Progress in Neurobiology 132 (2015) 59–80

Contents lists available at ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio

Review Article

Visual attention: Linking prefrontal sources to neuronal and behavioral correlates

Kelsey Clark [a], Ryan Fox Squire [b,c], Yaser Merrikhi [d], Behrad Noudoost [a,*]

[a] Montana State University, Bozeman, MT, United States
[b] Stanford University, Stanford, CA, United States
[c] Lumos Labs, San Francisco, CA, United States
[d] School of Cognitive Sciences (SCS), Institute for Research in Fundamental Sciences (IPM), Tehran, Iran

ARTICLE INFO

Article history:
Received 31 December 2014
Received in revised form 25 June 2015
Accepted 28 June 2015
Available online 6 July 2015

Keywords:
Prefrontal cortex
Visuospatial attention
Selective attention
Attention signatures
Attention deficit
Neglect

ABSTRACT

Attention is a means of flexibly selecting and enhancing a subset of sensory input based on the current behavioral goals. Numerous signatures of attention have been identified throughout the brain, and now experimenters are seeking to determine which of these signatures are causally related to the behavioral benefits of attention, and the source of these modulations within the brain. Here, we review the neural signatures of attention throughout the brain, their theoretical benefits for visual processing, and their experimental correlations with behavioral performance. We discuss the importance of measuring cue benefits as a way to distinguish between impairments on an attention task, which may instead be visual or motor impairments, and true attentional deficits. We examine evidence for various areas proposed as sources of attentional modulation within the brain, with a focus on the prefrontal cortex. Lastly, we look at studies that aim to link sources of attention to its neuronal signatures elsewhere in the brain.

Contents

Abbreviations: AC, anterior commissure; ACd, dorsal anterior cingulate area; CC, corpus callosum; D1R, D1-type dopamine receptors; D2R, D2-type dopamine receptors; dlPFC, dorsolateral prefrontal cortex; FEF, frontal eye field; Fr2, frontal cortical area; IT, inferotemporal cortex; LGN, lateral geniculate nucleus; LIP, lateral intraparietal area; LIP/d/v, lateral intraparietal area dorsal/ventral; MEF, medial eye field; MST, medial superior temporal area; MT, middle temporal visual area; PFC, prefrontal cortex; PMC, premotor cortex; RF, response field; SC, superior colliculus; TRN, thalamic reticular nucleus; VIP, ventral intraparietal area.

* Corresponding author.
E-mail address: bnoudoost@montana.edu (B. Noudoost).

http://dx.doi.org/10.1016/j.pneurobio.2015.06.006
0301-0082/© 2015 Published by Elsevier Ltd.

Attention is the means by which we focus on behaviorally relevant information, to select and enhance a subset of sensory information for further processing while ignoring the rest. Visual attention alters the processing of visual information (Carrasco et al., 2004; Carrasco, 2011; Yeshurun and Carrasco, 1998), prioritizing a location (spatial attention) or a particular feature (feature-based attention) based either on internally represented goals (top-down attention) or the physical salience of the stimulus (bottom-up attention). The focus of this review is on goal-driven, top-down modulations of visual processing: the changes in visual responses thought to underlie the behavioral benefits of attention, and the network of areas thought to drive these changes based on attentional cues. Specifically, our focus will be on the role of prefrontal cortex (PFC) in the top-down control of attention, as this area is critical for coordinating our goal-driven behavior. We will first address the attention-driven changes in visual processing and how they could benefit behavior (Section 1), then turn to some methodological concerns regarding measuring attention at a behavioral level (Section 2), review the evidence for several areas as sources of attentional modulation (Section 3), and finally examine experiments seeking to link attention in these source areas to the signatures previously discussed (Section 4).

1. Attention-driven changes in visual processing

1.1. Neuronal signatures of attention

Attention has long been known to modulate visual cortical responses (Moran and Desimone, 1985); since this initial report, attentional modulation has been reported in a wide range of visual cortical areas (Buffalo et al., 2010; Herrero et al., 2008; Sharma et al., 2014; Spitzer et al., 1988; McAdams and Reid, 2005; McAdams and Maunsell, 1999; Boudreau et al., 2006; Gregoriou et al., 2009b; Treue and Maunsell, 1996; Treue and Martínez Trujillo, 1999; Sheinberg and Logothetis, 2001), and as early in the visual hierarchy as the lateral geniculate nucleus (McAlonan et al., 2008). Attentional modulation has also been reported in a number of oculomotor structures with visual responses, including the lateral intraparietal area (LIP), superior colliculus (SC), frontal eye field (FEF), and dorsolateral PFC (dlPFC) (Goldberg and Wurtz, 1972; Bisley and Goldberg, 2003; Thompson et al., 2005; Buschman and Miller, 2007). Since attention is the means by which we select and enhance a subset of sensory information for further processing, a natural assumption is that this improvement in perception should be the result of an increase in the strength of sensory signals within visual areas. The first and most frequently reported effect of attention is an increase in visual responses when attention is directed toward the response field (RF) of a neuron (Moran and Desimone, 1985); however, a variety of other measures are increasingly included in attention studies (reviewed in Noudoost et al., 2010). In addition to increased visual responses, other reported signatures of attention include shrinkage of RFs containing the attended location (Womelsdorf et al., 2008; Anton-Erxleben et al., 2009), shifts of visual RFs toward the attended location (Womelsdorf et al., 2006a, 2008; Connor et al., 1997), decreases in trial to trial variability of individual neuron's responses (Mitchell et al., 2007; Cohen and Maunsell, 2009), enhanced contrast sensitivity (Reynolds et al., 2000), increased synaptic efficacy (Briggs et al., 2013), changes in noise correlations between neurons (Mitchell et al., 2009; Ruff and Cohen, 2014; Cohen and Maunsell, 2009), decreases in low-frequency LFP power and coherence (Fries et al., 2001, 2008; Mitchell et al., 2009), increases in gamma-band LFP power (Fries et al., 2008; Gregoriou et al., 2009a; Taylor et al., 2005), increases in gamma-band coherence both within and between areas (Fries et al., 2001, 2008; Gregoriou et al., 2009b; Womelsdorf et al., 2006b; Saalmann et al., 2007), decreases in response latency (Sundberg et al., 2012; Galashan et al., 2013), decreases in bursting activity (Anderson et al., 2013), and reductions in action potential height (Anderson et al., 2013). The question then becomes which of these changes in neuronal responses are functionally relevant for producing the behavioral benefits of attention.

1.2. Potential benefits of known signatures of attention

An enhanced neuronal representation of the target stimulus could underlie the behavioral benefits of attention, including greater sensitivity (Sridharan et al., 2014), greater spatial resolution (Carrasco, 2011), and faster response times (Posner, 1980). Here we summarize the potential representational benefits of the reported signatures of attention.

1.2.1. Attention enhances the visual representation at the level of single neurons

First, we consider the effects of attention on the responses of individual neurons: attention increases response magnitude, reduces neuronal latency, alters RFs, reduces burstiness, and reduces the variability of visual responses. From a signal processing perspective an increase in the difference in a neuron's response to its preferred vs. non-preferred stimuli can result in more reliable stimulus discrimination (Green and Swets, 1966). Computational models confirm that multiplicative-gain type increases in neuronal firing rates can produce a benefit when decoding population activity (Cohen and Maunsell, 2009; Mitchell et al., 2009; Ling et al., 2009). Attention also reduces the latency of neuronal responses (Sundberg et al., 2012; Galashan et al., 2013), which could potentially provide more information in a shorter amount of time, thus facilitating a faster reaction. More intense or higher contrast stimuli evoke shorter latency responses across numerous visual areas (Bell et al., 2006; Raiguel et al., 1999; Albrecht, 1995; Oram et al., 2002); thus attention, by reducing response latencies, effectively makes a stimulus resemble a higher contrast version of itself, similar to its effect on the contrast response function measured in firing rate (Reynolds et al., 2000). The response latencies of neurons in visual cortex are also directly correlated with reaction times on saccade tasks (Lee et al., 2010). Moreover, attention alters neuronal RFs, which could allocate more neuronal resources to the locus of attention. Attention causes a dynamic change in the RFs of neurons in several visual areas, shifting them toward the locus of attention and shrinking RFs at the attended location (Anton-Erxleben et al., 2009; Connor et al., 1996, 1997; Kusunoki and Goldberg, 2003; Womelsdorf et al.,