



Combined attention controls complex behavior by suppressing unlikely events

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ABSTRACT

Attention enables behavior by modulating both sensory inputs and task goals. Combining attentional resources from both of those sources exerts qualitatively large effects on manual performance. Here we tested how combined attention was represented in sensory processing, as reflected by the P1 component and associated activity in the alpha band. We measured performance and recorded EEG while participants' attention was engaged in an automated, endogenous, and combined (i.e., automated and endogenous) manner. Behavioral results replicated past reports with reliable effects of isolated automated and endogenous attention, as well as their qualitatively unique combined effect. ERP analyses indicated expected increases in P1 amplitude for validly relative to invalidly cued targets in automated and endogenous conditions. However, in the combined case, the P1 difference between validly relative to invalidly cued targets decreased. Analyses of target-locked alpha-band further revealed that this condition was associated with an increased synchrony in the alpha frequency for invalidly cued targets. This suggests that the large performance benefit observed when attentional systems combine is partly driven by suppressed processing of unexpected targets, dovetailing with the notion that in addition to increasing sensory gain of attended targets, attention may also modulate complex behavior by increasing suppression of unattended ones.

1. Introduction

Attentional systems facilitate complex behavior by allocating finite resources for processing of relevant perceptual and cognitive information. Research shows attentional systems are multifaceted and can be controlled in multiple ways.¹ The traditional modes of control include reflexive (e.g., Posner, 1980; Posner, 2014) and voluntary attention (e.g., Jonides, 1981), reflecting the capacity of the attentional systems to be engaged by unexpected sensory events (e.g., flash of light) and individual internal goals (e.g., task requirements). More recent work shows that attention can also be independently controlled by stimuli that carry a history of selection (e.g., Awah, Belopolsky, & Theeuwes, 2012; Kadel, Feldmann-Wüstefeld, & Schubö, 2017; Ristic & Kingstone, 2012). As an example, Ristic and Kingstone (2012) demonstrated that overlearning the meaning of common symbols like arrows results in automated attentional orienting, which is marked by consistent attentional shifts in response to common symbols, even when these symbols do not convey any task-relevant information (see also Ristic, Friesen, & Kingstone, 2002; Kingstone, Friesen, & Gazzaniga, 2000). Automated attention has been found to affect behavior independently from

reflexive and voluntary orienting (e.g., Ristic & Kingstone, 2012; Ristic, Landry, & Kingstone, 2012) and to facilitate both detection and perceptual discrimination of targets (Ristic & Landry 2015).

Most studies to date converge onto the finding that multiple attention control systems function in an interdependent manner (Ristic & Landry, 2015; Ristic & Kingstone 2009; Ristic & Kingstone 2012; Berger, Henik, & Rafal, 2005; Corbetta, Patel, & Shulman, 2008). This predicts that effects of attentional systems on performance may not only reflect their isolated, but also their combined influences. And while most studies conducted to date have investigated the conditions under which attentional systems may dissociate (e.g., Berger et al., 2005), Ristic and Kingstone (2006) were among the first to show that attentional systems may also combine. In 2006, the authors employed cuing methodology (e.g., Ristic & Kingstone, 2009; Posner, 1980; Posner, Snyder, & Davidson, 1980) to examine orienting elicited by automated attention, engaged by spatially nonpredictive arrows, and voluntary attention, engaged by spatially predictive digits. The sum of attentional orienting magnitudes from these two conditions (i.e., Invalidly cued – Validly cued Response Time) was compared to the magnitude of the combined effect in which spatially predictive arrows served as cues.

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¹ Abbreviations: EEG (Electroencephalography), IOR (Inhibition Of Return), ERS (Event Related Synchronization), ERD (Event Related Desynchronization), EOG (Electrooculogram), RT (Response Time), FFT (Fast Fourier Transform), ERS (Event Related Spectral Perturbations).

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This condition engaged both endogenous attention, as the cue was spatially informative, and automated attention, as the cue was an overlearned symbol. The results indicated that combined attention elicited superadditive effects on behavioral performance. That is, the magnitude of attentional orienting found in the combined condition was larger than the magnitudes of attentional orienting observed in each automated and endogenous condition, as well as the magnitude of their additive sum. Ristic and Landry recently (2015) found the same pattern of results when a shape cue was used to engage endogenous attention and participants were asked to perform a difficult target discrimination task.

What underlying processes contribute to the large performance effects observed for combined attention? One possibility is that these effects may be driven by correspondingly large combined increases in the sensory processing of attended or validly cued targets (e.g., Luck, Hillyard, Mangun, & Hillyard, 1990). A related possibility is that these behavioral effects may also be associated with an increased suppression of irrelevant or invalidly cued targets (e.g., Freunberger et al., 2008). Here we addressed this question by examining how combined attention effects were represented in target's sensory processing, as indexed by visually evoked P1 potentials, and the associated alpha-band activity.

One of the primary functional consequences of attentional selection is reflected in the increased sensory processing of attended targets. This can be demonstrated using electrocortical recordings (EEG) whereby the gains in target processing are indexed by the increased amplitude of the P1 component associated with attended relative to unattended targets, or the first positive event-related deflection occurring within 90–140 ms post-target (Barceló, Suwazono, & Knight, 2000; Brignani, Guzzon, Marzi, & Miniussi, 2009; Fu, Caggiano, Greenwood, & Parasuraman, 2005; Hillyard, Vogel, & Luck, 1998; Hopf & Mangun, 2000; Hopfinger & West, 2006; Luck et al., 1990; Mangun & Hillyard, 1991; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Martinez et al., 1999; Nobre, Sebestyen, & Miniussi, 2000; Ranzini, Dehaene, Piazza, & Hubbard, 2009; Wright, Geffen, & Geffen, 1995; Wykowska, Wiese, Prosser, & Müller, 2014). Such modulation in P1 amplitude has been associated with increases in the sensory visual processing of attended targets and attention-driven increases in signal-to-noise (Freunberger et al., 2008). Importantly, both automated (Hopf & Mangun 2000; Ranzini et al., 2009; Eimer, 1997; Tipper, Handy, Giesbrecht, & Kingstone, 2008) and endogenous attention (Brignani et al., 2009; Nobre et al., 2000) modulate the magnitude of the P1 component. That is, both automated orienting (Hopf & Mangun 2000; Ranzini et al., 2009) and voluntary orienting (Brignani et al., 2009; Nobre et al., 2000) lead to reliable increases in magnitudes of the attended (i.e., validly cued) target-related P1 amplitudes relative to those elicited by unattended (i.e., invalidly cued) targets.

These neural gains have generally connected well with behavioral effects. There are reliable positive correlations between the P1 ERP component amplitudes and the magnitudes of behavioral orienting, as reflected by participants' reaction time (Ranzini et al., 2009; Talsma, Mulckhuysen, Slagter, & Theeuwes, 2007), while factors that have been found to reduce or reverse the behavioral effects of attentional engagement, like IOR (Posner & Cohen, 1984) have been associated with the attenuation of P1 magnitude (Hopfinger & Mangun, 1998). Thus, attending to targets is typically associated with both facilitated behavior and increased sensory processing relative to instances in which attention is directed elsewhere.

In addition to facilitated sensory processing of validly cued targets, attentional facilitation of behavior may also depend on the suppression of invalidly cued or unexpected targets. This is often demonstrated by the activity in the alpha-band frequency (i.e., 8–12 Hz), as activity in this frequency range has been implicated as a marker of the suppression of task irrelevant responses and associated neural processing (Bengson, Mangun, & Mazaheri, 2012; Freunberger et al., 2008; Klimesch, 2012). For example, decreased alpha power has been associated with increases in target detection (e.g., MacLean & Arnell, 2011) while increased alpha

power has been associated with impaired target detection (e.g., Hanslmayr et al., 2007). Furthermore, ERS and a corresponding increase in alpha power have been observed in situations in which suppression might be necessary or helpful, such as during the appearance of task irrelevant stimuli. In contrast, ERD and a corresponding decrease in alpha power have been observed with increases in attentional processing, such as when participants are asked to classify a task relevant stimulus (Capotosto, Babiloni, Romani, & Corbetta, 2009; Freunberger et al., 2008; Klimesch, 2012).

To investigate the underlying mechanisms associated with the behavioral effects of combined attention, in the present study, we elicited automated, endogenous, and combined attention using established behavioral methods while recording participants' EEG activity. We expected to replicate past results showing typical effects of isolated automated and endogenous attention in both behavior and the P1. We also expected to replicate combined attention effects behaviorally. If this behavior was mostly related to gains in sensory processing of the validly cued target, we expected to find a correspondingly large increase in the magnitude of the target-related P1 for validly relative to invalidly cued targets. If, however, this behavior was driven by the suppression of task-unrelated or invalidly cued targets, we expected to observe increases in alpha ERS associated with invalidly cued targets. Our results supported the second alternative.

2. Materials and methods

2.1. Participants

Twenty adult volunteers (10 Female, Mean Age = 25; SD = 3.83) took part in the experiment. All participants were naive to the purpose of the experiment, reported normal or corrected-to normal vision, and no history of neurological or psychiatric disorders. All procedures were approved by the University's Research Ethics Board. Informed consent was obtained from all participants.

2.2. Apparatus and stimuli

EEG data were acquired using a BioSemi ActiveTwo system housed within an electrically shielded enclosure. The data were recorded from 64 Ag/AgCl electrodes positioned according to a 10–20 international system using a custom montage (see Fig. 1A).² The foundational channel configuration in this montage corresponds to BioSemi's 32-channel arrangement. An additional 32 channels have been added posterior to the midline. As such, this montage allows for recording from 64 channels while facilitating an increased inclusion of data from lateral and posterior electrodes typically associated with attentional effects (e.g., Brignani et al. 2009; Fu et al., 2005; Hietanen, Leppänen, Nummenmaa, & Astikainen, 2008; Mangun & Hillyard, 1991; Ranzini et al., 2009; Wykowska et al., 2014).

All stimuli were white line drawings shown against a 50% gray background, as illustrated in Fig. 1B. They were presented on a 16-inch CRT monitor and viewed from an approximate distance of 120 cm. Arrows and geometric shapes (i.e., circles and squares) served as cues. Arrows (2.9°) were comprised of a straight line (1.9°) with an arrowhead and arrow tail. Circles and squares were composed of an inner (0.8° × 2.3°) and outer frame (1.3° × 2.7°). Targets were black and white checkerboards (0.7°) (0.175°). Attentional cues were presented at fixation, and could indicate either the left or right side. Targets were presented peripherally in the upper left and right visual field, 2.9° horizontally and 2.9° vertically away from fixation. MATLAB's Psychophysics Toolbox (e.g., Brainard, 1997) was used to control the stimulus presentation sequence, event triggers, and response timing.

² Developed in collaboration with Dr. Barry Giesbrecht from the University of California Santa Barbara and Lloyd Smith from Cortech Solutions.

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