



Dissociating top-down attentional control from selective perception and action

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Abstract

Research into the neural mechanisms of attention has revealed a complex network of brain regions that are involved in the execution of attention-demanding tasks. Recent advances in human neuroimaging now permit investigation of the elementary processes of attention being subserved by specific components of the brain's attention system. Here we describe recent studies of spatial selective attention that made use of positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and event-related brain potentials (ERPs) to investigate the spatio-temporal dynamics of the attention-related neural activity. We first review the results from an event-related fMRI study that examined the neural mechanisms underlying top-down attentional control versus selective sensory perception. These results defined a fronto-temporal-parietal network involved in the control of spatial attention. Activity in these areas biased the neural activity in sensory brain structures coding the spatial locations of upcoming target stimuli, preceding a modulation of subsequent target processing in visual cortex. We then present preliminary evidence from a fast-rate event-related fMRI study of spatial attention that demonstrates how to disentangle the potentially overlapping hemodynamic responses elicited by temporally adjacent stimuli in studies of attentional control. Finally, we present new analyses from combined neuroimaging (PET) and event-related brain potential (ERP) studies that together reveal the timecourse of activation of brain regions implicated in attentional control and selective perception. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Selective attention is the ability to focus awareness on a portion of the vast array of potentially relevant stimuli in the environment. Attention can be directed voluntarily in a top-down manner, and visual attention can be focused on sensory stimuli based on attributes such as location, color, and/or higher-order form or object properties. Selective spatial attention (location selection) has been the subject of scientific investigation for more than a century. In the late 1800's, Hermann Von Helmholtz [61] provided experimental support for the idea that one could voluntarily focus awareness

upon a spatial location, even in the absence of eye movements (i.e. 'covert' spatial attention). More recently, Posner and colleagues [55] employed a simple paradigm that uses location expectancy to manipulate the focus of spatial attention. In the standard version of this paradigm a 'cue' stimulus occurs that provides information about where an upcoming 'target' stimulus is likely to occur, allowing participants to focus attention covertly (without saccades) upon the likely location prior to appearance of the target. Over the past 20 years, numerous variations of this paradigm have been used, and a wealth of experimental evidence now exists showing that selective spatial attention leads to faster and more accurate responses to stimuli at an attended location (see Pashler [50] for a review).

The mechanisms of covert spatial attention can be decomposed into a number of hypothetical, elementary

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mental operations. These may include but need not be limited to: disengaging attention from its current locus, moving attention to the desired location, selectively modulating the processing of new sensory inputs, and executing motor actions to target events [50,54]. Numerous studies in humans and animals have implicated a widespread set of cortical and subcortical brain regions in spatial attentional processing, leading to the view that attention is subserved by a highly specific but widely distributed attentional network [10,24,47]. The challenge is now to relate activity in specific parts of this attention network to particular component operations of attention.

Neuroimaging studies in humans, and lesion analysis in neurological patients and non-human primates, have shown that this spatial attention network may include the posterior parietal cortex [11,23,49,56] temporo-parietal junction [9,22], superior colliculus [47], thalamus [25,36,52], superior temporal sulcus [7,49,62], and regions of the frontal cortex [7,26]. While neuroimaging studies have identified the neural components of an attention-network in the healthy human brain, limitations in classical neuroimaging analysis methods have made it difficult to associate particular brain structures with specific attentional operations. Classical neuroimaging analysis methods often required tasks to be blocked over periods of many seconds or minutes. Within such block-design paradigms, top-down control and preparatory mechanisms are difficult to disentangle from the selective target processing that subsequently occurs as a result of attentional orienting. The advent of event-related methods of analysis in fMRI, however, has now enabled a more direct investigation of the neural substrates underlying the subcomponent processes of attention as for example, in the investigation of the neural mechanisms of top-down attentional control. In the next section we review recent evidence from our fMRI studies investigating the control circuitry of voluntary spatial attention.

2. Event-related fMRI study of attentional control and selective perception

2.1. Design and procedures

Recently, we used event-related functional magnetic resonance imaging (fMRI) to identify and dissociate the neural systems involved in top-down attentional control versus the subsequent selective processing of stimulus inputs [28]. In that study, a trial began with a cue presented at fixation for 500 ms that instructed participants where to covertly attend (randomly to the left or right; Fig. 1). Eye fixation was maintained on a central fixation cross during each trial. The cue consisted of overlapping isoluminant yellow and blue arrows point-

ing to opposite left and right field locations. This cue was used to control for simple sensory differences between leftward versus rightward directing cues. Each participant ($N = 6$) was instructed beforehand which color arrow was to be used to direct attention (half were instructed to use the blue arrow, half the yellow). After an interstimulus interval of either 1000 ms (17% of trials) or 8160 ms (83% of trials), checkerboard patterns were flashed bilaterally in the right and left visual fields (for 750 ms at a 4 Hz reversal rate). The task was to discriminate whether the checkerboard, at the attended location only, contained any gray checks or whether it was composed of only the standard white and black checks (a choice response was required on each trial). Flashing checkerboard patterns were used in order to ensure a strong response in visual processing regions of the brain [57], regardless of the presence or absence of the gray checks. The shorter ISI (1000 ms) was used to induce participants to shift attention as soon as the instructive cue appeared because the target could appear shortly after the cue. However, the hemodynamic response (responsible for the fMRI signal) is relatively slow to begin, peak and subside (on the order of seconds) in comparison to the underlying neural activity triggering the response (on the order of a few hundred milliseconds at most), and therefore the fMRI activity evoked by cue and target stimuli would overlap and be difficult to disentangle at the short ISI (but see Section 3.2 below for review of newer methods that allow for faster presentation-rate designs in fMRI). To avoid this and to permit cue and target activity to be distinguished, only the long ISI (8160 ms) trials were

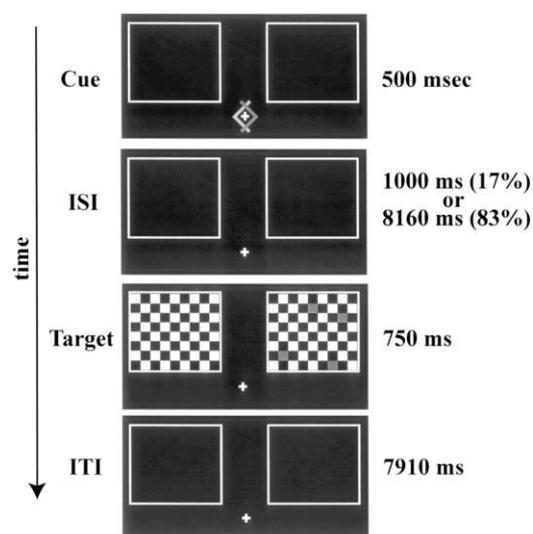


Fig. 1. Stimuli and procedure from Hopfinger et al. [28]. Cues consisted of overlapping isoluminant yellow and blue arrows that instructed subjects to covertly orient their attention to the location indicated. After a variable interstimulus interval (ISI), checkerboard target stimuli appeared within the outline boxes. The intertrial interval (ITI) was 7910 ms. See text for details.

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