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Review

Spatial neglect and the neural coding of attentional priority

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ABSTRACT

The concept of attentional priority plays an increasingly important role in theoretical interpretations of the neurophysiological mechanisms underlying attentional selection. A priority map is a feature-independent, spatiotopic representation of the environment that combines stimulus-driven information with goal-related signals. It emerges from the functional properties of parietal brain regions involved in spatial attention and saccade programming on the one hand, and reaching or grasping movements on the other hand. Here, we explore the value of this concept for the understanding of neuropsychological deficits of attention such as spatial extinction and neglect. We argue that these conditions reflect spatially graded, multisensory deficits affecting a processing level at which stimulus-driven and goal-driven signals interact. These attributes of neglect and extinction agree with the functional characteristics of attentional priority and suggest that components of both disorders can be understood as manifestations of damage or dysfunction affecting the parietal priority map.

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1. Introduction

One of the greatest mysteries of attention is its high degree of flexibility: attention may select almost any property of the environment, such as regions in space, surfaces, whole objects or isolated object features (Gilbert and Sigman, 2007). Selection may also be guided by expectations, action goals or preferences of the observer (Egeth and Yantis, 1997; Pashler et al., 2001; Simons, 2000). Attention may be focused on a small region or take a more distributed form (Eriksen and St. James, 1986; Pashler, 1998). It can be directed inwardly, such as when we focus on thoughts or emotions, or may actively track a stimulus in the environment. The almost infinite possibilities of attention present two fundamental challenges for theories of attentional selection: first, how can one explain that a single mechanism may succeed to select the 'right' one (whatever that be) among multiple stimuli characterized by sensory qualities as unlike as coloured text, a flying insect or the sound of an explosion? Second, how can one account for the capacity of attention to resolve the competition between external conditions (e.g., features defining the stimulus) and internal processes (e.g., action goals of the observer), such as the preference for a particular yellow hue when searching for a car on a parking filled with hundreds of cars of various colours? These questions delimit what may be considered as the *criterion problem* of attention: attention needs a selection threshold that is independent of specific stimulus features or attentional states of the observer (Ptak, 2012; Wolfe and Horowitz, 2004). Solving the criterion problem is an important step toward comprehending how humans select and act upon stimuli in a complex environment.

Providing answers to the criterion problem will not only advance the understanding of a wide range of phenomena related to attentional selection in healthy observers, but also contribute to a clearer picture of deficits associated with neuropsychological disorders of attention such as spatial neglect. Patients with neglect present a number of heterogeneous symptoms that have alternately been attributed to attentional, representational, or premotor factors. Many experimental studies have focused on dissociations between distinct patients or patient groups, and it is increasingly difficult to provide a common framework that would cover the totality of these symptoms. This is why the current review focuses on one of the core deficits characterizing neglect: the severe, lateralized impairment of spatial attention, which leads to a lack of awareness for visual, auditory or tactile stimuli presented contralateral to the brain damage (Corbetta and Shulman, 2011; Driver and Mattingley, 1998; Kerkhoff, 2001; Milner and McIntosh, 2005). Spatial attention deficits of neglect patients affect all sensory modalities and are easily modulated by goal-driven processes. A better understanding of neglect and other disorders of spatial attention might therefore provide important clues toward a solution of the criterion problem.

Here, we review neurophysiological findings that are of relevance for a better understanding of the criterion problem and we relate these to the deficits of spatial orienting and attention characterizing spatial neglect. We propose that brain regions lying along the dorsal visual stream build a reciprocal network that integrates sensory inputs and behavioural goals and computes an abstract representation of the environment – *a priority map*. We argue that attentional priority is computed prior to the full identification of a stimulus, and therefore constitutes a suitable mechanism for fast attentional selection. Finally, we propose that lateralized deficits of attention in spatial neglect can be understood as failures to compute the attentional priority of contralesional stimuli and events.

2. Spatial attention, the dorsal-ventral distinction and reentrant processing

Any theory addressing the neural basis of visual attention must attempt to integrate two highly influential ideas regarding the organisation of visual pathways. The first is that visual information is processed along a hierarchy of segregated areas, progressing from simple to increasingly complex visual features (Colby and Duhamel, 1991; Felleman and Van Essen, 1991; Van Essen and Maunsell, 1983). In parallel, there is a progressive increase of receptive field size from low-level to high-level areas, with the consequence that higher-order areas integrate information across a wide region of the visual field. The second idea concerns the distinction between a ventral object-processing system (what-stream) and a dorsal space-processing system (where-stream; Ungerleider and Mishkin, 1982; Ungerleider and Pasternak, 2003). Fig. 1 shows the visual areas located within the ventral and dorsal stream that are central for this review, as well as the main connections of the posterior parietal cortex (PPC), which is a high-level multisensory interface, with areas lying in premotor and prefrontal cortex.

Though the notions of functional segregation and hierarchical organization were extremely influential in the past and still provide the dominant framework for the understanding of many neurophysiological and behavioural observations, they both have their limitations. Several authors argued that the central role of the dorsal stream is to process visual signals necessary for the programming of visually guided action, including reaching and grasping (Kravitz et al., 2011; Milner and Goodale, 2006; Milner and Goodale, 2008; Rizzolatti and Matelli, 2003). At the neurophysiological level, this role of the dorsal stream becomes particularly evident in the intraparietal sulcus, where neural activity is associated with grasping in the anterior (AIP) and reaching in the middle part (MIP). Further, neurophysiological findings and human lesion studies show that the lateral intraparietal cortex (LIP) is involved in the programming and preparation of saccadic eye movements (Colby and Goldberg, 1999; Pierrot-Deseilligny et al., 1995). In addition, the degree of segregation of the ventral and dorsal stream itself is under question, and more fine-grained distinctions have been proposed. Thus Rizzolatti and Matelli (2003) distinguish two separate dorsal streams (a dorso-dorsal stream and a ventro-dorsal stream), which are involved in on-line control of action and visuo-spatial processing, respectively. Similarly, Rossetti et al. (2005) discriminate between two distinct visual 'routes to action' in the dorsal stream, a superior parietal route implicated in fast, automatic actions, and an inferior parietal route implicated in slow and delayed actions. This proposal fits well to the framework of Milner and Goodale (2006) who distinguish different routes to the PPC: an occipito-parietal route with the superior parietal lobule (SPL) as target and which is involved in reaching and grasping, and a distinct route to the inferior parietal lobule (IPL), which is important for visuo-spatial processing. These authors also emphasize the role of the IPL as a region of convergence of dorsal and ventral stream inputs. Finally, based on studies with parietal patients Battelli et al. (2007) propose that the right inferior parietal lobe plays a specific role in the analysis of event timing, and is thus part of a 'when'-pathway of the human brain. Thus, the classic distinction between a dorsal 'where'- and a ventral 'what'-pathway is now challenged by a more a complex framework, where the SPL is central for visuomotor transformations necessary for the fast programming of goal-directed manual actions and saccades while the ventral parietal lobe is important for visuospatial and temporal processing.

Similarly to the ventral-dorsal dichotomy, the hierarchical view of sensory processing has also found its critics. Inherent in the idea that visual processing is arranged hierarchically is the view

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