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Special issue: Research report

Neural processes underlying the orienting of attention without awareness



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ARTICLE INFO

Article history:

Received 15 February 2017

Reviewed 17 March 2017

Revised 20 May 2017

Accepted 16 July 2017

Published online 22 July 2017

Keywords:

Attention

Perceptual awareness

Object-substitution masking

N2pc

P1

ABSTRACT

Despite long being of interest to both philosophers and scientists, the relationship between attention and perceptual awareness is not well understood, especially to what extent they are even dissociable. Previous studies have shown that stimuli of which we are unaware can orient spatial attention and affect behavior. Yet, relatively little is understood about the neural processes underlying such unconscious orienting of attention, and how they compare to conscious orienting. To directly compare the cascade of attentional processes with and without awareness of the orienting stimulus, we employed a spatial-cueing paradigm and used object-substitution masking to manipulate subjects' awareness of the cues. We recorded EEG during the task, from which we extracted hallmark event-related-potential (ERP) indices of attention. Behaviorally, there was a 61 ms validity effect (invalidly minus validly cued target RTs) on cue-aware trials. On cue-unaware trials, subjects also had a robust validity effect of 20 ms, despite being unaware of the cue. An N2pc to the cue, a hallmark ERP index of the lateralized orienting of attention, was observed for cue-aware but not cue-unaware trials, despite the latter showing a clear behavioral validity effect. Finally, the P1 sensory-ERP response to the targets was larger when validly versus invalidly cued, even when subjects were unaware of the preceding cue, demonstrating enhanced sensory processing of targets following subliminal cues. These results suggest that subliminal stimuli can orient attention and lead to subsequent enhancements to both stimulus sensory processing and behavior, but through different neural mechanisms (such as via a subcortical pathway) than stimuli we perceive.

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<http://dx.doi.org/10.1016/j.cortex.2017.07.010>

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1. Introduction

At any given moment we are perceptually aware of relatively few of the multitude of sensory inputs that inundate us from the environment. Attention has been described as a “spotlight” that constantly scans our environment and selectively prioritizes the processing of behaviorally relevant stimuli (Posner, Snyder, & Davidson, 1980), often leading to awareness of those stimuli. However, despite long being of interest to both philosophers and scientists (James, 1890), the relationship between attention and awareness remains the subject of active investigation and some controversy, particularly regarding to what extent these phenomena are dissociable and, if so, how they interact (Cohen, Cavanagh, Chun, & Nakayama, 2012a, 2012b; Chica, Botta, Lupiáñez, & Bartolomeo, 2012; De Brigard & Prinz, 2010; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Koch & Tsuchiya, 2012; Koivisto, Kainulainen, & Revonsuo, 2009; Schettino, Rossi, Pourtois, & Müller, 2016; Tsuchiya, Block, & Koch, 2012; Van Boxtel, Tsuchiya, & Koch, 2010; Webb, Kean, & Graziano, 2016). Some of this controversy arises from differences in defining both “attention” and “awareness,” which is made difficult by the fact that neither are monolithic processes, nor are they particularly well-defined at the level of the brain.

Regardless, it is now well established that spatial attention can be oriented without awareness of the causative stimulus (Mulckhuyse & Theeuwes, 2010; Schettino et al., 2016; Schoeberl, Fuchs, Theeuwes, & Ansorge, 2014; Webb et al., 2016). Yet, most of this work has been based on behavior, and we have little understanding of how neural attentional processes differ when oriented consciously versus unconsciously. To address this issue, we employed a spatial-cueing paradigm and used a form of visual masking known as object-substitution masking (OSM) to manipulate subjects' awareness of the cues. We recorded EEG during the task, from which we extracted hallmark event-related-potential (ERP) indices of attention. This allowed us to use both behavioral and neural measures to directly compare the orienting of spatial attention with and without awareness.

In a classic paradigm for studying spatial attention (Posner, 1980), a cue stimulus orients attention (covertly, i.e., without an associated eye movement) either to the same location (validly cued) or a different location (invalidly cued) as that of a subsequent target stimulus to which subjects must respond. Behaviorally, many studies have shown that subjects are faster and more accurate responding to validly compared to invalidly cued targets (validity effect) (Posner, 1980). Neurally, the P1 sensory ERP component, which is generated in response to any visual stimulus and is associated with feed-forward visual processing in low-level extrastriate cortex (Luck & Kappenman, 2011), is larger in amplitude for validly versus invalidly cued targets (Hillyard & Anillo-Vento, 1998; Hopfinger & Mangun, 1998). These behavioral and neural enhancements to target processing are inferred to result from attention being oriented to the target location by the cue and biasing stimulus processing there (Desimone & Duncan, 1995). These enhancements are generally observed when a target follows an exogenous cue at short latencies (e.g., <~200 ms); at

longer latencies (>500 ms) the opposite pattern, termed inhibition of return, is often observed (Klein, 2000). Several studies have demonstrated behavioral validity effects in response to subliminal cues (reviewed in Mulckhuyse & Theeuwes, 2010; also see Herreros, Lambert, & Chica, 2017); however, to our knowledge, no study has examined the neural effects of unconsciously oriented attention on subsequent target neurosensory processing. In the present study, effects on both the target-evoked P1 and target detection (response time (RT) and accuracy) serve as dependent measures of attention.

In addition to cueing paradigms, attention has also been studied using visual search, in which subjects must find a target stimulus presented among an array of distractors (Treisman & Gelade, 1980). Both search and cueing paradigms have been used to measure the orienting of attention to laterally presented stimuli via the N2pc, a negative-polarity ERP wave that peaks between ~200 and 300 ms over posterior scalp contralateral to the target (Luck & Hillyard, 1994). The N2pc has been used extensively as an index of the lateralized orienting of attention (reviewed in Luck & Kappenman, 2011), and serves as a dependent measure of attentional orienting in this study.

While well established in studies with supraliminal stimuli, a few studies have also used the N2pc as an index of attentional orienting to subliminal stimuli (reviewed in Ansorge, Horstmann, & Scharlau, 2011; Harris, Ku, & Woldorff, 2013; Prime, Pluchino, Eimer, Dell'acqua, & Jolicoeur, 2011; Woodman & Luck, 2003). Woodman and Luck (2003) used OSM to manipulate subjects' awareness of lateralized shape targets in a search paradigm. In OSM, a four-dot mask surrounds a target, and both mask and target are presented among an array of distractors so that attention cannot be preallocated to any particular location, a requirement of the OSM effect (Enns & Di Lollo, 1997). In the unmasked condition, the mask and target onset and offset simultaneously (“co-termination” condition), and subjects suffer no impairment in target detection. Yet by simply delaying the offset of the mask relative to the target by a few hundred milliseconds (masked/“delayed offset” condition)—with no change to the target stimulus itself—subjects experience a marked decrease in their ability to detect the target (Enns & Di Lollo, 1997). Woodman and Luck (2003) found that both unmasked and masked targets elicited an N2pc, suggesting that attention was oriented to targets regardless of subjects' reported awareness.

An important methodological consideration for any study that seeks to manipulate subjects' awareness of stimuli is exactly how the conditions of awareness are defined and assessed. In OSM and several other forms of visual masking, the masked condition substantially reduces stimulus awareness, but does not lead to its total abolition. For OSM, stimulus detection or discrimination rates are typically reduced from ~90% in the unmasked condition to ~50–70% in the masked (Enns & Di Lollo, 1997; Harris et al., 2013; Prime et al., 2011; Woodman & Luck, 2003). Accordingly, even within the masked condition, subjects are still aware of the stimulus on half or more of the trials, and thus the unmasked and masked conditions cannot be equated simply with aware and unaware, respectively. The conditions of awareness should instead be based on the reported perceptual outcome of each trial within the masked condition, which is how we conducted

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