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Adult developmental trajectories of pseudoneglect in the tactile, visual and auditory modalities and the influence of starting position and stimulus length



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ABSTRACT

Pseudoneglect is a tendency to pay more attention to the left side of space, typically demonstrated on tasks like visuo-spatial line bisection, tactile rod bisection and the mental representation of numbers. The developmental trajectory of this bias on these three tasks is not fully understood. In the current study younger participants aged between 18 and 40 years of age and older participants aged between 55 and 90 years conducted three spatial tasks: (1) visuospatial line bisection - participants were asked to bisect visually presented lines of different lengths at the perceived midpoint; (2) touch-driven tactile rod bisection in the absence of vision - participants were asked to feel the length of a wooden rod with their index finger and bisect the rod at the perceived centre; and (3) mental number line bisection in the absence of vision - participants were asked to listen to a pair of numbers and respond with the numerical midpoint between the pair. The results showed that both younger and older participants demonstrated pseudoneglect (leftward biases) in the visual, tactile and mental number line tasks and that the magnitude of pseudoneglect for each group was influenced by physical or mentally represented starting side (start left versus start right) and stimulus length. We provide an exploration of pseudoneglect in younger and older adults in different tasks that vary in the degree to which mental representations are accessed and argue that pseudoneglect is a result of a right hemisphere attentional orienting process that is retained throughout adulthood. Our results indicate that, contrary to some current models of cognitive ageing, asymmetrical patterns of hemispheric activity may occur in older age.

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1. Introduction

Healthy young adults often pay more attention to the left-hand side of space when making spatial judgements, a bias known as pseudoneglect (Bowers & Heilman, 1980) which also occurs for mental representation. One key class of task on which pseudoneglect is observed are bisection tasks, in which a stimulus is presented and the participant is asked to identify the middle point of the stimulus. Pseudoneglect is consistently demonstrated on three main types of bisection tasks. Visuo-spatial line bisection involves centrally bisecting visually presented horizontal lines of

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different lengths (Benwell, Harvey, & Thut, 2014; for review see Jewell & McCourt, 2000), tactile rod bisection involves centrally bisecting wooden rods of different lengths using touch alone in the absence of vision (Baek et al., 2002; Brooks, Della Sala, & Logie, 2011; Hach & Schütz-Bosbach, 2012), and mental number line bisection involves mentally representing two or more numbers and bisecting the numerical distance between them (Loftus, Nicholls, Mattingley, & Bradshaw, 2008; Loftus, Nicholls, Mattingley, Chapman, & Bradshaw, 2009; Longo & Lourenco, 2007; Longo & Lourenco, 2010; see also Hubbard, Piazza, Pinel, & Dehaene, 2005). The magnitude of pseudoneglect has been found to be similar, at least for young adults, on visuo-spatial line bisection and mental number line bisection (Longo & Lourenco, 2007). The observation of pseudoneglect across different modalities is suggestive that a multimodal cognitive mechanism underlies the phenomenon.

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The most widely accepted theory of pseudoneglect is that the right cerebral hemisphere orients attention towards contralateral left space due to its dominant role in spatial processing (Heilman & Van Den Abell, 1979; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). This 'Attentional Orienting Hypothesis' is very well supported by behavioural data (Bultitude & Davies, 2006; Toba, Cavanagh, & Bartolomeo, 2011), neuroimaging data (Thiebaut de Schotten et al., 2005; Thiebaut de Schotten et al., 2011; Varnava, Dervinis, & Chambers, 2013) and clinical data – patients with right hemisphere damage err rightward not leftward on spatial tasks (Dormal, Schuller, Nihoul, Pesenti, & Andres, 2014; Manfredini, Mancini, Posteraro, & Savazzi, 2013; Robertson & Marshall, 1993).

The adult developmental trajectory of pseudoneglect, and hence attentional orienting, is a topic of current debate. There is no current agreement about whether or not leftward biases on spatial tasks like visuo-spatial line bisection, tactile rod bisection and mental number line bisection are observed across the full adult lifespan - though there are hints in the data. Jewell and McCourt (2000) noted that healthy older adults show rightward not leftward spatial biases in older age, though this conclusion was based on just two empirical studies that were available at that time (Fujii, Fukatsu, Yamadori, & Kimura, 1995; Stam & Bakker, 1990). There is now additional research to draw upon. Reduced or reversed rightward biases have been reported on visuo-spatial line bisection or landmark tasks (where participants classify pre-bisected line stimuli: Barrett & Craver-Lemley, 2008; Benwell, Thut, Grant, & Harvey, 2014; Goedert, Leblanc, Tsai, & Barrett, 2010; Schmitz & Peigneux, 2011; see also Schmitz, Dehon, & Peigneux, 2013). There is also evidence that males and females may produce differential patterns of pseudoneglect over aging, with older females exhibiting more consistent left biases, whilst older males may exhibit a drift into rightward bias with age (Chen et al., 2011; Varnava & Halligan, 2007). Meanwhile there is evidence for reduced lateral bias in older participants in lateralised visual detection tasks (Learmonth, Thut, Benwell, & Harvey, 2015; Nagamatsu, Carolan, Liu-Ambrose, & Handy, 2011; Nagamatsu, Munkacsy, Liu-Ambrose, & Handy, 2013).

Despite the foregoing, pseudoneglect has also been observed in *both* younger and older adults on visuo-spatial line bisection (Failla, Sheppard, & Bradshaw, 2003) – though it is to be noted that older adults, unlike younger adults, made errors in the direction of the hand used in bisection. Evidence of pseudoneglect on bisection tasks in older adults was also present in the study of Varnava and Halligan (2007) collapsing across gender, though line-length effects did interact with age.

Pseudoneglect has also been observed in older and younger adults in tactile rod bisection (Brooks, Della Sala, et al., 2011) and when recalling details from mentally represented real world scenes (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007). Additionally, neurologically intact control participants over the age of 60 years often produce leftward errors on tasks of a spatial nature (see Brooks, Della Sala, & Darling, 2014). Thus there is inconsistency in the literature on visual line bisection and aging, meanwhile although the relationship between aging and tactile and representational pseudoneglect is perhaps less unclear, only very limited systematic research has been carried out in well-matched tasks.

Assuming that pseudoneglect reflects the activity of lateralised cognitive processes, the observation of pseudoneglect in older adults challenges influential models of cognitive ageing. The Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model proposes that as the brain ages bilateral recruitment of the two hemispheres increases, especially in prefrontal cortex (Cabeza, 2002; Cabeza, Anderson, Locantore, & McIntosh, 2002; Cabeza et al., 1997; see also Collins & Mohr, 2013; McGregor, Craggs, Benjamin, Crosson, & White, 2009; Przybyla, Haaland, Bagesteiro,

& Sainburg, 2011; Toepper et al., 2014). HAROLD is consistent with recent evidence of age-related changes in attentional control in the left hemifield (Learmonth et al., 2015; Nagamatsu et al., 2011). With regard to pseudoneglect, the HAROLD model essentially predicts that cerebral asymmetry would decline over aging, and consequently so should lateral biases like pseudoneglect that may result from lateralised cognitive processing. The extent to which this attenuation of pseudoneglect should occur is also likely to reflect the degree of prefrontal involvement - hence tasks that have a high level cognitive component such as representational tasks are likely to be more affected than more perceptual tasks that are likely to be processed by more posterior brain regions. One alternative to HAROLD is the right hemi-ageing model of cognitive ageing which posits that the right hemisphere ages in a different way to the left hemisphere (for discussion see Dolcos, Rice, & Cabeza, 2002: Prodan, Orbelo, & Ross, 2007), Assuming that representational (compared to perceptual) processes engage cognitive networks involved in visual memory to a greater degree, and that these networks are represented to a substantive degree in frontal cortex (see e.g. Courtney, Petit, Ungerleider, Maisog, & Haxby, 1998), the right hemi-ageing approach makes fewer clear differenpredictions between representational and perceptual pseudoneglect, as it emphasises specific decreases in frontal asymmetry less than does the HAROLD model.

The CRUNCH hypothesis (Compensation Related Utilisation of Neural Circuits Hypothesis: Reuter-Lorenz & Cappell, 2008) proposes that more difficult tasks will recruit more cerebral activations, irrespective of brain side, and that on top of this, the level of difficulty at which these additional resources may be brought into use is likely to be lower in older adults. This pattern is actually consistent with the observation of HAROLD effects, if the assumption is made that the most likely areas to be recruited in difficult tasks would be functionally and anatomically corresponding contralateral regions (Berlingeri, Danelli, Bottini, Sberna & Paulesu, 2012). However, the CRUNCH approach is less specific as to patterns of brain activation in ageing, and hence can accommodate preserved lateral biases more easily.

Given the potential challenge to the HAROLD model of the observation of maintained pseudoneglect in older participants, the study reported in this paper aimed to investigate pseudoneglect in older adults across three different bisection tasks. We invited 60 older adults aged 55-90 years and 60 younger adults aged 18-40 to conduct three tasks: visuo-spatial line bisection, tactile rod bisection and mental number line bisection. The inclusion of mental number line bisection is of particular significance because there has been no previous investigation of performance on this task in older adults. Mental number line bisection can take the form of reporting a midpoint between two numbers in a pair (Gobel, Calabria, Farne, & Rossetti, 2006) or a making twoalternative forced choice about the numerical position (left or right) of a digit (Loftus et al., 2008). The task devised by Gobel et al. (2006) is more suitable for the current study because the task can be performed in the complete absence of visuo-spatial processing thus allowing us to explore a purely representational form of pseudoneglect. Representational forms of pseudoneglect, such as are required in the tactile and mental number line tasks, have the potential to be particularly enlightening with regard to the HAROLD hypothesis because they infer the operation of nonperceptual spatial representational or memory systems which are associated with prefrontal cortex (Courtney et al., 1998).

As a secondary aim we also examined the mediation of pseudoneglect across modalities. In line with the previous literature we systematically manipulated lateral starting position and stimulus length for both younger and older adults across task types. For visuo-spatial bisection starting *left* has been found to enhance leftward error (Brodie & Dunn, 2005; Brodie &

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