



Attentional control: Temporal relationships within the fronto-parietal network

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ABSTRACT

Selective attention to particular aspects of incoming sensory information is enabled by a network of neural areas that includes frontal cortex, posterior parietal cortex, and, in the visual domain, visual sensory regions. Although progress has been made in understanding the relative contribution of these different regions to the process of visual attentional selection, primarily through studies using neuroimaging, rather little is known about the temporal relationships between these disparate regions. To examine this, participants viewed two rapid serial visual presentation (RSVP) streams of letters positioned to the left and right of fixation point. Before each run, attention was directed to either the left or the right stream. Occasionally, a digit appeared within the attended stream indicating whether attention was to be maintained within the same stream ('hold' condition) or to be shifted to the previously ignored stream ('shift' condition). By titrating the temporal parameters of the time taken to shift attention for each participant using a fine-grained psychophysics paradigm, we measured event-related potentials time-locked to the initiation of spatial shifts of attention. The results revealed that shifts of attention were evident earlier in the response recorded over frontal than over parietal electrodes and, importantly, that the early activity over frontal electrodes was associated with a successful shift of attention. We conclude that frontal areas are engaged early for the purpose of executing an attentional shift, likely triggering a cascade through the fronto-parietal network ultimately, resulting in the attentional modulation of sensory events in posterior cortices.

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1. Introduction

The human visual system sorts through massive amounts of sensory input, which is sampled almost continuously, to arrive at a coherent perception of the scene. This process of searching through the environment for behaviorally relevant information is a ubiquitous component of sensory processing, and it reflects the remarkable ability of the perceptual system to select dynamically information that is compatible with the current goal of the organism. Such perceptual selectivity, referred to as attention, is considered central to cognition, with selected or attended information subsequently receiving preferential or enhanced processing. One of the key elements to understanding attentional selection is to determine what representations are engaged by this process such that they serve as potential candidates for selection. Several possible representations have been identified including those that are space- (Eriksen & Hoffman, 1972; Posner, Snyder, & Davidson, 1980; Yantis et al., 2002), feature- (Corbetta, Miezin, Dohmeyer,

Shulman, & Petersen, 1991; Liu, Slotnick, Serences, & Yantis, 2003), object- (Corbetta, Tansy, et al., 2005; Duncan, 1984; Kanwisher & Driver, 1992; Shomstein & Behrmann, 2006), and/or modality-based (Bushara et al., 1999; Shomstein & Yantis, 2004), and much recent psychophysical and imaging work has explored the similarities and distinctions between these forms of attentional selection and underlying representations.

Of all of these different potential candidate representations from which selection can occur, selection from space-based representations is perhaps the most pervasive and fundamental. Not only do space-based representations reflect topographical organization and layout of early visual cortex, but these representations describe the sensory environment with a unique set of 3D identifiers (i.e., each stimulus in the sensory environment occupies a unique set of spatial coordinates), thereby facilitating location-based selection in a direct and isomorphic manner. This space-based selection is reflected in multiple visual cortical areas as increased activity of neurons representing the attended location (Bisley & Goldberg, 2003; Moran & Desimone, 1985; Saalmann, Pigarev, & Vidyasagar, 2007; Somers, Dale, Seiffert, & Tootell, 1999; Treue & Maunsell, 1996). The behavioral benefit of this enhanced neural selectivity is that stimuli that appear in attended spatial locations are processed more efficiently and more accurately than stimuli that

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appear elsewhere (Chawla, Rees, & Friston, 1999; Posner, 1980; Treue & Martinez Trujillo, 1999; Yantis et al., 2002).

Despite the growing understanding of attentional selection gleaned from numerous studies, we do not yet have a full understanding of the mechanism that serves as the source to initiate the attentional orienting signal, which, ultimately, results in the neural modulation and behavioral benefit for attended locations. Investigations of this issue have uncovered a network of regions spanning frontal and parietal cortices that triggers a control signal for shifting from one representation to another, be it one that is space-based (Corbetta & Shulman, 2002; Hopfinger, Buonocore, & Mangun, 2000; Serences & Yantis, 2007), feature-based (Greenberg, Esterman, Wilson, Serences, & Yantis, 2010; Liu et al., 2003), or object-based (Shomstein & Behrmann, 2006). Although there is general consensus concerning regions that are engaged in this attentional shifting process, the relative contributions of the identified frontal and parietal regions have been difficult to characterize. Moreover, some studies have yielded conflicting findings, with several investigations suggesting that the initial spatial re-orienting signal is elicited by the frontal cortex, while others suggest that it is the parietal cortex that initiates the re-orienting signal with frontal cortex following suit (Brignani, Lepsien, Rushworth, & Nobre, 2009; Buschman & Miller, 2007; Green & McDonald, 2008; Simpson et al., 2011). It should be noted that while most investigations of bottom-up attentional capture have convincingly demonstrated that the shifting signal originates over the parietal cortex (Fu, Greenwood, & Parasuraman, 2005; Green, Doesburg, Ward, & McDonald, 2011; Hopfinger & Ries, 2005; Leblanc, Prime, & Jolicoeur, 2008; Ptak, Camen, Morand, & Schnider, 2011), most of the controversy regarding the temporal relationship between the source signals over frontal or parietal cortex has been exclusive to the investigations of top-down attentional control.

Part of the difficulty in determining the relative contribution of frontal and parietal regions to the attentional control signal lies in the fact that the neural profiles of these areas observed in response to the initiation of a spatial shift are similar, and, consequently, it is difficult to untangle and disambiguate their independent contributions. For example, both frontal and parietal regions contain topographically mapped priority maps. Single-unit physiology experiments with awake behaving monkeys have found evidence that both the frontal eye fields (FEFs) and the lateral intraparietal area (LIP) contain representations compatible with priority maps (Balan & Gottlieb, 2006; Bisley & Goldberg, 2010; Thompson & Bichot, 2005; Thompson, Bichot, & Sato, 2005), usually assumed to be the first step in triggering the shift signal. Concordantly, functional imaging studies in humans have found that corresponding frontal and parietal areas contain topographic representations related to saccade planning and attention (Chiu, Esterman, Gmeindl, & Yantis, 2011; Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009; Greenberg et al., 2010, 2012; Silver & Kastner, 2009), suggesting that these areas in humans may also contain priority maps utilized for the upcoming shift of attention. Moreover, the shift-related signal elicited over frontal and parietal regions is similar with the result that both regions are best described as initiating a transient signal, as measured by both fMRI and ERP. This identified transient signal is interpreted as being responsible for issuing, or initiating, an attention control signal to switch the current spatial focus of attention but a more detailed account of the dynamics of these disparate regions remains elusive (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger et al., 2000; Rushworth, Paus, & Sipila, 2001; Yantis et al., 2002).

One possible clue that might assist in uncovering the relative contribution of frontal and parietal areas to the control of spatial attention lies in the ability to identify the relative timing of the corresponding activations in the different regions. Measuring event-related potentials (ERP) provides an ideal opportunity to

exploit high temporal-resolution data and to examine the temporal relationship between the initiation of the spatial attentional control signal observed over the frontal and the parietal cortex. The goal of the present investigation was, thus, to elucidate the relative functional roles of two major nodes of the human attentional network, the frontal and parietal cortices, by focusing on the temporal relationships between these important subregions.

In order to assess the relative timing of the contribution of frontal and parietal cortices to spatial shifts of attention, we adopted a two-pronged approach. First, we conducted detailed psychophysical investigations to determine the timing thresholds required, on an individual-by-individual basis, to initiate a spatial shift of attention so as to delineate the particular switch signature for each participant. At the same time, we determined a threshold at which each participant was able to detect a target after the switch of attention so that the signal for trials in which the shift was successful could be separated from trials in which it was not. Second, in a separate session, each participant's neural activity was recorded by ERP, while the individual completed the behavioral attentional shifting task with the unique parameters for stimulus presentation adopted from the individual thresholding session. Critically, these attentional switch thresholds ensured that we were indexing the ERP components that occurred before the attentional shift initiation (i.e., source of the attentional shifting signal) as opposed to those components that occur after the execution of the shift. In this way, we can isolate the components that are related to the initiation of a spatial shift of attention, rather than a host of perceptual/post-perceptual processes that are involved in target detection, more generally.

Elucidating the neural mechanism of top-down spatial shifts of attention can also prove useful for understanding the behavioral deficits following damage to the parietal lobe. Clinical symptoms of hemispatial neglect have been strongly associated with damage to the parietal lobe including the temporo-parietal junction (TPJ) and the inferior parietal lobule (IPL) as well as connections between frontal and parietal cortices, all regions associated with shifts of spatial attention (Bartolomeo, Thiebaut de Schotten, & Doricchi, 2007; Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Friedrich, Egly, Rafal, & Beck, 1998; Ptak & Schnider, 2010; Shomstein, Lee, & Behrmann, 2010; Thiebaut de Schotten et al., 2005; Vallar & Perani, 1986).

2. Methods

2.1. Participants

Twelve neurologically healthy right-handed adults (ages 21–33, 5 female) with normal or corrected-to-normal visual acuity participated in two experimental sessions (psychophysical and ERP recording). Participants provided written consent to participate in the protocol that was approved by the Institutional Review Board of Carnegie Mellon University and were paid for their participation.

2.2. Paradigm

The behavioral task, depicted in Fig. 1, is a variant of a previously described rapid serial visual presentation (RSVP) task (Sperling & Reeves, 1980). In this task, two streams of letters appear on a computer screen, one to the right and one to the left of a central fixation cross. Stimuli were rendered in black on a gray background (RGB: 128, 128, 128) and presented at a rate of 8 Hz (125 ms, unless otherwise noted). Subjects were instructed to maintain fixation on a central cross, presented on a 19" CRT monitor with a refresh rate of 60 Hz and subtending 0.4° of visual angle from a viewing distance of 60 cm. At the beginning of each run, an attentional cue with the words "left" or "right" (presented for 10 s) instructed subjects which stream of letters was to be attended first. After the cue disappeared, the two streams of letters appeared 2.5° to the left and right of the fixation cross. Each letter in the stream changed identity synchronously every 125 ms. Letters were chosen at random from a predetermined set ('A', 'C', 'F', 'G', 'H', 'J', 'K', 'M', 'N', 'P', 'R', 'T', 'U', 'V', 'X', 'Y') and subtended approximately 0.5° horizontally and 0.6° vertically. Occasionally a digit ("4" or "2") appeared within the attended stream only.

The participants' task was twofold. Firstly, participants were to detect digits embedded among the stream of letters, and all letters, aside from 'S' (see below),

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