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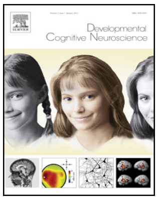

Review

The influence of executive functions on spatial biases varies during the lifespan

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ABSTRACT

Many perceptual processes, such as language or face perception, are asymmetrically organised in the hemispheres already in childhood. These asymmetries induce behaviourally observable spatial biases in which the observer perceives stimuli in one of the hemispaces more efficiently or more frequently than in the other one. Another source for spatial biases is spatial attention which is also asymmetrically organised in the hemispheres. The bias induced by attention is directed towards the right side, which is clearly demonstrated by patients with neglect but also in lesser degree by healthy observers in cognitively loading situations. Recent findings indicate that children and older adults show stronger spatial biases than young adults. We discuss how the development of executive functions might contribute to the manifestation of spatial biases during the lifespan. We present a model in which the interaction between the asymmetrical perceptual processes, the age-related development of the lateralised spatial attention and the development of the executive functions influence spatial perceptual performance and in which the development and decline of the executive processes during the lifespan modify the spatial biases.

Contents

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1. Introduction

Many perceptual processes such as language or face perception are lateralised predominantly either to the left or to the right hemisphere, inducing rightward or leftward spatial biases. However, regardless of the numerous behavioural and neuroimaging studies carried out to understand the development and the nature of the spatial biases other than those induced by language, the evidence and empirical support for many such biases are still diverse (e.g. see Takio and Hämäläinen, 2012). One of the possible but often neglected confounding processes influencing the performance in perceptual tasks is attention. Results from neglect patient studies (e.g. Corbetta et al., 2008; Corbetta and Shulman, 2002; Heilman et al., 1987; Proverbio et al., 1994), and healthy humans (Posner, 2008; Posner and Raichle, 1994) suggest that the hemispheres are asymmetrical also in attentional mechanisms. Furthermore, research on lateralisation has shown that the hemispheric asymmetries and spatial biases change during the lifespan presumably resulting from a complex interaction of biological and environmental factors. For example, language lateralisation (e.g., Andersson and Hugdahl, 1987; Hiscock and Kinsbourne, 1977, 1980; Sexton and Geffen, 1979) as well as the lateralisation of visuospatial functions (Everts et al., 2009) increase during childhood, and age-related changes in human structural and functional hemispheric asymmetry continue into old age (e.g. Dolcos et al., 2002). Regardless of the large body of lateralisation studies (for review see e.g. Boles et al., 2008), the variable results of the development of the asymmetries in literature make it difficult to determine the exact timing of lateralisation of different processes. Behind such inconsistency of the findings may be the development of executive functions that modulates perceptual performance and asymmetry differently across the lifespan (e.g. Hiscock and Kinsbourne, 1977; Hugdahl and Andersson, 1986). In the present paper, we introduce a theoretical model of the role and the interaction of asymmetrical bottom-up perceptual and attention mechanisms and of the age-related changes in executive functions in spatial biases. The spatial biases refer here to more efficient or frequent perception of stimuli in one side of the hemispace than in the other side.

2. Asymmetrical perceptual mechanisms and confounding processes

Left-hemisphere dominance in language processing is an essential source of the rightward spatial bias for auditory and visual linguistic perception in healthy adults (e.g. Calvo and Nummenmaa, 2009; Corballis, 2009; Koivisto, 1997). Such a rightward bias for language processing in the auditory modality is observable already at a very early age (Andersson and Hugdahl, 1987; Boles et al., 2008; Dehaene-Lambertz et al., 2002; Telkemeyer et al., 2009). Thanks to the proliferated expansion of functional neuroimaging studies, the findings of lateralisation and hemispheric asymmetry have extended to concern more elaborated and sophisticated aspects of perceptual processes. For example, the left hemisphere has been found to be specialised in the processing of local information and categorical spatial relationships of visual stimuli, while the right hemisphere is superior in the processing of global aspects and coordinate spatial relationships (Hellige et al., 2010; Ivry and Robertson, 1998). Nevertheless, still existing constraints of neuroimaging methods create uncertainty about determining whether the activated regions are truly associated with the processes in focus. For example, Martin and coworkers (2008) found right-hemisphere activation in both coordinate and categorical spatial tasks. They proposed that the right-hemisphere activation was indeed related to the lateralisation of spatial attention mechanisms rather than to the lateralisation of spatial coding mechanisms. Thus, the complexity of cognitive processing together with the yet existing limitations of behavioural and neuroimaging methods have raised questions of the confounding processes that put the earlier interpretations of lateralisation studies into a new light. Furthermore, while attention and memory functions are proposed to be such confounding factors in spatial biases (e.g. Callaert et al., 2011; Hiscock and Kinsbourne, 2011), they themselves are asymmetrically distributed in the brain (e.g. Kalpouzos and Nyberg, 2010).

3. Asymmetrical spatial attention mechanisms

3.1. Evidence from neurological patients

Neurophysiological and neuropsychological research has shown that the two cerebral hemispheres differ in the control of spatial attention (Corbetta et al., 2008; Driver and Vuilleumier, 2001; Heilman et al., 1987; Proverbio et al., 1994; Posner and Raichle, 1994). The clearest examples of the asymmetry of attentional behaviour are observed in neurological patients with unilateral neglect (Corbetta et al., 2008; Deouell et al., 2000; Heilman et al., 1987; Kinsbourne, 1987; Oliveri et al., 1999), callosotomy (split-brain) (Luck et al., 1989, 1994; Mangun et al., 1994; Proverbio et al., 1994) and attention deficit hyperactivity disorder (ADHD) (Chan et al., 2009; Hale et al., 2006).

According to the definition by Heilman and his coworkers (2000), neglect is a failure to report, respond, or orient to meaningful or novel stimuli. This failure is primarily for stimuli or actions that occur on the side contralateral to a hemispheric lesion" (p. 463), and cannot be attributed to either an elemental sensory or motor defect (see also Swan, 2001). In adult neglect patients suffering from unilateral right hemisphere injury, often a strong attentional bias towards the right hemispace is observed, whereas a leftward attentional bias after left unilateral hemisphere injury is considerably less often observed. Neural damages producing this kind of neglect behaviour can be localised at both cortical and sub-cortical areas and different levels of the neural system in right hemisphere, such as the posterior parietal cortex, frontal lobe, cingulate gyrus, striatum, thalamus, or brainstem nuclei (e.g. Swan, 2001; Posner and Petersen, 1990), suggesting that neglect can be explained by the physiological dysfunction of distributed cortical networks (Corbetta and Shulman, 2011; see also Corbetta et al., 2008). Visuospatial and motor neglect after