was not significant for the right ear (*t*(27) = 1.078, *p* = .291). Replicating the earlier experiments, the proportional difference for the binaural condition was not significantly different from zero (*t*(27) = .705, *p* = .487). A one-way ANOVA was used to compare the proportional difference between the binaural, monaural left ear, and monaural right ear listening conditions. Proportional bias was not significantly different across the three listening conditions (*F* (2, 81) = 1.558, *p* = .217).

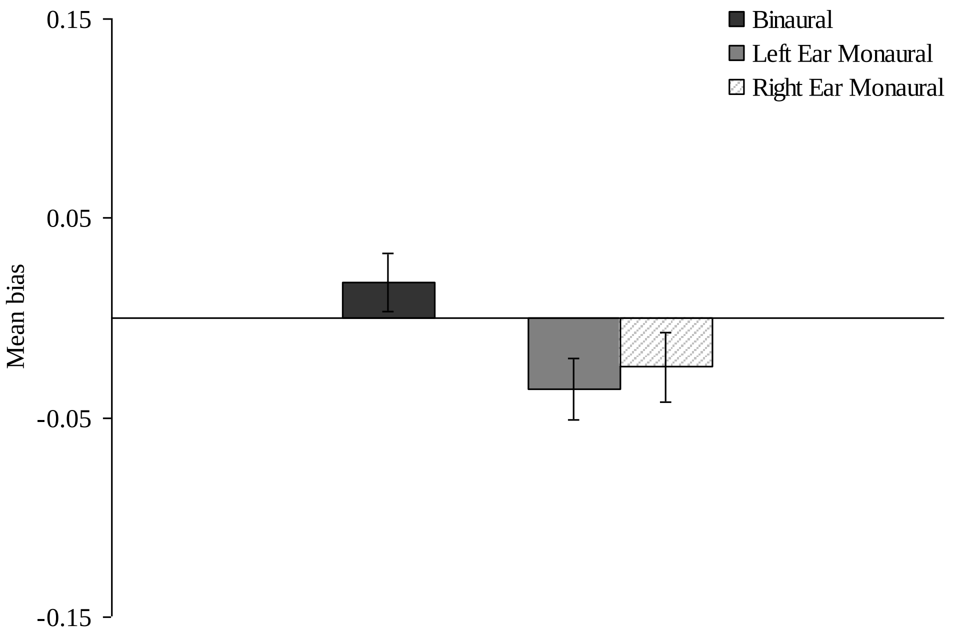

Figure 3.4. Proportional bias is shown for the separate binaural and monaural listening conditions in Experiments 5 and 6. Error bars indicate standard error of the mean.

Certainty

Certainty responses were then analysed in the same way as for Experiments 3 and 4[3]. Figure 3.5 shows that for all listening conditions certainty was greater for left-fuller compared to right-fuller stimuli. As in the earlier experiments, for the monaural condition there was a significant main effect of side fuller (*F*(1,27) = 6.303, *MSE* = .443, *p* = .018) with greater certainty for left-fuller compared to right-fuller stimuli. There was no significant effect of ear (*F*(1,27) = .233, *MSE* = .379, *p* = .633), or start side (*F*(1,27) = 1.620, *MSE* = .820, *p* = .214). In addition, there was no significant interaction between start side and side fuller (*F*(1,27) = .006, *MSE* = .367, *p* = .940), ear and side fuller (*F*(1,27) = .006, *MSE* = .258, *p* = .941), or ear, start side and side fuller (*F*(1,27) = .025, *MSE* = .286, *p* = .875). Participants did show a tendency to be more certain about left-fuller patterns in the binaural condition but there was no main effect of side fuller (*F*(1,27) = 0.23, *MSE* = .531, *p* = .881) although start side approached significance (*F*(1,27) = 3.936, *MSE* = .440, *p* = .058), with slightly greater certainty when the description started on the left-hand side than on the right-hand side. There was no interaction between start side and side fuller (*F*(1,27) = .888, *MSE* = .830, *p* = .354).

A repeated-measures ANOVA with start side and side fuller as the within-subject variables and listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted to compare differences between listening conditions. The interaction between side fuller and listening condition was not significant (*F*(2,81) = .933, *MSE* = .411, *p* = .398) and there was no interaction between start side and listening condition (*F*(2,81) = .284, *MSE* = .556, *p* = .753), nor start side, side fuller and listening condition (*F(*2,81) = .543, *MSE* = .494, *p* = .583).

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[3] A correct only analysis yielded similar results for both listening conditions.

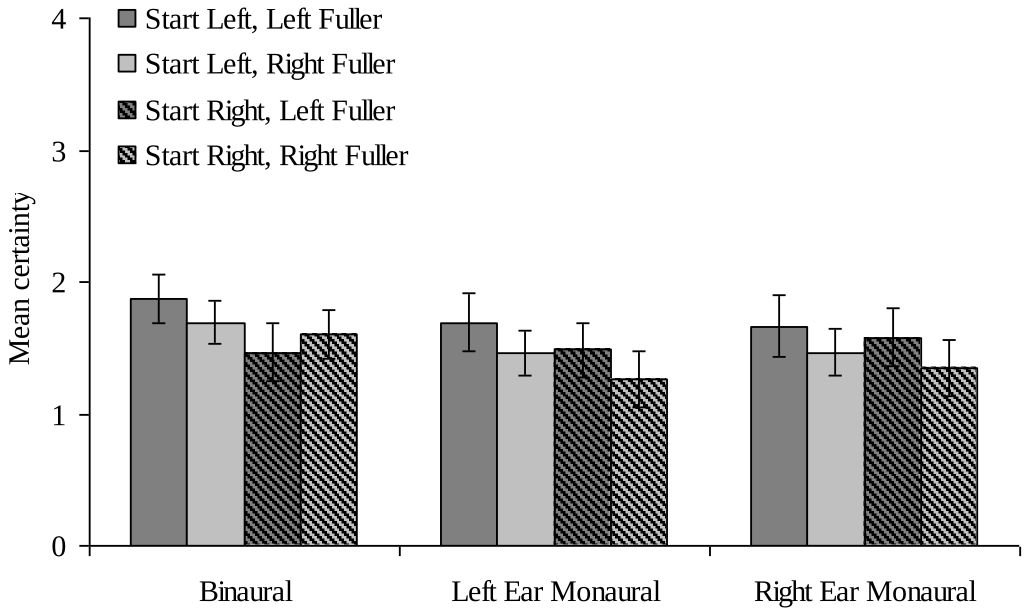


Figure 3.5. Mean certainty responses as a function of start side in Experiments 5 and 6. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left fuller and right fuller stimuli. Error bars indicate standard error of the mean.

Recall

Recall accuracy was assessed in terms of the rate of hits (cells correctly filled), false alarms (cells incorrectly filled), correct rejections (cells correctly left blank), and misses (cells incorrectly left blank). The calculation of Hit Rate (HR) is given below in Equation 1 and False Alarm Rate (FAR) is given below in Equation 2:

(1) Hits/(Hits + Misses)

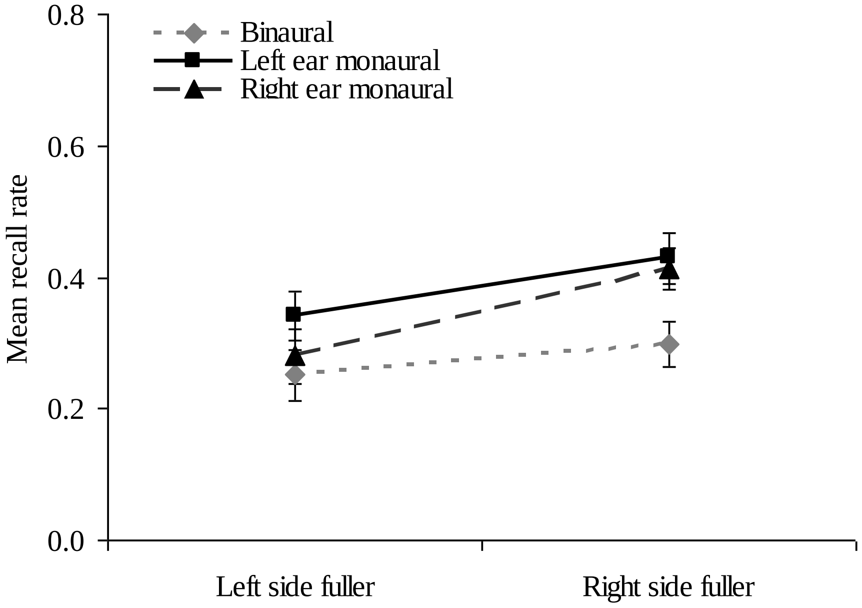
(2) False Alarms/(Hits+False Alarms)

Recall rate was then calculated as [HR – FAR] where higher values indicate more accurate replication of patterns (Figure 3.6). For the monaural listening condition, a repeated-measures ANOVA was conducted with start side and side fuller as the within-subject variables. There was no main effect of ear (*F*(1,27) = .003, *MSE* = .051, *p* = .953), start side (*F*(1,27) = 2.147, *MSE* = .041, *p* = .154), or side fuller (*F*(1,27) = .070, *MSE* = .019, *p* = .793), and no interaction between ear and start side (*F*(1,27) = 3.504, *MSE* = .021, *p* = .072), ear and side fuller (*F*(1,27) = .035, *MSE* = 0.21, *p* = .853), but a highly significant interaction between start side and side fuller (*F*(1,27) = 52.559, *MSE* = .014, *p* < .001) with the most accurate recall for the side that the verbal description ended on: when the description ended on the left-hand side (and started right) the recall rate was better for left-fuller patterns but when the description ended on the right-hand side (and started left) recall rate was better for right-fuller patterns. There was no interaction between ear, start side and side fuller (*F*(1,27) = .991, *MSE* = .038, *p* = .328). When the analysis was conducted for correct trials only the results for the monaural listening conditions were exactly the same with the only significant effect being an interaction between start side and side fuller (*F*(1,27) = 26.064, *MSE* = .035, *p* < .000). A repeated-measures ANOVA for the binaural condition with start side and side fuller as within-subjects factors found no significant effect of start side (*F*(1,27) = .317, *MSE* = .028, *p* = .578), side fuller (*F*(1,27) = .008, *MSE* = .022, *p* = .930) and no significant interaction between start side and side fuller (*F*(1,27) = 1.734, *MSE* = .040, *p* = .199), but when correct trials only were considered there was a significant interaction between start side and side fuller (*F*(1,27) = 6.678, *MSE* = .036, *p* = .016).

A post-hoc power analysis was performed for the binaural and monaural condition recall data using G*Power version 3.0.1 software (Heinrich-Heine-Universitat, Dusseldorf, Germany). The specified test-family was ‘F-test ANOVA: fixed effects, special, main effects and interactions’. For the monaural condition the power analysis was conducted with an alpha level of 0.05, an effect size of 0.25 (medium effect size), a value of 8 for the number of levels of the experimental design (i.e., 2 (ear) x 2 (start side) x 2 (side fuller)), and a total sample size of 224 (i.e., summed over all levels of the experimental design). The revealed power for the monaural analysis was 0.96 (equivalent to 96%). For the binaural condition the power analysis was conducted with an alpha level of 0.05, an effect size of 0.25 (medium effect size), a value of 4 for the number of levels of the experimental design (i.e., 2 (start side) x 2 (side fuller)), and a total sample size of 112. The revealed power was 0.75 (equivalent to 75%).

A repeated-measures ANOVA with start side and side fuller as the within-subject variables and listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted to compare differences between listening conditions. The interaction between side fuller and listening condition was not significant ($F(2,81) = .020$, $MSE = .020$, $p = .980$) and there was no interaction between start side and listening condition ($F(2,81) = 1.384$, $MSE = .030$, $p = .257$), nor start side, side fuller and listening condition ($F(2,81) = 1.945$, $MSE = .031$, $p = .150$).

(a) Start Left



(b) Start Right

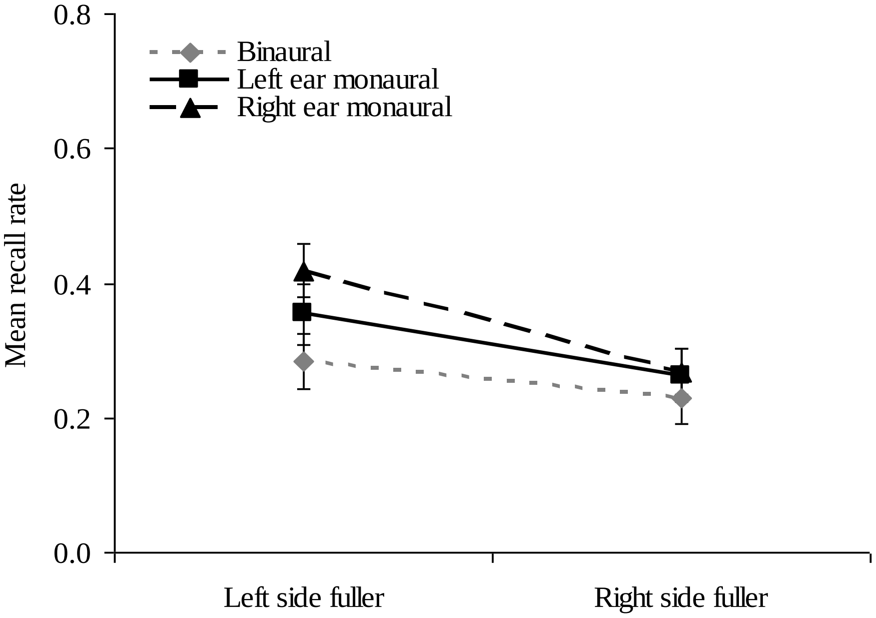


Figure 3.6. Mean recall rate as a function of start side in Experiments 5 and 6. Values represent mean recall rate for start left (a) and start right (b). Error bars indicate standard error of the mean.

3.3.5. Discussion

For the monaural listening conditions when participants made a relative judgement between the two sides of a verbally described pattern, there was some tendency to judge that the left side of the pattern was fuller and to be more certain that this was the case than for the right side of the pattern. However, the effect of monaural presentation to the left ear was the strongest enhancer of this effect. Despite this, the effect of having to maintain the pattern in greater detail rather than simply create a 'general impression' of the stimulus seemed to dampen the previously observed representational pseudoneglect in Experiments 3 and 4. In this experiment subjects were also explicitly required to maintain, for later recall, specific details on the left and right side of the pattern stimulus and it is possible that this maintenance by working memory mechanisms quashed the general impression of that stimulus. There was not greater accuracy in recalling the left side of the pattern and recall accuracy was greatly affected by recency with the side that the description finished on leading to a better rate of recall.

3.4. General Discussion

When participants made a relative judgement between two sides of a verbally described pattern (Experiments 3 and 4) there was a tendency to over-represent the left side, reflected in the fact that participants responded that this side was fuller more often than right side, and also that they were more certain when judging left-fuller patterns. The strongest effects were found for stimuli presented monaurally to the left ear. In Experiments 5 and 6, in addition to making a general judgement about which side was fuller, participants were also asked to recall the side judged to be fuller. Although participants showed some tendency to over-represent the left side of the pattern this over-representation did not translate into better accuracy in recall and the earlier observed effects in certainty judgements were only replicated for the monaural listening conditions as having to maintain the pattern in greater detail seemed to change the general impression of the stimulus.

The most common account of perceptual pseudoneglect is that the cerebral hemispheres differentially orient attention to contralateral space (Brodie & Pettigrew, 1996; Heilman & Van Den Abell, 1979; McCourt & Jewell, 1999) with the right hemisphere preferentially directing attention leftwards. The same theory can be used to explain the representational pseudoneglect observed in both Experiments 3 and Experiment 4. Imagining the spatial layout of the verbally described pattern stimulus may have engaged visuo-spatial processing mechanisms in the right hemisphere, preferentially facilitating the orienting of covert attention leftwards within working memory (e.g., McGeorge et al. 2007). As attention was oriented towards the left side of the stimulus this may have resulted in greater saliency for the left side which in turn resulted in increased certainty about the left side. The hypothesis is supported by the fact that monaural left ear presentation enhanced representational pseudoneglect as preferential engagement of the right hemisphere may have bolstered this process. Indeed, Schonwiesner et al. (2006) found that monaural pulsed noise to each ear preferentially engaged contralateral hemispheric regions – but when binaural pulsed noise was included this pattern was obliterated in the right hemisphere. This indicates that monaural presentation to the left ear may have increased activation in the right hemisphere which is also sensitive to spatial processing. The results therefore seem to suggest that attentional orienting can occur for a mental representation within visuo-spatial working memory that has been generated from an auditory verbal description, with monaural presentation to the left ear preferentially engaging the right hemisphere and enhancing attentional orienting. This account would argue that the right hemisphere was preferentially activated over the left hemisphere because of the spatial nature of the task given the right hemisphere’s well known role in spatial processing. In this way, the bias stems from a general ‘impression’ of the stimulus which may be driven by attentional orienting occurring in the right hemisphere.

The finding that there was no clear lateralised bias in recall performance suggests that the visual mental representation is equally detailed for both sides of the mentally constructed array. This reinforces the idea that the bias is in covert attention to the left of the mental representation in working memory rather than, for example, impoverished representation of detail for the right of the array. This finding is not wholly consistent with previous research showing better recall for the left side of temporary activation of visual information about familiar scenes (McGeorge et al. 2007) or in immediate visual memory for recently presented visual arrays (Della Sala et al. 2010). However, unlike those previous studies, the pattern stimuli in the present study were aurally described which means participants had no prior or current visuo-spatial experience of the stimuli. Also, in Experiments 5 and 6, there was a symmetrical effect of recency with the most recently described pattern side gaining better recall; it is possible that the recency effect - strongest when presentation was to the right ear (i.e., Burns & Manning, 1981; Taylor & Heilman, 1982) - helped to reduce sensitivity in the memory measure of representational pseudoneglect. As the bias was clear in the measure of certainty it is possible that certainty is simply a more sensitive measure of bias within this paradigm than is memory performance. It is clear that having to maintain details within a stimulus affects the general impression of that stimulus, but in order to explain why this is the case further research is required.

To this end, it would be interesting to explore ways of counterbalancing the recency effect in order to unmask any potential bias. One way to achieve this would be to increase or decrease the salience of one side of the pattern by making individual cells more salient; the hypothesis would be that salient cells would capture attention and contribute to representational pseudoneglect. Importantly, if the salient cells were contralateral to the finishing side of the description this could counterbalance the recency effect. The complexity of the patterns could be varied to create a test that is more sensitive to a difference in the level of detail encoded on the left and right. It may also be interesting to observe the performance of participants who read in the opposite direction – from right-to-left instead of from left-to-right. However, in the current study the leftward bias (i.e., representational pseudoneglect) was robust even when the stimulus description started on the right and moved leftward; this is the opposite direction to the participant's reading pattern which suggests that the bias is not simple a function of reading pattern. Nevertheless, it is worth considering for future research.

In conclusion, there are several possible theoretical accounts that could be explored in future studies. However, the focus here on reporting a robust phenomenon of representational pseudoneglect. In the two experiments here this phenomenon is manifest in the certainty with which participants make judgements about the number of items on either side of an array that has been presented as an aural verbal description. It is suggested that this reflects an over-representation or greater salience of the left side of the constructed mental representation of the array, and that monaural presentation to the left ear clearly enhances this effect. Moreover, the results have illustrated that the phenomenon of representational pseudoneglect is robust and merits further empirical investigation as well as consideration within current theories of the role of covert attention in visuo-spatial working memory.

Chapter 4

Representational pseudoneglect for imagined real word scenes driven by aural-verbal description.

Experiment 1 & 2 under review as:

Brooks, Brandimonte, & Logie. (*Under review*). Representational pseudoneglect for imagined real word scenes driven by aural-verbal description. *Quarterly Journal of Experimental Psychology*.

(Appendix A)

4.1. Introduction

The previous Chapter furthered our understanding of representational forms of pseudoneglect in an intriguing way; a representational form of pseudoneglect was found when participants were asked to make a lateralised general impression judgement of a mentally represented pattern stimulus but when participants were asked to extract details from the pattern no bias was demonstrated. On the basis of these results, it would seem that memory asymmetries are not simply a function of the representation held in visuo-spatial working memory but perhaps depend on *how* the representation is formed. One outstanding question is whether or not lateralised biases in memory only occur for highly familiar previously encountered stimuli because, here, there is a strong basis for visual imagery especially if that material was initially processed using vision. In contrast, a completely novel abstract stimulus may result in the formation of a less detailed visual representation less sensitive to the lateralised bias in memory but still sensitive to biases of general impression of spatial layout and/or in the confidence with which lateralised judgements are made. The main aim of the current study was to explore this issue. Experiment 7 and 8 followed the experimental design of Brooks, Logie, McIntosh, & Della Sala (*in press*, 2011) but also used highly imageable stimuli in familiar contexts to be more directly comparable with previous studies that have demonstrated representational pseudoneglect for working memory (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzzatti, 1978). Stimuli were aural-verbal descriptions of fictitious ‘city street’ scenes with highly imageable landmarks (‘shop’, ‘market’, ‘cafe’) on either side of the street, starting left or right (Urbanski & Bartolomeo, 2008). The design draws on previous research which has explored how people mentally represent spatial layout (i.e., Brunye & Taylor, 2008; Deyzac, Logie, & Denis, 2006). The participant's task was to decide which side of the street, left versus right, contained the most landmarks and then to provide a certainty score for this judgement before recalling the landmarks for the side that was perceived to contain the most landmarks. As in the previous Chapter the verbal description was presented monaurally or binaurally, as monaural presentation to each ear may preferentially engage the contralateral hemisphere whereas binaural presentation engages both hemispheres (Schönwiesner, Krumbholz, Rübsamen, Fink, & Yves von Cramon, 2007; Paiemont, Champoux, & Bacon et al. 2008). Boosting the engagement of the right hemisphere may also boost leftward attentional orienting by the right hemisphere. In contrast, Experiment 9 was a cued memory recall task where participants were asked to verbally recall the landmarks from either the left or right side of the imagined street while using a visual imagery strategy. In order to maximise the potential for visual imagery participants were given an active (i.e., walking) versus passive (i.e., standing still) visual imagery strategy while listening to the aural verbal descriptions. Experiment 10 was the same cued recall task as Experiment 9 but this time participants were asked to recall the landmarks from either the left or right side of the imagined street by *drawing* the street on a sheet of paper. The rationale for this experiment was to remove the possibility that participants were being forced access their mental representation using a verbal strategy; drawing is perhaps more synonymous with visuo-spatial processing since the visuo-spatial nature of the mental representation may be transferred from the mind's eye onto paper.

4.2. Experiments 7 and 8

4.2.1. Participants

There were 96 right-handed native English speaking undergraduate participants from the University of Edinburgh aged between 18-38 years with normal or corrected-to-normal vision and hearing. There were 48 participants in a binaural listening condition (Experiment 7) and 48 participants in a monaural listening condition (Experiment 8).

Participants were paid a £6 honorarium. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

4.2.2. Stimuli

There were 32 pre-recorded aural verbal descriptions of fictitious 'city streets' scenes which contained a mixture of landmarks on either side of the street (depicted in Figure 4.1). Please see Appendix C for the full stimulus set. The stimuli were recorded by a native English-speaking female in a sound-attenuated recording booth. The landmarks were generated using the MRC psycholinguistic database and chosen on the basis of having high imageability scores (> 550). The original landmarks were 'bank', 'bar', 'café', 'church', 'college', 'garden', 'hotel', 'market', 'office', 'school', 'shop', 'station'. In a pilot study 13 native English speaking right handed participants were asked to decide if each landmark could be easily visually imaged on a city street using a sliding scale of certainty [1 2 3 4 5 6 7]. For this scale, the number '1' represented 'very difficult to conjure up a visual image' and '7' represented 'very easy to conjure up a visual image'. Participants responded towards the low end of the scale (< 3) for 'office' and 'college' so these landmarks were removed from the cohort. The remaining ten landmarks (i.e., with scores > 3) were used for the experimental stimuli. On each trial, one side of the street, left or right, was fuller, that is, it had more landmarks than the other side. There were 8 'left fuller' city street scenes with either two, three, four, or five landmarks interspersed with the spoken word "house" on the left side of the street along with one, two, three, or four landmarks interspersed with the spoken word "house" on the right side of the street. There were also 8 'right fuller' street scenes which were designed in exactly the same way. There were always 6 items (a mixture of landmarks and houses) on each side of the street; 12 items in total. The landmarks were randomly distributed on each side of the street but the same landmark was not presented at the last/first position of the description on every trial. There were 16 descriptions that started on the left side of the street and 16 descriptions that started on the right side of the street; the description switched back and forth between each side of the street (e.g. on the left is a house, on the right is a bank, on the left is a garden, on the right is a house and so on). With regards to how the landmarks were assigned to each side of the street, the ten original landmarks were split into two matching groups of five stimuli based on their imageability scores. The landmarks for each side of the street were randomly picked from a pool of 'left side landmarks' and a pool of 'right side landmarks' which allowed the imageability for each side of the street to be matched on every trial. This was counterbalanced across participants so the left side landmarks were presented on the right and vice versa for the right side landmarks.

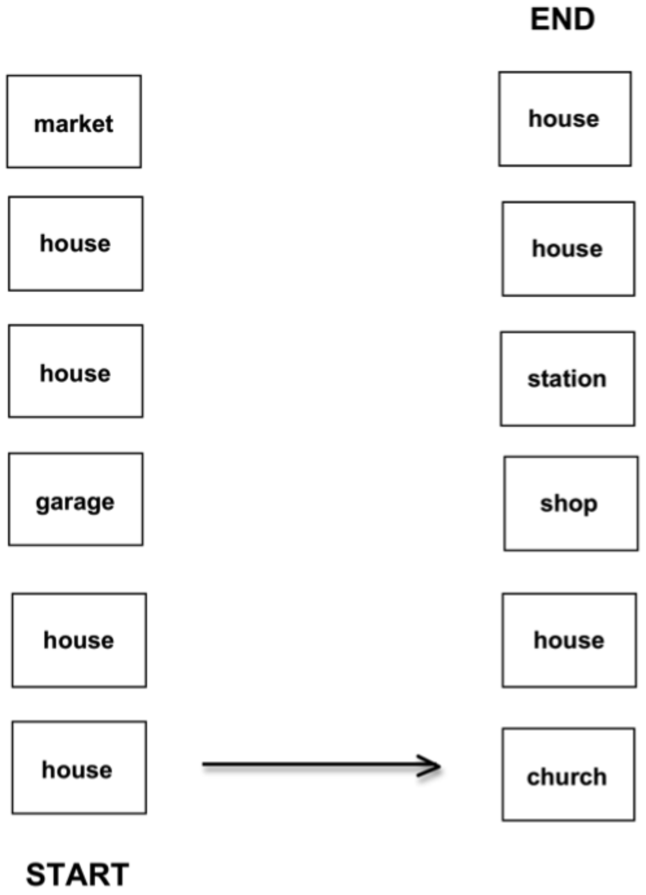


Figure 4.1. Illustration of the experimental stimulus in Experiments 7 and 8. The left side of the street has more landmarks than the right. The arrow indicates the direction of the description.

4.2.3. Procedure

There were 48 participants in a binaural listening condition (Experiment 7) and a separate group of 48 participants in a monaural listening condition (Experiment 8). Participants were given task instructions and shown a top-down depiction of a fictitious shopping street (Figure 4.1) removed before the experiment commenced. Participants were asked to mentally represent the street in whichever way they preferred. Participants were fitted with a pair of Sony noise-cancelling headphones and were asked to close their eyes and clasp their hands at the beginning of each trial. The experiment started when the spacebar was pressed. After a 1s pause, a pre-recorded verbal description was played either binaurally or monaurally. When the description was complete, participants were asked to open their eyes and decide which side of the street, left or right, had the most landmarks and rated their certainty on a certainty scale presented on the keyboard. The certainty scale consisted of nine keys [4 3 2 1 0 1 2 3 4]. If the left side of the street was perceived to have the most landmarks and participants were absolutely certain about this, they were asked to press ‘4’ on the left side of the keyboard – vice versa for the right side. If participants were uncertain about which side of the street had the most landmarks, they were asked to press ‘0’ on the scale. The other numbers from ‘1’ to ‘3’ represented an incremental increase on the certainty scale. All the participants completed the certainty scale judgement. Half of the participants (24 binaural and 24 monaural) stopped at this point and simply moved on to the next trial. The other half of the participants in each listening condition were asked to perform an additional task: to recall the landmarks for the side of the street they thought had the most landmarks. If they had responded that the left side of the street had the most landmarks, they were asked to recall the landmarks on the left and vice versa for the right side of the street. There was some suggestion in Brooks et al. (*in press*, 2011) that performing the recall task, therefore mentally representing the stimulus with the intention to recall details, reduced sensitivity to representational pseudoneglect so it was important to have the opportunity to explore this within the current design. Participants verbally responded into a centrally positioned microphone and there was no time limit for recall. When recall was complete, participants pressed the spacebar for the next trial, closed their eyes, and clasped their hands. Start side (start left vs. start right) was a within-subject variable and trials were blocked by starting side and counterbalanced across participants. For the monaural listening condition, ear (left or right) was a within-subject variable and trials were also blocked by ear and counterbalanced across participants. Trial order was randomly shuffled. One randomly selected trial was used for practise.

4.2.4. Results

For the relative judgement task, the total number of 'left fuller' responses from all 96 participants in the binaural (Experiment 7) and monaural (Experiment 8) condition was subtracted from the total number of 'right fuller' responses and then divided by the overall number of responses to yield a measure of 'proportional bias', with a negative proportional bias indicating a tendency to respond 'left fuller' more often than 'right fuller' but a positive value reflecting the opposite tendency (Brooks et al. *in press,* 2011). An initial analysis showed no significant difference in proportional bias between participants who completed only the certainty task versus those who completed certainty plus recall so the data were collapsed within each listening condition.

Figure 4.2 displays mean proportional bias for the binaural and separate monaural listening conditions. Proportional bias was significantly different across the three listening conditions (F (2, 141) = 4.235, p = .016). There was a significant difference between the left and right ear (p = .014) but no significant difference between the binaural and left ear (p = .608) or the binaural and right ear (p = .141). There was a clear leftward trend for the left ear and this was significantly different from zero (t(47) = -

2.722, *p* = .009), but not for the binaural condition (*t*(47) = -.713, *p* = .480) nor for the right ear condition (*t*(47) = 1.704, *p* = .095).

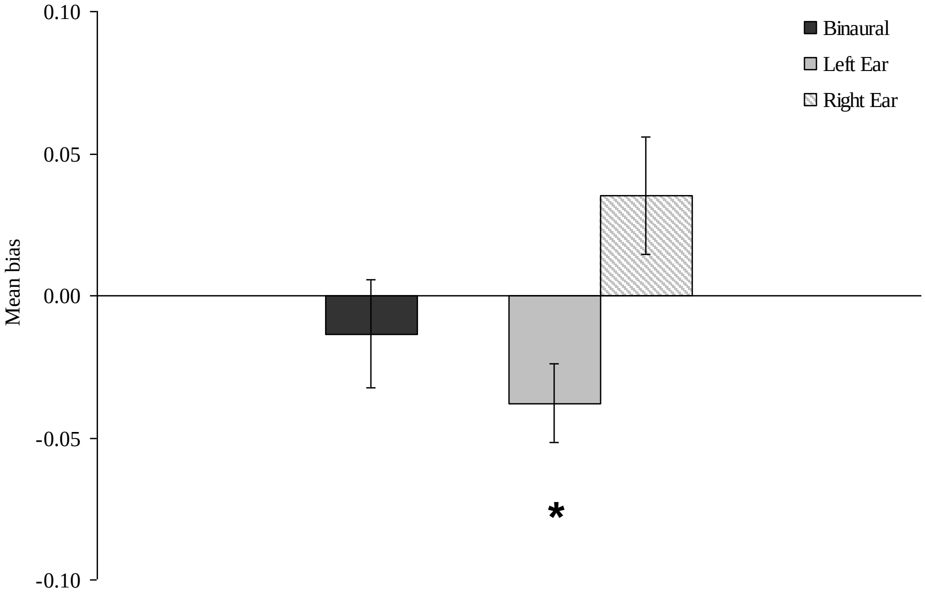


Figure 4.2. Proportional bias is shown for the separate binaural and monaural listening conditions in Experiments 7 and 8. Asterisk indicates significance. Error bars indicate standard error of the mean.

Certainty responses were then recoded as a correct judgement (e.g. participants responded ‘left side more landmarks’ correctly) or an incorrect judgement (e.g. participants responded ‘left side more landmarks’ incorrectly); correct judgements were assigned positive values whereas incorrect judgements were assigned negative values, creating a certainty index (Brooks et al., *in press*, 2011). The certainty analysis for participants in the binaural condition and monaural condition was conducted with correct and incorrect trials combined because a tendency to be more certain about the landmarks on the left side of the street should occur regardless of whether or not participants were correct or incorrect in their responses. An initial analysis showed no significant difference in certainty between each task group of participant so the data were collapsed within each listening condition. Figure 4.3 displays mean certainty for the binaural and monaural conditions. For the monaural listening condition, there was a significant interaction between ear and side fuller (*F*(1,47) = 7.277, *MSE* = .556, *p* = .010) and start side and side fuller (*F*(1,47) = 5.541, *MSE* = .786, *p* = .023), as when presentation was to the left ear certainty was greater for left fuller stimuli - especially when the description started on the left - but the exact opposite was observed when presentation was to the right ear with certainty being greater for right fuller stimuli and a start right description. There was no significant main effect of ear alone (*F*(1,47) = .124, *MSE* = .951, *p* = .726), side fuller (*F*(1,47) = .086, *MSE* = .517, *p* = .770), or start side (*F*(1,47) = 2.195, *MSE* = .813, *p* = .145), and no interaction between ear and start side (*F*(1,47) = 3.435, *MSE* = .799, *p* = .070), or ear, start side and side fuller (*F*(1,47) = .033, *MSE* = .476, *p* = .856). For the binaural condition there was no significant main effect of side fuller (*F*(1,47) = .255, *MSE* = .565, *p* = .616) or start side (*F*(1,47) = 3.055, *MSE* = .679, *p* = .087) but the interaction between start side and side fuller approached significance (*F*(1,47) = 3.929, *MSE* = .782, *p* = .053). Consistently, there was a significant interaction between side fuller and listening condition (*F*(2,141) = 3.878, *p* = .023) driven by noticeably different performance when presentation was to the right ear.

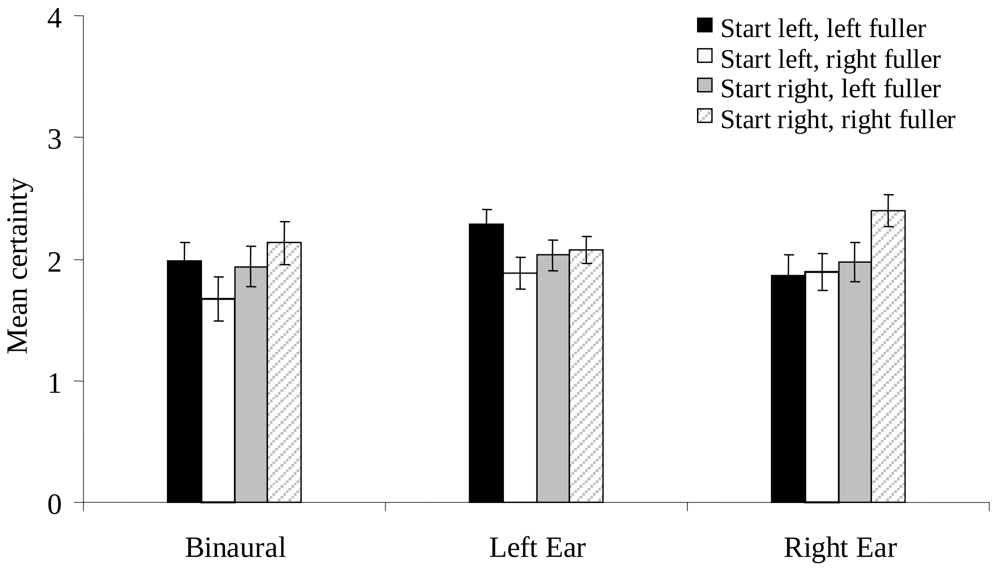


Figure 4.3. Mean certainty response as a function of start side in Experiments 7 and 8. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left fuller and right fuller stimuli. Error bars indicate standard error of the mean.

Recall accuracy was analysed for participants in the binaural condition (N=24) and monaural condition (N=24) in terms of the rate of hits (landmarks correctly recalled), false alarms (landmarks incorrectly recalled), correct rejections (landmarks correctly not recalled), and misses (landmarks not recalled but missed). The calculation of Hit Rate (HR) is given in Equation 1 and False Alarm Rate (FAR) in Equation 2:

(1) Hits/(Hits + Misses)

(2) False Alarms/(Hits+False Alarms)

Recall rate was then calculated as [HR – FAR] where higher values indicate more accurate recall of landmarks. Figure 4.4 displays mean recall rate for the binaural and monaural listening conditions. For the monaural condition, there was a significant main effect of start side (*F*(1,23) = 9.964, *MSE* = .041, *p* = .004) with recall rate being better for the start right condition (description moved from right-to-left and finished on the left) compared to the start left condition (description moved from left-to-right and finished on the right). There was no significant main effect of ear alone (*F*(1,23) = .276, *MSE* = 0.67, *p* = .605) or side fuller (*F*(1,23) = 1.670, *MSE* = .067, *p* = .209), and no interaction between ear and start side (*F*(1,23) = 1.982, *MSE* = .038, *p* = .173) or ear and side fuller (*F*(1,23) = .001, *MSE* = .040, *p* = .971) or ear, start side and side fuller (*F*(1,23) = 0.62, *MSE* = .030, *p* = .805). For the binaural condition, there was no significant main effect of side fuller (*F*(1,23) = .082, *MSE* = .043, *p* = .777) or start side (*F*(1,23) = .002, *MSE* = .022, *p* = .968) and no interaction between start side and side fuller (*F*(1,23) = .657, *MSE* = .128, *p* = .426). When listening condition was added as a between-group variable there were no significant effects.

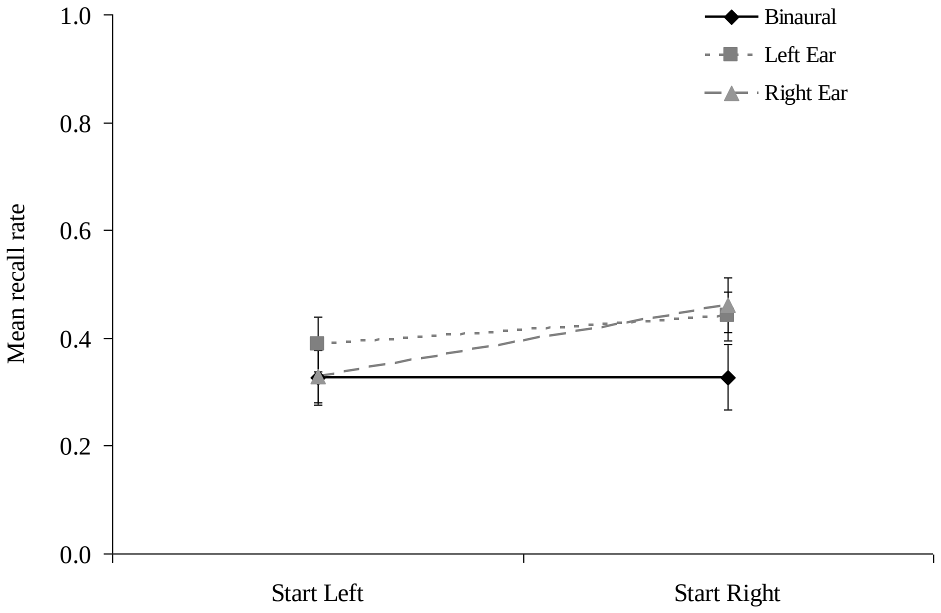


Figure 4.4. Mean recall rate as a function of start side in Experiment 7 and 8. Values represent mean recall rate. Error bars indicate standard error of the mean.

4.2.5. Discussion

When participants made a relative judgement between the two sides of a verbally described street scene there was a significant effect of listening condition: when presentation was monaural to the left ear judgements erred towards the left side of the street (i.e., 'the left side of the street has the most landmarks') but when presentation was binaural or monaural to the right ear, there was no bias. Despite the significant leftward trend for the left ear condition, or representational pseudoneglect, recall accuracy was similar across all listening conditions. This is an important finding since the mental representation was based on highly imageable landmarks and not an abstract stimulus as in the previous experimental Chapter. The relative judgement results are consistent with right hemisphere attentional orienting. The formation of temporary representations in visuo-spatial working memory based on novel highly imageable material, however, does not seem to be subject to an attentional orienting process. The next experiment, Experiment 9, was designed to explore whether or not recall cued to one side, left or right, would be a more sensitive measure of recall biases. The rationale for this experiment was that asking participants to base their judgements on which side of the street they perceived as fuller (i.e., which had the most landmarks) may have made the mental representation *goal-directed* in that as they were building the representation they may have been continually assigning and then updating a 'which side has more landmarks?" judgement. This may have affected sensitivity to representational pseudoneglect for memory recall. Furthermore, Experiment 9 aimed to 'bootstrap' participants' ability to build and maintain a mental representation of a novel stimulus by providing participants with a visual imagery strategy, as well as taking into account participants' own self-reported idea of their mental representation ability. The initial procedure for introducing the participants to the task was the same as the previous experiments but presentation was binaural and there were three important changes to the procedure: 1) there was no certainty scale judgement, 2) recall was cued to the left or to the right, 3) participants completed the task using a given visual imagery strategy, 4) self-reported mental representation ability was taken into account when the data were analysed.

4.3. Experiment 9

4.3.1. Participants

There were 64 right-handed native English speaking undergraduate participants from the University of Edinburgh selected in exactly the same way as Experiments 7 and 8. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

4.3.2. Stimuli

There were 12 unique pre-recorded aural verbal descriptions of made-up shopping streets (six start left description and six start right description) which contained a mixture of landmarks and houses on either side of the street designed using the same landmarks and in exactly the same way as Experiments 7 and 8 with one exception: there were always the same number of landmarks and houses on each side of the street (please see Appendix D for the full stimulus set). There were either two, three, or four landmarks on the left side of the street and either two, three, or four landmarks on the right side of the street. The six start left stimuli and six start right stimuli were heard twice: once with recall cue ‘LEFT’ and once with recall cue ‘RIGHT’. There were also ‘filler’ stimuli (three start left and three start right) designed in exactly the same way as the experimental stimuli which served to prevent participants from becoming too familiar with the experimental stimuli; the filler stimuli contained different landmarks namely:

‘bench’, ‘bin’, ‘car’, ‘fence’, ‘park’, ‘pond’, ‘tree’, ’truck’ also interspersed with the word ‘house’. The filler stimuli always had the recall cue ‘ALL’ and were not repeated.

4.3.3. Procedure

The initial procedure for introducing the participants to the task was the same as Experiments 7 and 8 but were then three important changes to the procedure: 1) there was no certainty scale judgement, 2) recall was cued to the left or to the right, 3) participants completed the task using a given visual imagery strategy. There were two visual imagery strategies: active imagery and passive imagery. In the active imagery condition participants were asked to imagine themselves walking along the street in line with the aural-verbal description of the street. Participants were asked to imagine the street from a birds-eye perspective, that is, they were asked to imagine what they would actually see with their eyes if they walked along the street as opposed to *watching* themselves or *looking down* at themselves walking along the street. In the passive imagery condition participants were asked to imagine themselves standing still at one end of the street while it was verbally described and, again, view the street from a bird’s eye perspective but imagine that they were not moving. Half the After participants had listened to the aural verbal description of the street scene, following a 1s pause, a recall cue was presented in the centre of the screen for 2 seconds; the participants were not aware of which side of the street the cue would relate to until the end of the trial meaning they needed to represent both sides of the street in equal detail. If the recall cue was ‘LEFT’ participants were to recall the landmarks on the left side of the street and vice versa if the cue was ‘RIGHT’. If the cue was ‘ALL’ (filler stimuli only) participants were asked to recall all the landmarks on both sides of the street. Participants were asked to respond as quickly as possible by speaking clearly into a microphone attachment which was the same as Experiments 7 and 8. Participants’ responses were recorded in an individual sound file for each trial. Participants then pressed spacebar for the next trial, closed their eyes, and clasped their hands. Trials were blocked by imagery condition (active vs. passive) and then by start side (start left vs. start right) counterbalanced across participants. Trial order (within each block) was randomly shuffled. There were thus 48 trials in total divided into four blocks: 1) 12 trials active imagery start left (plus 3 filler stimuli start left); 2) 12 trials active imagery start right (plus 3 filler stimuli start right); 3) 12 trials passive imagery start left (plus 3 filler stimuli start left); 4) 12 trials passive imagery start right (plus 3 filler stimuli start right);. These four experimental blocks were preceded by one practise trial.

One week following the experiment participants were emailed with two questions about visual imagery. These questions were adapted from Garden, Cornoldi, & Logie (2002) and were as follows: Question 1) ‘Think about the way you orient yourself in different environments around you. Would you describe yourself as a person who tries to create a ‘mental map’ of the environment?’ Participants were asked to answer on a sliding scale of certainty with a number between from 1 (not at all) to 5 (very much). Question 2) ‘Think of an unfamiliar city. Write the name here. Now try to classify your representation of the city – is the representation like that of a map?’ Participants were asked to answer on a sliding scale of certainty with a number between from 1 (not at all) to 5 (very much). Participants were divided into three groups on the basis of the answer to the second question. If participants responded either ‘1’ or ‘2’ they were classified as poor mental mappers. If participants responded either ‘4’ or ‘5’ they were classified as good mental mappers. If participants responded ‘3’ they were classified as neutral. The rationale for using Question 2 (Q2) instead of Question 1 (Q1) was because Q2 was a more accurate reflection of what participants *actually did* as opposed to what they thought they did. Both questions were asked, however, to engage participants with considering the type of mental representation that they generally make. The answers were statistically compared.

4.3.4. Results

The recall data for 64 participants was analysed across all trials, overall, and as a function of mental mapping group in the same way as Experiments 7 and 8 by calculating the recall rate. Figure 4.5 shows the recall rate as a function of start side, cue side, and imagery strategy overall for 64 participants.

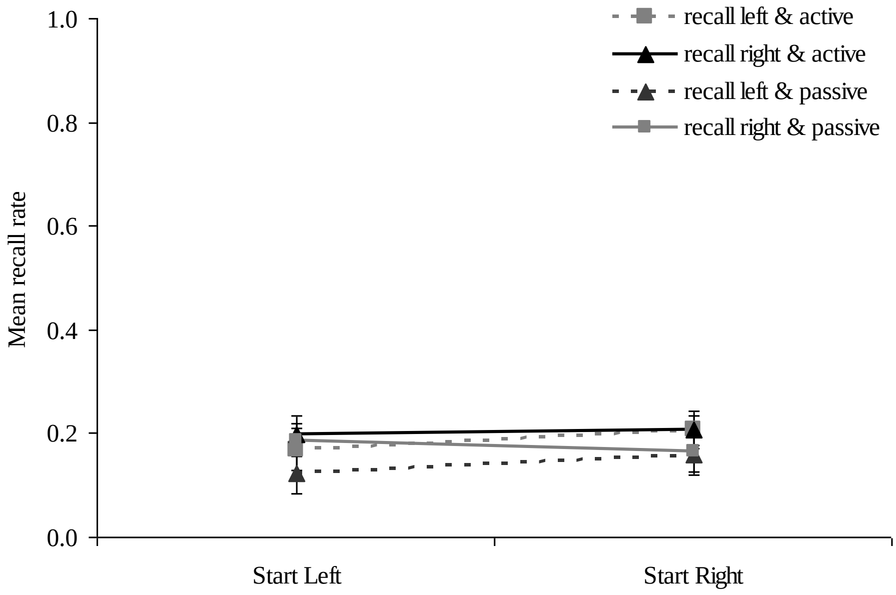


Figure 4.5. Mean recall rate as a function of start side, cue side, and imagery strategy in Experiment 9. Values represent mean recall rate. Error bars indicate standard error of the mean.

A repeated-measures ANOVA with imagery condition (passive vs. active), start side (left vs. right) and side of recall (left vs. right) showed no main effect of imagery condition (*F*(1,63) = 2.831, *MSE* = .063, *p* = .097), start side (*F*(1,63) = .432, *MSE* = .061, *p* = .514), or side of recall (*F*(1,63) = .921, *MSE* = .086, *p* = .341) and no significant interaction between imagery condition and start side (*F*(1,63) = .179, *MSE* = .038, *p* = .674), imagery condition and recall side (*F*(1,63) = .375, *MSE* = .040, *p* = .542), start side and recall side (*F*(1,63) = 1.185, *MSE* = .054 , *p* = .280), imagery condition, start side and recall side (*F*(1,63) = .137, *MSE* = .047 , *p* = .712).

Mental mapping data was available for 60 of the 64 participants (four participants did not answer the question). There were 33 participants classified as *poor mental mappers* on the basis of their answer to Q2 (i.e., participants responded ‘1’ or ‘2’ to question 2). There were 10 participants classified as *neutral mental mapper* on the basis of their answer to Q2. There were 17 participants classified as *good mental mapper* on the basis of their answer to Q2. There was an unbalanced number of participants in each mental mapping group who started left versus start right first and also for imagery condition. For the simplicity of analysis recall rate was collapsed across start side but, given the nature of the analysis, imagery condition was retained as a within-subject variable along with cue side. A comparison was first made between the overall scores for Q1 and Q2. The score of each participant for Q2 was subtracted from the score of each participant for Q1 giving one of three numerical values: zero (i.e., the scores were the same for each question), a positive numerical value (i.e., Q2 received a higher score than Q1), or a negative numerical value (i.e., Q2 received a lower score than Q1). A one-sample t-test on the mean difference (*M* = -.18, *SD* = .93) showed that there was no significant difference between the scores for Q1 and Q2 (*t*(59) = -1.528, *p* = .132).

Figure 4.6 shows the recall rate for participants classified as good, neutral and poor mental mappers on the basis of their answer to Q2. For poor mental mappers (N33) a repeated-measures ANOVA with imagery condition (passive vs. active) and side of recall (left vs. right) showed no main effect of imagery condition (*F*(1,32) = .231, *MSE* = .035, *p* = .634), recall side (*F*(1,32) = .562, *MSE* = .041, *p* = .459) and no significant interaction between imagery condition and side of recall (*F*(1,32) = .575, *MSE* = .019, *p*

= .454). For neutral mental mappers (N10) a repeated-measures ANOVA showed no main effect of imagery condition ($F(1,9) = .334$, $MSE = .036$, $p = .578$), recall side ($F(1,9) = .354$, $MSE = .066$, $p = .566$) and no significant interaction between imagery condition and side of recall ($F(1,9) = .296$, $MSE = .019$, $p = .600$). For good mental mappers (N17) repeated-measures ANOVA showed no main effect of imagery condition ($F(1,16) = 1.494$, $MSE = .025$, $p = .239$), recall side ($F(1,16) = .014$, $MSE = .034$, $p = .908$) and no significant interaction between imagery condition and side of recall ($F(1,16) = .635$, $MSE = .015$, $p = .437$). A further analysis was undertaken in order to compare whether recall accuracy of good and poor mappers was statistically different; in order to make a sensible comparison 17 participants were selected from the poor mental mapping group and matched, as far as possible, to the participants from the good mental mapping group on the basis of which imagery condition they had completed first. A one-way ANOVA showed no significant difference between groups in the active imagery condition when cued to recall left ($F(1,32) = .396$, $p = .548$) or right ($F(1,32) = .424$, $p = .520$) or in the passive imagery condition when cued to recall left ($F(1,32) = .000$, $p = .984$) or right ($F(1,32) = .284$, $p = .598$).

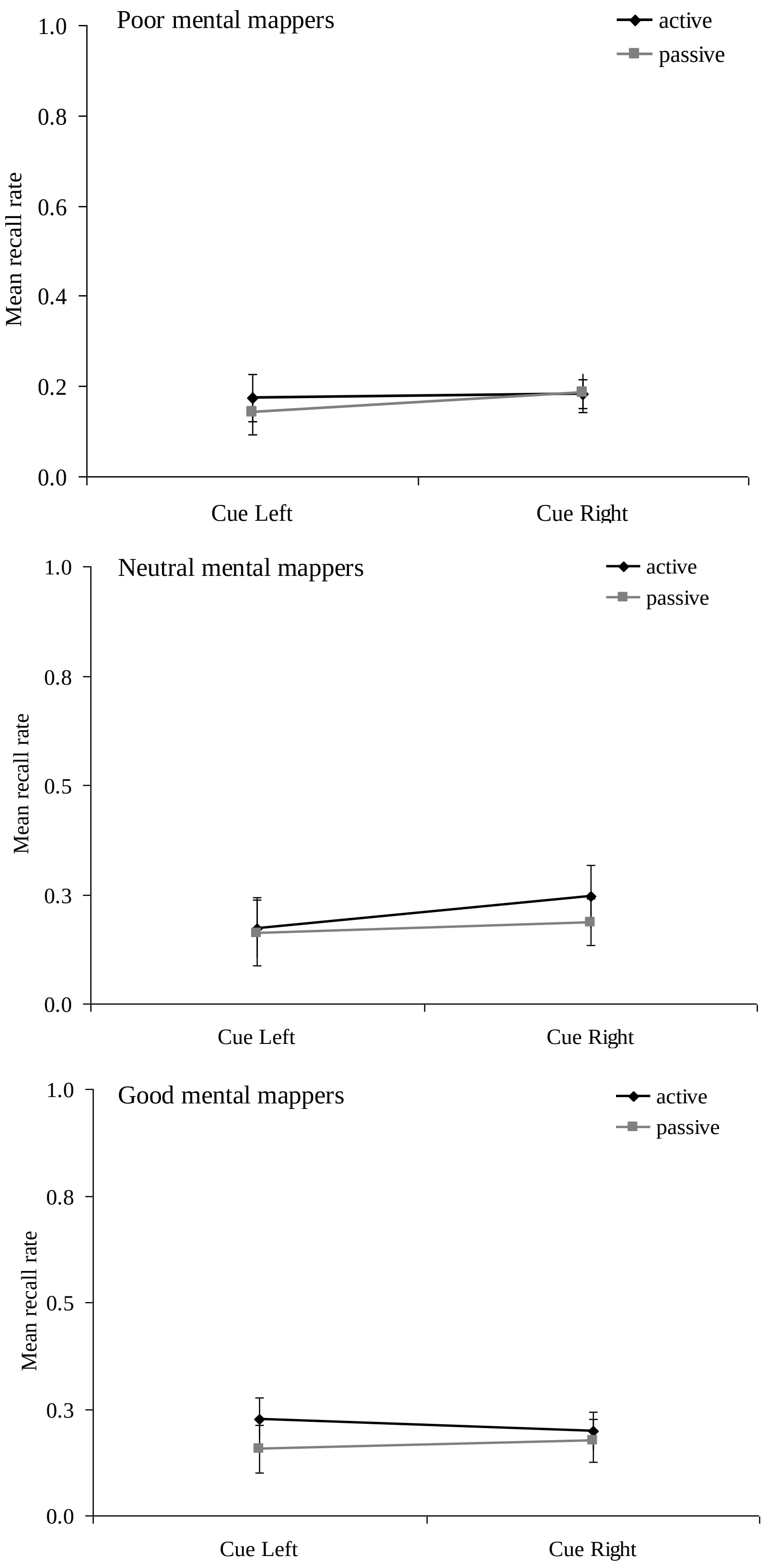


Figure 4.6. Mean recall rate by mental mapping group as a function of cue side and imagery strategy (active and passive) in Experiment 9. Values represent mean recall rate. Error bars indicate standard error of the mean.

4.3.5. Discussion

Despite the fact that recall was cued, participants completed the task using a given visual imagery strategy, and that self-reported mental representation ability was taken into account there were no significant lateralised memory biases. The data are completely in line with Experiments 7 and 8 and also the experiments reported in the previous Chapter and, again, indicate that the temporary activation of novel material held in working memory is not subject to attentional orienting. The final experiment in this series, Experiment 10, was conducted to confirm that the method of recall was not influential.

4.4. Experiment 10

4.4.1. Participants

There were 16 right-handed native English speaking undergraduate participants from the University of Edinburgh selected in exactly the same way as Experiments 7 and 8. Ethical approval was granted for the experiment from the University of Edinburgh ethics committee.

4.4.2. Stimuli

Exactly the same stimuli as Experiment 9.

4.4.3. Procedure

The procedure was exactly the same as Experiment 9 with two exceptions: 1) participants recalled the landmarks by drawing the street and landmarks on a sheet on paper, 2) no visual imagery strategy was given. There were therefore two blocks of 12 experimental stimuli, a start left block and a start right block, and also 3 filler trials. A booklet of A4 paper containing a total of 31 sheets of paper (24 experimental trials, plus six filler trials and one practise trial) was placed in-between the participant and the computer monitor in landscape orientation. Participants were informed they could change the orientation of the paper if it helped them to better recall the landmarks. Following the cue on the screen to recall 'LEFT', 'RIGHT', or 'ALL' participants were asked to draw a road on the page in any orientation they desired but the road should be defined by two lines with a gap between them and then to draw, in any way desired, the landmarks on the left, right, or both sides of the street. Participants were invited to draw the landmarks in terms of written words, as outline depictions, or as more complex pictures. When the drawing was completed participants turned the A4 sheet of paper over and placed it to their right-hand side. Participants then closed their eyes, pressed spacebar and clasped their hands for the next trial. Trial order (within each block) was randomly shuffled. Start side (start left vs. start right) was a within-subject variable and was blocked and counterbalanced across participants.

4.4.4. Results and discussion

Figure 4.7 shows the recall rate. The data for 16 participants was analysed overall using a repeated-measures ANOVA with start side (left vs. right) and side of recall (left vs. right) as the within-subject variables' there was n significant effect of start side (*F*(1,15) = .063, *MSE* = .048, *p* = .805) or side of recall (*F*(1,15) = .206, MSE = .048, *p* = .656) and no significant interaction between start side and side of recall (*F*(1,15) = .014, MSE = .045, *p* = .907). The data are completely in line with the experiments reported in this Chapter and also the Experiments reported in the previous Chapter and fully suggest that the temporary activation of novel material held in working memory is not subject to attentional orienting.

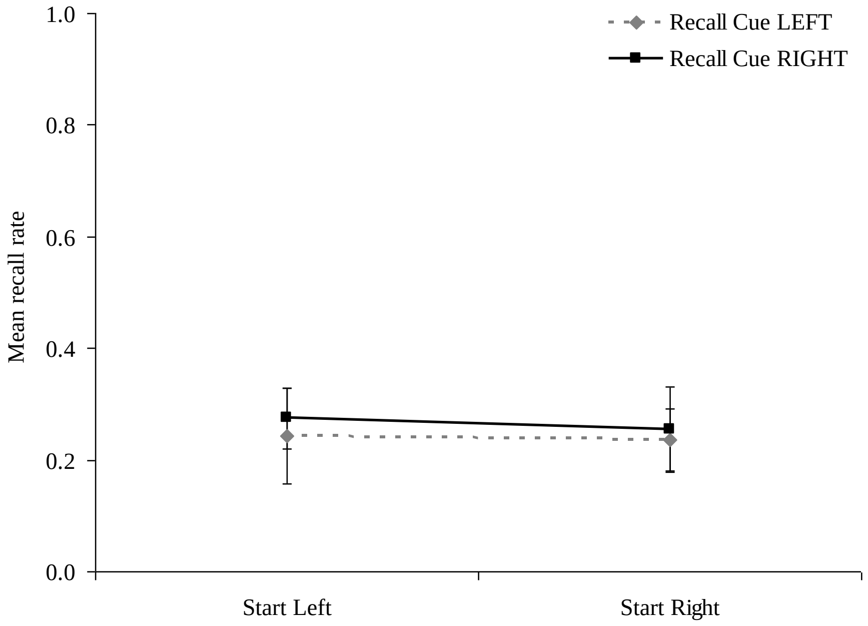


Figure 4.7. Mean recall rate as a function of start side and cue side in Experiment 10. Values represent mean recall rate. Error bars indicate standard error of the mean.

4.5. General Discussion

The main aim of the current research was to explore asymmetries in visuo-spatial working memory for the temporary activation of highly imageable information. In Experiments 7 and 8 healthy participants listened binaurally or monaurally to aural-verbal descriptions of novel ‘city street’ scenes which contained highly imageable landmarks (e.g., “shop”, “market”, “school”) on either side of the street (left vs. right) and were asked to create a visuo-spatial mental representation of the street as it was described. Participants were then asked to decide which side of the street contained the most landmarks, provide a certainty score for this judgement, and recall the landmarks on the side of the street that was perceived to contain the most landmarks. The results showed a significant effect of listening condition: when presentation was monaural to the left ear judgements erred towards the left side of the street (i.e., ‘the left side of the street has the most landmarks’) but when presentation was binaural or monaural to the right ear, there was no bias. Despite the significant leftward trend for the left ear condition, or representational pseudoneglect, recall accuracy was similar across all listening conditions. In Experiment 9 the initial procedure was the same as Experiments 7 and 8 but were thus three important changes to the procedure: 1) there was no certainty scale judgement, 2) recall was cued to the left or to the right, 3) participants completed the task using a given visual imagery strategy, and 4) self-reported mental representation ability was taken into account when the data were analysed. Despite these changes, recall accuracy was similar for the left and right cued side, across both visual imagery conditions, and regardless of the participants self-reported mental representation ability. Experiment 10 showed that the method of recall (i.e., aural verbal vs. drawing) did not influence this pattern of results.

The current studies explored whether lateralised memory biases could be found for the temporary activation of completely novel, non-visual, highly imageable material. The main aim was the recall task and the results completely complement Brooks et al. (*in press,* 2011) as, importantly, there was no lateralised memory bias even though the stimuli were highly imageable and, arguably, familiar in terms of context (i.e., McGeorge et al., 2007). As there was no clear lateralised recall bias, this suggests that the street scene stimulus was equally detailed (or equally impoverished) on both sides. This is an important finding as it indicates that regardless of the imageability of the stimuli lateralised memory biases were not observed – under a variety of different conditions. The landmarks were not more salient on the left side of the street despite the implied asymmetry in salience when participants made a relative judgement in the first part of the task of Experiment 7 and 8 for monaural left ear presentation. The results of the relative judgement task are also consistent with Brooks et al. (*in press,* 2011) showing a significant leftward bias, or representational pseudoneglect, for the monaural left ear condition (favouring the right hemisphere) but no significant bias for the binaural or monaural right ear condition (favouring the left hemisphere). For Experiments 7 and 8, the results for the relative judgement task, at least for the left ear, can be interpreted within the theoretical framework that the right hemisphere directs attention preferentially leftward in spatial tasks (Kinsbourne, 1970; Heilman & Van Den Abell, 1979; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990) especially under conditions that enhance its activation. Interestingly, although Brooks et al. (*in press*, 2011) did not find a large rightward bias when their stimuli were presented monaurally to the right ear, there was a clear indication that presentation to the right ear resulted in reduced sensitivity to representational pseudoneglect compared to monaural left ear or binaural presentation. It is therefore possible that the high imageability of the stimuli somehow boosted this ‘desensitivity’. It is possible that because the landmarks were also high frequency words left hemisphere activity, and thus contralateral attentional orienting, was particularly enhanced. Finally, when the direction of the description was theoretically consistent with that of attentional orienting, from right-to-left, recall rate was significantly enhanced. It is possible that the start side effect was a signature of an underlying attentional orienting effect that could lead to asymmetries in recall performance, especially for the left ear condition, but that any such effect is overshadowed by the serial order nature of the aural verbal description. While the results could perhaps be interpreted as lateralised ‘spatial cuing’ with presentation to each ear drawing attention to each side of the street stimulus, the current paradigm does not allow us to make strong enough inferences in this direction but is an interesting question for future research and one that has been addressed for perceptual pseudoneglect (i.e., Nicholls & McIlroy, 2010).

In conclusion, the current study implies that when temporary visual representations are formed from auditory verbal descriptions of highly imageable, familiar stimuli, then lateralised asymmetries are present in the judgements that people make about the contents of those representations, but are not present in the accuracy of recall. This points to the intriguing possibility of a lateralized attentional bias in metamemory rather than in the temporary memory representations themselves, suggesting a potentially fruitful avenue for future research on the topic of representational pseudoneglect.

Chapter 5

What the eyes do during the mental representation of natural scenes held in working memory.

5.1 Introduction

Chapters 3 and 4 found, across a series of experiments, a lateralised bias in judgements of certainty for novel spatial layouts from aural-verbal descriptions in the absence of vision, but no evidence for lateralised working memory biases, which is inconsistent with the previous research that has demonstrated lateralised memory biases for visually processed scenes for healthy participants - though not for aural-verbal descriptions (Bourlon, Duret, & Pradat-Diehl et al. 2010; Della Sala, Darling, & Logie, 2010; McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007). The results may suggest, therefore, that in the absence of previous visuo-spatial processing lateralised memory biases are either difficult to demonstrate, or simply do not exist.

The aim of the next experiment was two-fold. The first aim was to assess whether lateralised memory biases could be more readily observed for completely novel scenes that were *visually* processed. The second aim was to track participants' eye movements during visual processing and also during memorisation in order to gain additional hints about any potential spatial biases that arose. To this end, participants were asked to recall two different types of information from a visually processed natural-world scene - perceptual (i.e., colour) or spatial information (i.e., side). Natural scenes were used in order to bring the task in-line with previous real-world research in the field (i.e., McGeorge et al. 2007) and also because of the second aim – to track participants' eye movements during the task - would arguably be more natural under these conditions. The rationale for exploring eye movements stems from the fact that if lateralised memory biases *are* demonstrated then this observation may be accompanied by a specific pattern of eye movements biased towards the left side of space, which may hint towards lateralised memory biases being a function of visuo-spatial processing. Eye movements have been used to explore a wide range of cognitive processes (Hautala, Hyönä, & Aro, 2011; Martini, Furtner, & Sachse, 2011) and it has already been shown that leftward bias on certain tasks – like facial recognition – may be accompanied by leftward eye movements (Butler, Gilchrist, & Burt et al. 2005). This has also been noted for mental number line tasks (Loetscher, Bockisch, & Brugger, 2008; see also Fischer, Warlop, Hill, & Fias, 2004; Sullivan, Jurhasz, Slatterly, & Barth, 2011). Moreover, memory may be linked to the number of fixations or duration of fixations during free viewing (Huebner & Gegenfurtner, 2010; Loftus, 1972) and that patterns of eye movements made during free viewing are often similar to those during memorisation (Brandt & Stark, 1997; Laeng & Teodorescu, 2002). Previously, no single study has explored lateralised memory recall, associated patterns of fixation, and the relationship between these two factors during a period of visual processing versus mental representation.

Participants were presented with a natural scene and asked to fully explore the stimulus using vision and then, when the stimulus was removed from view, hold a mental representation of the stimulus in working memory before recalling specific details from the scene with regards to a target object on the left or right hand side. In Participants were asked two types of questions - perceptual and spatial. The perceptual question was “what colour was the…” followed by the name of the relevant target object (i.e., “bench”) and the spatial question was “what side was the…” followed by the name of the relevant target object (i.e., “bench”). The eyes were tracked throughout the entire trial.

5.2 Experiment 11

5.2.1. Participants

There were 12 subjects with normal or corrected-to-normal vision and normal hearing, who spoke English as a native language, were aged between 18 and 38 years old, and were exclusively right handed. Ethical approval for the experiment was obtained from the University of Edinburgh ethics committee.

5.2.2. Stimuli

The stimuli were 18 full-colour photographs of unique natural locations taken by the experimenter using a Canon EOS 350D digital camera (8 mega pixel resolution). Some of the images were of the same scene (i.e., living room) but each scene was completely unique (i.e., more than one living room scene was used but the living rooms in each case were different). Within each image an object was chosen to be the 'target' object. The target objects were unique in terms of colour, size, and absolute position (Table 5.1; see Appendix E for full stimulus set).

Image	Scene	Target
1	Market	Basket
2	Park	Bench
3	Bedroom	Lampshade
4	Living room	Lampshade (Figure 5.1)
5	Café	Door
6	Street	Lamp
7	Café	Man's T-shirt
8	Park	Bench (Figure 5.1)
9	Market	Bag
10	Park	Flowers
11	Concert stage	Cushion
12	Living room	Bottle
13	Kitchen	Mug
14	Living room	Bin
15	Café	Man's T-shirt
16	Ocean	Buoy
17	Street	Car
18	Park	Clock

Table 5.1. The experimental images with the target object listed.

Nine images contained a target object left of the image midline and nine images contained a target object right of the image midline. The target object was always exclusive to one side of the image (the target did not appear on both sides) but the exact position on the left or right varied randomly from image to image. Target side was also completely counterbalanced across subjects by mirror-reversing the 18 original images to form a separate set of stimuli as illustrated in Figure 5.1.

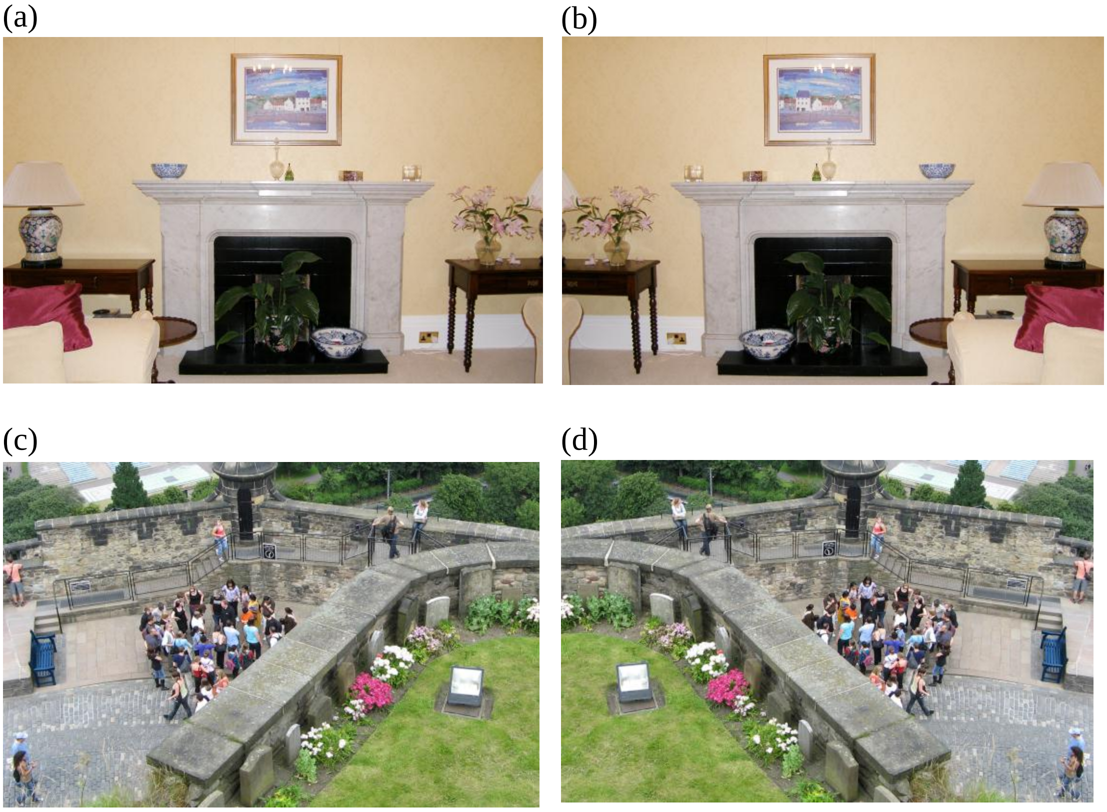


Figure 5.1. Illustration of the experimental stimuli in Experiment 11. Both (a) and (c) show experimental images in normal orientation and in (b) and (d) the same images in mirror reversed rotation. In (a) and (b) the target is the lamp-shade/lamp. In (c) and (d) the target is the bench.

Objects that were either too obvious or too inconspicuous were not chosen as targets. There were two types of questions asked about each target object. The perceptual question was “what colour was the…” followed by the name of the relevant target object (e.g., “lamp-shade”) and the spatial question was “what side was the…” followed by the name of the relevant target object (e.g., “lamp”). Nine images were randomly assigned the perceptual question and nine images were randomly assigned the spatial question.

5.2.3. Apparatus

A Tower-mounted Eyelink 2000 © 2005-2007 SR Research Ltd monocular eye tracker was used to track participant’s eye-movements. An infrared mirror directs the infrared beam to the eye and the angle of camera-to-pupil can be adjusted for optimal tracking. The eye camera was positioned above the participant’s head so arm and hand movements were not restricted, though this was not required in the current experiment. The sampling rate of the eye tracker was 2000 Hz. The eye tracker automatically records the position of the chosen eye in terms of x and y coordinates on the computer screen every 50ms. A fixation was defined as stationary gaze for more than 50ms in one location. Horizontal fixation midline was defined as 512 pixels (range 0 to 1024 pixels) with values less than 512 pixels indicating fixation towards the left side of space and values greater than 512 pixels indicating fixation towards the right side of space – fixations were therefore analysed as a function of left versus right side of midline. Vertical fixation midline was defined as 384 pixels with values less than 384 indicating fixation towards the lower visual field and values greater than 384 indicating fixation towards the upper visual field - fixations were therefore analysed as a function of lower versus upper position relative to midline. The eye-tracker was positioned on a black table in a room that was painted black on the walls adjacent to the eye-tracker, with a non-adjustable chin-rest and a non-swivel adjustable chair positioned at the same end as the eye tracker. There was also a flat-screen computer monitor, the display screen, with resolution 1280 x 1024 pixels positioned at a distance of 60cm from the eye-tracker. The host computer, which controlled the eye-tracker, was positioned directly behind the participant on a table where the experimenter was also seated (Figure 5.2). From the host computer screen one eye, left or right, was selected for tracking, the eye-tracking device was optimised in terms of ensuring the pupil was detected by the camera and the pre-experimental procedures of Calibration, Validation, and Drift Checking were controlled.

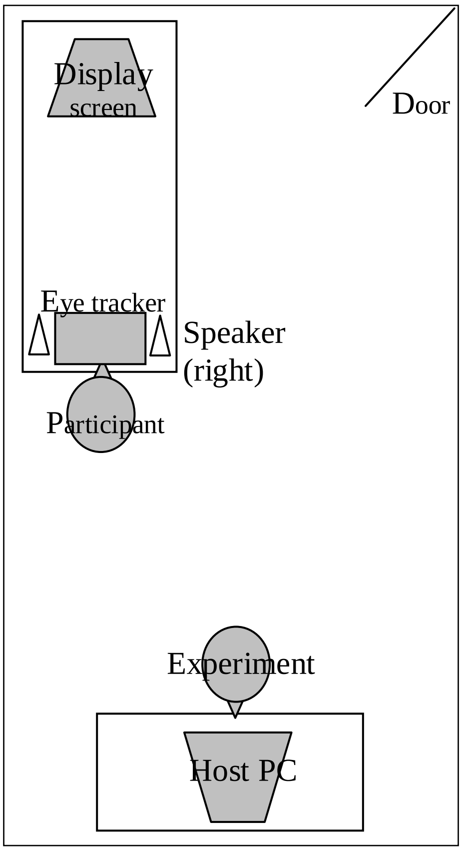


Figure 5.2. Illustration of the experimental set-up for Experiment 11.

5.2.4.Procedure

After being given the task instructions and signing a consent form participants were asked to place their chin on a chin rest - always fixed in line with the participants’ body vertical midline – and to rest their forehead flush with the forehead resting bar of the Tower eye-tracker mount. The chin and forehead rest kept the participant's head as still as possible during the experiment. Participants were encouraged to adjust the height of the chair vertically to a comfortable position. The lights in the testing room were then dimmed to near darkness. The right eye was tracked in 11 subjects and the left eye in one subject who had an eye infection in the right eye. A real-time image of the eye was projected to the host computer with a rectangle ‘tracking window’ superimposed over the eye - this was adjusted by the experimenter until optimal focus of the pupil was obtained. A Calibration procedure, provided by the manufacturers of the eye-tracker (SR Research), was then conducted. Participants were asked to visually fixate on a series of nine target dots which were presented one at a time in different pre-programmed horizontal and vertical positions on the display screen. The Calibration procedure was started by the experimenter on the host computer and the participant was asked to fixate on each target dot on the display screen as it appeared until it disappeared; participants were asked not to anticipate the location of the next target dot and to wait for the next dot to be visually presented before moving the eyes. For each fixation dot, the position of the fixation in *x* and *y* coordinates was recorded automatically and this information was sent to the host computer. The Calibration automatically terminated after nine dots were fixated. If fixation position was not recorded for a given target dot there was the option to restart the Calibration procedure. The Validation procedure, also provided with the eye-tracker (SR Research), was then conducted to check the fixation information recorded during Calibration using the same procedure. These two procedures were necessary to ensure that the participants’ eyes were being accurately tracked at all x-y positions on the display screen. Finally, the Optical Drift was calculated by asking participants to fixate on a centrally presented target dot and the fixation position for this target dot compared to that calculated during Calibration; if the difference was large an error message was automatically generated and these three procedures were started from the beginning. These procedures were slightly more difficult when the participant was wearing glasses - for two participants it was impossible to track the eyes because the glasses contained an anti-reflective coating which prevented infra-red wavelengths reaching the pupil. In these cases, the experiment was terminated and the participants were replaced.

Each experimental trial began with participants being asked to fixate centrally on a target dot – the fixation position could be seen by the experimenter on the host computer (i.e., Optical Drift procedure) seated behind the subject. If fixation was central the experimenter pressed a key on the host computer to start the trial. The recording of eye movements started at this point. In terms of the actual dynamics of the eye tracking, the position of the eyes was updated every 50ms in terms of x and y pixel coordinates on the display screen and also in terms of fixation duration. During the ‘visual processing period’ an image was presented at full screen size on the display screen for 6 seconds, during which time participants were instructed to view the image, move their eyes over the image, and try to remember as much as possible about the image. Images were controlled using Experiment Builder (SR Research). Immediately following the visually processing period there was a ‘mental representation period’ with a blank white background presented at full resolution for 4 seconds, during which time participants were asked to mentally represent the image that had just been viewed. During the mental representation period there was nothing on the computer screen – it was completely blank. Participants were asked to keep their eyes open and were informed they could move their eyes if desired providing the eye movements were within the realms of the display screen. Participants were told a blank screen would be presented during this time. At 10 seconds into the trial participants heard a pre-recorded aural-verbal question (spatial or perceptual) played over a pair of speakers – one speaker located at either side of the participant. There were two types of questions - perceptual and spatial. The perceptual question was “what colour was the…” followed by the name of the relevant target object (i.e., “bench”) and the spatial question was “what side was the…” followed by the name of the relevant target object (i.e., “bench”). Nine images were randomly assigned the perceptual question and nine images were randomly assigned the spatial question. Question type was counterbalanced across subjects so this means the perceptual question become a spatial question for nine images and the spatial question became a perceptual question for nine images. Every question was a different length depending on the target object name (i.e., “what colour was the bench?” versus “what colour was the man’s t-shirt?”). During this time the display screen remained blank. The question was followed by a 2 seconds of silence and then a tone (frequency 400 hertz) was played from both speakers to prompt the participants to verbally respond with the answer (i.e., “brown” or “white” respectively). Participants were asked, at the start of the experiment, to provide an answer that was clear with relation to the colour of the target, that is, participants were asked to respond with clear colour names (i.e., blue, red, green, white) rather than secondary colour names (i.e., turquoise, fuchsia, cream). The recording of eye movement was automatically stopped at the tone. The subject’s response was physically recorded by the experimenter on a sheet of paper. The display screen remained blank until the experimenter pressed a key on the host computer and the centrally positioned target dot appeared again. The participant then was asked to fixate centrally and the next trial was initiated by the experimenter. There were 18 trials for each participant which were presented in a randomised order with one practise trial randomly selected. The 12 participants were rotated around four counterbalanced stimulus sets: 1) original/perceptual-spatial, 2) original/spatial-perceptual, 3) mirror-reversed/perceptual-spatial, 4) mirror-reversed/spatial-perceptual. The behavioural within-subject variables were question type (perceptual vs. spatial) and target side (left versus right).

5.3. Results

Behavioural data

The behavioural data consisted of 12 participants' responses for 18 trials to the perceptual (nine trials) or spatial question (nine trials). Responses were either correct or incorrect. There were only two "don't know" responses (from the same participant) - these were classified as 'incorrect'. For the perceptual question the response was always a colour and care was taken not to reject plausible responses to visual questions; for example, if the target colour was 'white' but a participant responded 'cream' this was considered a correct answer (this happened on just three trials across all participants). For the spatial question the response was always either "left" or "right". The percentage of correct responses overall was 78.04 %. In order to compare the proportion of correct responses for the perceptual and spatial question, for each participant, the total number of correct responses for the perceptual question was subtracted from the total number of correct responses for the spatial question and the resulting value was divided by the total number of correct responses overall to give the 'proportional difference'. The mean proportional difference (M = .12, SD = .13) was positive indicating a higher number of correct responses for the spatial question - this was confirmed as significant ($t(11)$ = 3.220, p = .008), so participants were more accurate on spatial questions than on visual feature questions. Using the same method, the total number of correct responses when the target was on the left was subtracted from the total number of correct responses when the target was on the right for each question type. In this comparison, a negative proportional difference would indicate more correct responses when the target was on the left hand-side whereas a positive proportional difference would indicate the opposite. Figure 5.3. illustrates the proportional difference for the perceptual and spatial questions. For the perceptual question the mean proportional difference was not significantly difference from zero ($t(11)$ = .168, p = .870) and for the spatial question the mean proportional difference was not significantly difference from zero (*t*(11) = .304, *p* = .767), indicating that the side of the target object did not influence the number of correct responses.

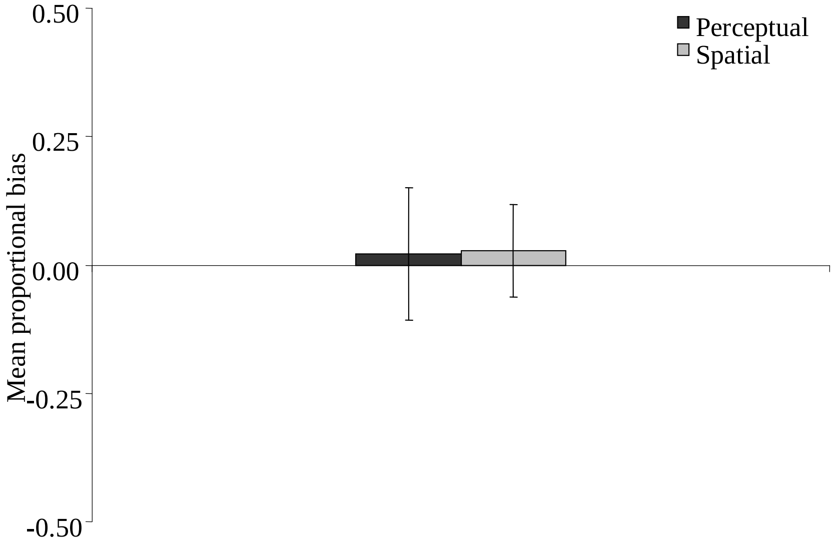


Figure 5.3. Proportional bias is illustrated for the perceptual and spatial question for Experiment 11. Error bars represent standard error of the mean.

Fixations: Entire trial

It had been originally planned to analyse fixations immediately following the onset of the word “colour” or “side” in order to assess anticipatory eye movements, for example, but due to a programming ‘time stamp’ error it was impossible to determine fixation position from the aural-verbal onset of the keyword “colour” versus “side” of the target question. Eye movements were analysed in terms of fixations across 18 trials for 12 participants using EyeLink® Data Viewer across the entire trial and during the visual processing and mental representation period individually. In total there were 6008 fixations across all participants but 230 (3.83%) fixations were removed due to errors in recording (i.e., participants moved their eyes off the screen). The mean number of fixations when the question was answered correctly (*M* = 26.70, *SD* = 3.11) was compared to the mean number of fixations when the question was answered incorrectly (*M* = 27.07, *SD* = 3.49) - the difference was not significant (*t*(11) = -.598, *p* = .562). When side was compared, left versus right, the mean number of fixations left of midline (*M* = 13.25, *SD* = 3.23) and right of midline (*M* = 13.57, *SD* = 1.96) did not significantly differ (*t*(11) = -.252, *p* = .806) indicating a balanced mean number of fixations to the left and right of midline. The mean number of fixations below midline (*M* = 12.61, *SD* = .2.73) and above midline (*M* = 14.19, *SD* = 1.23) also did not differ significantly (*t*(11) = -1.853, *p* = .091). The mean fixation position (pixels) was then analysed: if there was a tendency to explore the left side to greater leftward extremes compared to the right, or vice versa, this should be reflected in the mean pixel position as it should be weighted in one direction (i.e., left of midline) or another (i.e., right of midline). Figure 5.4 shows the distribution of fixations across the horizontal plane (a) and vertical plane (b) for the entire trial. The overall mean horizontal fixation position (*M* = 521.70, *SD* = 25.09) was towards the right side of midline but was not significantly different from midline (*t*(11) = 1.338, *p* = .208). However, the mean vertical fixation position (*M* = 397.24, *SD* = 16.36) was significantly above midline (*t*(11) = 2.804, *p* = .017) indicating that, on average, participants explored above midline to greater extents than below midline.

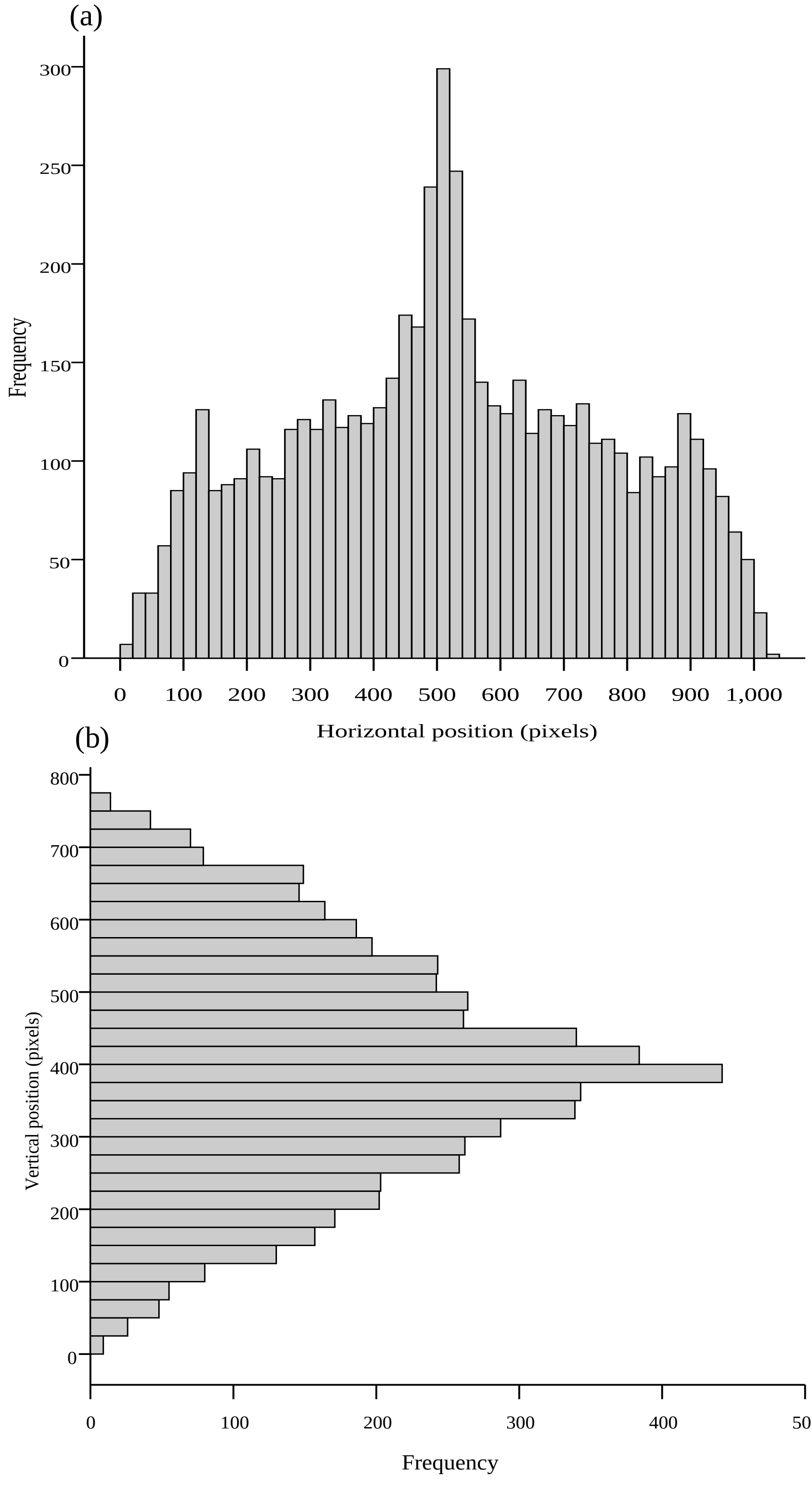


Figure 5.4. The distribution of fixations in Experiment 11. In (a) values represent fixations on the horizontal plane and in (b) values represent fixations on the vertical plane. The midpoint in each case is indicated by a solid back line.

Figure 5.5 shows the distribution of fixations by duration (ms); according to the previous literature (Henderson, 2000) most fixation durations should fall between 200ms and 600ms - this was indeed the case.

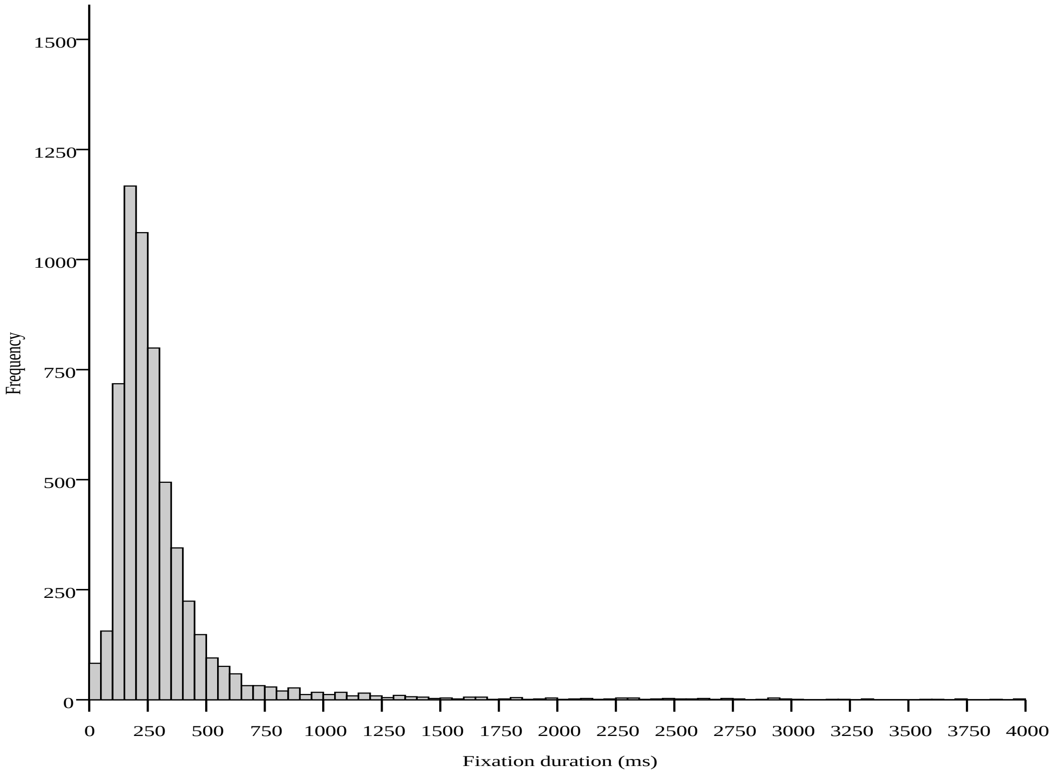


Figure 5.5. The frequency of fixation duration (ms) in Experiment 11.

In Figure 5.6 the average fixation duration (ms) on the left and right hand-side of midline and also above and below midline is illustrated. The overall duration for fixations left of midline and right of midline did not significantly differ from one another (*t*(11) = .471, *p* = .647). However, the overall duration for fixations below of midline and above midline were significantly different (*t*(11) = 3.613, *p* = .004) with longer fixations below midline compared to above midline.

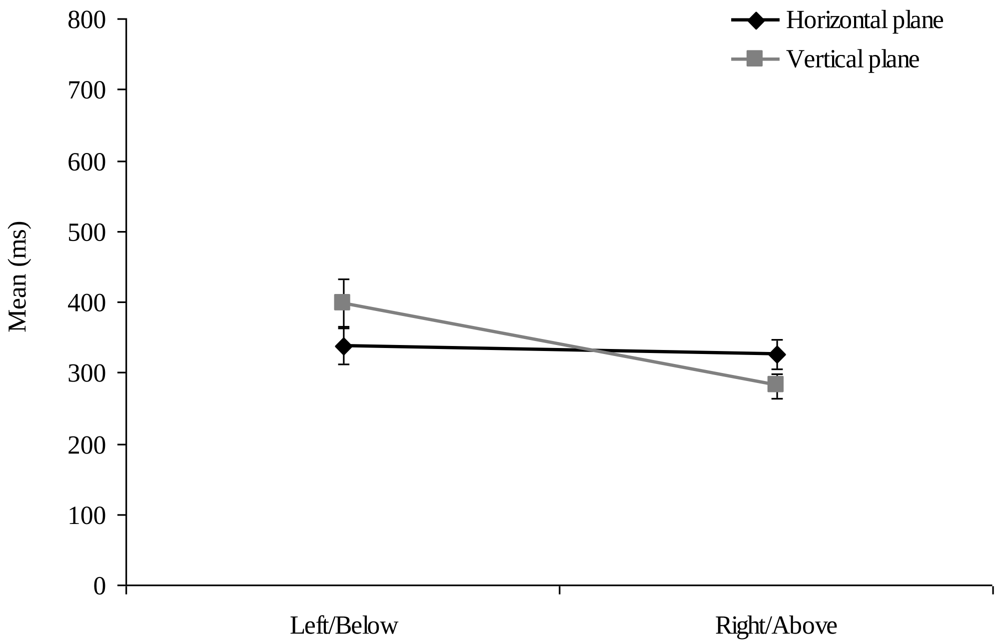


Figure 5.6. The mean fixation duration for fixations on the horizontal and vertical plane in Experiment 11.

Fixations: Visual processing versus mental representation

Fixations were then analysed in exactly the same way for the visual processing period (0 to 5999ms of the trial) and the mental representational period (6000 to 10000ms of the trial). Figure 5.7 illustrates the mean number of fixations left and right of midline on the horizontal plane, and above and below midline on the vertical plane, for the visual processing and mental representation period.

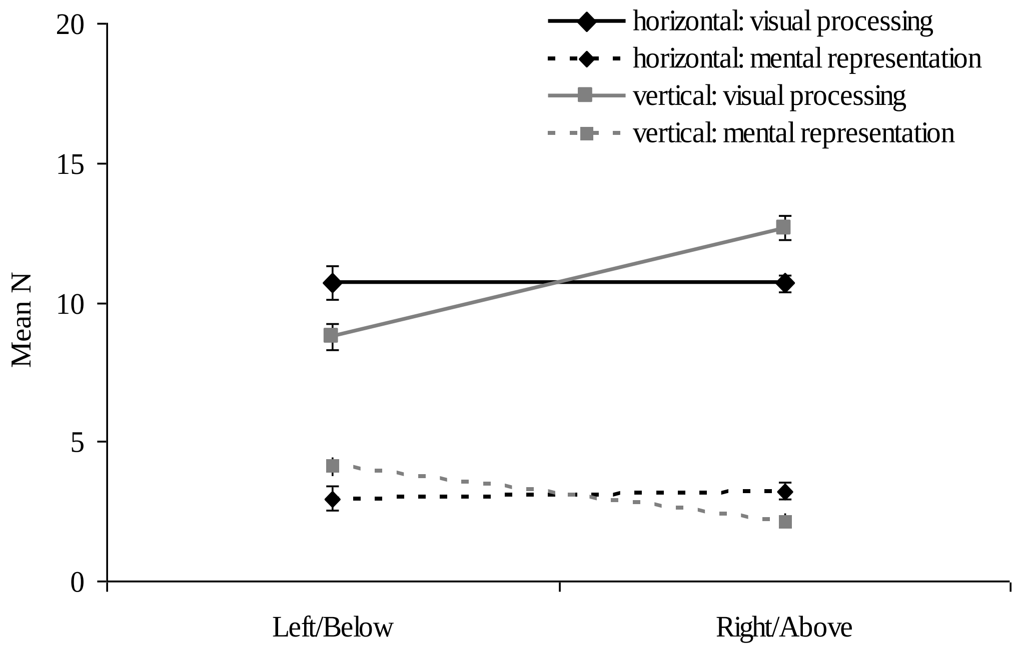


Figure 5.7. The mean number of fixations on the horizontal and vertical plane for each processing period in Experiment 11.

A repeated-measures ANOVA with period (visual processing vs. mental representation) and side (left vs. right) as the within-subject variables showed a main effect of period ($F(1,11) = 565.12$, $MSE = 1.219$, $p < .001$) indicating that there were significantly more fixations during the visual processing period compared to the mental representation period. There was no main effect of side ($F(1,11) = .046$, $MSE = 3.901$, $p = .834$) and no interaction between period and side ($F(1,11) = .211$, $MSE = 1.100$, $p = .655$). A repeated-measures ANOVA with period (visual processing vs. mental representation) and vertical position (below vs. above) as the within-subject variables showed a significant main effect of period ($F(1,11) = 473.97$, $MSE = 1.443$, $p < .001$), a significant main effect of position ($F(1,11) = 5.268$, $MSE = 2.177$, $p = .042$) and a significant interaction between period and position ($F(1,11) = 66.06$, $MSE = 1.569$, $p < .001$). The mean fixation position (pixels) for the visual processing and mental representation period was then analysed.

Figure 5.8 shows the mean horizontal fixation position left and right of midline, as well as the mean vertical position below and above midline, for the visual processing and mental representation period. The mean horizontal fixation position was not significantly different from midline for the visual processing period ($t(11) = .828$, $p = .425$) nor the mental representation period ($t(11) = 1.612$, $p = .135$). The mean vertical fixation position was significantly above midline during visual processing ($t(11) = 6.182$, $p < .001$) but significantly below midline during mental representation ($t(11) = -4.060$, $p = .002$) - this difference was also significant (t(11) = 5.816, p < .001).

The mean fixation duration (ms) for the visual processing and mental representation period was then analysed. Table 5.2 presents the mean duration (ms) for fixations left and right of midline as well as below and above midline during visual processing and during mental representation. A repeated-measures ANOVA with period (visual processing vs. mental representation) and side (left vs. right) as the within-subject variables showed a significant main effect of period ($F(1,11) = 16.692$, $p = .002$), indicating that there were significantly longer fixations during the mental representation period compared to the visual processing period. There was no significant main effect of side ($F(1,11) = 1.494$, $p = .247$) and no significant interaction between period and vertical position ($F(1,11) = 1.422$, $p = .258$). A repeated-measures ANOVA with period (visual processing vs. mental representation) and vertical position (below vs. above) as the within-subject variables showed a significant main effect of period ($F(1,11) = 16.548$, $p = .002$), a significant main effect of vertical position ($F(1,11) = 8.790$, $p = .013$), indicating significantly longer fixations above midline compared to below, and a significant interaction between period and vertical position ($F(1,11) = 9.000$, $p = .012$), indicating that during visual processing there were longer fixations above midline but that during mental representation this effect was reversed with longer fixations below midline.

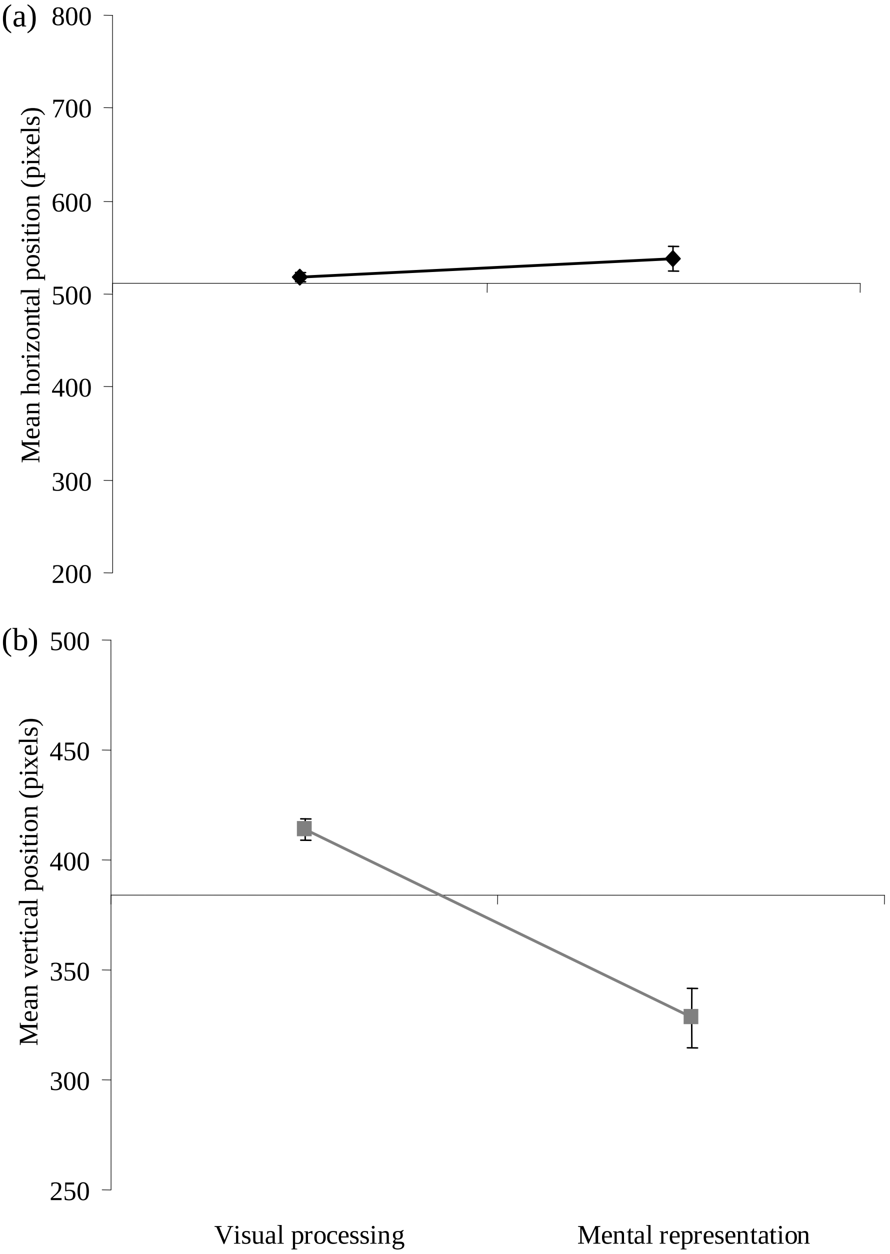


Figure 5.8. The mean fixation position in Experiment 11. The mean position (pixels) on the horizontal plane (a) and vertical plane (b) during each processing period is shown. Error bars represent standard error of the mean.

Condition	Mean (ms)	(SD)
Horizontal plane		
Visual processing fixation left	251.29	(31.85)
Visual processing fixation right	250.13	(31.89)
Mental representation fixation left	757.20	(503.91)
Mental representation fixation right	645.60	(320.36)
Vertical plane		
Visual processing fixation below	249.39	(26.09)
Visual processing fixation above	251.50	(35.17)
Mental representation fixation below	764.79	(451.30)
Mental representation fixation above	509.50	(272.13)

Table 5.2. The mean duration of fixations of eye movements in the horizontal and vertical plane.

5.4. Discussion

The results can be summarised as follows. The experiment showed no lateralised memory biases when participants were asked to recall either perceptual (“what colour was the…”) or spatial (“what side was the…”) information from a visually processing natural world scene. Although recall accuracy was balanced when recalling these two types of information from the left versus the right side, there were more correct responses for the spatial question (i.e., “what side was the…”) compared to the perceptual question (i.e., “what colour was the…”). Overall, the participants’ horizontal eye movements reflected the behavioural data with no overall left versus rightward biases. There was a balanced number of fixations to the left and right side of the scene, each side of the scene was explored to the same extent, and each side of the scene was explored for the same duration. There was a significant difference in the number of fixations (i.e., fixation count) when participants were visually processing the natural scene compared to mentally representing it, with fewer fixations during mental representation, but again there was no lateralised bias. In terms of vertical eye movements while a similar number of fixations were made above and below midline, the upper section of the scene was explored to a greater extent than the lower section (i.e., greater fixation distance) but fixation duration (i.e., time length of the fixation) was longer below midline; this seemed to be predominantly driven by the mental representation period for which fixations below midline were particularly long in duration.

The behavioural results in the current study are entirely consistent with the research reported throughout this thesis but are inconsistent with the previous literature that has clearly found lateralised biases for the recall of details from highly familiar imagined scenes and novel spatial layouts that have been processed visually (Bourlon et al. 2011; Della Sala et al. 2010; McGeorge et al. 2007). The results suggest, therefore, that even with direct visuo-spatial processing lateralised memory biases are somewhat difficult to demonstrate and indicate that these lateralised biases perhaps occur under very specific conditions. It is possible that lateralised memory biases for natural scenes are simply a product of familiarity with repeated attentional orienting towards the left hand-side of the scene leading to deeper encoding of a leftward visuo-spatial bias. But it has also been suggested in other research by Della Sala et al. (2010) that lateralised memory biases can occur for completely *novel* visually processed stimuli. It is important to note, however, that the lateralised biases in this research study were found for a feature binding task that involved remembering characteristics like shape, colour, and location of a previously presented visual stimulus within an artificial display - the measure was the recall error in selecting matching aspects from a subsequently presented array (i.e., six possible colours and six possible shapes). Arguably, this is not the same as retrieving information entirely from a mental representation with no visual-perceptual prompt. That is not to say that these results were due to a bias in visuo-spatial perception as, in fact the authors showed in an additional experiment that this was unlikely; rather, it most likely highlights that the type of retrieval in each case is different. Moreover, it is possible that memorising information from different types of spatial layout - artificial versus natural scenes - elicits different patterns of recall. One reason for this could relate to the sheer amount of detail in natural scenes as, arguably, there is far more competition between elements of natural scenes than artificial displays. Indeed, in the current study the lower number of correct responses for the perceptual condition could be a result of ‘colour competition’ at the point of recall; the higher number of responses for the spatial question may have been a result of less competition at the point of recall, that is, fewer items that could have been perceived as potential targets. Time to response onset for the perceptual versus spatial question would have been a perfect measure of this, with longer responses for the perceptual question (i.e., more competition) in comparison to the spatial question (i.e., less competition).

The eye movement data from the current study do not agree with the previous literature that has shown a significant tendency to make more fixations on the right hand-side but produce significantly longer fixations on the left when free viewing visual images (Harvey, Gilchrist, Olk, & Muir, 2003) and an association between the number of fixations and recall accuracy (Loftus, 1972). The current study did complement the previous research in terms of longer fixations during mental representation than during visual processing (i.e., Henderson & Hollingworth, 1999) but differs from the previous literature in that similar patterns of eye movements were not clearly found during mental representation compared to visual processing (Brandt & Stark, 1997; Laeng & Teodorescu, 2002). With regards to this last point, it is also possible that memorising information from different types of spatial layout, such as artificial checkerboard (Brandt

& Stark, 1997; Laeng & Teodorescu, 2002) versus natural scenes (current study), elicits different patterns of eye movements. Indeed, the difference in the number of fixations (i.e., fixation count) between the visual processing and mental representation period in the current study (in addition to the difference in fixation duration) could indicate something important about mental representation: that eye movements interfere with the ability to accurately mentally represent and retrieve information. Suppressing eye movements may help participants to better mentally represent the scene - this has already been demonstrated in the previous literature (Rode, Revol, Rossetti, Boisson, & Bartolomeo, 2000). It is possible that participants use a visual imagery strategy to memorise natural real-world scenes with greater detail and thus reduce the number of eye movements required to preserve the image. On the other hand, participants may use a visual scanning strategy for mentally representing more abstract artificial stimuli – moving their eyes over a virtual checkerboard pattern, for example, in the same way as during visual processing in order to preserve the image. Of course, it is possible that in the current experiment the difference between the number of fixations during visual processing and mental representation may simply be due to the fact that participants were specifically instructed to move their eyes around the scene to memorise as much information about the scene as possible, but in the latter they were given no instruction about eye movements. Finally, asking participants to recall material from either the left or the right-hand side of the natural may have been too insensitive a measure; the addition of a certainty scale within the current paradigm (as in Chapter 3 and 4) may give rise to greater sensitivity to lateralised memory biases.

The finding of a significant number of fixations above midline is consistent with the previous research in the pseudoneglect domain that has shown participants demonstrate biases towards the upper visual field when bisecting vertical lines (Bradshaw, Nettleton, Nathan, & Wilson, 1985; Fink, Marshall, Weiss, & Zilles, 2000; Shelton, Bowers, &

Heilman, 1990). However, during mental representation the current study showed that participants fixated more often *below* midline. This is novel, and one interesting possibility is that allowing the eyes to drift downward may be a signature of a highly controlled attentional system that aims to ‘shut-out’ further information processing; looking downward could potentially reduce the amount of additional processing if, from an evolutionary point of view, the upper visual field is specialised for distance-in-depth vision (e.g., Previc, 1990).

In conclusion, the current study implies that when temporary visuo-spatial representations are formed from the direct visual processing of natural scenes, lateralised asymmetries are not readily observed in recall regardless of whether perceptual or spatial information is retrieved. The current study has, however, provided hints that spatial information may be easier to retrieve than perceptual information, albeit equally so for each side of space. In addition, patterns of eye movements during mental representation are not necessarily the same as those during visual processing and this may be related to the type of spatial layout in question. Taken together, the behavioural and eye tracking results indicate the need for further research in this field.

Chapter 6

How internal attentional-orienting influences external attentional orienting.

6.1. Introduction

The focus of the thesis so far has been on demonstrating purely representational forms of pseudoneglect, that is, pseudoneglect in the complete absence of direct visual processing. It has also been argued throughout this thesis that the most fitting account of representational pseudoneglect is the activation-orientation hypothesis (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). The activation-orientation hypothesis has enjoyed clear support from studies that show the portion of a visually presented horizontal line, left or right, which receives the most attention is perceived as longer (Bultitude & Davies, 2006; Toba, Cavanagh, & Bartolomeo, 2011). There have been similar findings for stimuli that are mentally represented (Nicholls & McIlroy, 2010). Probably the most convincing support for the activation-orientation hypothesis comes from brain imaging and neuro-conduction studies that clearly implicate the involvement of the right hemisphere during line bisection tasks, both with and without direct visual processing, in healthy participants (Cattaneo, Silvanto, Pascual-Leone, & Battelli, 2009; Çiçek, Deouell, & Knight, 2009; Fink, Marshall, Weiss, & Zilles, 2001; Gobel, Calabria, Farne, & Rossetti, 2006). In the current Chapter, Experiments 12 and 13, the spotlight is on how *internal* attentional orienting can influence *external* attentional orienting. The aim is to conduct an initial exploration into whether attentional orienting can be shared between two tasks at the same time or whether attentional orienting is prioritised for one task over the other in a competitive setting.

Adult participants and children were asked to perform two pseudoneglect tasks at the same time, traditional visual line bisection (external attentional orienting) and mental number line representation (internal attentional orienting). Both of these tasks are assumed to tap into attentional orienting mechanisms in the right hemisphere but in different ways, that is, via direct visual processing or through mental representation. Visual and mental number line bisection, therefore, provide a strong basis for making assumptions about whether attentional orienting is additive because we have a comprehensive understanding of each task individually to begin with. There are several possible outcomes: the magnitude of pseudoneglect on visual line bisection may remain *constant* which may suggest that attentional orienting can be efficiently engaged in parallel for two pseudoneglect tasks. Pseudoneglect on visual line bisection may be *enhanced* which may indicate that when attentional orienting is doubly engaged there is additional ‘excitation’ of these mechanisms. Pseudoneglect on visual line bisection may also be *attenuated* which may suggest that when the two tasks are paired, mental number line bisection is prioritised for attentional orienting over visual line bisection.

Several studies have shown that healthy participants display similar magnitudes of pseudoneglect on visual and mental number line bisection (Longo & Lourenco, 2007; Longo & Lourenco, 2010) which indicates that similar mechanisms do indeed underlie each form of the bias – an assumption of the current paradigm. There have been several demonstrations of pairing tasks that explore representational forms of pseudoneglect (Laeng, Buchtel, & Butter, 1996; Lourenco & Longo, 2009; Loftus, Nicholls, Mattingley, & Bradshaw, 2008; Nicholls, Loftus, & Gevers, 2008) but there are no studies comparing how *representational* and *visual* pseudoneglect directly interact with one another. Most studies of visual pseudoneglect have been more focused on how the bias is mediated by characteristics of the stimulus (McCourt & Jewell, 1999), the mode of presentation (Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Luh, 1995; McCourt, Garlinghouse, & Butler, 2000; McCourt & Jewell, 1999), line length (Chokron & Imbert, 1993; Manning, Halligan, & Marshall, 1990; McCourt & Jewell, 1999) or the hand used to perform the bisection (Bradshaw, Bradshaw, Nathan, Nettleton, & Wilson, 1986; Brodie, 2010; Brodie & Pettigrew, 1996; McCourt, Freeman, Tahmahkera-Stevens, & Chaussee, 2001). Another important reason for selecting these two particular tasks was in order to explore a competition account of attentional orienting across age. It is interesting to compare the trade-off between visual and representational attentional-orienting as a function of age because it is already known that age affects both forms of pseudoneglect individually, but it is unknown how age affects the interplay between the two. On visual line bisection, for instance, it has been shown that performance for children on visual line bisection is far more variable than for adults; leftward biases have been shown for children aged five to six years old (De Agostini, Curt, Tzortzis, & Dellatolas, 1999) whereas many other studies with children less than 12 years of age have shown that biases on visual line bisection occur in the direction of hand – towards the left or right depending on which hand is used (Bradshaw, Nathan, Nettleton, Wilson, & Bradshaw, 1987; Dellatolas, Coutin, & De Agostini, 1996; Failla, Sheppard, & Bradshaw, 2003; Hausmann, Waldie, & Corballis, 2003). Interestingly, children and adults are also thought to have differential representations of the mental number line. There is a linear representation of the number line for adults but a logarithmic representation or two linear representations – one for double digits and one for single digits – for children (Berteletti et al., 2010; Ebersbach, Luwel, Frick, Onghena, & Verschaffel, 2007; Moeller, Pixner, Kaufmann, & Nuerk, 2009). It has already been shown in this thesis that a representational form of pseudoneglect can be demonstrated across lifespan; if this was *also* shown in the current context it would provide stronger evidence for the existence of attentional orienting across lifespan.

Participants in the current study were adults aged between 18 and 38 years (Experiment 12) and children aged between 4 and 10 years (Experiment 13). Participants were asked to conduct a horizontal visual line bisection task and at the same time perform a task that involved mentally representing a number line (mental number bisection was only for adult participants).

6.2. Experiment 12

6.2.1. Participants

There were 30 healthy adult participants recruited from the University of Edinburgh with normal or corrected-to-normal vision and normal hearing, who spoke English as a native language, were aged between 18 and 38 years old, and were exclusively right handed as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). Ethical approval for the experiment was obtained from the University of Edinburgh ethics committee.

6.2.2. Stimuli

There were eight different horizontal lines measuring 8, 10, 12, 14, 16, 18, 20, 22cm printed in black on A4 paper in landscape orientation. There were four horizontal lines per page randomly staggered across the page in the same way as previous research (Jewell & McCourt, 2000). Lines 8 to 14cm were printed on the same page and lines 16 to 22cm were printed on the same page. The reason for this grouping was to avoid obvious differences between the lines (i.e., 8 and 22cm) which may have influenced participants' bisection judgements. There were therefore two A4 pages each containing four horizontal lines – these pages formed one stimulus set. The sheets of paper were white and were presented on a white board which was cut to the size of the experimental table and firmly attached. The aim of presenting the white paper on the white board was to prevent the participant from using the edges of the paper as a reference point for judging the centre of the lines. There were also 64 unique number pairs with a numerical interval of 36 (i.e., 11_47; 74_92). The interval of 36 was chosen randomly and tested in a small pilot study (N3) conducted to assess whether participants would realise that the same interval was being used on every trial; they did not. The lowest true midpoint was 29 and the highest true midpoint was 92.

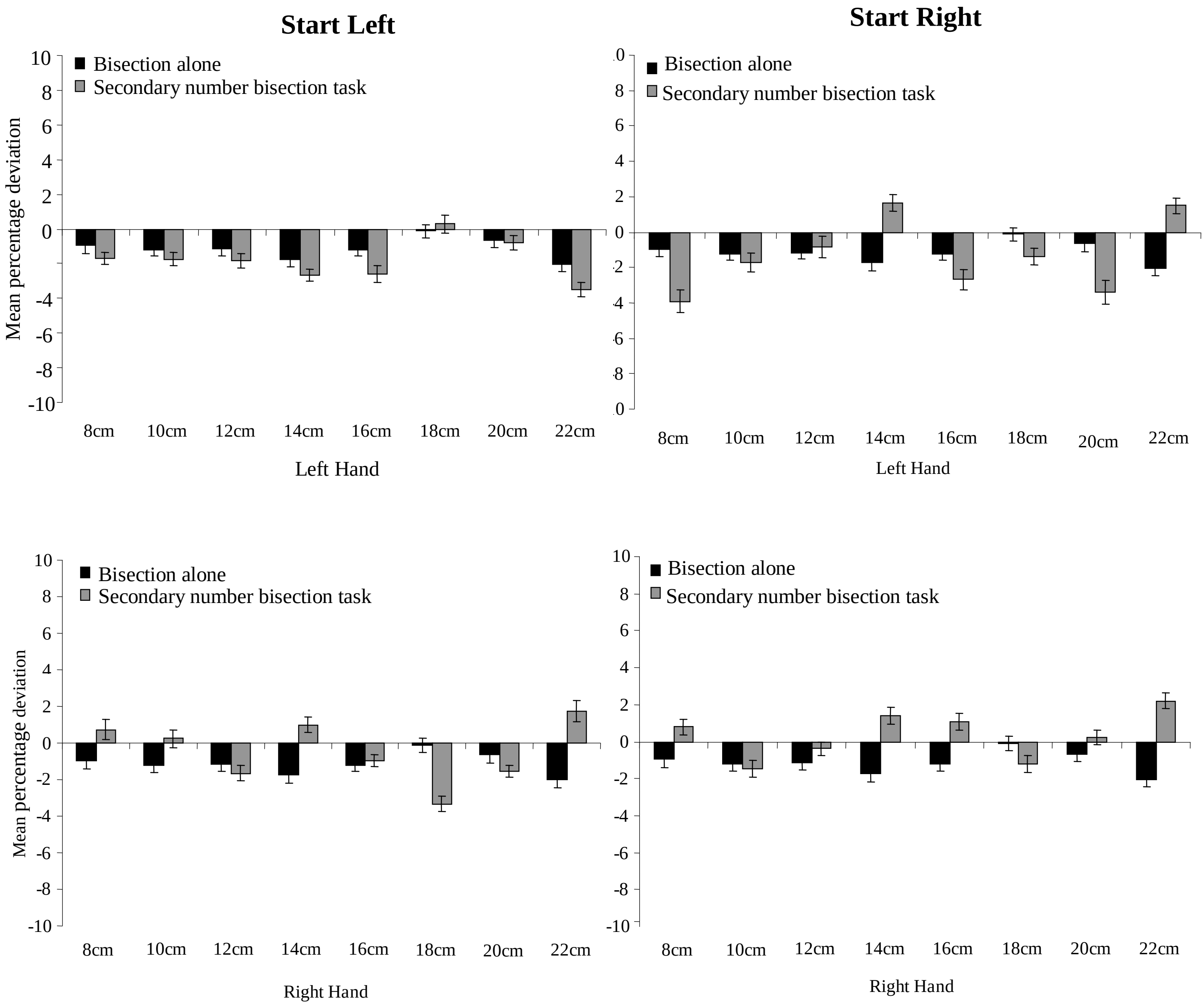
6.2.3. Procedure

Participants were seated in a quiet room on a non-swivel chair at the experimental table and given written task instructions. Following the instructions the participant carefully aligned his/her body midline with the centre of the white board marked by a small black target cross (+) as directed by the experimenter who was seated on the opposite side of the table. There were two different starting positions, left and right, and all participants completed the task under both start side positions. The start left position was indicated by a small black dot drawn on the board 20cm to the horizontal left of the black target cross; an identical start right dot was drawn 20cm to the horizontal right of the target cross. The participants completed the task using the left hand and the right hand in both starting positions (counterbalanced across participants). The trial began when the experimenter placed one of the two pages from the stimulus set directly in front of the participant. The centre of the page was aligned with the centre of the participant’s body midline. Four small marks, representing A4 landscape orientation, were centred around the black target cross to help the experimenter achieve this with ease. There were three conditions under which participants bisected each line on the page. In the *baseline condition* participants were required to bisect the visually presented horizontal lines on the page, one at a time, at their own speed, by marking a vertical line through the perceived centre of the horizontal line. Participants were asked to return to the starting position, left or right, before bisecting each line. Once completed, the page was removed from view and replaced with another by the experimenter. In the *mental number line (small or large number first)* the participant placed his/her hand on the left/right starting position and the experimenter presented the participant with an aural-verbal number pair (i.e., 11_47) spoken in monotone with a slight pause between the numbers. The small number in the pair was presented first for half the trials (N1) and the larger number in the pair was presented first for half the trials (N2). The participant was instructed to hold the number pair in mind whilst bisecting the first horizontal line on the page and then, after bisecting, immediately respond with the perceived midpoint between the two numbers without actively calculating. The midpoint was recorded by the experimenter on paper. The participant then returned the hand to the starting position and the next trial began. The numerical interval between the numbers in the pair was always 36. The presentation of the small or larger number first was blocked across trials. All participants heard exactly the same number pairs in each case but in a randomised order. The within-subject variables were hand (left hand vs. right hand), starting position (start left vs. start right), condition (baseline vs. N1 and N2), and line length (x 8). Trials were blocked by hand then starting position then condition. Participants always started with the right hand in a start left condition but the experimental condition (baseline vs. N1 and N2) was fully counterbalanced. The experiment took 45 minutes to complete.

6.2.4. Results

Visual line bisection

For visual line bisection the directional bias from the true midpoint was calculated as a percentage of the line length. This is a standard method of computing line bisection performance (Failla et al., 2003; Hausmann et al., 2002; 2003) and takes into account the magnitude of bias as a function of stimulus length. The resulting score is negative or positive: negative scores indicate a leftward bias while positive values indicate a rightward bias (relative to the true centre). A score of zero reflects no bias. For visual line bisection the overall mean percent deviation was negative (M = *-.78* SD = 1.05), indicating a leftward bias, and significantly different from zero ($t(29) = -4.072$, $p < .001$). An initial exploration of the secondary mental number line task found that the mean percent deviation when the small number was presented first (M = -.80, SD = 1.17) and the mean percent deviation when the larger number was presented first (M = -.84, *SD* = 1.26) were not significantly different (*t*(29) = .312, *p* = .757) and so the data were collapsed across small/large number first. An initial exploration also showed that the overall mean percent deviation for the left hand (*M* = -1.43, *SD* = 1.55) and right hand (*M* = -.13, *SD* = 1.06) were significantly different from one another (*t*(29) = -1.30, *p* < .001) so the data were further explored for each hand separately. Figure 6.1 shows the mean percent deviation for visual line bisection for the left hand (top panel) and right hand (bottom panel) as a function of condition (baseline vs. number secondary task) and line length (8 to 22cm) for the Start Left condition and Start Right condition respectively.



Start Left

Start Right

Figure 6.1. The mean percent deviation for visual line bisection in Experiment 12. The mean values are shown for the left hand (top panel) and right hand (bottom panel) as a function of condition and line length in the Start Left and Start Right conditions. Error bars indicate standard error of the mean.

For the *left hand*, a repeated-measures ANOVA with start side (start left vs. start right), condition (baseline vs. mental number line) and line length (x8) as the within-subject variables showed no significant effect of start side (*F*(1,29) = .620, *MSE* = 19.683, *p* = .438), but a significant effect of condition (*F*(1,29) = 5.863, *MSE* = 7.503, *p* = .022) with greater leftward bias when performing the secondary mental number line bisection task at the same time as visual line bisection. There was a highly significant effect of line length (*F*(7,203) = 10.503, *MSE* = 4.755, *p* < .001) with increasing leftward bias as line length increased. There was no significant interaction between start side and condition (*F*(1,29) = 4.139, *MSE* = 3.424, *p* = .051), but a highly significant interaction between start side and line length (*F*(7,203) = 26.106, *MSE* = 5.648, *p* < .001) with a clear increase in bias as line length increased in the start left but not the start right condition. There was a significant interaction between condition and line length (*F*(7,203) = 2.868, *MSE* = 2.909, *p* = .007) and a highly significant interaction between start side, condition and line length (*F*(7,203) = 5.670, *MSE* = 2.451, *p* < .001) driven by the fact that the greatest leftward biases were for start left, when the secondary mental number line bisection task was performed in parallel with visual line bisection, and for the longest line lengths. For the *right hand*, a repeated-measures ANOVA with start side (start left vs. start right), condition (baseline vs. mental number line) and line length (x8) as the within-subject variables showed a significant main effect of start side (*F*(1,29) = 8.532, *MSE* = 17.332, *p* = .007) with more consistent leftward biases in the start left position, but no significant main effect of condition (*F*(1,29) = .808, *MSE* = 10.785, *p* = .376). There was a highly significantly effect of line length (*F*(7,203) = 13.900, *MSE* = 6.801, *p* < .001) with increasing bisection error for longer line lengths mostly in the start left condition, no significant interaction between start side and condition (*F*(1,29) = .009, *MSE* = 5.965, *p* = .926) but a highly significant interaction between start side and line length (*F*(7,203) = 5.722, *MSE* = 4.690, *p* < .001) driven by the fact that the line length effect was far more obvious when starting left. There was also a significant interaction between condition and line length (*F*(7,203) = 8.806, *MSE* = 3.576, *p* < .001) and a highly significant interaction between starting position, condition and line length (*F*(7,203) = 2.960, *MSE* = 2.662, *p* = .006) driven by the fact that the greatest leftward biases were for start left, when mental number line bisection was performed in parallel, and when line length was the longest.

Mental number line bisection

The data for the secondary mental number line bisection task were also analysed in order to ensure that participants showed a leftward bias which is important if inferences are to be made about competition between attentional orienting mechanisms. For the mental number line bisection the directional bias from the true midpoint was calculated in terms of numerical distance from the true midpoint; if the true numerical midpoint was ‘29’ but participants responded with a perceived midpoint of “26” this would be a negative directional bias of ‘-3’ (towards the smaller number in the pair) but a response of “31” would yield a positive directional bias of ‘3’ (towards the larger number in the pair). The overall mean bias (*M* = -1.27, *SD* = 1.42) was towards the smaller number in the pair and was significantly different from zero (*t*(29) = -4.897, *p* < .001). The data were then analysed in the same way as the visual line bisection data in order to assess whether the perceived midpoint deviation also changed with factors of start side (left vs. right), condition (small or large number first) and line length. Figure 6.2 shows the mean bias for mental number line bisection for the left hand (top panel) and right hand (bottom panel) as a function of condition (small number first vs. large number first) and line length (8 to 22cm) for the Start Left condition and the Start Right condition.

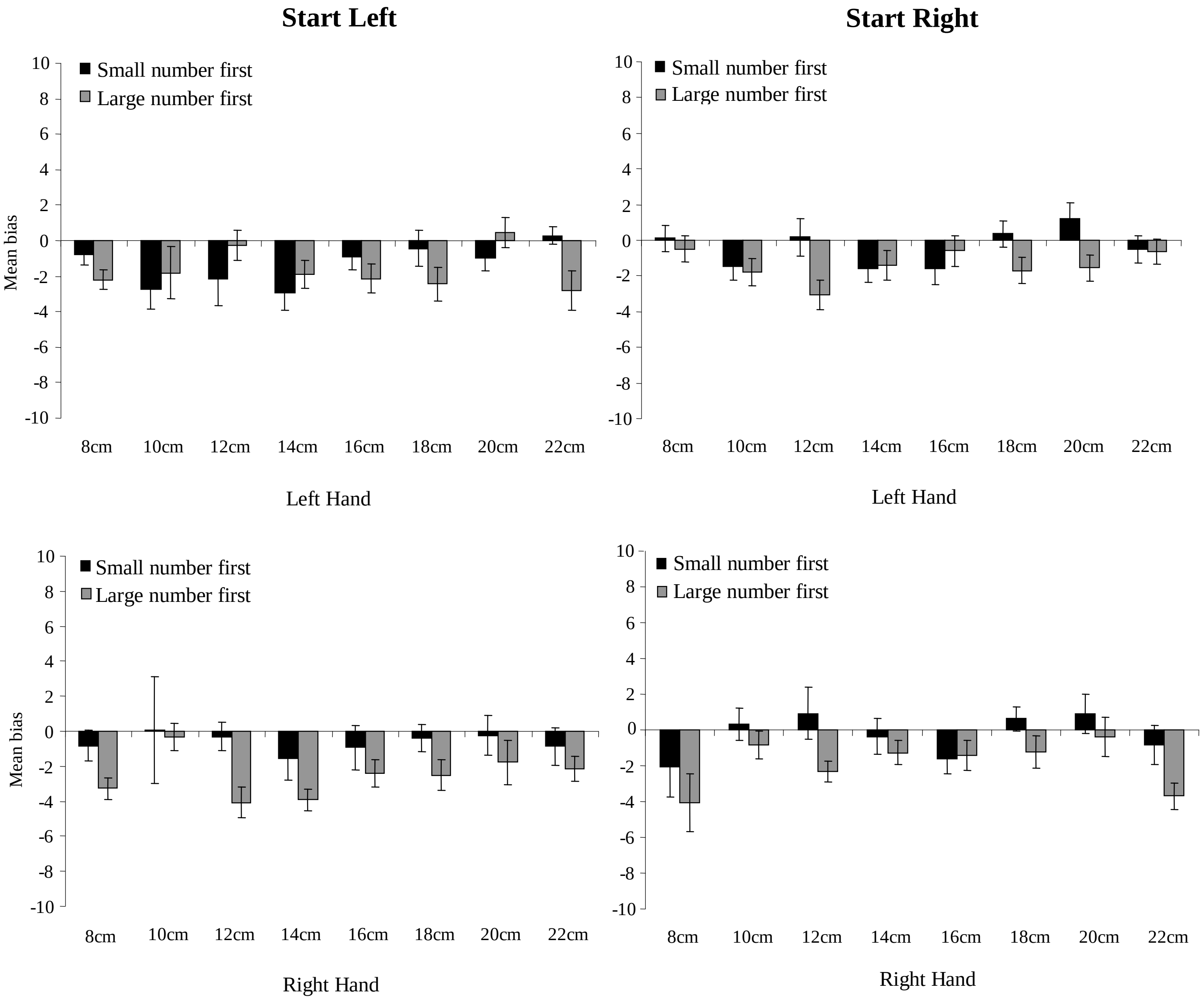


Figure 6.2. The mean bias for mental number line bisection in Experiment 12. Mean values are shown for the left hand (top panel) and right hand (bottom panel) as a function of condition and line length in the Start Left and Start Right conditions. Error bars indicate standard error of the mean.

During *left hand* response a repeated-measures ANOVA with start side (start left vs. start right), condition (small number first vs. large number first), line length (x 8) showed no significant effect of start side (*F*(1,29) = 2.001, *MSE* = 40.120, *p* = .168), but a highly significant main effect of condition (*F*(1,29) = 5.058, *MSE* = 20.201, *p* = .032), with the presentation of a larger number first eliciting a greater leftward bas, a marginal significant effect of line length (*F*(7,203) = 2.128, *MSE* = 18.775, *p* = .042), no significant interaction between starting position and condition (*F*(1,29) = .871, *MSE* = 33.350, *p* = .358), start side and line length (*F*(7,203) = .343, *MSE* = 20.265, *p* = .933), condition and line length (*F*(7,203) = 1.073, *MSE* = 22.885, *p* = .382), but a significant interaction between start side, condition and line length (*F*(7,203) = 2.883, *MSE* = 20.874, *p* = .007). During *right hand* response a repeated-measures ANOVA with start side (start left vs. start right), condition (small number first vs. large number first), line length (x 8) showed no significant effect of start side (*F*(1,29) = 1.873, *MSE* = 33.686, *p* = .182), but a highly significant main effect of condition (*F*(1,29) = 10.274, *MSE* = 74.559, *p* = .003), no significant effect of line length (*F*(7,203) = 1.974, *MSE* = 39.160, *p* = .060), no significant interaction between starting position and condition (*F*(1,29) = .219, *MSE* = 18.676, *p* = .643), start side and line length (*F*(7,203) = .915, *MSE* = 38.860, *p* = .495), condition and line length (*F*(7,203) = .765, *MSE* = 32.066, *p* = .617), and no significant interaction between start side, condition and line length (*F*(7,203) = .247, *MSE* = 34.234, *p* = .973). A further exploration also showed that the overall mean bias for the left hand (*M* = -1.20, *SD* = 1.50) and right hand (*M* = -1.33, *SD* = 1.57) was not significantly different (*t*(29) = .614, *p* = .544). Finally, a correlation was performed to assess the relationship between the mean bias for mental number line bisection and the percent deviation for visual line bisection; there was no correlation (*r(*19) = -.037, *p* = .847).

6.2.5. Discussion

The results from Experiment 12 were very interesting and completely unique. Overall, there was a significant leftward bias on visual line bisection, enhanced by increasing line length and when the left hand was used to respond, which is consistent with the right hemisphere orienting attention towards the left side of space – because attention was oriented towards the left-hand side. The main finding was that when participants used the left hand to bisect a visually presented line performing a mental number line bisection task caused pseudoneglect to be further enhanced. To this end, the effect of the secondary task was particularly strong and consistent in a start left condition and increased as a function of line length. For the right hand, however, performing a mental number line bisection task while during visual line bisection did not have the same clear effect though there was some influence of the secondary task for longer line lengths in a start left condition; indeed in a start right condition the performance of the secondary task caused pseudoneglect to become ‘neglect’ for the longer lines (i.e., leftward bias became rightward bias). The results also showed a significant leftward bias on mental number line bisection, enhanced when a larger number was presented first relative to a smaller number, and is consistent with the right hemisphere orienting attention leftward within the mental representation. Taken together, the results provide evidence that attentional orienting on one task can influence attentional orienting on the other. These results suggest that attentional orienting can be shared between two different tasks at the same time and that when attentional orienting is doubly engaged there is a greater overall leftward bias for visual line bisection; critically, however, this seems to depend on a certain level of excitation for the right hemisphere by using the left hand or starting on the left side of space.

Experiment 13 explored exactly the same issue in children; if the same results were observed, especially when using the left hand, this would provide strong evidence that the capacity sharing mechanisms that underlie attentional orienting develop from a very early stage.

6.3. Experiment 13

6.3.1. Participants

There were 35 children aged between 4 and 10 years old recruited from a primary school. Handedness was assessed in the children by simply asking each child to pick up a pencil and draw an object of their choice on a sheet of paper and then asking whether they use that hand all the time to draw and write. There were 28 children classified as right handed. Of these, one participant was four years of age; three participants were five years of age; three participants were six years of age; three participants were seven years of age; eight participants were eight years of age; two participants were nine years of age; and eight participants were 10 years of age. There were 7 children classified as left handed. Of these, the age of one participant was unrecorded; there was one participant five years of age; two participants six years of age; two participants eight years of age, and one participant 10 years of age. All children had normal or corrected-to-normal vision and normal hearing, and spoke English as a native language. Ethical approval for the experiment was obtained from the University of Edinburgh ethics committee.

6.3.2. Stimuli

The visual line bisection stimuli consisted of six different horizontal lines measuring 10, 12, 14, 16, 18, 20cm. A smaller cohort of lines was utilised in order to reduce the number of trials for the children. Also, there was just one single line printed on a sheet of paper because a small pilot study (N2) showed that the younger children didn’t understand that they were supposed to bisect one line at a time and tended to draw a line across the middle of the page. The mental number line task was also slightly different.

The children were given a set of numbers that were individually printed on square pieces of card (4 x 4cm) in black typeface font size 20 arranged randomly on the experimental table. The numbers were 1, 3, 4, 6, 8, 10, 20, and 30. The children were asked to look at the numbers and then put the numbers in a straight line from left to right. A demonstration was not provided by the experimenter. All the children understood the instructions. The children were told they could put the numbers in a line in any order they liked and were told “line up the numbers in a way that makes sense to you”. All children, even those aged 4 and 5 years, put the numbers in a line with ease and in ascending order though the youngest child (aged 4) mixed the occasion number. The aim of this procedure was to prime the children to mentally represent numbers in a horizontal line.

6.3.3. Procedure

The experiment was conducted in a quiet classroom in the presence of a Teaching Assistant who was a full-time member of staff at the primary school. The child carefully aligned his/her body midline with the centre of a white board marked by a small black target cross (+) as directed by the experimenter in the same way as Experiment 12. The experimenter was seated on the opposite side of the table. In the *baseline condition* visual line bisection was conducted in the same way as Experiment 1 with the exception that the children only used their dominant hand, either left or right, and started from a central position which was aligned with the body midpoint and marked by a black target dot. The trial began when the experimenter placed an A4 sheet of paper on the experimental table (carefully aligned with the participants’ body mid-line as in Experiment 1). The child was asked to place a vertical line using a pencil through the middle of the horizontal line and was told “try to be as close to the middle as possible”. A practise trial confirmed that the child understood the task. Once the bisection had been made the child was asked to return the hand to the central position. Each A4 sheet containing one horizontal line was presented one at a time to the child until all sheets were completed. In the m*ental number line condition* each child was given a number from the line of earlier numbers. The dialogue at this point was as follows:

> Experimenter: "Okay, now I'm going to give you a number. The number '2'. Can you repeat that number for me?"
>
> Child: "Two".
>
> Experimenter: "That's great! Now what I want you to do is keep thinking about that Number and where it was on the line you made earlier on and keep repeating it while you mark the middle of the next line with your pencil".

The child kept verbally repeating the number and then marked the middle of the line before returning to the central starting position and receiving the next number. The mental number line task was conducted in this way because the task used for adults would have been too complicated for the children; the main point of the task was that the children mentally represented a mental number line while performing the visual line bisection task. For this particular experiment the aim was to merely explore the possibility that attention would be automatically oriented leftward when a line of numbers was held in the mind's eye. Each child completed 12 trials - there were 6 lines bisected in the baseline condition and 6 lines in the number condition.

6.3.4. Results

For visual line bisection the directional bias from the true midpoint was calculated as a percentage of the line length in the same way as Experiment 12 for 6 left handed participants and 27 right handed participants (the data for one left handed and one right handed subject was not included in the analysis because the participants in question did not finish the experiment due to tiredness). Figure 6.3 shows the percentage deviation as a function of condition (baseline vs. mental number line) and line length for left handed and right handed participants separately.

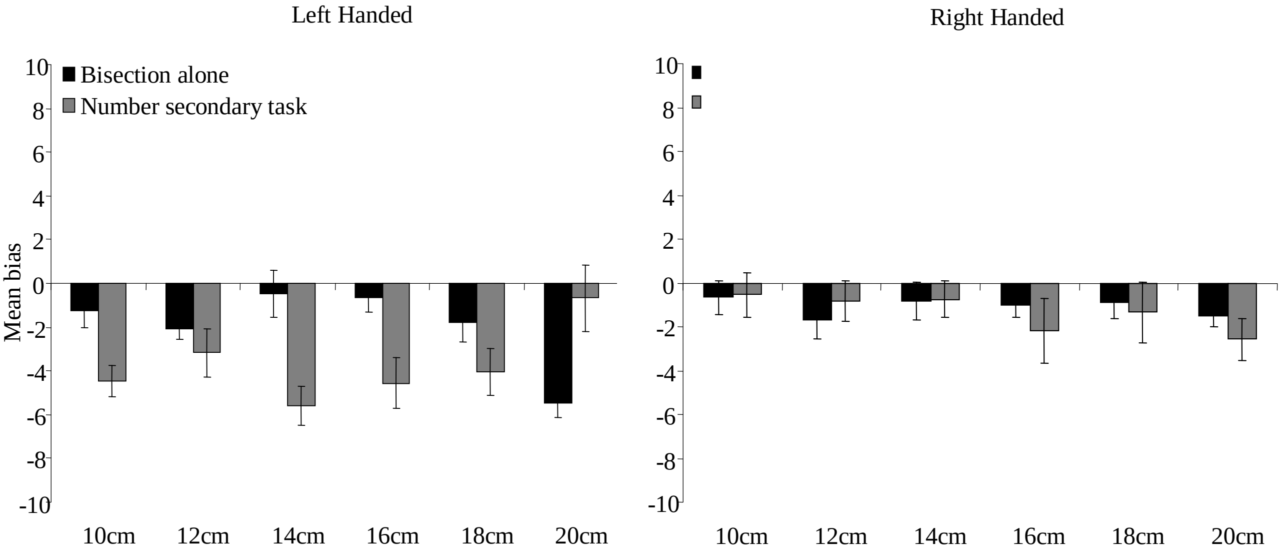


Figure 6.3. The mean percent deviation on visual line bisection in Experiment 13. The mean values are shown for left handed children participants (left panel) and right handed participants (right panel) as a function of condition and line length (8 to 22cm). Error bars indicate standard error of the mean.

A repeated-measures ANOVA was conducted on the percentage deviation for the visual line bisection data as a function of condition (baseline vs. number secondary task) and line length (x 6) for left and right handed participants separately. For *left handed participants* (N6) there was a significant effect of condition (*F*(1,5) = 7.698, *MSE* = 7.489, *p* = .039), with significantly greater leftward biases when a number was repeated out loud, but no significant effect of line length (*F*(5,25) = .026, *MSE* = 19.067, *p* = 1.00), and no significant interaction between condition and line length (*F*(5,25) = 1.778, *MSE* = 20.917, *p* = .154). For *right handed participants* (N27) there was no significant effect of condition (*F*(1,26) = .215, *MSE* = 33.494, *p* = .647), no significant effect of line length (*F*(5,130) = 1.240, *MSE* = 11.962, *p* = .294), and no significant interaction between condition and line length (*F*(5,130) = .814, *MSE* = 10.191, *p* = .542). When hand (left hand vs. right hand) was added to the repeated-measures ANOVA there was only a significant interaction between condition (baseline vs. number representation), line length, and hand (*F*(5,155) = 3.021, *MSE* = 11.921, *p* = .012).

6.3.5. Discussion

Strikingly, the results complement Experiment 12 and are also completely unique. Overall, there was a significant leftward bias on visual line bisection for both left handed and right handed children. In the current study, the leftward biases for right handed children were less than those for left handed children and for those children using the left hand performing a secondary number-based task during visual line bisection caused pseudoneglect to be further enhanced - with the exemption of the longest line (20cm). However, for both left handed and right handed children the leftward biases were consistent across all line lengths which is different from that of adults. The results provide further evidence that attentional orienting on one task can influence attentional orienting on the other, albeit no measure of actual attentional orienting for the children is available here. Following this assumption, the effect of the secondary task seems to depend on the right hemisphere being particularly activated over the left hemisphere by using the left hand.

6.4. General Discussion

The aim of the experiments reported here was to scrutinise the mechanisms that underlie attentional orienting using a unique dual-task paradigm in participants of different ages. In a novel and unique paradigm participants were asked to perform two pseudoneglect tasks at the same time, visual line bisection and mental number line representation, both of which are assumed to tap into attentional orienting mechanisms in the right hemisphere. For adults as well as children there was an overall significant leftward bias on visual line bisection. For adults pseudoneglect on visual line bisection was enhanced by increasing line length, when the left hand was used to respond, and when the starting position was on the left-hand side. For children pseudoneglect on visual line bisection was greatest for participants using the left hand but was not influenced by line length. For both adults and children performing the secondary mental number line task boosted the magnitude of pseudoneglect on visual line bisection when the left hand was used to bisect. For adults there was also an overall significant leftward bias on mental number line bisection (this was not performed by children).

For adult participants the finding of pseudoneglect on visual line bisection entirely complements the previous research (Jewell & McCourt, 2000) especially since pseudoneglect was enhanced by increasing line length (Chokron & Imbert, 1993; Luh, 1995; McCourt & Jewell, 1999) and when using the left hand (Bradshaw et al. 1986; Brodie & Pettigrew, 1996; Brodie, 2010; McCourt et al. 2001). Likewise, the finding of pseudoneglect on mental number line bisection also complements the previous literature (Loftus, Nicholls, Mattingley & Bradshaw, 2008; Loftus, Nicholls, Mattingley, Chapman, & Bradshaw, 2008; Zorzi et al. 2002). These results clearly indicate that attentional orienting (Reuter-Lorenz et al. 1990) was engaged, and shared, between the two tasks at the same time. It is also clear that attentional orienting was *mediated* in a similar way for both tasks given that the same variables, starting on the left and increasing line length, enhanced the degree of pseudoneglect on both tasks independently - despite the fact that the task demands were individually very different. The leftward bias on mental number line bisection was significantly greater when a larger number was presented first in the number pair which has been shown in previous research (Loftus et al. 2008a). This did not translate into a significantly larger impact on visual line bisection indicating that some uniqueness in engaging attentional orienting mechanisms within each task was retained. It could be argued that the increase of the leftward biased observed on visual line bisection was a function of simply performing a ‘secondary task’ but this seems very unlikely for the following reasons. If this were the case we would expect the secondary task to have the same influence when the left and the right hand was used to respond and when starting left as well as starting right - clearly this was not the case. Furthermore, dual-task research that has shown, across a range of tasks, that if two tasks performed in conjunction tap into the same cognitive resources (i.e., working memory) then performance on one or both tasks is likely to decline (Pashler, 1994). In this case the ‘decline’ of performance was manifested by significantly greater pseudoneglect or, in other words, greater bias.

The start side results in the current research are also entirely consistent with the previous research that has demonstrated favouring the right hemisphere leads to increased pseudoneglect. It has also been discussed within this thesis how boosting the engagement of the right hemisphere through the motor and visual pathways can increase the magnitude of pseudoneglect; that is exactly what happened here when the left hand started within the left hemifield. Although the previous research has noted the importance of starting right (Bowers & Heilman, 1980; Baek et al. 2002) these observations were for tactile rod bisection in the complete absence of visual processing. Similar observations of starting right have been reported for visual line bisection – but for neglect patients (Urbanski & Bartolomeo, 2008). In the previous experiments reported in this thesis it has been argued that "if the direction of bisection is consistent with the direction of attentional orienting (bisecting from the right) the lateralised bias will be enhanced" but, again, this is relevant to the representation of spatial layout in the absence of direct visual processing where it is arguably more difficult to favour the right hemisphere; though this was achieved with this thesis by presenting aural-verbal stimuli to the left ear monaurally.

For children the results also complement the previous research since leftward biases on visual line bisection were shown for both left handed and right handed participants (De Agostini et al. 1999). In fact, overall bisection results are also consistent with the research that has reported symmetrical biases in the direction of hand for children ages less than 12 years, since in the current study the biases were noticeable *less leftward* for participants using the right hand compared to the left hand (Bradshaw et al. 1987; Dellatolas et al. 1996; Failla et al. 2003; Hausmann et al. 2003). Strikingly, the effect of secondary task that involved mentally representing the number line produced the same effect for children as for adults: number line representation conducted in parallel caused pseudoneglect on visual line bisection to be significantly enhanced but only when the bisection was conducted by the left hand. It is difficult to argue that the task was simply a verbal task and that mental number line representation was not elicited. If so, there should have been no difference in performance between the two conditions (i.e., Laeng et al. 1996) since each task would have tapped into different cognitive resources. Moreover, if so, the same effect should have been seen for right and left handed participants *or even reversed* since using the right hand may preferentially engage the left hemisphere which in this case may have been more activated than the right hemisphere given the verbal nature of the task.

Taken together, the results tentatively suggest that capacity sharing mechanisms underlie attentional orienting and that these develop from a very early stage. Most importantly, internal attentional orienting can boost external attentional orienting when conditions favour the right hemisphere: this is a completely novel and unique finding.

There are, however, shortcomings of the current research. There was no baseline condition for the adult participants for mental number line bisection which would have allowed a more complete comparison between how the two tasks, visual and representational, interact as well as mediate one another. In order to provide a completely convincing account participants would need to perform a non-related dual-task; a secondary task that does not tap into attentional orienting mechanisms. Finally, dual-tasking is widely assumed to ‘load’ the central executive of working memory (Baddeley, 2007) and so it would have been interesting to explore each individual’s working memory capacity and use this as a correlation measure with overall task performance for each task individually and also for the effect of the secondary task (i.e., Cowan, Fristoe, Elliot, Brunner, & Saults, 2006). There is some recent evidence to suggest that when children’s working memory capacity is ‘loaded’ with additional information visual attention is not allocated in the same way as when unloaded; in this case children seem to allocate attention in the same way as adults (Cowan, Morey, Aubuchon, Zwilling, & Gilchrist, 2010). The present research is inconsistent with these findings because children *did* allocate attention in the same way as adults. It would thus be interesting to explore the model working memory further within the current paradigm.

In conclusion, the mechanisms that underlie attentional orienting seem to be enabled for parallel processing, sharing is allowed with an interplay between internal and external attentional orienting. Overall, further research is encouraged to continue to explore this extremely interesting paradigm of competition for right hemisphere attentional orienting.

Discussion of Thesis

7.1. Evidence of representational pseudoneglect

The main aim of the research reported here was to build our understanding of representational forms of pseudoneglect and the extent to which attentional orienting by the right hemisphere underlies the bias, by exploring some core but as yet unanswered questions in the field. While the individual Chapters of this thesis achieved this aim in a number of different ways the overall endeavour was the same: to consider how representational forms of pseudoneglect in the absence of direct visual processing can be demonstrated and mediated. The aims were happily achieved and the results point towards some novel, unique, and extremely interesting possibilities for how spatial attention is oriented in the healthy ageing human brain in the complete absence of visual input.

In Chapter 2 the effect of age on tactile rod bisection was investigated in an attempt to fully understand lateralized biases that are not driven by prior experience or visual processing across lifespan; the first time that this has been explored in the absence of vision. In Experiment 1 healthy participants aged between 3 and 84 years of age, divided into eight age groups, used touch alone without vision to bisect one wooden rod. Participants across all age groups, except those approaching or in adolescence, showed pseudoneglect on tactile rod bisection. In Experiment 2 healthy participants aged between 6 and 96 years old, divided into three age groups, used touch alone without vision to bisect three wooden rods of different length. Experiment 2 showed pseudoneglect across the full adult life span and most notably in the oldest participants. For the youngest participants there was no significant pseudoneglect bias but there was a significant effect of gender with females showing greater leftward bias than males. When participants scanned and bisected the rods starting from the right-hand side, pseudoneglect was significantly enhanced; again this bias interacted with age. These results make a novel and important new suggestion: that the right hemisphere has an early capacity to orient attention contralaterally and that this capacity continues in middle and older adulthood which is inconsistent with current models of cognitive ageing. This is the first time that age has been shown to *directly* enhance the magnitude of pseudoneglect for a novel stimulus explored using touch in the complete absence of visual processing.

In Chapter 3 the main aim was to explore lateralised biases in mental representations of matrix patterns formed from aural verbal descriptions in the absence of vision. In Experiments 3 and 4 healthy participants listened, either monaurally or binaurally respectively, to verbal descriptions of 6 by 3 matrix patterns and were asked to form a mental representation of each pattern, judge which half of the matrix, left or right, contained more filled cells and to rate the certainty of their judgement. Participants tended to judge that the left side was fuller than the right and showed significantly greater certainty when judging patterns that were fuller on the left. This tendency was particularly strong for left ear presentation. In Experiments 5 and 6 participants conducted the same task as Experiments 3 and 4 but were also asked to recall the pattern for the side judged as fuller. Participants were again more certain in judging patterns that were fuller on the left – particularly for left ear presentation - but were no more accurate in remembering the details from the left. These unique results suggest that the left side of the mental representation was represented more saliently but it was not remembered more accurately.

In Chapter 4 the main aim was to explore asymmetries in visuo-spatial working memory for the temporary activation of highly imageable information in the absence of vision. In Experiments 7 and 8, 96 healthy participants listened, binaurally or monaurally respectively, to aural-verbal descriptions of novel real-world street scenes which contained highly imageable landmarks (e.g., “shop”, “market”, “school”) and were asked to create a visuo-spatial mental representation of the stimulus as it was described.

Participants were then asked to decide which side of the street contained the most landmarks, provide a certainty score for this judgement, and recall the landmarks on the side of the street that was perceived to contain the most landmarks. The results showed a significant effect of listening condition: when presentation was monaural to the left ear judgements erred towards the left side of the street (i.e., ‘the left side of the street has the most landmarks’) but when presentation was binaural or monaural to the right ear, there was no bias. Despite the significant leftward trend for the left ear condition, or representational pseudoneglect, recall accuracy was similar across all listening conditions. In Experiment 9 participants completed the same task using a visual imagery strategy and, in addition, self-reported ‘mental mapping’ ability was taken into account; but again no lateralised memory biases were found. Experiment 10 showed that the method of landmark recall (i.e., aural verbal vs. drawing) did not influence this pattern of results. These intriguing results also suggest that the left side of the mental representation was represented more saliently but it was not remembered more accurately - regardless of the imageablity of the stimuli, the context that the stimuli were presented in, visual imagery strategy, or mental mapping ability.

In Chapter 5 the main aim was to explore hints about lateralised biases in mental repetition by recording participants’ eye movements while they visually processed and then memorised natural real-world scenes. Experiment 11 not only showed no lateralised memory bias when participants were asked to recall colour or spatial information from a previously viewed visual scene but also no lateralised bias in participants’ eye movements. These results again support the previous research reported in the literature but importantly extend the debate showing that lateralised recall biases are also not readily demonstrated for novel material even when it is visual in nature. Lateralised memory biases therefore seem to occur under very specific conditions.

Finally, Chapter 6 aimed to explore in an innovative and original paradigm how orienting attention *internally* can bias the orienting of attention *externally*. In Experiment 12, children and adults participants performed two pseudoneglect tasks at the same time. When a secondary mental number line representation task was performed in conjunction with visuo-spatial line bisection the magnitude of pseudoneglect was significantly enhanced for children and adults but only when using the left hand. These remarkable results suggest that attentional orienting mechanisms can be fully engaged in parallel for two tasks at the same time but, most importantly, that attentional orienting may be *additive* for both children as well as adults. This is the first time that internal attentional orienting has been shown to *directly* enhance the magnitude of external attentional orienting.

7.2. An activation-orientation account of representational pseudoneglect

The activation-orientation hypothesis (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; see also Kinsbourne, 1970) posits that pseudoneglect arises from contralateral attentional orienting by the right hemisphere towards the left side of space. Taken together, the unique collection of results within the current thesis strongly suggests that attention can be oriented in a similar way within a spatial representations created from tactile exploration or aural-verbal description in the complete absence of visual processing, for completely novel stimuli and across the entire adult lifespan. The activation-orientation hypothesis seems to be the best account of the results of Chapter 2 on tactile rod bisection; the results of Chapters 3 and 4 with regard to the mental representation of spatial layout from aural-verbal description; and the results from pseudo-dual task within the final Chapter 6 for the following reasons. A critical assumption of the activation-orientation hypothesis is that pseudoneglect arises due to the orienting of visual attention towards the left portion of a stimulus which is subsequently perceived as *longer*. For visuo-spatial line bisection this critical assumption has been shown to hold under direct scrutiny (Bultitude & Davies, 2006; Toba, Cavanagh, & Bartolomeo, 2011) and some evidence along the same lines has also been provided for mental number line bisection (Nicholls & McIlroy, 2010). The results of the experiments reported here are very consistent with this critical assumption. Experiments 1 and 2 showed that when participants were required to bisect a wooden rod at its middle using only touch there was a significant leftward bias for adults; this is arguably consistent with attentional orienting since if more attention was directed to the right portion of the rod the midpoint would arguably have been perceptually shifted, in sensory terms, towards the right-hand side of midline (i.e., Bultitude & Davies, 2006; Toba et al., 2011). Importantly, because the task was conducted in the absence of vision this is consistent with a form of pseudoneglect for a *spatial representation* of the stimulus. The fact that this assumption appeared to hold across the entire adult lifespan is extremely interesting and will be discussed in due course, along with the differences in performance for males versus female children. The previous research on tactile rod bisection in the absence of vision also acknowledges that attentional orienting by the right hemisphere plays an important role in pseudoneglect on tactile rod bisection (Laeng, Buchtel, & Butter, 1996; Sampaio & Chokron, 1992; Sampaio & Philip, 1991) and that the right hemisphere is dominant for attentional orienting even in the long-term blind (Cattaneo, Fantino, & Tini, 2011). Of course, there are likely additional processes involved in tactile rod bisection such as internal mental scanning (Laeng et al., 1996), proprioceptive or motor feedback (Sampaio & Chokron, 1992; Sampaio & Philip, 1991) which may contribute to the magnitude of directional error. Experiments 3 to 8, which did not involve motor-driven exploration, also convincingly showed that leftward biases emerge when participants are asked to create a mental representation of spatial layout from aural-verbal description and make a relative judgement between the left and right side of that representation (abstract pattern or more contextualised real-world stimulus with highly imageable landmarks). Importantly, because the task was conducted in the absence of vision this is also consistent with pseudoneglect for a *spatial representation* of the stimulus. The aural-verbal results are also highly consistent with the critical assumption of attention orienting if the perception of ‘longer’ is considered synonymous with perceiving the left side of an aural-verbally described stimulus as ‘fuller’ or containing ‘more’ target stimuli (i.e., landmarks). The fact that healthy participants were able to build abstract or real world spatial layouts from aural verbal descriptions complements the previous literature (Denis, Pazzaglia, Cornoldi, & Bertolo, 1998; Noordzij, Zuidhoek, & Postma, 2006). Moreover, Experiments 3 to 6 (aural-verbal description of abstract pattern stimulus) clearly demonstrate the flexibility of tasks like the Visual Pattern Test (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999). Experiments 12 and 13 can also be explained by the same critical assumption since participants showed a leftward bias on visuo-spatial line bisection which is typically explained by right hemisphere attentional orienting (Jewell & McCourt, 2000), and adults showed a leftward bias when reporting the midpoint between two mentally represented numbers - towards the smaller number on the mental number line. All the tasks were inherently different: each task importantly involved a different *type* of spatial representation (the representation was driven by motor-feedback, aural-verbal description, or direct visual processing) but despite this leftward biases were seen across the collection of tasks. Neither a scanning hypothesis (Halligan, Manning, & Marshall, 1991) nor motor activation account (Heilman & Valenstein, 1979) could directly account for the pseudoneglect observed on the mental number line, for example, since there was no internal starting position and no motor response. Neither the scanning nor motor-activation account could fully explain the results of tactile rod bisection since the bias was completely asymmetrical regardless of starting side (biased towards the left) and the leftward biases were observed even though participants all bisected using their right hand which would in theory preferentially activate the left hemisphere not the right) hemisphere. A motor-activation account could also not explain the biases observed for mental representation created from aural-verbal description since no motor-response was required, though there was an internal starting position.

In order to be more certain that right hemisphere attention-orientating could account for the data a demonstration would be required showing that pseudoneglect was enhanced under conditions that favoured the activation of the right hemisphere. Numerous previous studies have demonstrated exactly this during visuo-spatial line bisection. For instance, using the left hand enhances pseudoneglect (Bradshaw, Bradshaw, Nathan, Nettleton, & Wilson, 1986; Brodie & Pettigrew, 1996; Brodie, 2010; MacLeod & Turnbull, 1999; McCourt, Freeman, Tahmahkera-Stevens, & Chaussee, 2001) and presenting the stimuli in left hemispace (Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Luh, 1995; McCourt & Jewell, 1999) as well using the left eye or looking towards the left increases the bias (McCourt, Garlinghouse, & Butler, 2000; Nielsen, Intriligator, & Barton, 1999). Under these conditions the right hemisphere seems to be favoured due to the anatomical and functional pathways that connect hemispace to hemisphere. In the current thesis the same relationship has been demonstrated. Representational forms of pseudoneglect were significantly boosted under conditions that preferentially favoured the activation of the right cerebral hemisphere. In Experiments 3 to 8, during aural-verbal description, monaural presentation to the left ear significantly enhanced the magnitude of pseudoneglect for both mentally represented abstract patterns and real-world street scenes. Monaural presentation has been shown in the previous literature to induce contralateral hemispheric activity (Gilmore, Clementz, & Berg, 2009; Lazzouni, Ross, Voss, & Lepore, 2010; Paiemont, Champoux, & Bacon et al., 2008; Schönwiesner, Krumbholz, Rübsamen, Fink, & Yves von Cramon, 2007) in a similar way as visual presentation to each visual field (Kimura, 1966; Bryden, 1966; Ellis, Brooks, & Lavidor, 2005); but this is the first time that monaural presentation has been shown to *directly* enhance the magnitude of pseudoneglect for a novel stimulus in the complete absence of visual processing. As the monaural left ear effect was shown across a large number of participants with completely different stimuli (pattern stimuli vs. real-world natural scenes) this is arguably strong evidence that the effect was not simply an artefact of some methodological aspect of the experiment. But what are the mechanisms of this? It is conceivable that monaural presentation to the left ear boosted the activation of the already engaged right hemisphere (due to the spatial aspect of the task) and thus augmented attentional orienting. This could arguably happen if the presentation of stimuli to the left ear activated an underlying neural network in the right hemisphere which *overlapped* with parietal regions. Indeed, in the healthy brain spatial neural networks overlap several right hemisphere regions (Himmelbach, Erb, & Karnath, 2006). As mentioned in the Literature Review functional Magnetic Resonance Imaging (MRI) studies have consistently revealed that regions of the right hemisphere's parietal cortex are actively engaged during visuo-spatial line bisection (Bjoertomt, Cowey, & Walsh, 2002; Çiçek, Deouell, & Knight, 2009; Fink, Marshall, & Shah et al. 2000; Fink, Marshall, & Weiss et al. 2000; Fink, Marshall, Weiss, & Zilles, 2001; Foxe, McCourt, & Javitt, 2003). Consistently, Gilmore, Clementz and Berg (2009) found that during monaural left ear presentation of auditory tone stimuli the right temporo-parietal area was preferentially activated. Moreover, Hirano, Naito and Okazawa (1997) found that left ear stimulation (white noise and speech) activated the right superior temporal gyrus and, critically, a number of studies have shown that lesions in the right superior temporal gyrus are associated with neglect (Karnath, 2001; Dankert & Ferber, 2006). It follows, then, that the underling functions in those regions (attentional orienting) may have been exacerbated due to enhanced cortical arousal in general. It may be expected in this case that the relationship would also work in the opposite direction with attentional-orienting exacerbating left ear dichotic listening; this is an interesting question for future research.

In returning to the argument that pseudoneglect was enhanced under conditions that favoured the activation of the right hemisphere, throughout all the experiments reported in this thesis starting side was often found to be crucial for the magnitude of pseudoneglect. Starting *right* during tactile exploration (Experiments 1 and 2) was found to elicit greater pseudoneglect; starting right also interacted with other variables like age, with older participants showing the greatest magnitude of pseudoneglect in a start right condition (Experiment 1 and 2). With regards to tactile rod bisection the previous research has also noted the importance of tactile scanning from the right (Bowers & Heilman, 1980; Baek, Lee, & Kwon et al. 2002). As mentioned, for tactile rod bisection, these results cannot be interpreted as ‘overshooting’ the middle of the rod (i.e., Baek et al. 2002) since there was not a symmetrical bias when *starting left* on the same task for the same participants. It is entirely possible that if the direction of physical or imagined movement is consistent with the theoretical direction of attentional orienting, from right to left, then the amount of attention directed towards the left-hand side will increase. Baek and colleagues explained their tactile rod bisection findings in terms of attentional arousal and suggest that attentional arousal may be higher during anticipatory movement such as the exploration of rod length during the initial search. Cattaneo et al. (2011) note that the ‘overshoot phenomenon’ - in terms of underlying mechanisms - is not entirely clear, Baek and colleagues notion of anticipatory attentional arousal could be combined with directional attentional-orienting. In a start left condition (moving and bisecting towards the right) there may *only* be anticipatory attentional arousal which alone would not produce strong (rightward) directional error. In a start right condition (moving and bisecting towards the left) there is anticipatory attentional arousal *as well as* attentional orienting which does lead to strong (leftward) directional error. Another possibility relates to Sampaio and Chokron's (1992) report that directly using the index finger during tactile rod bisection prompts participants to imagine the stimulus as a whole prior to bisecting but using a cursor to conduct the bisection prompts participants to map the duration of movement into a length estimate. The former sensory strategy is perhaps more consistent with visuo-spatial line bisection in which the whole stimulus is perceived all at once. The latter strategy could be interpreted as a temporal order strategy. In the same way, building a stimulus from aural-verbal description (Experiments 3 to 10) is also a temporal-order task with the participants being required to keep track of the number of filled cells within the matrix or the different landmarks on a 'street' by building the stimulus sequentially. One important difference between the tasks, however, is that in the former tactile rod bisection the participants controlled the speed at which the stimulus was explored; in the case of aural-verbal description the participants had no choice but to follow the description at the given speed. Could this have been influential? The fact that the same leftward biases arose in both temporal-order tasks indicates that the orienting of attention towards the left-hand side of a stimulus is an automatic and involuntary process – regardless of speed of scanning. Moreover, in Experiments 3 and 4 the speed of the description was shown *not* to affect the degree of pseudoneglect on the relative judgement task.

Interestingly, starting *left* during mental representation from aural-verbal description (Experiments 3 to 10) was found to elicit greater pseudoneglect and this was further enhanced by presentation to the left ear which elicited the greatest degree of pseudoneglect overall (Experiment 3 to 8). This is of particular interest because the start side was *imagined*. In this case the argument of anticipatory arousal combined with attentional-orienting does not hold since anticipatory arousal and attentional-orientating could have, in theory, cancelled one another out – participants imagined that the description was moving from left-to-right but attention would have been oriented right-to-left. This is an important finding as it suggests that the observation of pseudoneglect on each task may be underlain by different mechanisms. So how could these differences be explained? For aural-verbal description the starting left effect was shown across a larger number of participants with completely different stimuli (pattern stimuli vs. real-world natural scenes), so the finding was arguably not an artefact of the experimental procedure. It has been previously suggested that mentally representing spatial layouts from highly familiar scenes activated a visuo-spatial representation (McGeorge et al., 2007) and that learning spatial descriptions involving landmarks in particular engages visual imagery (Deyzac, Logie, & Denis, 2006). One interesting possibility is that during aural-verbal description visuo-spatial mechanisms were activated in the right hemisphere which could suggest that the left side of the visuo-spatial mental representation ‘behaved’ in the same way as an actual visuo-spatial stimulus (i.e., a horizontal line). For visually presented stimuli like horizontal lines starting left has already been documented to elicit a greater degree of pseudoneglect (Jewell & McCourt, 1999). Consistent with this, starting *left* also facilitated the degree of pseudoneglect in Experiment 12 for adults who completed visuo-spatial line bisection. It is plausible that if participants visualised the matrix pattern or street scene in their mind’s eye then the mechanisms underlying the tasks were, in fact, very similar or the same as visuo-spatial line bisection. This adds to an existing debate in the field with regards to whether the same mechanisms do, in fact, underlie both representation and visuo-spatial forms of pseudoneglect. Longo and Lourenco (2007) showed that mental number line bisection biases for healthy participants were related to visual line bisection biases and Longo and Lourenco (2010) found that both physical line bisection and mental number line bisection were modulated by viewing distance. The neglect literature, however, would not necessarily agree with this assumption given that perceptual and representational forms of pseudoneglect have been found independently of one another (Beschin, Basso, & Della Sala, 2000; Beschin, Cocchini, Della Sala, & Logie, 1997; Logie, Della Sala, Beschin, & Denis, 2005) but it is likely that there is a *pathological* origin for this dissociation; indeed, it is often difficult to define critical lesion sites for neglect (Dankert & Ferber, 2006).

If sensory information (aural-verbal) was remapped into a visuo-spatial representation why did mental mapping ability or visual imaging strategy (Experiment 9) not impact upon performance? Surely those participants with better mental mapping ability should be better at mental representation and thus less susceptible to pseudoneglect bias, following the previous literature that has shown participants who perform better on visuo-spatial tasks may have superior visual-imagery abilities (Dean & Morris, 2003; Garden, Cornoldi, & Logie, 2002). However, there was no actual measure of visual imagery and it is possible that the measure of *mental mapping* was simply not sensitive enough. A measure like the Vividness of Visual Imagery Questionnaire (Marks, 1973) may have been more sensitive as there are a large range of questions specifically designed to assess visual imagery ability. In addition, there is no way of knowing that participants actually implemented these visual imaging strategies during the processing of the aural-verbal description and the building of the mental representation. It would be of great interest to further pursue the influence of strategy for tasks designed to measure representational pseudoneglect from either tactile rod bisection or indeed aural-verbal description. It is nevertheless highly likely that mentally represented information from different types of spatial layout, visuo-spatial versus aural-verbal gives rise to different strategies which may be further exuberated by aspects such as familiarity, context, visuo-spatial imaging, and strategy.

In the context of tactile rod bisection Cattaneo et al. (2011) note that although the participants’ strategy may be to locate the point of subjective equality they actually perceive the point of subjective *inequality* instead. Strategy is something that has been implemented for visuo-spatial line bisection and mental number line bisection but, critically, it doesn’t seem to prevent the occurrence of pseudoneglect which suggests that pseudoneglect is indeed an underlying and automatic attentional phenomenon. Varnava and Halligan (2009) found that regardless of the strategy used participants deviated towards the left-hand side in visuo-spatial line bisection; Nicholls, Mattingley and Bradshaw (2005) found the same for luminance judgements on the Greyscales task when participants were forced to use a ‘comparison strategy’ (i.e., explicitly compare left and right portion of a stimulus with separated left and right portions) versus a ‘global strategy’ (i.e., view stimulus as a whole not separated). In the current aural-verbal experiments participants arguably used a ‘comparison strategy’ to compare the left and right side to answer the question ‘which side is fuller?’ and it could also be interpreted that a more ‘global strategy’ was always used when participants were required to retrieve the details *globally* from one side of the stimulus. To this end, the differences between the two tasks are highly relevant when discussing the lack of bias in the recall data, since one task produced lateralised biases whereas the other did not.

7.3. Limitations of an activation-orientation account for representational forms of pseudoneglect

Lateralised memory biases have also been found for imagined highly familiar material (Bourlon, Duret, & Pradat-Diehl et al. 2010; McGeorge et al., 2007) and also for novel visually processed scenes (Della Sala, Darling, & Logie, 2010). The research reported within this thesis, however, consistently showed balanced recall for stimuli on the left and right side of mentally represented scenes from aural-verbal description - despite the fact that in a relative judgement task immediately prior to recall there was a consistent leftward bias. Experiments 5 to 6 categorically showed no lateralised memory bias for retrieval of information from mental representations of abstract pattern spatial layout built from aural-verbal description; Experiments 7 to 10 showed that even when the abstract pattern was replaced with a real-world scene and highly imageable stimuli in the form of landmarks as well as a familiar context (i.e., city street) there were still no lateralised biases. Experiment 11 also showed that even when details are retrieved from a visuo-spatial representation of a visually processed real-world scene there were no lateralised biases. Although the previous research has shown that eye movements can be biased towards the left side of space during visual processing (i.e., Harvey, Gilchrist, Olk, & Muir, 2003) the current research also found no evidence to suggest that eye movements are biased towards one side of space - left versus right. These results prompt the suggestion of a new interpretation of the activation-orientation hypothesis within the following framework.

It is possible that contralateral attentional orienting by the right hemisphere may lead to the left side of the stimulus being more *heavily weighted* than the right side which leads to greater salience for the left side of the stimulus - manifested as a leftward bias when a judgement of *magnitude* is made. Here, salience is interpreted as a purely attentional phenomenon whereby the left side ‘stands out’ relative to the right side which could be considered relatively more ‘fuzzy’. In this case, each side of the stimulus is represented in equal detail in working memory; during retrieval there is no lateralised bias because the same amount of information is *available* on each side of the stimulus. The bias arises because the available information can be *attended* to in different ways. This is visually illustrated in Figure 1 for the pattern stimuli and real-world scene stimuli that were aural-verbally described in Experiments 3 to 8, though the premise also holds for tactile rod bisection and any other stimulus in any modality.

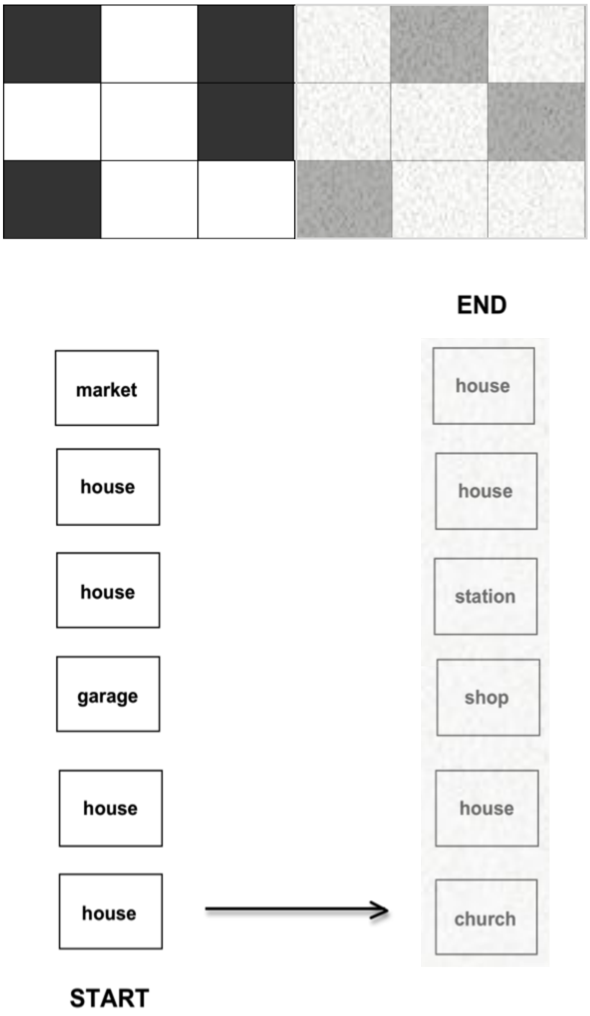


Figure 7.1. A new interpretation of attentional orienting. In the top panel the pattern stimulus from Chapter 3 is shown and in the bottom panel the street scene stimulus from Chapter 4 is shown. In each case, both the left and right sided details of each stimulus are clearly visible but the left side stands out more than the right side which is ‘fuzzy’.

The advantage of this interpretation is that it allows us to explain the results of the relative judgement task as well as why there was no lateralised bias in memory when participants were asked to access specific details from mentally represented stimuli built from aural-verbal description, and would account for the fact that regardless of the imageability of the stimuli lateralised memory biases were not observed. It is possible that, over time, consistent attentional orienting towards the left-hand side makes the visuo-spatial representation super salient or extra weighted and this eventually causes impoverishment to the maintenance of the less-attended-to right side due to lack of 'exercise' which may explain why lateralised memory biases are more readily observed in tasks which require healthy participants to recall information from highly familiar scenes held in long-term memory (Bourlon et al. 2010; McGeorge et al., 2007). This wouldn't directly explain why lateralised memory biases are found for novel tasks (Della Sala et al. 2010) though in this particular case the stimuli were processed using vision in artificial displays, making a direct comparison non applicable. Experiment 9 did indeed provide some control for how participants 'mentally mapped' their world (i.e., Garden, Logie, & Cornoldi, 1992) and found that, regardless of whether participants classified themselves as good, neutral or poor mental mappers, recall remained balanced between the left and right side of the mental representation. The interpretation of one side of the mental representation being fuzzy also falls in line with postulations from the neglect literature that representational neglect arises from impairment to visuo-spatial working memory (Della Sala, Logie, Beschin, & Denis, 2004; Logie, Della Sala, Beschin, & Denis, 2005). In the current thesis the participants were healthy and so there was no damage to visuo-spatial working memory and hence no lateralised bias. In the case of aural-verbal description there was a symmetrical effect of recency with the most recently described pattern side gaining better recall; it is possible that the recency effect (Burns & Manning, 1981; Taylor & Heilman, 1982) helped to reduce sensitivity to lateralised memory biases. To this end, it would be interesting to explore ways of counterbalancing the recency effect by increasing or decreasing the salience of one side of the pattern or street scene by making individual cells even more salient. This should allow us to test the assumption that one side of the stimulus is indeed more salient than the other, since more salient cells should further capture attention and increase the degree of representational pseudoneglect. If increased salience was ipsilateral to starting side (contralateral to the finishing side) this may counterbalance the recency effect and unearth sensitivity to lateralised recall biases. However, given the consistency between the experiments within this thesis in terms of demonstrating representational forms of pseudoneglect this seems unlikely to change the pattern of results. Previous research has indicated that there are different types of spatial processing: fine-grained (i.e., 'coordinate processing') or more relative (i.e., 'categorical processing') (Kosslyn, 1987). The relative judgement task may be synonymous with a categorical task and this task elicited greater pseudoneglect due to right hemisphere attentional orienting which would also suggest that the categorical task was a function of the right hemisphere. However, both categorical and coordinate spatial processing have been found to be lateralised - but in the opposite way - with categorical processing being a function of the left hemisphere and coordinate processing being a function of the right hemisphere (Kessels, Kappelle, de Haan, & Postma, 2002; Rinck & Denis, 2004; van Asselen, Kessels, Kappelle, & Postma, 2008). For this reason, the distinction does not really hold for the current data unless, of course, these experiments have uncovered a modality-dependent factor for categorical and coordinate spatial processing. There is little evidence to support this assumption, however, and it seems far more likely that left side of the stimulus was more *heavily weighted* than the right side but only when a judgement of *magnitude* is made.

Taken together, these results are intriguing. The right hemisphere seems able to preferentially orient attention leftward in the absence of direct visuo-spatial processing but only when making a relative judgement about magnitude. Moreover, attentional orienting does not lead directly to lateralised working memory biases.

7.4. The mediation of activation-orientation for representational forms of pseudoneglect

The current data suggest a representational form of pseudoneglect occurs across the entire adult lifespan - this was a critical finding of this thesis. This observation can allow us to make important inferences about the early, middle, and late developmental trajectory of attentional orienting in the *complete absence of visual processing*. As already discussed, the activation-orientation hypothesis is arguably the best account of the data and this suggests that there is a continuing role for the mechanisms in the right hemisphere that orient attention in the absence of vision. The results from Experiment 2 suggest that younger participants aged between 6 to 13 years old do not orient attention in exactly the same way as an adult which suggests that attentional orienting may be the signature of a more mature system. If so this capacity, to orient attention leftward regardless of age, should arguably be acknowledged in current models of cognitive ageing like HAROLD (Cabeza, 2002) as the bias indicates that certain functions do not become less asymmetrical with increasing age contrary to popular belief (Cabeza, 2002; Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Cabeza, Grady, & Nyberg et al., 1997; Cabeza, McIntosh, Tulving, Nyberg, & Grady, 1997; Madden, Turkington, & Provenzale et al., 1999). If anything, the bias indicates that certain functions become *more* asymmetrical. This is not the only study that has hinted towards this possibility as Johnson, Logie and Brockmole (2010) demonstrated that verbal memory may remain modality-specific in older adulthood for example. In order to explain why older participants showed a greater degree of bias compared to younger adults it is possible to draw again on the serial-order aspects of tactile rod bisection. Temporal-order working memory across a wide range of tasks has been found to decline in older age (Hartman &Warren, 2005; Poliakoff, Shore, Lowe, & Spence, 2006) as well as working memory function in general (Park, Lautenschlager, & Hedden, 2002; Johnson, Logie, & Brockmole, 2010). It is possible that having to maintain information about the distance that has been travelled along each length of the rod in each direction and then using this information to estimate the middle of the rod is a task that heavily engages working memory (Baddeley & Hitch, 1974; Baddeley & Logie, 1999; Logie, 2011a; 2011b). If, however, those working memory mechanisms were unreliable in older adults this may mean they were more susceptible to *attentional* aspects of the task – like the orienting of attention towards the left. It is also possible that older adults ‘forget’ about earlier explored portions of the rod; but this should lead to symmetrical biases when starting on either side (starting left vs. starting right) and this was clearly not observed. While working memory mechanisms undoubtedly play some role in tactile rod bisection the role of attentional orienting seems to predominantly drive the bias here. One clear result was that older adults were particularly sensitive to the start right condition. It is possible that in a start right condition (moving and bisecting towards the left) older adults were particularly sensitive to anticipatory attentional arousal *as well as* attentional orienting which led to strong (leftward) directional error because the left side was more heavily weighted in the mind’s eye. To what extent could internal mental scanning explain this? Personnier, Kubicki, Laroche and Papaxanthis (2010) found that older adults (71 years of age) relative to younger adults (25 years of age) significantly over-estimated imagined walking in a motor-imagery experiment relative to a physical condition. It is possible that older participants in the tactile rod bisection also over-estimated an internal scan path (i.e., Laeng et al., 1996) but did so more when starting right due to the combination of anticipatory attentional arousal and attentional orienting.

One interpretation of tactile rod bisection by Bowers and Heilman (1980) is that “each hemisphere may have its own spatial coordinate frame for mapping out the contralateral hemispace” (pg. 496). Here, ‘hemispace’ is based on an egocentric coordinate system relative to the individual participant with the perceived body mid-line serving as divider[1]. It is also possible that during tactile rod bisection participants employ a strategy of using their body mid-line as an external reference point from which to base judgments about the perceived centre of the rod; critically, this may change with age. This supposition can be explained as follows. Previous research has shown that tactile stimulation may be remapped into an external spatial frame of reference relating to the posture of the body (Azañón, Camacho, & Soto-Faraco, 2010; Azañón & Soto-Faraco, 2008). When the left hand is in left space and the right hand is in right space the external position of the hands corresponds to an internal spatial map of left and right space. But when the left hand is crossed-over the body mid-line in right space and vice versa for the right hand in left space a re-mapping process is required in order to 'untangle' the conflict between egocentric and external spatial frames of reference. The extent, speed, or accuracy of this remapping process may be related to age; it is relevant to tactile rod bisection because in each case participants were required to physically *cross the body midline* (i.e., when exploring the rod). It is possible that older adults were less able to re-map as effectively as mid-age adults or children. The fact that the remapping process changes with age in general was recently demonstrated by Pagel, Heed and Röder (2009) who found that older but not younger children (5 to 10 years) displayed a crossed hand effect. Interestingly, the crossed hand effect has also been shown to be stronger for females than for males (Cadieux, Barnett-Cowan, & Shore, 2010) so it would be interesting to establish to what extent this tactile remapping affected not only participants of different ages but also participants of different gender. Indeed, Experiment 2 showed significant gender differences in bisection performance for the youngest age group (aged 6 to 13 years) with females showing a significantly greater

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[1] 'Hemispace' is not necessarily the same as 'hemifield' which is anatomically fixed at the retinal level. For example, Split fovea theory is the idea that the fovea is split into two portions, both anatomically and functionally, so that visual input to the left of fixation is preferentially projected to the right hemisphere but visual information to the right of fixation is preferentially projected to the left hemisphere (Ellis, 2010).

degree of pseudoneglect compared to males (see also Van Vugt, Fransen, Creten, & Paquier, 2000).

So can it be concluded that attention is oriented in the same way across lifespan? The findings from tactile rod bisection do not necessarily suggest that children and adults orient attention in different ways, since there was still a trend towards the left-hand side for children though the bias was non-significant. For visuo-spatial line bisection on the other hand children *did* allocate attention in the same way as adults. Rather, the data suggest that children and adolescents, when compared to adults, may orient attention leftward to *different degrees*. One reason for this could relate to corpus callosum immaturity (Hausmann, Waldie, & Corballis, 2003; Pulsipher, Seidenberg, & Hermann, 2009) or changes in brain function and structure during cognitive development (Sisk & Zehr, 2005; see also Giorgio, Watkins, & Chadwick et al. 2010) which may impact on right and left hemisphere functions like the way in which internal and external spatial frames of reference are synchronised and the way that attention is oriented. With regards to how age affects attentional-orienting this thesis has provided some clues on how internal attentional orienting seems to influence external attentional orienting in both children and adults – but, again, to different degrees. In Experiment 12 and 13 both adults and children showed leftward biases on both visuo-spatial line bisection which are consistent with the previous literature (Jewell & McCourt, 2000) and pseudoneglect for adults was similarly mediated by increasing line length (Chokron & Imbert, 1993; Manning et al., 1990; McCourt & Jewell, 1999; Luh, 1995). For right-handed children the leftward biases that were found in visuo-spatial line bisection were also in line with the previous research (De Agostini, Curt, Tzortzis, & Dellatolas, 1999; Varnava & Halligan, 2007). But the results for adults as well as children offered a striking new finding: a hint towards the fact that number line representation conducted in parallel caused pseudoneglect on visual line bisection to be significantly enhanced when bisection was conducted with the left hand. So even though children's working memory capacity is 'loaded' with additional information visual attention was, in fact, allocated in the same way as adults (Cowan, Morey, Aubuchon, Zwilling, & Gilchrist, 2010). For adults it was clear that attention was oriented on both visuo-spatial line bisection and mental number line bisection in parallel as evidenced by the significant leftward biases on both tasks; for children the assumption that attention was oriented in both tasks is based on the fast that they did access a 'mental line of numbers' in the way instructed. To this end, one clear finding of Experiments 12 and 13 was that there seems to be a *threshold of sensitivity* for this relationship between internal and external attentional orienting. When attentional orienting mechanisms were shared between two tasks then overall activation may have been somehow reduced. But using the left hand to respond preferentially activated the right hemisphere (Brodie, 2010) and provided the supplementary level of activation that is required for attentional orienting. It has been shown in previous visuo-spatial literature that using the left hand to respond during visuo-spatial line bisection promotes a larger degree of pseudoneglect (Bradshaw, Bradshaw, Nathan, Nettleton, & Wilson, 1986; Brodie & Pettigrew, 1996; Brodie, 2010; MacLeod & Turnbull, 1999; McCourt, Freeman, Tahmahkera-Stevens, & Chaussee, 2001). Indeed, the observation of a large effect is also consistent with the fact that participants typically respond faster to smaller numbers with the left hand but faster to larger numbers with the right hand – demonstrated by Dehaene, Bossini and Giraux (1993) who coined the term Spatial Numerical Association of Response Codes (SNARC) to describe this observed relationship (for review see Hubbard, Piazza, Pinel, & Dehaene, 2005). Interestingly, it is possible that because participants were orienting attention towards the left side of the mental number line this elicited a preferential response in the left hand. Because the task was to bisect the line – and not a parity task – this response may have been manifested as a larger bias on visuo-spatial line bisection.

The critical finding here is that, based on these assumptions, internal attentional orienting can bias external attentional orienting in both children and adults. This is the first time that this has been hinted towards and thus presents a very intriguing possibility for future research. Loftus, Nicholls, Mattingley and Bradshaw (2008) and Nicholls, Loftus and Gevers (2008) have shown that internal attentional orienting can influence external attentional orienting on the Greyscales task. Lourenco and Logo (2009) have shown that participants who held in mind small numbers in working memory whilst performing the traditional mental number line bisection task showed larger degrees of pseudoneglect – a neat demonstration of additive attentional orienting. Probably the closest example comes from De Hevia and Spelke (2009) who asked adults (25 years of age) and children (5 and 7 years of age) to perform a visual line bisection when Arabic numerals such as ‘2’ and ‘9’ presented on the left versus right side of the line; adult participants were biased in the direction of the larger number or the larger dot array and all children showed a bias towards the larger dot array (though this would be consistent with a rightward bias). The current findings of the thesis certainly add to this expanding plethora of research that will eventually lead us towards a greater and more in-depth understanding of attentional orienting and how it is mediated.

7.5. Summary & Conclusions

The aim of this thesis was to learn more about representational forms of pseudoneglect and whether or not attentional orienting underlies the bias, as well as discovering what mediates the bias. The research reported here has shown some novel, unique, and extremely interesting findings and has contributed to our understanding of representational forms of pseudoneglect tremendously. This thesis has presented several important discoveries: that a representational form of pseudoneglect can exist across the full adult lifespan in the complete absence of visual processing; that while the left side of a spatial mental representation created from aural-verbal description may be represented more saliently, it is not remembered more accurately; that representational forms of pseudoneglect can be significantly mediated by favouring the right cerebral hemisphere in terms of presenting stimuli to the left ear, using the left hand, or starting on one side of space; and that internal attentional orienting can enhance the magnitude of external attentional orienting in both adults as well as children.

This body of evidence is best explained by an activation-orientation account of representational pseudoneglect which is based on the left side of a spatial mental representation being heavier or more salient than the right. The current thesis recommends that this fresh perspective of attentional orienting is adopted by researchers in the field and that current models of cognitive ageing provide for the possibly that certain right hemisphere functions remain asymmetrical in older age and exert a capacity at an early age. As research in this field continues, our understanding of the inner workings and mechanisms of pseudoneglect (and neglect) will increase, shedding more light into the way the human mind works, develops and ages. This thesis has hopefully contributed to this endeavour and will help pave the way for observations and discoveries that can help us further improve our knowledge of how spatial attention is oriented in the healthy human brain.

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Appendix A

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Tactile rod bisection in the absence of visuo-spatial processing in children, mid-age and older adults

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ABSTRACT

The effect of age on tactile rod bisection is explored in an attempt to fully understand lateralized biases that are not driven by prior experience or visual processing. In Experiment 1, a total of 549 healthy participants aged between 3 and 84 years of age, divided into eight age groups, used touch alone without vision to bisect one wooden rod. Participants across all age groups, except those approaching or in adolescence, showed pseudoneglect on tactile rod bisection. In Experiment 2 a total of 72 healthy participants aged between 6 and 96 years old, divided into three age groups, used touch alone without vision to bisect three wooden rods of different length. Experiment 2 showed pseudoneglect across the full adult life span and most notably in the oldest participants. For the youngest participants there was not a significant pseudoneglect bias but there was a significant effect of gender with females showing greater leftward bias than males. When participants scanned and bisected the rods starting from the right-hand side, pseudoneglect was significantly enhanced; again this bias interacted with age. The results suggest that the right hemisphere exerts an early capacity to orient attention contralaterally and that this capacity continues in middle and older adulthood which is inconsistent with current models of cognitive ageing. The findings are discussed in terms of how the right hemisphere preferentially orients attention leftward in the absence of direct visuo-spatial processing across lifespan and how this may be modulated by variables like gender and starting position.

1. Introduction

Previous research has reported that healthy adults often show biases on visual line bisection, tending to bisect horizontal visually presented lines towards the left-hand side of true centre (*for review see* Jewell & McCourt, 2000). This phenomenon is known as 'pseudoneglect' (Bowers & Heilman, 1980). One explanation of errors on visual line bisection relates to the theory that each hemisphere orients attention towards contralateral space (Heilman & Van Den Abell, 1979; Kinsbourne, 1970; Reuter Lorenz, Kinsbourne, & Moscovitch, 1990), with the right hemisphere preferentially directing attention leftward. Evidence in support of this theory of pseudoneglect comes from functional Magnetic Resonance Imaging studies with healthy adults that implicate right parietal regions in visual line bisection (Finke, Bublak, & Zihl, 2006; Fink, Marshall, Weiss, & Zilles, 2001). Further evidence comes from the observation that when the right parieto-frontal regions are damaged, patients make *rightward* errors on visual line bisection (Halligan & Robertson, 1999). Moreover, the involvement of the right hemisphere in spatial processing has been well documented (Della Sala, Logie, Beschin, & Denis, 2004; Gobel, Calabria, Farnè, & Rossetti, 2006; Halligan & Marshall, 1989).

Recent studies have demonstrated that there is a form of pseudoneglect that is representational in nature, appearing when participants recall characteristics of recently viewed stimuli (Della Sala, Darling, & Logie, 2010) or information from highly familiar scenes (Bourlon et al., 2011; McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzzatti, 1978), and also when participants predicted the position of a moving target which disappeared from view in a virtual reality environment (Cocchini, Watling, Della Sala, & Jansari, 2007). In number based tasks a preference is also observed towards smaller numbers thought to be represented on the left-hand side of the mental number line (Loftus, Nicholls, Mattingly, Chapman, & Bradshaw, 2008; *for review see* Hubbard, Piazza, Pinel, & Dehaene, 2005). Recently, pseudoneglect has even been suggested for auditory descriptions of imagined spatial arrays (Brooks, Logie, McIntosh, & Della Sala, in press). Representational pseudoneglect has also been demonstrated on *tactile-driven* rod bisection (Bowers & Heilman, 1980; Bradshaw, Nathan, Nettleton, Wilson, & Pierson, 1987; Bradshaw, Nettleton, Nathan, & Wilson, 1985; Brodie & Pettigrew, 1995; Sampaio &

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Chokron, 1992; see also MacLeod & Turnbull, 1999) which is not directly affected by factors such as familiarity, previous experience, or, in some cases, visual processing.

One unanswered question is what happens to representational forms of pseudoneglect across lifespan? The existence of pseudoneglect across lifespan, in general, is an important observation since current models of cognitive ageing have no provision for spatial biases that can be *enhanced* by age. The Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model (Cabeza, 2002) is a widely accepted model of cognitive ageing and argues that, with increasing age, general cognitive functioning becomes less lateralised. There is much support for HAROLD with a plethora of neuroimaging studies showing bilateral activation in older adults but asymmetrical activation in younger participants for similar tasks (Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010; *for review see* Eyler, Sherzai, Kaup, & Jeste, 2011). In contrast, the right hemiageing model argues that the two hemispheres age differentially with the right hemisphere ageing faster or more detrimentally than the left hemisphere (*for review see* Dolcos, Rice, & Cabeza, 2002). The right hemiageing model has support from studies showing good performance on left hemisphere lateralised tasks (i.e., language) but poorer performance on right hemisphere lateralised tasks (i.e., visuo-spatial).

The empirical observation of pseudoneglect *across lifespan* on tactile rod bisection would be of particular importance for several reasons. Firstly, it would indicate that a representational form of pseudoneglect, *independently of vision*, is retained in older age which has implications for current models of cognitive ageing. Secondly, it would indicate that motor-driven lateralised biases are retained in older age which is of interest since lateralised motor responses, in general, are thought to become less lateralised with age (i.e., McGregor, Craggs, Benjamin, Crosson, & White, 2009; Przybyla, Haaland, Bagesteiro, & Sainburg, 2011; Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010). Thirdly, it would allow us a more complete understanding of the developmental trajectory of pseudoneglect between modalities which is important for understanding how right hemisphere attentional orienting operates and is modulated as a whole.

While our knowledge of the developmental trajectory of pseudoneglect on mental representational tasks is lacking there are some hints, albeit inconsistent ones, regarding the impact of age on pseudoneglect in the literature on visual line bisection. Visual pseudoneglect has been reported in participants aged 5–94 years old (De Agostini, Curt, Tzortzis, & Dellatolas, 1999; Varnava & Halligan, 2007). Other visual line bisection studies have reported symmetrical neglect, that is, when the left hand is used the bias is towards the left-hand side but when the right hand is used the bias is towards the right-hand side. Symmetrical errors on line bisection have been shown in children aged around 5 years of age (Bradshaw, Nettleton, Wilson, & Bradshaw, 1987; Dellatolas, Coutin, & De Agostini, 1996), in children aged 5–7 years as well as older adults aged 60–70 years (Failla, Sheppard, & Bradshaw, 2003), and also in older children aged 10–12 years (Hausmann, Waldie, & Corballis, 2003). In children symmetrical biases are suggestive of an 'immature' attentional orienting system (Hausmann, Waldie, & Corballis, 2003) but for older adults symmetrical biases are certainly in line with HAROLD. However, some studies on visual line bisection have reported rightward biases for older adults (Fujii, Fukatsu, Yamadori, & Kimura, 1995; Schmitz & Peigneux, 2011; Stam & Bakker, 1990); this is in line with the view that the right hemisphere may be more sensitive to cognitive ageing than the left.

The influence of age on tactile rod bisection is addressed in the context of current models of cognitive ageing. Following HAROLD, older participants should display less bias on tactile rod bisection compared to younger participants. Following the right hemiageing model, older participants should display reversed pseudoneglect, that is, rightward biases on tactile rod bisection. Alternatively, pseudoneglect may be maintained or enhanced on tactile rod bisection in older age.

In the current study participants were asked to use their index finger to explore wooden rods in the horizontal plane while keeping their eyes closed, and indicate their judgement as to the position of the centre point of the rod. Previous research has demonstrated the importance of starting side on line bisection (Bowers & Heilman, 1980; Brodie & Pettigrew, 1996; Urbanski & Bartolomeo, 2008) but also the importance of the direction in which the bisection is actually made (Baek et al., 2002). Therefore, a secondary aim was to explore how performance on tactile rod bisection can be mediated by the spatial direction from which the judgement was made in younger, mid-age and older participants. In Experiment 1 the performance of 549 healthy right-handed participants aged between 3 and 84 years of age who bisected a single horizontal rod with the right index finger in the absence of direct visuo-spatial processing was assessed. Experiment 2 assessed the performance of 72 right handed participants aged between 6 and 96 years of age who bisected three horizontal rods of different length over a larger number of trials with the right index finger in the absence of direct visuo-spatial processing. In Experiment 2 gender was controlled because there is some suggestion that pseudoneglect in young adults is influenced by gender (Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Laeng, Buchtel, & Butter, 1996; see also Van Vugt, Fransen, Creten, & Paquier, 2000).

2. Experiment 1

2.1. Method

2.1.1. Participants

A total of 549 right-handed native English speaking participants were divided into eight different age groups; the rationale for these age groups was to provide an illustration of bisection performance across lifespan. There were 72 participants between 3 and 6 years of age ($M = 5.36$, $SD = .76$), 108 participants between 7 and 8 years of age ($M = 7.48$, $SD = .50$), 95 participants between 9 and 10 years of age ($M = 9.49$, $SD = .50$) and 59 participants between 11 and 12 years of age ($M = 11.25$, $SD = .44$): all these participants were recruited from primary schools in the United Kingdom and the annual Edinburgh International Science Fair. There were 22 participants between 13 and 20 years of age ($M = 15.50$, $SD = 2.60$) recruited from secondary schools in the United Kingdom and the Edinburgh International Science Fair. There were 86 participants between 22 and 40 years of age ($M = 34.94$, $SD = 4.72$) recruited from universities in Scotland and the Edinburgh International Science Fair; there were 79 participants between 41 and 60 years of age ($M = 47.08$, $SD = 5.22$) recruited from the Edinburgh International Science Fair. Finally, there were 28 participants between 61 and 84 years of age ($M = 70.82$, $SD = 6.87$) recruited from public libraries in Edinburgh and the Edinburgh International Science Fair. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). The calculation of the handedness score was achieved using the formula $(R - L/R + L) \times 100$ with a score of +100 indicating exclusive right handedness and a score of −100 indicating exclusive left handedness. All participants were right-handed, reported normal or corrected-to-normal vision and hearing and did not report a history of dyslexia, spatial disorder, dementia, or memory loss. All participants were naive to the study hypothesis. The younger children were given a pencil for participating.

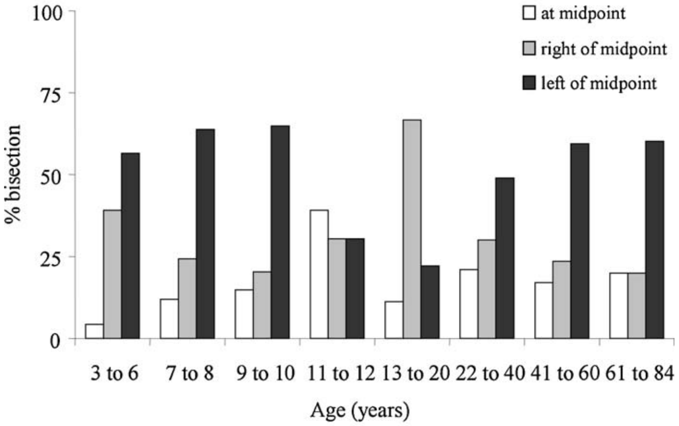
2.1.2. Materials

A custom-made portable tactile rod bisection task was devised for the purpose of the experiment. There was one wooden dowling rod measuring 32 cm in length and 2 cm in diameter. A rectangular wooden stopper was firmly attached to the end of each rod to stop the participants overshooting the ends of the rod during tactile exploration. The rod was held in place using a custom-made wooden base. The true centre of the rod was carefully measured and defined by a 0.5 mm black line drawn on the side of the rod facing the experimenter, but that was not visible to the participants.

2.1.3. Procedure

Participants were tested in three locations: at a table set aside from the main exhibition area at the Edinburgh Science Festival (a large, annual interactive exhibition of science for the general public); in a quiet area of a classroom within a school; or in a quiet room set aside in a library. In all cases the testing location was similar and the stimuli were set-up in exactly the same way. In each case, the stimulus was positioned on the testing table with the wooden rod centrally aligned with the

(a) Start left



(b) Start right

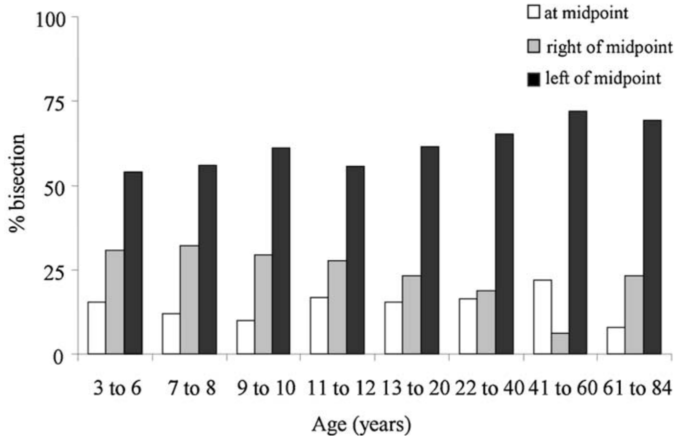


Fig. 1. This figure displays the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint in Experiment 1.

participants' midsaggital plane. The experimenter was positioned opposite the participant with the wooden rod in-between the participants and the experimenter. Participants were asked to place their right index finger at a central location on the testing table, in line with the participant's body mid-line, which was the starting point of each trial. Participants were asked to keep their non-dominant hand by their side and close their eyes. The experimenter was careful to monitor compliance with this last request: if participants opened their eyes at any time during a trial their data were not included for analysis (this happened for three participants). The reaching distance to the rod was approximately 15 cm. The experimenter guided the participant's right index finger from the central location to the extreme left-hand side of the wooden rod or the extreme right-hand side of the wooden rod. The experimenter then let go of the participant's index finger which was the participant's cue to begin moving the index finger along the entire length of the rod either from left to right (i.e., start left condition) or from right to left (i.e., start right condition). Start side was counterbalanced across participants. Participants moved their index finger along the entire length of the rod (i.e., from left to right) and then re-traced this path in the opposite direction for the entire length of the rod (i.e., from right to left) as many times as preferred before moving their index finger back to the perceived middle of each rod. The number of times each participant moved along the rod was not recorded (i.e., in line with the previous line bisection literature). The participant was required to leave their index finger at the perceived middle until directed by the experimenter who recorded the position as belonging in one of three categories: 'left of midpoint' or 'right of midpoint' or 'at midpoint'. The experimenter recorded the measurement on paper. Each participant completed a single trial with start side (start left versus start right) counterbalanced across participants.

2.2. Results

Fig. 1 shows the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint when starting on the left side of the rod (a) or when starting on the right side of the rod (b).

For the start right condition there was a clear trend for participants in all age groups to bisect the rod towards the left hand side; there was no significant difference in bisection performance across age group (χ^2(14, N254) = 11.27, p = .664), However, for the start left condition the same effect was observed for younger (aged 3–10 years) and adult participants (aged 22–84 years) but not for adolescence participants (aged 11–20 years) who showed a different pattern of performance. Hence, there was a significant difference in bisection performance across age group (χ^2(14, N295) = 28.72, p = .011). A further analysis was considered in order to fully counterbalance – for each age group – the number of participants who started either left or right. There was no significant effect for the start right condition (χ^2(14, N237) = 12.44, p = .571) nor start left condition (χ^2(14, N237) = 29.29, p = .010).

2.3. Discussion

The results of Experiment 1 suggest that when bisection starts on the right hand-side the right hemisphere exerts an early capacity to orient attention contralaterally and that this capacity persists in middle and older adulthood. The results of Experiment 1 also demonstrate that the performance of adolescents is different from that of younger children or older adults when starting and bisecting from the left hand-side. Indeed, it is probable that this variability in performance may arise from changes in hormonal levels, or even brain structure, during adolescence which indirectly influence cognitive processes like attentional orienting (Giorgio et al., 2010; *for review see* Sisk & Zehr, 2005).

Experiment 2 sought to address two further questions motivated by Experiment 1. Experiment 2 assessed the magnitude of bias over a larger number of trials across lifespan (rather than using the proportion of participants showing a bias that was adopted for Experiment 1) with gender and start side completely counterbalanced. In Experiment 1 tactile scanning of the rod was unrestricted and the direction from which the scan was made was unknown despite starting on the left-hand side or right-hand side. In Experiment 2 tactile scanning was therefore restricted to one complete scan of the rod before the bisection was made from the same direction as the starting position. This means that when the scan started from the left-hand side of the rod the bisection also started from the left-hand side (and vice versa when the scan started from the right-hand side).

3. Experiment 2

3.1. Method

3.1.1. Participants

A total of 72 right-handed native English speaking participants were divided into three different age groups. None of these participants had taken part in Experiment 1. The rationale for these age groups was to provide an illustration of bisection performance during early development, middle adulthood, and older adulthood; the main concern was exploring early and late attentional biases but an intermediate age group was included for comparison. As participants aged 11–12 years in Experiment 1 did not preferentially bisect the rod in either direction it was decided to include participants of this age in Experiment 2 as bisection performance was explored across a larger number of trials instead of just one single trial. One participant who turned 13 years old on the day of testing was included in Experiment 2 but there were no other participants aged between 13 and 17 years old in order to reduce the suggested variability in bisection performance for the start left condition in Experiment 1. There were 24 participants between 6 and 13 years of age (M = 9.42, SD = 1.55) recruited from primary schools in the United Kingdom; there were 24 participants between 18 and 55 years of age (M = 30.29, SD = 12.93) recruited from universities in Scotland; and there were 24 participants between 60 and 96 years of age (M = 74.17, SD = 11.20) recruited from public libraries in Edinburgh and through personal acquaintance of the experimenter. All participants were right-handed (Edinburgh Handedness Inventory), reported normal or corrected-to-normal vision and hearing and did not report a history of dyslexia, spatial disorder, dementia, or memory loss. All participants were naive to the study hypothesis. The participants aged 6–13 years were offered a pencil for participating. All of the adult participants were given a small honorarium.

3.1.2. Materials

A custom-made portable adjustable tactile rod bisection task was devised for the purpose of the experiment (Fig. 2). There were three wooden dowling rods measuring 24 cm, 32 cm, and 40 cm in length and 2 cm in diameter. A rectangular wooden stopper was firmly attached to the end of each rod to stop the participants overshooting the ends of the rod during tactile exploration. Strips of high quality Velcro (i.e., hook-and-loop fasteners) were affixed along the entire underside of each rod and in a horizontal line across a solid wooden base measuring 40 cm × 30 cm × 1.5 cm. These Velcro strips allowed each rod to be held in a sturdy horizontal position during tactile exploration. The true centre of each rod was carefully measured and defined by a 0.5 mm black line that was not visible to the participants but visible to the experimenter since the experimenter was seated opposite the participant.

3.1.3. Procedure

Participants were tested in three locations: at a table in a quiet area of a classroom within a school; in a quiet room set aside in a library; or in a quiet room within the university. In all cases the testing rooms were similar and the stimuli were set-up in exactly the same way. Participants aged 6–13 years were tested in pairs but seated on opposite sides of the room (with two experimenters) due to the require-

Fig. 2. This figure displays the rod stimulus in Experiment 2.

ments of one primary school; this design was replicated across all participants in that particular age group for the sake of consistency. Adult participants aged 18–96 years were tested alone. Participants were seated at a table directly in front of the wooden base affixed to the table and centrally aligned with the participant's midsaggital plane. The experimenter was seated opposite the participants on the other side of the table with the wooden rod in-between the experimenter and the participant. Participants were asked to place their right index finger on the wooden base at a central location which was the starting point of each trial. Participants were asked to keep their non-dominant hand on their lap and close their eyes. Participants were not blindfolded due to the requirements of one primary school so we decided to replicate this design across all participants for consistency. All participants were carefully watched by the experimenter throughout the trial in order to ensure the participant did not open their eyes. This happened on a small number of occasions (N5 trials) across older, but not younger participants, and the data for that trial were discarded and the trial was repeated at the end of the block. The experimenter then attached a wooden rod, horizontally, to the strip of Velcro on the wooden base. The reaching distance to the rod was approximately 15 cm and the middle of the rod was centrally aligned with the participants' midsaggital plane. The experiment started when the experimenter guided the participant's right index finger from the central baseline position to the extreme left-hand side of the wooden rod or the extreme right-hand side of the wooden rod. The experimenter then let go of the participant's index finger which was the participant's cue to begin moving the index finger along the entire length of the rod either from left to right (i.e., start left condition) or from right to left (i.e., start right condition). Start side was counterbalanced across participants and participants were given a 3-min break in between start side conditions (after 15 trials). During this break participants were allowed to open their eyes but the stimuli and testing table were hidden from sight using a large black cloth. Participants were restricted to one complete scan of the rod. This meant that the participants moved their index finger along the entire length of the rod (i.e., from left to right) and then re-traced this path in the opposite direction for the entire length of the rod (i.e., from right to left). Then participants were asked to move their index finger back to the perceived middle of each rod. When the exploration started left, the bisection was also made from the left and when the exploration started right the bisection was also made from the right. The participant was required to leave their index finger at the perceived middle until directed by the experimenter who used a stainless steel half millimetre ruler to measure the position of the subjective midpoint relative to the objective middle. Bisection was recorded 'at midpoint' when the index finger was aligned with the objective middle. The experimenter recorded the measurement on paper. The participant then guided the participant's index finger back to the central location on the wooden base, removed the rod, attached another rod (according to a pre-determined random order) and began the next trial by placing the participant's right index finger on the extreme (left or right) end of the rod.

Each participant completed 30 trials in total: 15 start left trials and 15 start right trials, with start side blocked across participants and rod length randomised across participants. Importantly, there were an equal number of males and females across the counterbalanced design (i.e., the same number of males and females start left or right first in each age group). Each rod length was repeated five times for each start side condition.

3.2. Results

First, for comparative purposes with Experiment 1, the total number of participants in each age group (N24) who bisected at 'midpoint', 'left of midpoint', and 'right of midpoint' for the first trial only (there were missing data for one person in the age group 60–96 years), with start side combined, was analysed. Fig. 3 shows the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint. The results complement Experiment 1 and across age groups there was no significant difference in the proportion of participants who bisected left of midpoint, right of midpoint or at midpoint ($\chi^2(4, N71) = 1.321$, $p = .85$).

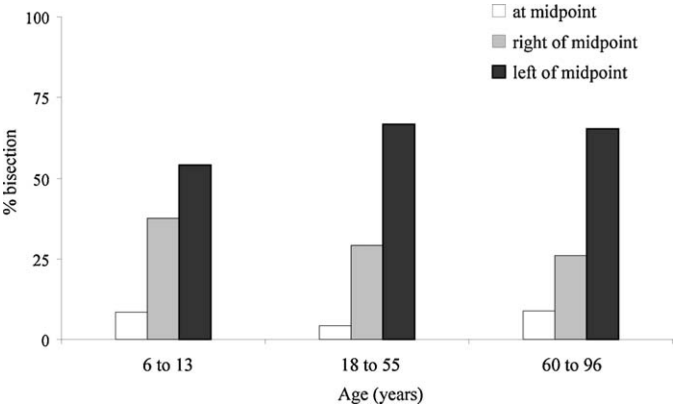


Fig. 3. This figure displays the proportion of participants in each age group who bisected the rod left of midpoint, right of midpoint, and at midpoint in Experiment 2.

For each age group the directional bias from midpoint was calculated as a percentage of the rod length. This is a standard method of computing line bisection performance (see Failla et al., 2003; Fujii et al., 1995; Hausmann et al., 2002, 2003) and takes into account the magnitude of bias as a function of stimulus (i.e., rod) length. This is important to consider because a bias of 5 cm, for example, would be proportionally greater for a 24 cm rod compared to a 40 cm rod. The resulting score is negative or positive: negative scores indicate a leftward bias while positive values indicate a rightward bias (relative to the true centre). A score of zero reflects no bias. Fig. 4 displays the mean percent deviation scores for each group.

For participants aged 6–13 years the bias was not significantly different from zero ($t(23) = -.691$, $p = .496$). In order to ensure that there was no indication of a hidden developmental stage in bisection performance participants aged 6–13 were further divided into two smaller age groups: aged 6–9 years (N13) and aged 10–13 years (N11). The overall mean bias for the 6–9 year olds ($M = -1.66$, $SD = 7.38$) was not significantly different from zero ($t(12) = -.811$, $p = .433$) and the mean bias for the 10–13 year olds ($M = .09$, $SD = 4.17$) was also not significantly different from zero ($t(10) = .074$, $p = .942$). For participants aged 18–55 years the bias was significantly different from zero ($t(23) = -2.657$, $p = .014$) and for participants aged 60–96 years the bias was highly significantly different from zero ($t(23) = -3.409$, $p = .002$). There was a trend for the bias to increase with age and this difference fell short of significance ($F(2,71) = 2.840$, $p = .065$).

A comparison was also made between the overall bias for males (N12) and females (N12) in each age group. Fig. 5 displays the mean percent deviation scores for each group split by gender. There was a significant difference between male and female bisection performance for participants aged 6–13 years ($F(1,22) = 5.097$, $p = .034$) with females showing a greater leftward bias compared to males who showed a rightward bias but this was not significantly different from zero ($t(11) = 1.145$, $p = .277$). There was no significant difference between male and female bisection performance for participants aged 18–55 years ($F(1,22) = .692$, $p = .414$) and neither for participants aged 60–96 years ($F(1,22) = 1.390$, $p = .251$), although

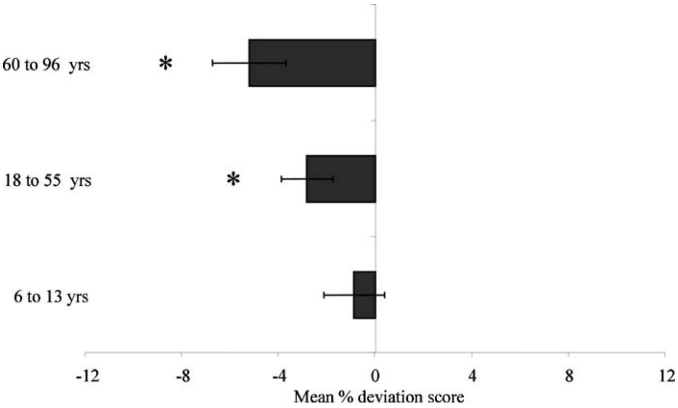


Fig. 4. This figure displays the mean percent deviation scores for participants in each age group in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias. Error bars indicate standard error of the mean.

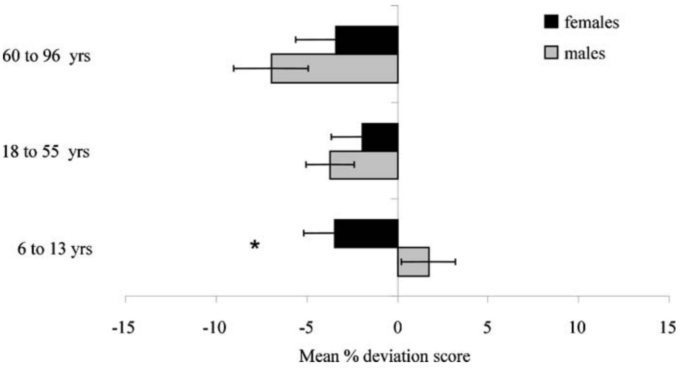


Fig. 5. This figure displays the mean percent deviation scores for male and female participants in each age group in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias. Error bars indicate standard error of the mean.

there was a tendency for males to show larger leftward biases compared to females. A comparison of bisection performance for males and females across age groups confirmed a significant interaction between gender and age group ($F(2,66) = 3.364$, $p = .041$). Post-hoc comparisons were conducted using Tukey HSD. For *males* the bias for participants aged 60–96 years was significantly different to that of participants aged 6–13 years ($p = .002$) but not to participants aged 18–55 years ($p = .359$). The bias for participants aged 6–13 years was not significantly different to the bias of participants aged 18–55 years ($p = .069$). For *females* the bias for participants aged 60–96 years was not significantly different to that of participants aged 6–13 years ($p = 1.000$) nor participants aged 18–55 years ($p = .843$). The bias for participants aged 6–13 years was not significantly different to that of participants aged 18–55 years ($p = .839$).

The influence of starting side was then explored. Fig. 6 displays the mean percent deviation scores for each group as a function of start side (start left versus start right). As shown in Fig. 6, when participants started right and bisected from the right (and physically moved the index finger towards the left) bisection error was noticeably leftward in all age groups – but particularly so for the participants aged 60–96 years. A mixed ANOVA was conducted with rod length (24 cm, 32 cm, 40 cm) and start side (start left versus start right) as the within-subject variables and age-group as the between-subject variable and gender as a covariate. There was a highly significant main effect of start side ($F(1,68) = 7.645$, $MSE = 323.39$, $p = .007$) and a highly significant interaction between start side and group ($F(2,68) = 13.919$, $p < .001$). There was no significant main effect of rod length ($F(2,136) = .677$, $MSE = 24.08$, $p = .510$), no interaction between rod length and group ($F(4,136) = .684$, $p = .604$) or rod length and start side ($F(2,136) = .120$, $MSE = 34.68$, $p = .887$), rod length, start side, and group ($F(4,136) = 1.478$, $p = .212$). There was no significant interaction between gender and rod length ($F(2,136) = .503$, $p = .606$) or gender and start side ($F(1,68) = .815$, $p = .370$). Post-hoc comparisons were conducted using Tukey HSD. For the start right condition the leftward bias for the participants aged 60–96 years was significantly different to the bias of participants aged 6–13 years ($p < .001$) and 18–55 years ($p = .034$). The leftward bias for participants aged 6–13 years was also significantly different to that for the participants aged 18–55 years ($p = .046$). For the start left condition the bias for participants aged 60–96 years was significantly different to the bias for participants aged 6–13 years ($p = .017$) but not to the bias for participants aged 18–55 years ($p = .392$). Likewise, the bias for participants aged 6–13 years was not significantly different to the bias for participants aged 18–55 years ($p = .291$).

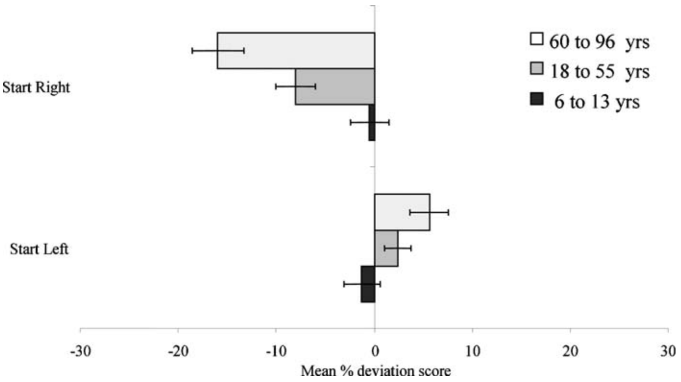


Fig. 6. This figure displays the mean percent deviation scores for participants in each age group as a function of start side (start left versus start right) in Experiment 2. Negative values indicate a leftward bias while positive values indicate a rightward bias. Error bars indicate standard error of the mean.

3.3. Discussion

Experiment 2 showed, for the first time, the presence of pseudoneglect on tactile rod bisection, in the absence of visual input, across the full adult life span and most notably in the oldest participants. This form of representational pseudoneglect was not as clear for the youngest participants who also displayed a gender difference in bisection performance, with greater pseudoneglect for female participants. The results of Experiment 2 suggest that the right hemisphere exerts an early capacity to orient attention contralaterally and that this capacity continues in middle and older adulthood; this empirical observation is at odds with the notion that there is more bilateral recruitment during cognitive tasks in older adults. It is also inconsistent with the argument that the right hemisphere is more sensitive to cognitive ageing than its left hemisphere counterpart.

Experiment 2 also showed that side from which the bisection started was crucial for mediating the bias: when participants started and bisected from the right-hand side (consistent with the direction of attentional orienting) the lateralised bias towards the left was significantly enhanced. Again the oldest participants were far more sensitive to this effect compared to the other two groups. However, when participants started and bisected from the left-hand side (inconsistent with the direction of attentional orienting) the bias was not simply reversed in the opposite direction which is evidence that the bias is not simply a product of over-estimation.

4. General discussion

The main aim of the current study was to explore tactile line bisection across lifespan while taking into account the influence of starting position and gender. Experiment 1 showed representational pseudoneglect on tactile rod bisection across a large number of younger and older participants, but the results were dependant on starting side with adolescents showing different performance when bisection started on the left-hand side. In Experiment 2 clear representational pseudoneglect was demonstrated on tactile rod bisection with older participants aged 60–96 years showing the largest bias and the youngest participants aged 6–13 years being statistically unbiased in their bisection performance overall. However, Experiment 2 also showed that tactile rod bisection performance in male and females was different for participants aged 6–13 years but this difference was not as clearly observed for participants aged 18–55 years or participants aged 60–96 years. Experiment 2 also showed that when participants started from the right to undertake tactile scanning and bisection representational pseudoneglect was significantly increased; again this bias was significantly enhanced by age.

The data from Experiments 1 and 2 provide evidence for a representational form of pseudoneglect for adults not driven by direct visual attention but by the creation and maintenance of a mentally represented spatial layout. Interestingly, there is evidence to suggest that tactile input can be readily mapped onto an external visuo-spatial framework (Azañón, Camacho, & Soto-Faraco, 2010; Pagel, Heed, & Röder, 2009) which poses a question as to whether or not the pseudoneglect observed in the present study was really ‘representational’ in nature. Indeed, if a visuo-spatial framework was activated this may have engaged visuo-spatial mechanisms in the right hemisphere and resulted in preferential right hemisphere attentional orienting from visuo-spatial attention. While this is a possibility, it is unlikely to account for the effect observed. Line length effects have been well documented to have a critical effect on visual line bisection (Jewell & McCourt, 2000) and so, arguably, if the rod was translated into a visual representation, a similar effect may have been expected here. But there was no significant effect of rod length in Experiment 2. Although previous research has documented a significant effect of rod length during tactile line bisection (Laeng, Buchtel, & Butter, 1996; Sampaio & Chokron, 1992) other tactile-driven studies have not directly reported rod length effects (Baek et al., 2002; Bowers & Heilman, 1980; Sampaio & Philip, 1991). Also, we did not vary spatial position of the rod (e.g., Laeng, Buchtel, & Butter, 1996) and it is possible that tactile-visual mapping would be more likely to occur when a tactile stimulus is perceived in a more spatially complex orientation. Certainly, body posture has been shown to influence pseudoneglect on both visual and tactile rod bisection (Bradshaw et al., 1985).

The results from Experiment 2 suggest a more symmetrical bias for participants aged 6–13 years old, dependant on starting and bisecting direction, which supports the notion that leftward asymmetries in attentional orienting may be the signature of a more mature system. The present study suggests that the mechanisms that underlie representational pseudoneglect may be engaged in older age and that this capacity should be included in current models of cognitive ageing like HAROLD (Cabeza, 2002). Indeed, the fact that pseudoneglect occurs for older adults on a motor-driven task is somewhat surprising; a related finding is that motor responses become less lateralised in older age (McGregor et al., 2009; Przybyla et al., 2011; Vallesi et al., 2010). Our results also indicate that for older participants the process of 'dedifferentiation' – reliance on a broader range of cognitive resources – may be selective. The selective nature of age-related dedifferentiation has been reported for other tasks. Johnson, Logie, and Brockmole (2010) demonstrated that in older adults individual variation in *verbal* immediate memory capacity is accounted for by task-specific variance whereas individual variation in *visual* immediate memory shares common variance with a range of other working memory tasks. This suggests that while visual immediate memory is modality specific early in adulthood but subject to dedifferentiation with age, verbal memory remains modality-specific in older adults.

Experiment 2 showed significant gender differences in bisection performance for the youngest age group (aged 6–13 years) with females showing a significantly greater degree of pseudoneglect compared to males. In line with these results is a study with 650 healthy children suggested that males were more accurate than females on horizontal visual line bisection (Van Vugt et al., 2000). Interestingly, our results suggest a trend in the opposite direction for adults; this has also been recently suggested for visual line bisection (Brodie, 2010). However, the degree of pseudoneglect demonstrated by males and females on visual line bisection has been shown to be influenced by the hand used (Hausmann et al., 2002). The effect of response hand was not addressed in the current study as the research was motivated by a different question – to explore whether representational pseudoneglect is present across lifespan – but the age at which pseudoneglect on both visual and tactile bisection is first demonstrated in children, when controlling for gender and hand, would benefit from further scrutiny.

Previous research has demonstrated the importance of starting side on line bisection (Bowers & Heilman, 1980; Urbanski & Bartolomeo, 2008) and in Experiment 2 starting side (start left versus start right) was controlled and, in addition, the direction from which the bisection was made. Importantly, the results of Experiment 2 showed the influence of starting side was crucial for the magnitude of pseudoneglect: starting from the right and bisecting from the right enhanced this bias, especially for the oldest adult participants. We argue that if the direction of bisection is consistent with the direction of attentional orienting (bisecting from the right) the lateralised bias will be enhanced; but if the direction of bisection is inconsistent with the direction of attentional orienting (bisecting from the left) the lateralised bias will be reduced or even observed in the opposite direction. As the bias was not simply symmetrical when start side and bisection was counterbalanced this strongly suggests that the bias is not simply a product of over-estimation, or the 'overshoot phenomenon' (Baek et al., 2002), but rather stems from a 'weighted' influence of the left side of the rod. Indeed, this may be increased when the left side of his rod is being anticipated. If anticipation alone was driving the bias then the opposite pattern of results should be observed when starting, and bisecting, from the opposite direction (left towards the right). Again, the bias was not symmetrically reversed. An exploration of why older adults would be more sensitive to this effect is an important question for future research.

There is little doubt that tactile rod bisection involves additional or different processes compared to visual line bisection related to sequential mental scanning (Sampaio & Chokron, 1992) and it is highly likely that these are related to working memory. During tactile rod bisection participants must retain information about the distance that they have travelled along each rod in each direction and then use this information to estimate the middle of the rod; it is likely that working memory mechanisms (Baddeley & Hitch, 1974; Baddeley & Logie, 1999; Logie, 2011a) were involved in the creation and maintenance of this spatial layout. Working memory function is well known to decline with age (e.g., Park et al., 2002; Johnson, Logie, & Brockmole, 2010) which means that relatively older adults may be more likely to 'forget' about earlier explored portions of the rod leading to an impoverished representation of earlier spatial layout compared with younger adults or children. While working memory mechanisms may play some role in tactile rod bisection it is more likely that the role of attentional orienting predominantly drives the bias observed here. If the bias resulted purely from an impoverished representation of earlier spatial layout we would expect to observe symmetrical biases in each direction when starting and bisecting from each side: this was clearly not the case. Rather, the bias observed for adults is more consistent with an over-representation of the left side of the rod in visuo-spatial working memory (i.e., Della Sala et al., 2010; Logie, 2011b) driven by attentional mechanisms and perhaps synonymous with the formation of a 'general impression' of the stimulus which may be more salient in attentional terms for the left side (Mattingley et al., 2004). A related question is the extent to which visual imagery was used by participants of different ages during the scanning of the rod, as in a motor imagery task elderly adults with a mean age of 71 years performed considerably worse than younger adults with a mean age of 25 years (Personnier, Kubicki, Laroche, & Papaxanthis, 2010).

It would be interesting to explore the strategy that is used during bisection tasks and whether this differs for males compared to females. Varnava and Halligan (2009) conducted a study to explore the strategy used during visual line bisection and found that the reported strategies including making a direct comparison of the perceived leftward and rightward portions of the line as well as using the body as a reference to find the middle of the line. It is possible that during tactile rod bisection participants employ a strategy of using their body mid-line as an external reference point from which to base judgments about the perceived centre of the rod; critically, this may change with age and be different in males versus females. In addition, given that tactile rod bisection is a temporal-order task it is possible that participants adopted a counting strategy; the strategy may have been to count during movement from one end of the rod to the other and then take the median number as representative of the rod's middle. Needless to say, whichever strategy was used it was arguably unsuccessful.

In conclusion, the present study has provided evidence that pseudoneglect in non-visual motor-driven tactile rod bisection appears throughout the adult age range but not necessarily in adolescents or younger children. Moreover, the results have illustrated that the phenomenon of representational pseudoneglect is robust and calls for further empirical investigations into tactile rod bisection, in the absence of vision, across lifespan.

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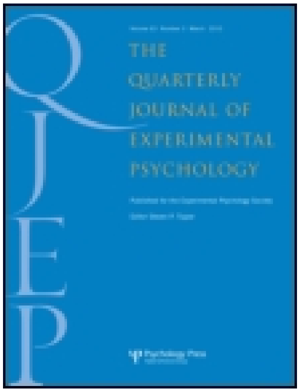

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Representational pseudoneglect in an auditory-driven spatial working memory task

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Representational pseudoneglect in an auditory-driven spatial working memory task

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Two experiments explored lateralized biases in mental representations of matrix patterns formed from aural verbal descriptions. Healthy participants listened, either monaurally or binaurally, to verbal descriptions of 6 by 3 matrix patterns and were asked to form a mental representation of each pattern. In Experiment 1, participants were asked to judge which half of the matrix, left or right, contained more filled cells and to rate the certainty of their judgement. Participants tended to judge that the left side was fuller than the right and showed significantly greater certainty when judging patterns that were fuller on the left. This tendency was particularly strong for left-ear presentation. In Experiment 2, participants conducted the same task as that in Experiment 1 but were also asked to recall the pattern for the side judged as fuller. Participants were again more certain in judging patterns that were fuller on the left—particularly for left-ear presentation—but were no more accurate in remembering the details from the left. These results suggest that the left side of the mental representation was represented more saliently but it was not remembered more accurately. We refer to this lateralized bias as "representational pseudoneglect". Results are discussed in terms of theories of visuospatial working memory.

Keywords: Representation; Pseudoneglect; Auditory; Spatial; Working memory; Mental.

Healthy participants often bisect visually presented horizontal lines to the left of the line's true centre (review in Jewell & McCourt, 2000). This phenomenon has been termed "pseudoneglect" (Bowers & Heilman, 1980) by analogy to the performance of right-hemisphere-impaired patients who neglect the left side of space and demonstrate rightward biases on line bisection (Halligan & Robertson, 1999). Pseudoneglect on physical line bisection tasks has been explored extensively (Brodie & Pettigrew, 1996; Liouta, Smith, & Mohr, 2008; MacLeod & Turnbull, 1999; McCourt, Freeman, Tahmahkera-Stevens, & Chausse, 2001; McCourt & Garlinghouse, 2000; Varnava, McCarthy, & Beaumont, 2002). One recent study (Della Sala, Darling, & Logie, 2010) has demonstrated a related, but different, phenomenon in visuospatial working memory, with healthy participants having better memory for material on the left of a briefly presented

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visual array. This leftwards bias in memory could not be explained in terms of any visual encoding bias and appeared to be a specific phenomenon of immediate visuospatial memory, which we refer to here as "representational pseudoneglect". This empirical observation raises questions about the characteristics of visuospatial working memory that are not considered in current theoretical developments. However, to be confident that the lateralized bias is not driven by visual perception, it would be crucial to explore the phenomenon in the absence of visual input. We explore here whether this bias in visuospatial representations arises when these representation are based on auditory descriptions of visual arrays with no visual perceptual input.

There are additional hints in the previous literature of lateralized biases in visual memory. For example, when healthy participants were asked to recall details from a highly familiar imagined scene (the Piazza del Duomo in Milan), they reported significantly more details from the left side of the imagined scene than from the right; this bias was independent of viewpoint (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzzatti, 1978). Arguably, this could be evidence for the existence of a pseudoneglect that is *representational* and not dependent on visual perceptual input. Moreover, given the familiar nature of the stimulus, this suggests that temporary activation of visual information held in long-term memory is also subject to the bias. Similarly, when asked to report the midpoint between a pair of mentally represented numbers, healthy participants also consistently show a preference towards the smaller number in the pair (Loftus, Nicholls, Mattingley, Chapman, & Bradshaw, 2008). Since numbers are thought to be mentally represented with smaller numbers to the left and larger numbers to the right (for review see Hubbard, Piazza, Pinel, & Dehaene, 2005), this is also argued to be indicative of a leftward representational spatial bias. Furthermore, leftward biases have been demonstrated for mental alphabet lines (Nicholls & Loftus, 2007), for finger counting habits (Fischer, 2008), and in listing cities of a country from different imagined viewpoints (Bourlon et al., 2011).

While these studies indicate that pseudoneglect can occur in the absence of direct visual input immediately prior to the behavioural response, the experimental paradigms were based on visual information that was highly familiar and stored in long-term memory. An unanswered question is whether or not the same phenomenon can be seen with completely novel stimuli generated from an aural verbal description and held in visuospatial working memory. Although the asymmetry reported by Della Sala et al. (2010) was demonstrated for novel stimuli held in visuospatial working memory, the initial input was visual in nature. Moreover, it is unclear how such asymmetries may be maximized or mediated. To address these issues, the current study used aural verbal descriptions of completely novel stimuli. Participants were asked to create a mental visual representation of the stimulus during the aural verbal description and, when the description was complete, retrieve certain details from the left and right side of the stimulus held in visuospatial working memory.

The main aim of the current study was to explore the possibility that the left side of the mental representation constructed from an aural verbal description was more salient than the right side of the mental representation and also incorporated greater and more accurate detail due to a leftwards bias in visuospatial working memory.

To explore this, participants were asked to imagine a verbally described matrix pattern. As the stimuli were both novel and aurally described, this removed any confounding effect of previous visual–perceptual processing or prior visual experience. The primary task was to judge which side of the pattern contained the greatest number of filled cells. The rationale for asking participants to make a relative side fuller judgement stems from similar perceptual tasks, such as the greyscales task (Mattingley et al., 2004), in which participants typically show a tendency to perceive the left side of a stimulus as darker in terms of light intensity than the right side. In the current task, if the left side of the pattern was represented more saliently this may be manifested as a tendency to judge that the left side was fuller than the right. In this view, overrepresentation may be driven by attentional mechanisms and is synonymous with the formation of a "general impression" of the stimulus, which may be more salient for the left side. Additionally, working memory mechanisms may maintain the left side of the stimulus in more detail.

In order to maximize potential representational pseudoneglect, the verbal description started on either the left-hand side of the stimulus or the right-hand side of the stimulus, bringing the task in line with previous research that has demonstrated that starting position strongly influences biases on line bisection (Urbanski & Bartolomeo, 2008). Furthermore, given the aural–verbal nature of the task, stimuli were presented either monaurally or binaurally. Indeed, monaural presentation to each ear has been shown to produce asymmetrical performance on certain auditory tasks such as ignoring irrelevant acoustic stimuli (Beaman, Bridges, & Scott, 2007; Hadlington, Bridges, & Beaman, 2006; Hadlington, Bridges, & Darby, 2004). Monaural presentation is known to induce contralateral hemispheric activity while binaural presentation induces bilateral activity (Paiement et al., 2008; Schonwiesner, Krumbholz, Rübsamen, Fink, & Yves von Cramon, 2006). If presentation to the left ear preferentially engages the right hemisphere, this may lead to increased sensitivity of encoding or maintaining the left side of the mental representation given the widely documented involvement of the right hemisphere in spatial processing (Chokron et al., 2002; Della Sala, Logie, Beschin, & Denis, 2004; Fink et al., 2000; Finke, Bublak, & Zihl, 2006; Göbel, Calabria, Farnè, & Rossetti, 2006; Halligan & Marshall, 1989; Ishiai, Koyama, Seki, Hayashi, & Izumi, 2006).

Experiment 1 was a relative judgement task that involved comparing the left and right halves of a verbally described pattern and responding, on a certainty scale, to indicate which side of the pattern was fuller. Experiment 2 was a recall task in which participants physically replicated the side perceived as fuller as accurately as possible.

EXPERIMENT 1

Method

Participants

There were 112 right-handed native English-speaking undergraduate participants from the University of Edinburgh. There were 56 participants in the binaural listening condition and a separate 56 participants in the monaural listening condition. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), with a score of +100 indicating exclusive right-handedness and a score of −100 indicating exclusive left-handedness: All participants scored over +65 on the handedness questionnaire. All participants were aged 18−38 years with normal or corrected-to-normal vision and hearing. Participants were paid a £6 honorarium.

Apparatus and stimuli

The stimuli were aural verbal descriptions of 36 patterns designed by the experimenters. Each side of the pattern (left and right) consisted of 3 × 3 cells (Figure 1). Each cell was either "filled" or "empty". The filled or empty cells on each side were chosen at random. The pattern of filled and empty cells for each stimulus was unique within the stimulus set. Each pattern was verbally described by a prerecorded female voice, in a snake-like manner, starting either from the top left ("start left" description), or from the top right corner ("start right" description). For instance, a start left verbal description of the pattern in Figure 1 would be "*filled empty filled empty filled empty filled empty empty filled empty empty filled empty empty filled empty empty*".

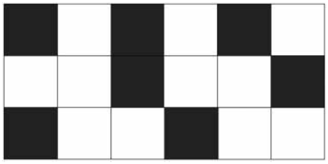

Figure 1. *Illustration of the pattern stimulus from Experiment 1 and Experiment 2. The left side of the pattern (defined within a 3 × 3 matrix) is fuller than the right side (also defined within a 3 × 3 matrix).*

Start side (start left vs. start right) and side fuller (left fuller vs. right fuller) were within-subject variables. Each participant performed two blocks of 18 trials. Two of the trials had 4 filled cells on each side of the pattern (i.e., neutral trials); these trials were included in order to encourage use of the full certainty scale (including certainty = 0). For the remaining 16 trials, 8 had 4 filled cells on the left side and 2, 3, 5, or 6 filled cells on the right, with each combination presented once with a start left and once with a start right description. The other 8 trials followed the same format except that the 4 filled cells were on the right. Therefore, within each block, there were 8 "left-fuller" and 8 "right-fuller" trials. Trial order within each block was randomly shuffled.

Listening condition was a between-subjects variable with 56 participants in a binaural condition and 56 in a monaural condition. Within the monaural condition, ear of presentation (left, right) was blocked, with one block per ear, and block order was counterbalanced across participants. Finally, half of the participants in each listening condition had patterns presented at a relatively slow speed (16 s per pattern) and the other half at a faster speed (11 s per pattern).

Procedure

Participants were seated in front of a computer monitor at a comfortable viewing distance of approximately 60 cm. The monitor and keyboard were centrally aligned with the participants' body midline. Participants were asked to close their eyes and clasp their hands in front of them on their lap or on the table at the beginning of each trial. The experiment started when the spacebar was pressed. After a 1-s pause, a prerecorded verbal pattern description was played over a pair of Sony noise-cancelling headphones at the same volume for each participant binaurally or monaurally. When the description was completed, there was a 1-s pause, and then participants opened their eyes, unclasped their hands, and reported which side of the pattern, left or right, contained the most filled cells using a graded scale of certainty [LEFT 4 3 2 1 0 1 2 3 4 RIGHT] presented at the centre of the screen. The scale was physically replicated on the computer keyboard. Participants were to choose 0 if they were completely uncertain. If participants thought there were more filled cells on the left side of the stimulus they were to choose a number from 1 (slightly certain) to 4 (absolutely certain) on the left-hand side of the scale, whereas if they judged there to be more filled squares on the right side of the stimulus they were to chose a number from 1 (slightly certain) to 4 (absolutely certain) on the right-hand side of the scale. In order to differentiate between certainty on each side of the response scale, responses on the left side were assigned negative values, and responses on the right side were assigned positive values. A randomly selected pattern was used as a practice trial. All participants heard exactly the same stimulus patterns in a random order.

Results

Proportional bias

For the 56 participants in the binaural condition and 56 participants in the monaural condition, the total number of left-side fuller responses was subtracted from the total number of right-side fuller responses and then divided by the overall number of responses (including the neutral trials), to yield a measure of "proportional bias". A negative proportional bias therefore indicates a tendency to respond left fuller more often than right fuller, whereas a positive value would reflect the opposite tendency. An initial analysis showed that the proportion of left-fuller versus right-fuller responses in both the binaural and monaural listening conditions was not significantly affected by the speed of the stimulus description, so the data were therefore collapsed across this factor to simplify subsequent analyses.

Figure 2, left panel, displays mean proportional bias for participants in the binaural condition and separate monaural condition. All mean values were negative, indicating that participants were more likely to respond left-fuller than right-fuller. The proportional bias was significantly different from zero for the left ear, $t(55) = -4.286$, $p < .001$, but not for the right ear, $t(55) = -0.394$, $p = .695$. In contrast for the binaural condition, proportional

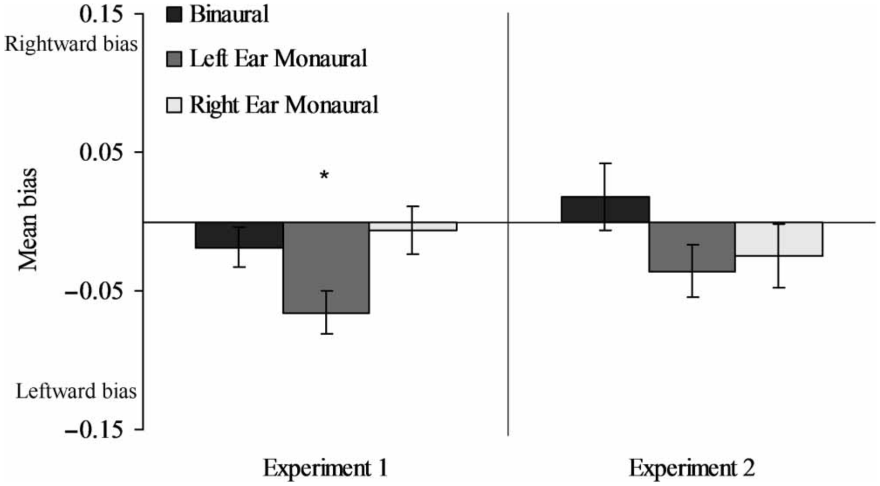

Figure 2. *Proportional bias in Experiment 1 and Experiment 2. Proportional bias is shown for the separate binaural and monaural listening conditions. Asterisk indicates significance. Error bars indicate standard error of the mean.*

bias was not significant, $t(55) = -1.204, p = .234$.[1] A one-way analysis of variance (ANOVA) was used to compare the proportional difference between the binaural, monaural left ear, and monaural right ear listening conditions. Proportional bias was significantly different across the three listening conditions, $F(2, 165) = 3.825, p = .024$.

Certainty

Certainty responses were then recoded according to whether certainty related to a correct judgement (e.g., participants responded left fuller when it was in fact left fuller) or an incorrect judgement (e.g., participants responded left fuller when the right side was in fact fuller). Correct judgements were assigned positive values and incorrect judgements negative values (i.e., negative responses reflect certainty in an incorrect response), creating a "certainty index". The certainty analysis was conducted with correct and incorrect trials binned together because a tendency to overrepresent the left side of the pattern should occur regardless of whether or not participants were correct or incorrect in their responses. Certainty was compared for left-fuller patterns and right-fuller patterns for 28 participants at both Speed 1 and Speed 2 in the binaural condition and 28 participants at both Speed 1 and Speed 2 in the monaural condition. An initial analysis showed that certainty for left-fuller versus right-fuller responses in both the binaural and monaural listening conditions was not significantly affected by the speed of the stimulus description, so the data were therefore collapsed across this factor to simplify subsequent analyses.

Figure 3 shows mean certainty for 56 participants in the binaural and monaural conditions overall.[2] For the monaural condition, side fuller was analysed as a function of ear and start side. There was a highly significant main effect of side fuller, $F(1, 55) = 27.573$, $MSE = 0.361$, $p < .001$, with significantly greater certainty for left-fuller than for right-fuller stimuli. There was also a significant interaction between start side and side fuller, $F(1, 55) = 8.351$, $MSE = 0.745$, $p = .006$, with a noticeable increase in

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[1] The neutral trials were included in the experimental stimulus set purely to encourage full use of the certainty scale; for this reason there were too few trials per participant (i.e., four per participant) to analyse the neutral trials in isolation.

[2] A separate analysis was conducted on correct trials only (i.e., when the left side of the pattern was fuller, and participants responded that it was fuller, or when the right side of the pattern was fuller, and participants responded that it was fuller). Certainty was greater for left-fuller stimuli than for right-fuller stimuli in each listening condition.

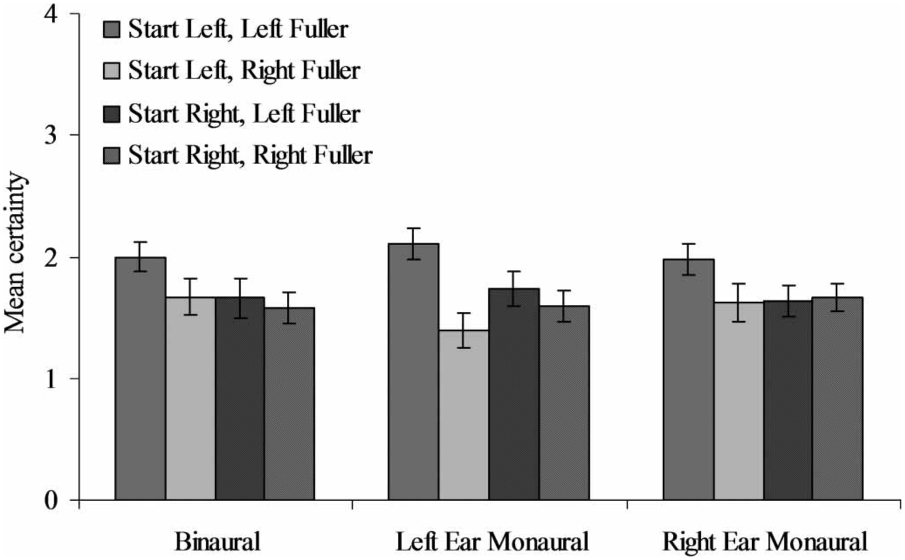

Figure 3. *Mean certainty responses as a function of start side in Experiment 1. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left-fuller and right-fuller stimuli. Error bars indicate standard error of the mean.*

certainty for left-fuller patterns when the description started left. There was also a significant interaction between ear and side fuller, $F(1, 55) = 4.098$, $MSE = 0.488$, $p = .048$, with presentation to the left ear strongly enhancing the tendency to be more certain about left-fuller stimuli. The effect of ear alone was not significant, $F(1, 55) = 0.057$, $MSE = 0.620$, $p = .812$, and neither was start side, $F(1, 55) = 2.237$, $MSE = 0.709$, $p = .140$. Side fuller as a function of start side was then analysed for the binaural condition using a repeated measures ANOVA. Replicating the monaural condition, there was a significant main effect of side fuller, $F(1, 55) = 5.045$, $MSE = 0.456$, $p = .029$, with certainty being reliably greater for left-fuller than for right-fuller stimuli. There was no main effect of start side, $F(1, 55) = 3.892$, $MSE = 0.665$, $p = .054$, and no significant interaction between start side and side fuller, $F(1, 55) = 1.626$, $MSE = 0.513$, $p = .208$.

A repeated measures ANOVA with start side and side fuller as the within-subject variables and listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted. The interaction between side fuller and listening condition was not significant, $F(2, 165) = 2.692$, $MSE = 0.435$, $p = .071$, and there was no interaction between start side and listening condition, $F(2, 165) = 0.390$, $MSE = 0.606$, $p = .678$, nor between start side, side fuller, and listening condition, $F(2, 165) = 0.689$, $MSE = 0.554$, $p = .504$.

Discussion

For all listening conditions, when participants made a relative judgement between the two sides of a verbally described pattern, there was a tendency to overrepresent the left side of the pattern. This was reflected in the fact that participants responded “left fuller” more often than “right fuller” and also that participants were more certain when judging left-fuller patterns. The predictions were therefore supported as it can be argued that there was greater saliency for the left side of the pattern.

The certainty results could not have arisen because participants were only using one side of the certainty response scale; if participants were only using one side of the scale (i.e., the left), this would have been reflected as a systematic pattern of certainty across all conditions, but this was clearly not the case, which suggests that any differences between the ratings of each side arose as a genuine refection of the impression that participants had in their representation of each side.

It is also unlikely that the results were based on merely the last three instructions of "empty" or "filled" on either side because every pattern was unique, and, indeed, for some patterns the last three cells were blank. The contents of late-presented cells were chosen at random, which makes it difficult to conduct a separate analysis on how the contents of late-presented cells influenced certainty given that these were not counterbalanced across stimuli. While it is possible that the contents of the late-presented cells played some role in certainty responses, there was no symmetrical recency effect demonstrated for any listening condition, which indicates that certainty judgements were based on a genuine impression of each stimulus side.

The findings from Experiment 1 therefore appear to support the hypothesis that there is a lateralized bias towards the left in visual mental representations, even if they did not involve visual input.

EXPERIMENT 2

The results of Experiment 1 were clear, but leave open the question as to whether the bias observed in certainty judgements would also appear in a test of memory for each side of the pattern. The result is also new, and so it is important to demonstrate that it replicates with different participants and with a modified paradigm. However, it is possible that when participants are required to maintain the details of the pattern, this changes the general impression of the stimulus and therefore may reduce the likelihood to respond "left fuller" over "right fuller" and lead participants to be less certain about the general impression of the stimulus. Therefore, Experiment 2 was designed partly to replicate the results of Experiment 1 and also to explore whether overrepresentation of the left side resulted in more accurate maintenance and retrieval of the left side of the pattern.

Method

Participants

A total of 56 right-handed native English-speaking undergraduate participants were recruited for the experiment. There were 28 participants in a binaural listening condition and 28 participants in a separate monaural condition. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), with a score of +100 indicating exclusive right-handedness and a score of −100 indicating exclusive left-handedness: All participants scored over +65 on the handedness questionnaire. All participants were aged 18−38 years and from the University of Edinburgh, with normal or corrected-to-normal vision and hearing. Participants were paid a £6 honorarium.

Apparatus and stimuli

These were the same as those in Experiment 1.

Design and procedure

Two separate groups of 28 participants each performed the task in either a binaural or a monaural listening condition at Speed 2, the higher speed (11 s per pattern). The design and procedure were the same as those for Experiment 1 with the exception of an additional recall response demand.

After a prerecorded aural verbal pattern description had been played over a pair of Sony noise-cancelling headphones at the same volume for each participant binaurally or monaurally, there was a 1-s pause, and then participants opened their eyes, unclasped their hands, and reported which side of the pattern contained the most filled cells using the same graded scale of certainty [LEFT 4 3 2 1 0 1 2 3 4 RIGHT] as that in Experiment 1. Following their certainty response, participants recalled the pattern for the side they perceived fuller using a paper booklet situated between the participant and the keyboard. The booklet consisted of 19 A4 sheets of paper in landscape orientation stapled together at the top centre (1 practice trial plus 18 experimental trials). On each sheet of paper, there was an outline of a 6 × 3 cell matrix in black ink printed centrally both horizontally and vertically. The left and right

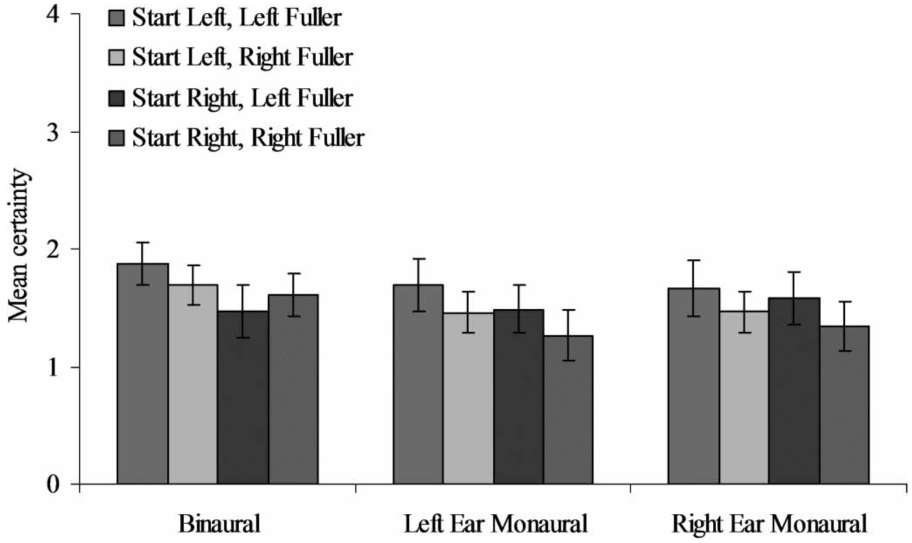

Figure 4. *Mean certainty responses as a function of start side in Experiment 2. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left-fuller and right-fuller stimuli. Error bars indicate standard error of the mean.*

sides of the matrix were separated by a thicker black line. If participants perceived the left side of the stimulus to be fuller, they recalled the left side of the pattern using the left side of the matrix by making a cross (×) inside the blank cells to designate a filled cell. If participants perceived the right side of the stimulus to be fuller, they recalled the right side of the pattern using the right side of the matrix by making a cross (×) inside the blank cells to designate a filled cell. If participants were not sure which side was fuller (and thus had pressed "0" on the response scale), they were not required to recall the pattern. Following recall, participants turned over the page in the booklet, closed their eyes, pressed the spacebar, and clasped their hands ready for the next trial.

Results

Proportional bias

The proportional bias was calculated for each of the 28 participants in the binaural and monaural listening conditions across all trials (Figure 2, right panel). As in Experiment 1, all mean values for the monaural condition were negative, indicating that participants were more likely to respond left fuller than right fuller. For the binaural listening condition, the mean value was positive, indicating the opposite trend. The proportional bias for the left ear approached significance, $t(27) = -1.841$, $p = .077$, and was not significant for the right ear, $t(27) = 1.078$, $p = .291$. Replicating Experiment 1, the proportional difference for the binaural condition was not significantly different from zero, $t(27) = 0.705$, $p = .487$. A one-way ANOVA was used to compare the proportional difference between the binaural, monaural left ear, and monaural right ear listening conditions. Proportional bias was not significantly different across the three listening conditions, $F(2, 81) = 1.558, p = .217$.

Certainty

Certainty responses were then analysed in the same way as for Experiment 1.[3] Figure 4 shows that for all listening conditions, certainty was greater for left-fuller than for right-fuller stimuli. As in Experiment 1, for the monaural condition there was a significant main effect of side fuller, $F(1, 27) = 6.303$, $MSE = 0.443$, $p = .018$, with greater certainty for left-fuller than for right-

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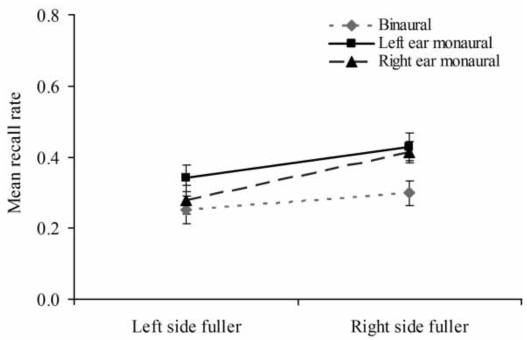
[3] A correct-only analysis yielded similar results for both listening conditions.

(a) Start Left



(b) Start Right

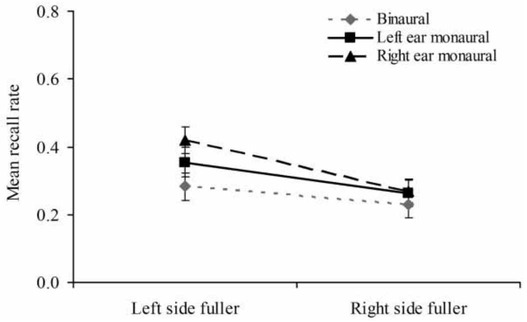


Figure 5. *Mean recall rate as a function of start side in Experiment 2. Values represent mean recall rate for start left (a) and start right (b). Error bars indicate standard error of the mean.*

fuller stimuli. Like Experiment 1, there was no significant effect of ear, $F(1, 27) = 0.233$, $MSE = 0.379$, $p = .633$, or start side, $F(1, 27) = 1.620$, $MSE = 0.820$, $p = .214$. In addition, there was no significant interaction between start side and side fuller, $F(1, 27) = 0.006$, $MSE = 0.367$, $p = .940$, ear and side fuller, $F(1, 27) = 0.006$, $MSE = 0.258$, $p = .941$, or ear, start side, and side fuller, $F(1, 27) = 0.025$, $MSE = 0.286$, $p = .875$.

Participants did show a tendency to be more certain about left-fuller patterns in the binaural condition but there was no main effect of side fuller, $F(1, 27) = 0.23$, $MSE = 0.531$, $p = .881$, although start side approached significance, $F(1, 27) = 3.936$, $MSE = 0.440$, $p = .058$, with slightly greater certainty when the description started on the left-hand side than on the right-hand side. There was no interaction between start side and side fuller, $F(1, 27) = 0.888$, $MSE = 0.830$, $p = .354$.

A repeated measures ANOVA with start side and side fuller as the within-subject variables and listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted to compare differences between listening conditions. The interaction between side fuller and listening condition was not significant, $F(2, 81) = 0.933$, $MSE = 0.411$, $p = .398$, and there was no interaction between start side and listening condition, $F(2, 81) = 0.284$, $MSE = 0.556$, $p = .753$, nor between start side, side fuller, and listening condition, $F(2, 81) = 0.543$, $MSE = 0.494$, $p = .583$.

Recall

Recall accuracy was assessed in terms of the rate of hits (cells correctly filled), false alarms (cells incorrectly filled), correct rejections (cells correctly left blank), and misses (cells incorrectly left blank). The calculation of hit rate (HR) is given below in Equation 1, and false-alarm rate (FAR) is given below in Equation 2:

$$\mathrm{HR} = \mathrm{hits}/(\mathrm{hits} + \mathrm{misses}) \tag{1}$$

$$\mathrm{FAR} = \mathrm{false\ alarms}/(\mathrm{hits} + \mathrm{false\ alarms}) \tag{2}$$

Recall rate was then calculated as HR − FAR, where higher values indicate more accurate replication of patterns (Figure 5). For the monaural listening condition, a repeated measures ANOVA was conducted with start side and side fuller as the within-subject variables. There was no main effect of ear, $F(1, 27) = 0.003$, $MSE = 0.051$, $p = .953$, start side, $F(1, 27) = 2.147$, $MSE = 0.041$, $p = .154$, or side fuller, $F(1, 27) = 0.070$, $MSE = 0.019$, $p = .793$, and no interaction between ear and start side, $F(1, 27) = 3.504$, $MSE = 0.021$, $p = .072$, ear and side fuller, $F(1, 27) = 0.035$, $MSE = 0.21$, $p = .853$, but a highly significant interaction between start side and side fuller, $F(1, 27) = 52.559$, $MSE = 0.014$, $p < .001$, with the most accurate recall for the side that the verbal description ended on:

When the description ended on the left-hand side (and started right), the recall rate was better for left-fuller patterns, but when the description ended on the right-hand side (and started left), recall rate was better for right-fuller patterns. There was no interaction between ear, start side, and side fuller, $F(1, 27) = 0.991$, $MSE = 0.038$, $p = .328$. When the analysis was conducted for correct trials only, the results for the monaural listening conditions were exactly the same with the only significant effect being an interaction between start side and side fuller, $F(1, 27) = 26.064$, $MSE = 0.035$, $p < .000$.

A repeated measures ANOVA for the binaural condition with start side and side fuller as within-subjects factors found no significant effect of start side, $F(1, 27) = 0.317$, $MSE = 0.028$, $p = .578$, side fuller, $F(1, 27) = 0.008$, $MSE = 0.022$, $p = .930$, and no significant interaction between start side and side fuller, $F(1, 27) = 1.734$, $MSE = 0.040$, $p = .199$, but when correct trials only were considered there was a significant interaction between start side and side fuller, $F(1, 27) = 6.678$, $MSE = 0.036$, $p = .016$.

A post hoc power analysis was performed for the binaural and monaural condition recall data using G*Power Version 3.0.1 software (Heinrich-Heine-Universitat, Dusseldorf, Germany). The specified test-family was "*F*-test ANOVA: fixed effects, special, main effects and interactions". For the monaural condition, the power analysis was conducted with an alpha level of .05, an effect size of 0.25 (medium effect size), a value of 8 for the number of levels of the experimental design—that is, 2 (ear) × 2 (start side) × 2 (side fuller)—and a total sample size of 224 (i.e., summed over all levels of the experimental design). The revealed power for the monaural analysis was .96 (equivalent to 96%). For the binaural condition, the power analysis was conducted with an alpha level of .05, an effect size of 0.25 (medium effect size), a value of 4 for the number of levels of the experimental design—that is, 2 (start side) × 2 (side fuller)—and a total sample size of 112. The revealed power was .75 (equivalent to 75%).

A repeated measures ANOVA with start side and side fuller as the within-subject variables and listening condition (binaural, monaural left ear, monaural right ear) as the between-subject variable was then conducted to compare differences between listening conditions. The interaction between side fuller and listening condition was not significant, $F(2, 81) = 0.020$, $MSE = 0.020$, $p = .980$, and there was no interaction between start side and listening condition, $F(2, 81) = 1.384$, $MSE = 0.030$, $p = .257$, nor start side, side fuller, and listening condition, $F(2, 81) = 1.945$, $MSE = 0.031$, $p = .150$.

Discussion

For the monaural listening conditions when participants made a relative judgement between the two sides of a verbally described pattern, there was some tendency to judge that the left side of the pattern was fuller and to be more certain that this was the case than for the right side of the pattern. However, the effect of monaural presentation to the left ear was the strongest enhancer of this effect. Despite this, the effect of having to maintain the pattern in greater detail rather than simply create a "general impression" of the stimulus seemed to dampen the previously observed representational pseudoneglect in Experiment 1. In Experiment 2, subjects were also explicitly required to maintain, for later recall, specific details on the left and right sides of the pattern stimulus, and it is possible that this maintenance by working memory mechanisms quashed the general impression of that stimulus. There was not greater accuracy in recalling the left side of the pattern, and recall accuracy was greatly affected by recency with the side that the description finished on leading to a better rate of recall.

GENERAL DISCUSSION

When participants made a relative judgement between two sides of a verbally described pattern, there was a tendency to overrepresent the left side, reflected in the fact that participants responded that this side was fuller more often than right side and also that they were more certain when judging left-fuller patterns. The strongest effects were found for stimuli presented monaurally to the left ear. In Experiment 2, in addition to making a general judgement about which side was fuller, participants were also asked to recall the side judged to be fuller. Although participants in Experiment 2 showed some tendency to overrepresent the left side of the pattern, this overrepresentation did not translate into better accuracy in recall, and the earlier observed effects in certainty judgements were only replicated for the monaural listening conditions, as having to maintain the pattern in greater detail seemed to change the general impression of the stimulus.

The most common account of perceptual pseudoneglect is that the cerebral hemispheres differentially orient attention to contralateral space (Brodie & Pettigrew, 1996; Heilman & Van Den Abell, 1979; McCourt & Jewell, 1999) with the right hemisphere preferentially directing attention leftwards. The same theory can be used to explain the representational pseudoneglect observed in both Experiment 1 and Experiment 2. Imagining the spatial layout of the verbally described pattern stimulus may have engaged visuospatial processing mechanisms in the right hemisphere, preferentially facilitating the orienting of covert attention leftwards within working memory (e.g., McGeorge et al., 2007). As attention was oriented towards the left side of the stimulus, this may have resulted in greater saliency for the left side, which in turn resulted in increased certainty about the left side (Experiments 1 and 2).

The hypothesis is supported by the fact that monaural left ear presentation enhanced representational pseudoneglect as preferential engagement of the right hemisphere may have bolstered this process. Indeed, Schonwiesner et al. (2006) found that monaural pulsed noise to each ear preferentially engaged contralateral hemispheric regions—but when binaural pulsed noise was included, this pattern was obliterated in the right hemisphere. This indicates that monaural presentation to the left ear may have increased activation in the right hemisphere, which is also sensitive to spatial processing. The results therefore seem to suggest that attentional orienting can occur for a mental representation within visuospatial working memory that has been generated from an auditory verbal description, with monaural presentation to the left ear preferentially engaging the right hemisphere and enhancing attentional orienting. This account would argue that the right hemisphere was preferentially activated over the left hemisphere because of the spatial nature of the task, given the right hemisphere's well-known role in spatial processing. In this way, the bias stems from a general "impression" of the stimulus, which may be driven by attentional orienting occurring in the right hemisphere.

The finding that there was no clear lateralized bias in recall performance suggests that the visual mental representation is equally detailed for both sides of the mentally constructed array. This reinforces the idea that the bias is in covert attention to the left of the mental representation in working memory rather than, for example, impoverished representation of detail for the right of the array. This finding is not wholly consistent with previous research showing better recall for the left side of temporary activation of visual information about familiar scenes (McGeorge et al., 2007) or in immediate visual memory for recently presented visual arrays (Della Sala et al., 2010). However, unlike those previous studies, the pattern stimuli in the present study were aurally described, which means participants had no prior or current visuospatial experience of the stimuli. Also, in Experiment 2, there was a symmetrical effect of recency with the most recently described pattern side gaining better recall; it is possible that the recency effect—strongest when presentation was to the right ear (i.e., Burns & Manning, 1981; Taylor & Heilman, 1982)—helped to reduce sensitivity in the memory measure of representational pseudoneglect. As the bias was clear in the measure of certainty, it is possible that certainty is simply a more sensitive measure of bias within this paradigm than is memory performance. It is clear that having to maintain details within a stimulus affects the general impression of that stimulus, but in order to explain why this is the case, further research is required.

To this end, it would be interesting to explore ways of counterbalancing the recency effect in order to unmask any potential bias. One way to achieve this would be to increase or decrease the salience of one side of the pattern by making individual cells more salient; the hypothesis would be that salient cells would capture attention and contribute to representational pseudoneglect. Importantly, if the salient cells were contralateral to the finishing side of the description, this could counterbalance the recency effect. The complexity of the patterns could be varied to create a test that is more sensitive to a difference in the level of detail encoded on the left and right.

It may also be interesting to observe the performance of participants who read in the opposite direction—from right to left instead of from left to right. However, in the current study the leftward bias (i.e., representational pseudoneglect) was robust even when the stimulus description started on the right and moved leftward; this is the opposite direction to the participant's reading pattern, which suggests that the bias is not simply a function of reading pattern. Nevertheless, it is worth considering for future research.

In conclusion, there are several possible theoretical accounts that could be explored in future studies. However, we focus here on reporting a robust phenomenon of representational pseudoneglect. In the two experiments here, this phenomenon is manifest in the certainty with which participants make judgements about the number of items on either side of an array that has been presented as an aural verbal description. We suggest that this reflects an overrepresentation or greater salience of the left side of the constructed mental representation of the array, and that monaural presentation to the left ear clearly enhances this effect. Moreover, the results have illustrated that the phenomenon of representational pseudoneglect is robust and merits further empirical investigation as well as consideration within current theories of the role of covert attention in visuospatial working memory.

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Representational pseudoneglect for imagined real word scenes driven by aural-verbal description.

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Representational pseudoneglect for imagined real word scenes driven by aural-verbal description.

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ABSTRACT

The main aim of the current research was to explore asymmetries in visuo-spatial working memory for the temporary activation of highly imageable information. In the current study, 96 healthy participants listened binaurally or monaurally to aural-verbal descriptions of novel ‘city street’ scenes which contained highly imageable landmarks (e.g., “shop”, “market”, “school”) on either side of the street (left vs. right) and were asked to create a visuo-spatial mental representation of the street as it was described. Participants were then asked to decide which side of the street contained the most landmarks, provide a certainty score for this judgement, and recall the landmarks on the side of the street that was perceived to contain the most landmarks. The results showed a significant effect of listening condition: when presentation was monaural to the left ear judgements erred towards the left side of the street (i.e., ‘the left side of the street has the most landmarks’) but when presentation was binaural or monaural to the right ear, there was no bias. Despite the significant leftward trend for the left ear condition, or representational pseudoneglect, recall accuracy was similar across all listening conditions. Results are discussed in terms of right hemisphere attentional orienting and the formation of temporary representations in visuo-spatial working memory of novel, highly imageable material from auditory presentation.

Representational pseudoneglect for imagined real word scenes driven by aural-verbal description.

It has been previously shown that when healthy participants are asked to report details from an imagined highly familiar scene (e.g. Piazza del Duomo in Milan) more details are reported from the left than from the right-hand side - a bias independent of imagined viewpoint (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; see also Bisiach & Luzatti, 1978). A similar bias has been suggested when healthy participants were asked to recall cities from highly familiar countries (Bourlon, Duret, Pradat-Diehl et al., 2011). Healthy participants have also been found to have better immediate memory for material briefly presented on the left-hand side of a visual array, an effect based on the mental representation that was formed after the visual stimulus had been removed (Della Sala, Darling & Logie, 2010). These studies suggest that lateralised biases can occur during the temporary activation of information in working memory and point towards a form of ‘pseudoneglect’ (Bowers & Heilman, 1980) that is purely representational. Perceptual pseudoneglect has been widely demonstrated as a leftward bias on visuo-spatial line bisection (*for review see* Jewell & McCourt, 2001) and is typically explained by the right hemisphere preferentially orienting attention to contralateral left space (Kinsbourne, 1970; Heilman & Van Den Abell, 1979; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). An important question is whether or not these observed memory asymmetries really do arise from the temporary representations in working memory or whether they are a product of biases in visual attention when processing the visual array. This question was recently addressed by Brooks, Logie, McIntosh, & Della Sala (*in press*, 2011) who asked participants to mentally represent a novel square matrix that contained either filled-in or empty cells created from aural verbal description. There was a significant tendency for participants to respond that the left side of the pattern contained the most filled-in cells and to be more certain about judgements for the left-hand side of the pattern; this was enhanced by monaural left ear presentation (favouring the right hemisphere). However, there was no advantage in recall accuracy for pattern on the left side. It would seem that memory asymmetries are not simply a function of the representation held in visuo-spatial working memory but perhaps depend on how the representation is formed.

One outstanding question is whether or not lateralised biases in memory only occur for highly familiar previously encountered stimuli because, here, there is a strong basis for visual imagery especially if that material was initially processed using vision. A completely novel abstract stimulus may result in the formation of a less detailed visual representation, less sensitive to the lateralised bias in memory but still sensitive to biases of general impression and/or in the confidence with which lateralised judgements are made. One experiment is reported which followed the experimental design of Brooks et al. (*in press*, 2011) but also used highly imageable stimuli in familiar contexts to be more directly comparable with McGeorge et al., (2007). Stimuli were aural-verbal descriptions of fictitious ‘city street’ scenes with highly imageable landmarks (‘shop’, ‘market’, ‘cafe’) on either side of the street, starting left or right (Urbanski & Bartolomeo, 2008), drawing on previous research which has explored how people mentally represent spatial layouts (i.e., Brunye & Taylor, 2008; Deyzac, Logie, & Denis, 2006). In the current study, the task was to decide which side of the street, left versus right, contained the most landmarks and then to provide a certainty score for this judgement before recalling the landmarks for the side that was perceived to contain the most landmarks. Like Brooks and colleagues the verbal description was presented monaurally or binaurally; monaural presentation may preferentially engage the contralateral hemisphere whereas binaural presentation engages both hemispheres (Schönwiesner, Krumbholz, Rübsamen, Fink, & Yves von Cramon, 2007; Paiement et al., 2008).

METHOD

Participants

There were 96 right-handed native English speaking participants from the University of Edinburgh aged between 18-38 years with normal or corrected-to-normal vision and hearing. Participants were paid a £6 honorarium.

Stimuli

There were 32 pre-recorded aural verbal descriptions of fictitious ‘city streets’ scenes containing a mixture of landmarks on either street side (depicted in Figure 1). The stimuli were recorded by a native English-speaking female in a sound-attenuated recording booth. The landmarks were generated using the MRC psycholinguistic database and chosen on the basis of having high imageability scores (> 550). The original landmarks were ‘bank’, ‘bar’, ‘café’, ‘church’, ‘college’, ‘garden’, ‘hotel’, ‘market’, ‘office’, ‘school’, ‘shop’, ‘station’. In a pilot study 13 native English right handed participants were asked to decide if each landmark could be easily visually imaged on a city street using a sliding scale of certainty [1 2 3 4 5 6 7]. For this scale, the number ‘1’ represented ‘very difficult to conjure up a visual image’ and ‘7’ represented ‘very easy to conjure up a visual image’. Participants responded towards the low end of the scale (< 3) for ‘office’ and ‘college’ so these were removed from the cohort. The remaining ten landmarks (with scores > 3) were used for the experimental stimuli. For each stimulus, one side of the street was always ‘fuller’ with more landmarks on one side than the other. There were 8 ‘left fuller’ street scenes with either two, three, four, or five landmarks interspersed with the spoken word “house” on the left side of the street along with one, two, three, or four landmarks interspersed with the spoken word “house” on the right side of the street. There were also 8 ‘right fuller’ street scenes designed in exactly the same way. There were always 6 items (a mixture of landmarks and houses) on each side of the street; 12 items in total. The landmarks were randomly distributed but the same landmark was not presented at the last/first position of the description on every trial. There were 16 descriptions that started on the left side of the street and 16 descriptions that started on the right side of the street; the description switched back and forth between each side of the street (e.g. on the left is a house, on the right is a bank, on the left is a garden, on the right is a house and so on). The ten original landmarks were split into two matching groups of five stimuli based on their imageability scores. The landmarks for each street side were randomly picked from a pool of 'left side landmarks' and a pool of 'right side landmarks' which allowed the imageability for each street side to be matched on every trial (counterbalanced so that the left side landmarks were presented on the right and vice versa for the right side landmarks).

----- Insert Figure 1 about here -----

Procedure

There were 48 participants in a binaural listening condition and a separate group of 48 participants in a monaural listening condition. Participants were given task instructions which contained a top-down depiction of a fictitious shopping street (Figure 1). Participants were asked to mentally represent the street in whichever way they preferred. Participants were fitted with a pair of Sony noise-cancelling headphones and closed their eyes and clasped their hands ready to begin. The experiment started when the spacebar was pressed. After a 1s pause, a pre-recorded verbal description was played either binaurally or monaurally. When the description was complete, participants were asked to open their eyes and decide which side of the street, left or right had the most landmarks and rated their certainty on a scale presented on the keyboard. The certainty scale consisted of nine keys [4 3 2 1 0 1 2 3 4]. If the left side of the street was perceived to have the most landmarks and participants were absolutely certain about this, they were asked to press ‘4’ on the left side of the keyboard – vice versa for the right side. If participants were uncertain about which side of the street had the most landmarks, they were asked to press ‘0’ on the scale. The other numbers from ‘1’ to ‘3’ represented an incremental increase on the scale. All the participants completed the certainty scale judgement. Half of the participants (24 binaural and 24 monaural) stopped at this point and moved on to the next trial. The other half of the participants in each listening condition were asked to perform an additional task: to recall the landmarks for the side of the street they thought had the most landmarks. If they had responded that the left side of the street had the most landmarks, they were asked to recall the landmarks on the left and vice versa for the right side of the street. Brooks et al. (*in press,* 2011) suggested that performing the recall task, therefore mentally representing the stimulus with the intention to recall details, reduced sensitivity to representational pseudoneglect so we wanted the opportunity to explore this as well. Participants verbally responded into a centrally positioned microphone and there was no time limit for recall. When recall was complete, participants pressed the spacebar for the next trial, closed their eyes, and clasped their hands. Start side (start left vs. start right) was a within-subject variable and trials were blocked by starting side and counterbalanced across participants. For the monaural listening condition, ear was a within-subject variable and trials were also blocked by ear (counterbalanced across participants). Trial order was randomly shuffled.

RESULTS

For the relative judgement task, the total number of ‘left fuller’ responses from all 96 (binaural and monaural) participants was subtracted from the total number of ‘right fuller’ responses and then divided by the overall number of responses to yield a measure of 'proportional bias', with a negative proportional bias indicating a tendency to respond 'left fuller' more often than 'right fuller' but a positive value reflecting the opposite tendency (Brooks et al. *in press,* 2011). There was no significant difference in proportional bias between participants who completed only the certainty task versus those who completed certainty plus recall so the data were collapsed within each listening condition. Figure 2 displays mean proportional bias for the binaural and separate monaural listening conditions. Proportional bias was significantly different across the three listening conditions (F (2, 141) = 4.235, p = .016). There was a significant difference between the left and right ear (p = .014) but no significant difference between the binaural and left ear (p = .608) or the binaural and right ear (p = .141). There was a clear leftward trend for the left ear and this was significantly different from zero (t(47) = -2.722, p = .009), but not for the binaural condition (t(47) = -.713, p = .480) nor for the right ear condition (t(47) = 1.704, p = .095).

----- Insert Figure 2 about here -----

Certainty responses were then recoded as a correct judgement (e.g. participants responded 'left side more landmarks' correctly) or an incorrect judgement (e.g. participants responded 'left side more landmarks' incorrectly); correct judgements were assigned positive values whereas incorrect judgements were assigned negative values, creating a certainty index (Brooks et al., *in press*, 2011). The certainty analysis for participants in the binaural condition and monaural condition was conducted with correct and incorrect trials combined because a tendency to be more certain about the landmarks on the left side of the street should occur regardless of whether or not participants were correct or incorrect in their responses. An initial analysis showed no significant difference in certainty between each task group of participant so the data were collapsed within each listening condition. Figure 3 displays mean certainty for the binaural and monaural conditions. For the monaural listening condition, there was a significant interaction between ear and side fuller (*F*(1,47) = 7.277, *MSE* = .556, *p* = .010) and start side and side fuller (*F*(1,47) = 5.541, *MSE* = .786, *p* = .023), as when presentation was to the left ear certainty was greater for left fuller stimuli - especially when the description started on the left - but the exact opposite was observed when presentation was to the right ear with certainty being greater for right fuller stimuli and a start right description. There was no significant main effect of ear alone (*F*(1,47) = .124, *MSE* = .951, *p* = .726), side fuller (*F*(1,47) = .086, *MSE* = .517, *p* = .770), or start side (*F*(1,47) = 2.195, *MSE* = .813, *p* = .145), and no interaction between ear and start side (*F*(1,47) = 3.435, *MSE* = .799, *p* = .070), or ear, start side and side fuller (*F*(1,47) = .033, *MSE* = .476, *p* = .856). For the binaural condition there was no significant main effect of side fuller (*F*(1,47) = .255, *MSE* = .565, *p* = .616) or start side (*F*(1,47) = 3.055, *MSE* = .679, *p* = .087) but the interaction between start side and side fuller approached significance (*F*(1,47) = 3.929, *MSE* = .782, *p* = .053). Consistently, there was a significant interaction between side fuller and listening condition (*F*(2,141) = 3.878, *p* = .023) driven by noticeably different performance when presentation was to the right ear.

----- Insert Figure 3 about here -----

Recall accuracy was analysed for participants in the binaural condition (N=24) and monaural condition (N=24) in terms of the rate of hits (landmarks correctly recalled), false alarms (landmarks incorrectly recalled), correct rejections (landmarks correctly not recalled), and misses (landmarks not recalled but missed). The calculation of Hit Rate (HR) is given in Equation 1 and False Alarm Rate (FAR) in Equation 2:

(1) Hits/(Hits + Misses)

(2) False Alarms/(Hits+False Alarms)

Recall rate was then calculated as [HR – FAR] where higher values indicate more accurate recall of landmarks. Figure 4 displays mean recall rate for the binaural and monaural listening conditions. For the monaural condition, there was a significant main effect of start side ($F(1,23) = 9.964$, $MSE = .041$, $p = .004$) with recall rate being better for the start right condition (description moved from right-to-left and finished on the left) compared to the start left condition (description moved from left-to-right and finished on the right). There was no significant main effect of ear alone ($F(1,23) = .276$, $MSE = 0.67$, $p = .605$) or side fuller ($F(1,23) = 1.670$, $MSE = .067$, $p = .209$), and no interaction between ear and start side ($F(1,23) = 1.982$, $MSE = .038$, $p = .173$) or ear and side fuller ($F(1,23) = .001$, $MSE = .040$, $p = .971$) or ear, start side and side fuller ($F(1,23) = 0.62$, $MSE = .030$, $p = .805$). For the binaural condition, there was no significant main effect of side fuller ($F(1,23) = .082$, $MSE = .043$, $p = .777$) or start side ($F(1,23) = .002$, $MSE = .022$, $p = .968$) and no interaction between start side and side fuller ($F(1,23) = .657$, $MSE = .128$, $p = .426$). When listening condition was added as a between-group variable there were no significant effects.

----- Insert Figure 4 about here -----

DISCUSSION

The current study explored whether lateralised memory biases could be found for the temporary activation of completely novel, non-visual, highly imageable material. The main aim of the current study was the recall task: the results of the recall task completely complement Brooks et al. (in press, 2011) as, importantly, there was no lateralised memory bias even though the stimuli were highly imageable and, arguably, familiar in terms of context. As there was no clear lateralised recall bias, this suggests that the street scene stimulus was equally detailed (or equally impoverished) on both sides. The landmarks were not more salient on the left side of the street despite the implied asymmetry in salience when participants made a relative judgement in the first part of the task for monaural left ear presentation.

The results of the relative judgement task are also consistent with Brooks et al. (in press, 2011) showing a significant leftward bias, or representational pseudoneglect, for the monaural left ear condition (favouring the right hemisphere) but no significant bias for the binaural or monaural right ear condition (favouring the left hemisphere). These results, at least for the left ear, can be interpreted within the theoretical framework that the right hemisphere directs attention preferentially leftward in spatial tasks (Heilman & Van Den Abell, 1979; Reuter-Lorenz, Kinsbourne, and Moscovitch, 1990). Interestingly, although Brooks et al. did not find a large rightward bias when their stimuli were presented monaurally to the right ear, there was a clear indication that presentation to the right ear resulted in reduced sensitivity to representational pseudoneglect compared to monaural left ear or binaural presentation. It is therefore possible that the high imageability of the stimuli somehow boosted this ‘desensitivity’. It is also possible that because the landmarks were also high frequency words left hemisphere activity, and thus contralateral attentional orienting, was particularly enhanced. When the direction of the description was theoretically consistent with that of attentional orienting, from right-to-left, recall rate was significantly enhanced. It is possible that the start side effect was a signature of an underlying attentional orienting effect that could lead to asymmetries in recall performance, especially for the left ear condition, but that any such effect is overshadowed by the serial order nature of the aural verbal description. While the results could perhaps be interpreted as lateralised ‘spatial cuing’ with presentation to each ear drawing attention to each side of the street stimulus, the current paradigm does not allow us to make strong enough inferences in this direction but this is an interesting question for future research (see also Nicholls & McIlroy, 2010).

In conclusion, the current study implies that when temporary visual representations are formed from auditory verbal descriptions of highly imageable, familiar stimuli, then lateralised asymmetries are present in the judgements that people make about the contents of those representations, but are not present in the accuracy of recall. This points to the intriguing possibility of a lateralized attentional bias in metamemory rather than in the temporary memory representations themselves, suggesting a fruitful avenue for future research on representational pseudoneglect.

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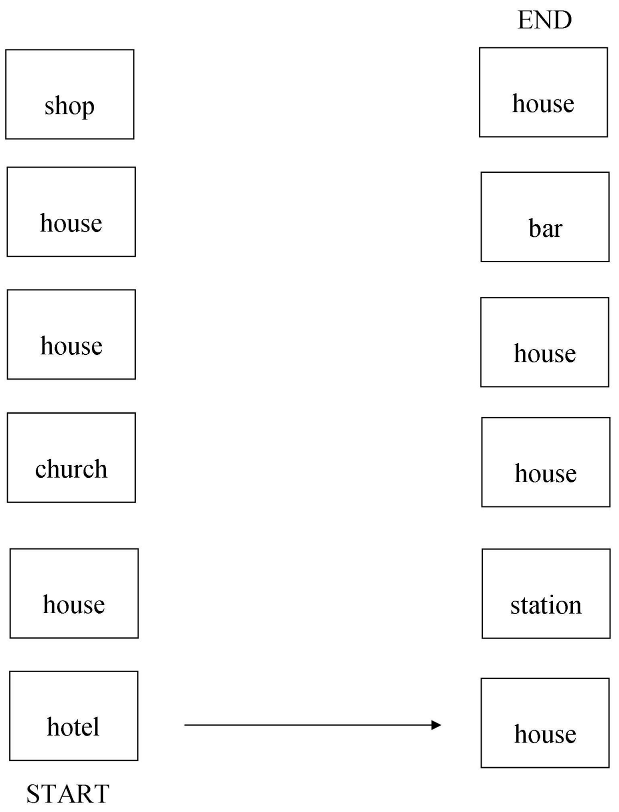
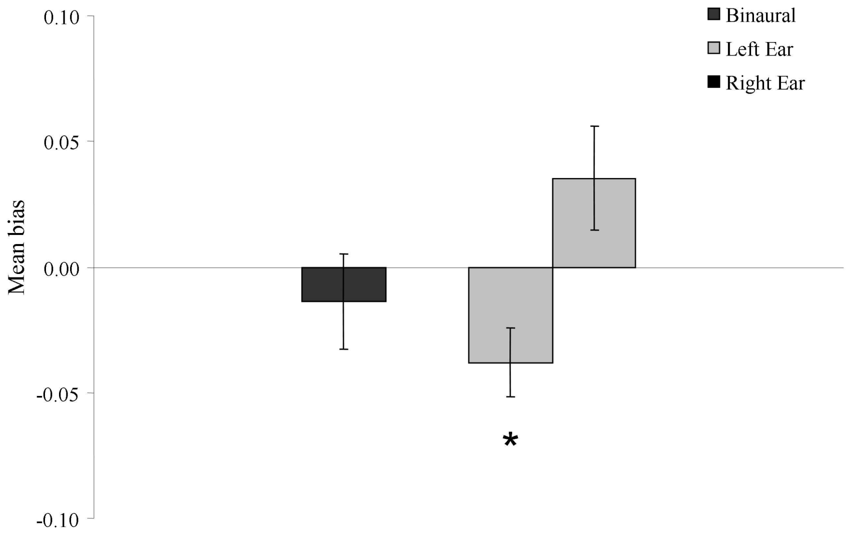
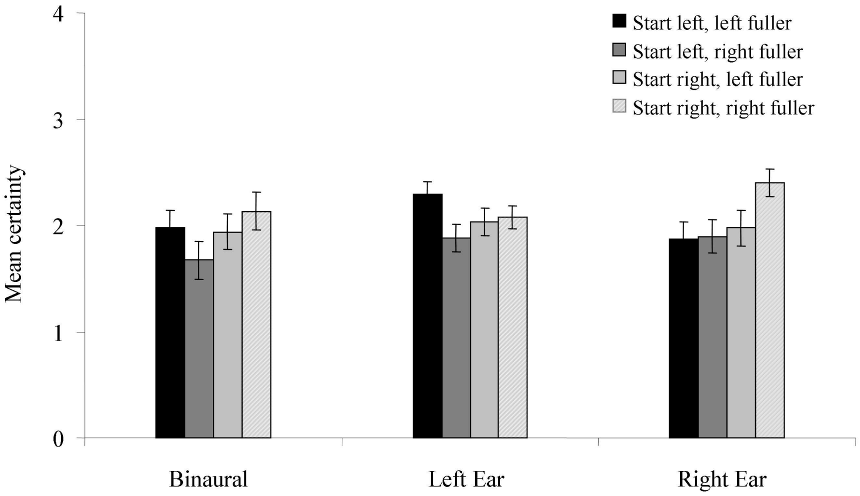


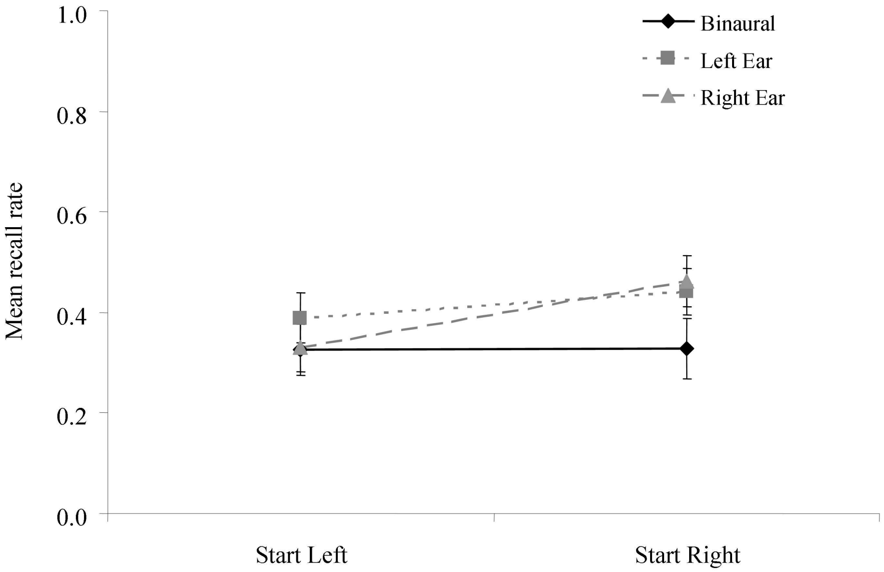
Illustration of the experimental stimulus. The left side of the street has more landmarks than the right.
190x254mm (300 x 300 DPI)



Proportional bias is shown for the separate binaural and monaural listening conditions. Asterisk indicates significance. Error bars indicate standard error of the mean.
274x190mm (284 x 284 DPI)



Mean certainty responses as a function of start side. Values represent mean certainty on a 4-point scale (4 = maximum certainty, 0 = minimum certainty) for left fuller and right fuller stimuli. Error bars indicate standard error of the mean.
274x190mm (284 x 284 DPI)

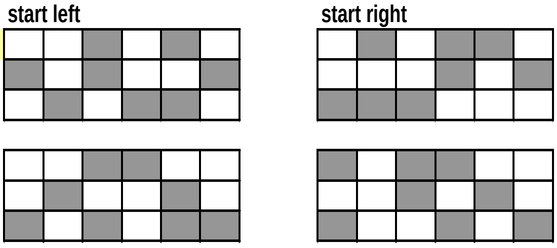


Mean recall rate as a function of start side. Values represent mean recall rate for start left (a) and start right (b). Error bars indicate standard error of the mean.
274x190mm (284 x 284 DPI)

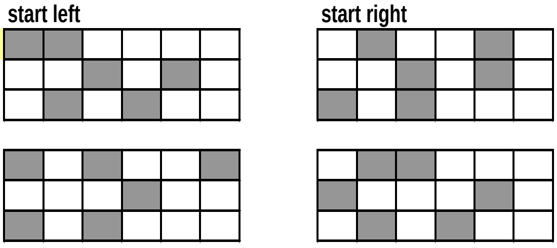
Appendix B

Appendix B: Pattern Stimuli (Experiments 3 to 6)

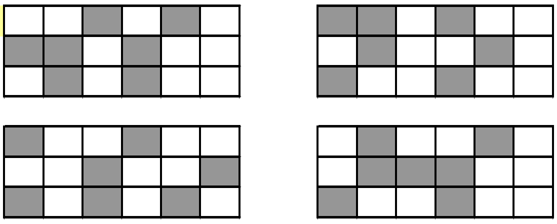
BASELINE LEFT RIGHT 4 FILLED



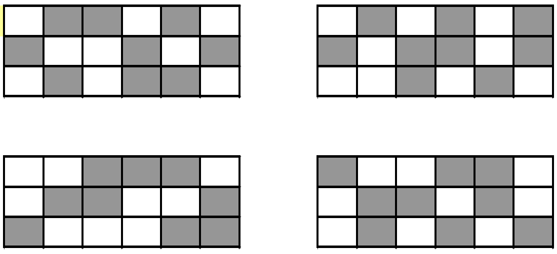
LEFT 4 FILLED - RIGHT 2 FILLED



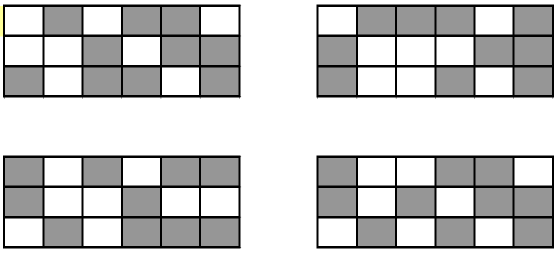
LEFT 4 FILLED - RIGHT 3 FILLED



LEFT 4 FILLED - RIGHT 5 FILLED

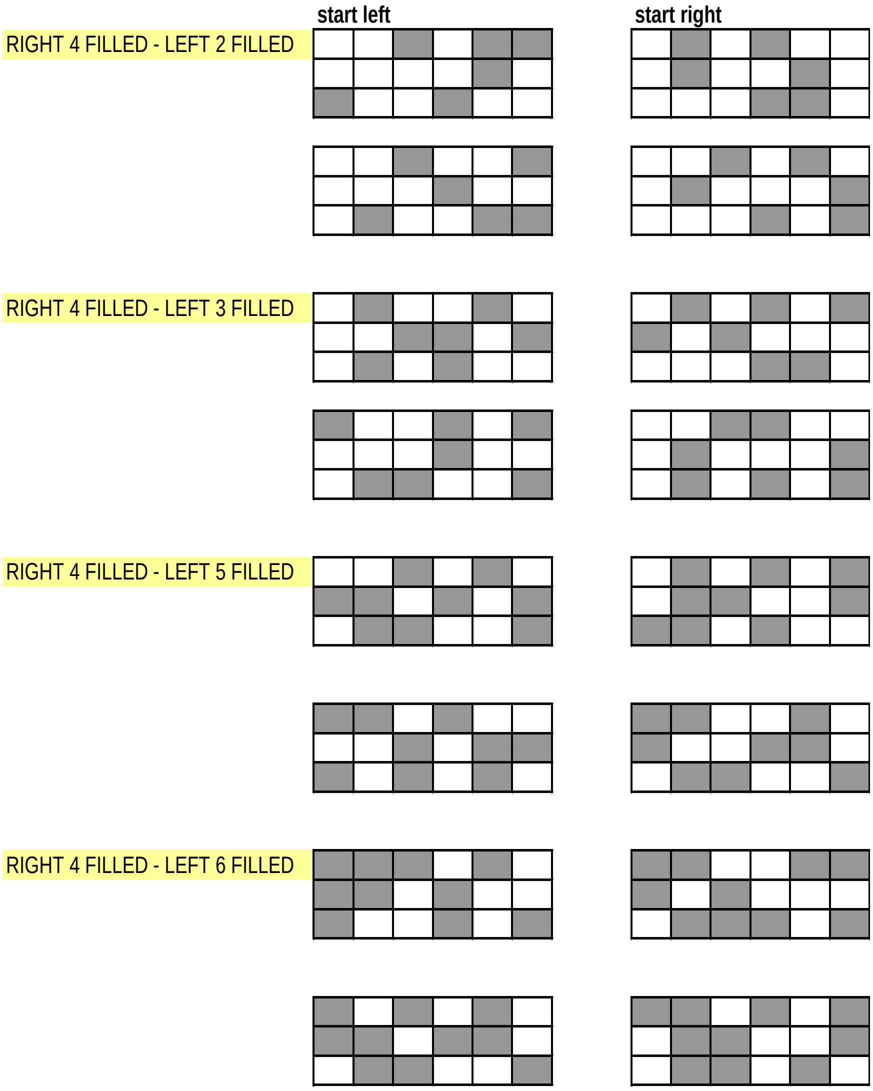


LEFT 4 FILLED - RIGHT 6 FILLED



These pattern stimuli were aural-verbally described as having ‘filled’ or ‘empty’ cells

APPENDIX B PATTERN STIMULI



These pattern stimuli were aural-verbally described as having ‘filled’ or ‘empty’ cells

Appendix C

Appendix C: Street Stimuli (Experiments 7 and 8)

START LEFT

LEFT LARGER

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6			6	SHOP (11)	STATION (12)	6	BANK (11)	BAR (12)	6	BANK (11)	BAR (12)
5	BANK (9)		5			5	CAFE (9)		5	CAFE (9)	
4	CAFE (7)		4	CHURCH (7)		4		SCHOOL (8)	4		SCHOOL (8)
3		SCHOOL (6)	3		BAR (6)	3	HOTEL (5)	GARDEN (6)	3	HOTEL (5)	GARDEN (6)
2			2	HOTEL (3)		2			2	SHOP	
1			1			1	CHURCH (1)		1	CHURCH (1)	MARKET

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6	CAFE (11)	STATION (12)	6	SHOP (11)		6		STATION (12)	6		STATION (12)
5			5			5	BANK (9)	SCHOOL (10)	5	BANK (9)	MARKET
4	SHOP (7)		4			4	HOTEL (7)		4	HOTEL (7)	
3			3	BANK (5)	MARKET (6)	3	CAFE (5)		3	CAFE (5)	
2			2	HOTEL (3)		2	CHURCH (3)	GARDEN (4)	2	CHURCH (3)	GARDEN (4)
1			1		BAR (2)	1			1	SHOP	BAR

RIGHT LARGER

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6			6			6		MARKET	6		MARKET
5			5	SHOP (9)	STATION (12)	5	BANK (11)	BAR (10)	5	BANK (11)	BAR (10)
4		SCHOOL (8)	4		BAR (6)	4	CAFÉ		4	CAFÉ	
3	HOTEL (5)		3			3		GARDEN (2)	3		GARDEN (2)
2			2		GARDEN (2)	2	SHOP	SCHOOL (4)	2	SHOP	SCHOOL (4)
1		MARKET (2)	1	CHURCH (3)		1			1	HOTEL	STATION

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6			6		STATION (12)	6			6	HOTEL	
5			5	BANK (9)	MARKET (10)	5	CHURCH (9)	STATION (10)	5	CHURCH (9)	STATION (10)
4			4			4		SCHOOL (8)	4		SCHOOL (8)
3		MARKET	3	HOTEL (5)	BAR (6)	3	CAFE (5)		3	CAFE (5)	BAR
2	CHURCH		2			2		MARKET (4)	2		MARKET (4)
1		GARDEN (2)	1			1	SHOP (1)	GARDEN (2)	1	SHOP (1)	GARDEN (2)

START RIGHT

LEFT LARGER

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6			6	HOTEL (12)		6	CHURCH (12)	GARDEN (11)	6	CHURCH (12)	GARDEN (11)
5			5		GARDEN (9)	5			5		
4			4	CHURCH (8)		4	CAFE (8)	STATION (7)	4	CAFE (8)	STATION (7)
3	HOTEL (6)		3		BAR (5)	3	HOTEL (6)		3	HOTEL (6)	
2	BANK (4)		2	CAFE (4)		2	BANK (4)	BAR (3)	2	BANK (4)	BAR (3)
1		MARKET (1)	1			1			1	SHOP	MARKET

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6		SCHOOL (11)	6	HOTEL (12)	MARKET (11)	6	BANK (12)	GARDEN (11)	6	BANK (12)	GARDEN (11)
5	SHOP (10)		5			5	CHURCH (10)		5	CHURCH (10)	
4			4			4		BAR (7)	4		BAR (7)
3	CAFÉ (6)		3	SHOP (6)		3	CAFE (6)		3	CAFE (6)	
2			2			2	SHOP (4)	MARKET (3)	2	SHOP (4)	MARKET (3)
1			1	BANK (2)	STATION (1)	1			1	HOTEL	SCHOOL

RIGHT LARGER

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6			6	HOTEL (12)		6	CHURCH (12)	GARDEN (11)	6	CHURCH (12)	GARDEN (11)
5		SCHOOL (9)	5		GARDEN (9)	5			5		MARKET
4			4	CHURCH (8)		4		STATION (7)	4	SHOP	
3	HOTEL (6)	MARKET (5)	3		BAR (5)	3		SCHOOL (5)	3		SCHOOL (5)
2			2			2	BANK (4)	BAR (3)	2	HOTEL	BAR (3)
1			1		SCHOOL (1)	1	CAFE (2)		1	CAFE (2)	STATION (7)

	Left Street	Right Street		Left Street	Right Street		Left Street	Right Street		Left Street	Right Street
6		STATION (11)	6	CHURCH (12)	MARKET (11)	6		GARDEN (11)	6	HOTEL	GARDEN (11)
5	SHOP (10)		5			5	BANK (10)		5	BANK (10)	SCHOOL
4			4			4		BAR (7)	4		BAR (7)
3		SCHOOL (5)	3	SHOP (6)	SCHOOL (5)	3	CAFE (6)	MARKET (5)	3	CAFE (6)	MARKET (5)
2			2			2	SHOP (4)	STATION (3)	2	SHOP (4)	STATION (3)
1			1		STATION (1)	1			1		

These stimuli were also mirror-reversed so landmarks on the left became landmarks on the right and vice versa.

Appendix D

Appendix D: Street Stimuli (Experiments 9 and 10)

START LEFT	end right
6	SCHOOL
5	
4 CAFE	
3	MARKET
2 BANK	
1	

START LEFT	end right
6	STATION
5 SHOP	
4	
3	BAR
2 CHURCH	
1 HOTEL	GARDEN

START LEFT	end right
6 BANK	MARKET
5 CAFE	BAR
4 HOTEL	
3	
2 CHURCH	SCHOOL
1	GARDEN

START LEFT	end right
6	
5 CAFE	
4	
3	STATION
2 SHOP	
1	GARDEN

START LEFT	end right
6	
5 BANK	MARKET
4 SHOP	
3	
2	BAR
1 HOTEL	STATION

START LEFT	end right
6 SHOP	
5	STATION
4	SCHOOL
3 CAFE	
2 CHURCH	MARKET
1 BANK	GARDEN

START RIGHT	end left
1	
2	SCHOOL
3	
4 HOTEL	
5 BANK	
6	MARKET

START RIGHT	end left
1 HOTEL	
2	GARDEN
3 CHURCH	
4	BAR
5 CAFE	
6	SCHOOL

START RIGHT	end left
1 CHURCH	GARDEN
2	
3	STATION
4 SHOP	
5 BANK	BAR
6 CAFE	MARKET

START RIGHT	end left
1	STATION
2 SHOP	
3	
4	GARDEN
5	
6 CAFÉ	

START RIGHT	end left
1 HOTEL	MARKET
2	
3	
4 SHOP	SCHOOL
5	
6 BANK	STATION

START RIGHT	end left
1	GARDEN
2 CHURCH	
3	BAR
4 CAFE	MARKET
5 SHOP	STATION
6 BANK	

These stimuli were also mirror-reversed so landmarks on the left became landmarks on the right and vice versa.

Appendix E

Appendix E: Real-world Images (Experiment 11)

The order of the images (with target) matches Table 5.1 if viewed line by line left-to-right.