cortex 102 (2018) 14–25

Available online at www.sciencedirect.com

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Journal homepage: www.elsevier.com/locate/cortex

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

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 & Anllo-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 our experiment. In addition, while some studies subsequent to Woodman and Luck (2003) have similarly reported an N2pc in response to masked stimuli (using a variety of masking methods) (Prime et al., 2011; reviewed in Ansorge et al., 2011), others have found it to be substantially reduced when accounting for the perceptual variability within the masked condition (Harris et al., 2013). Thus, it is currently unclear if the N2pc reliably indexes unconsciously oriented attention.

Masking paradigms such as OSM also allow for the comparison of neural activity in response to stimuli that are physically identical but of which subjects are either aware or unaware on a given trial. With OSM, however, this is only true when comparing within but not across masking conditions, which we do here by examining aware versus unaware trials within the masked condition only. Two ERP components in particular have been consistently associated with visual awareness: an enhanced negativity measured at posterior scalp sites around 200 ms, known as the visual awareness negativity (VAN), and an enhanced positivity measured at parietal sites around 400 ms, called the late positivity (LP) (reviewed in Koivisto & Revonsuo, 2010). In addition, OSM in particular is thought to disrupt awareness not by affecting initial feedforward sensory processing (as indexed by the P1), but by disrupting later feedback/reentrant activity (as indexed by the longer-latency VAN and LP) (Di Lollo, Enns, & Rensink, 2000; Harris et al., 2013). Together with subjects' reported awareness, the presence of the VAN and LP can provide additional support that stimuli are being processed differently in the brain as a function of awareness. Trial-by-trial awareness reports, the VAN, and the LP serve as dependent measures of awareness in this study.

Given the inconclusive evidence for unconsciously oriented attention as indexed by the N2pc, the neural mechanisms that lead to the observed behavioral facilitation in response to subliminal cues are unclear. Two issues in particular remain unresolved: whether the N2pc reliably indexes unconsciously oriented attention, and whether there is a subsequent enhancement of target sensory processing—as with conscious orienting—thereby reflecting a processing-amplification mechanism that leads to behavioral facilitation. Here, we directly compare the full cascade of attentional processes—the cue-induced N2pc, behavioral facilitation, and, importantly, the target-evoked P1—with versus without awareness.

2. Materials and methods

2.1. *Subjects*

Fifty healthy subjects with normal or corrected-to-normal visual acuity participated in this study. We needed to exclude one subject due to a technical problem during data acquisition, and 14 subjects due to insufficient trial counts within some task conditions (<40 trials in any condition), leaving 35 subjects for inclusion in the final analyses (17 female, 32 right-handed, mean age 21 years, range 18–35). Of the 35 included subjects, 25 participated in the main experiment and 10 participated in a separate control experiment (see Section 2.2.1.). We recruited subjects through the Duke University Psychology Subject Pool and local advertisements, and obtained informed consent for all subjects for their credited or paid participation in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board.

2.2. *Stimuli and task*

Subjects were seated 60 cm in front of a 24-in stimulus presentation monitor (60 Hz refresh rate) in a dimly lit, electrically shielded room. Each experimental session comprised 1000 total trials spread evenly across 25 blocks. The sequence of events in a trial is shown in Fig. 1.

We instructed subjects to fixate continuously on a white square in the center of a medium gray background. Each trial began with a fixation screen (duration 900–1100 ms). Next, an array ("cue array") consisting of 14 distractor images and two potential cue/target locations, designated by four-dot masks ($3.5^\circ \times 3.5^\circ$ visual angle), was presented for 17 ms (one screen refresh). The distractors were circular scrambled face and house images, each 3° diameter and jittered $\pm .67^\circ$ in the X and Y dimensions on each trial. The two cue/target locations were always symmetric across the vertical midline, and were both randomly in either the upper or lower visual hemifield on a given trial (50% each) so that subjects could not preallocate their attention to any particular location, a requirement for the OSM effect (Enns & Di Lollo, 1997). A cue was presented within one of the masks on 80% of trials (random 50% left or right); cues were circular face or house images (random 50% each; 3° diameter) chosen randomly from sets of 20 each. The remaining 20% of trials had a blank inside both masks, resulting in a no-cue condition.

To have enough trials to examine the perceptual variability within the masked condition, the main experiment consisted solely of masked trials, in which the offset of the masks was delayed by 500 ms relative to the offset of the rest of the cue array. Following the offset of the cue array and an interstimulus interval of 200–300 ms, a white square-border target (3.5° per side) was presented (duration 100 ms) within one of the masks, both of which remained on the screen for 500 ms following offset of the cue array. The target was randomly presented in either the same location (valid condition) or the opposite location (invalid condition) as the previously presented cue (50% each). Targets were not presented on 30% of trials that had a cue presented, resulting in a cue-only condition, which was important for isolating target-evoked activity (see Section 2.3.2.). Subjects used the index and middle fingers of their right hand to press the left and down arrows, respectively, on a standard keyboard to indicate the location (left or right) of the target (100–1000 ms response window post-target). We instructed subjects to respond as quickly and accurately as possible.

Following their response to the target, subjects were presented with an untimed, three-alternative forced choice (3AFC) report screen and told to indicate whether they had or had not seen a cue on that trial (by indicating the side, "left" or "right," or by indicating "no"). Subjects entered this report with their left hand using the Z ("left"), X ("no"), and C ("right") buttons on the keyboard. Importantly, we created conditions of awareness (cue-aware and cue-unaware) based on this report: trials were cue-aware if a cue had been presented and

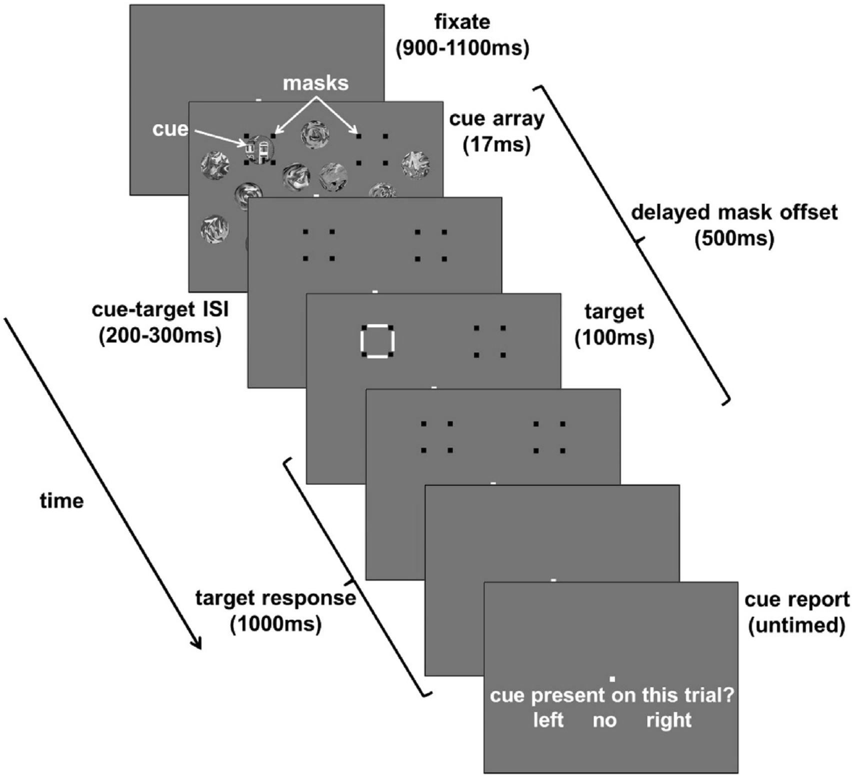

Fig. 1 – Sequence of events in a trial. Shown is a valid trial with both a cue and a target presented. Cue-target validity was 50%. No cue was presented on 20% of trials, and no target was presented on 30% of trials (cue-only trials). ISI: interstimulus interval.

the subject correctly reported its location. Trials were cue-unaware if a cue had been presented but the subject reported that one had not been. We excluded from further analysis trials in which a cue was presented but subjects incorrectly reported its location, as subjects' awareness was ambiguous to determine in these cases. We instructed subjects to look for the cue on each trial, but explicitly stated that a cue would not be presented on every trial. We coached subjects extensively on detecting and responding to both the cue and the target, and had them complete a practice run of 80 trials before beginning the task to ensure proficiency in responding to both stimuli.

2.2.1. *Control experiment*

We also ran a control experiment that had the two standard OSM conditions (randomly interleaved): masked trials as in the main experiment, and unmasked trials, in which the entire array, including cue and masks, offset simultaneously. We replicated the classic OSM masking effect in this control experiment (see Section 3.1.1. and Fig. 2), validating our decision to use only masked trials in the main experiment.

2.3. *Data acquisition and analysis*

2.3.1. *Behavioral data*

We calculated mask effectiveness as the proportion of cue-aware trials out of the total number of cue-aware and cue-unaware trials. In the control experiment, we compared mask effectiveness between the unmasked and masked conditions using a two-tailed paired *t*-test. In the main experiment, we compared mask effectiveness in the sole masked condition using a two-tailed *t*-test against chance (3AFC = 33%).

For the target-detection RT analyses, we excluded trials with incorrect responses and outliers (RTs greater than twice the subject's interquartile range, i.e., twice Q3 minus Q1). This outlier-rejection procedure also ensured that no anticipatory responses (RTs <200 ms) were included in the analysis. To statistically evaluate target-detection RTs and accuracy, we used separate, within-subjects, two-factor, repeated-measures analyses of variance (rANOVAs), with the factors cue-target validity (valid and invalid) and cue awareness (cue-aware and cue-unaware). We used two-tailed paired *t*-tests for planned comparisons examining the validity effects separately for the cue-aware and cue-unaware conditions.

2.3.2. *EEG data*

We recorded EEG from a 64-channel, custom-designed, extended-coverage cap (Woldorff et al., 2002) using active electrodes (actiCAP, Brain Products GmbH, Gilching, Germany), an online right-mastoid reference, and a 500 Hz sampling rate using a three-stage cascaded integrator-comb filter with a corner frequency of 130 Hz (actiCHamp, Brain Vision LLC, Cary, NC, USA). We used two horizontal electro-oculogram (EOG) channels lateral to the outer canthus of each eye and one vertical EOG channel below the left eye to monitor for horizontal eye movements and blinks, respectively.

Offline, we preprocessed the data by segmenting it into 3 s epochs, re-referencing to the algebraic average of the left and right mastoid electrodes, bandpass filtering between .1 and 30 Hz, and downsampling to 250 Hz. We then baseline-corrected the epoched data from −100 to 0 ms. We excluded from further analysis trials with blinks or eye movements that occurred around stimulus presentation (±100 ms), and used independent component analysis to correct for eye-related artifacts occurring across the rest of the epoch. We also excluded trials with high-amplitude noise or excessive muscle activity (>±75 μV), and interpolated excessively noisy channels using a spherical spline procedure (Perrin, Pernier, Bertrand, & Echallier, 1989). We performed the data preprocessing using a combination of the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes.

To examine cue-evoked activity, we selectively averaged trials time-locked to cue-array onset as a function of laterality of electrodes with respect to the cue (contralateral and ipsilateral) and/or cue awareness, and collapsed across all other conditions (i.e., face and house cues and upper- and lower-visual-field presentation). For the early cue-evoked effects (P1 and VAN), we included both cue-only trials and cue-and-target trials in which the target was presented >250 ms after the cue. This allowed us to have more trials while avoiding activity overlap from the target, since the earliest visual evoked potential (C1) does not occur until 50–70 ms after stimulus onset (Luck & Kappenman, 2011). For the later effects (LP and N2pc), we included only cue-only trials, which allowed us to examine the cue-evoked activity without any activity overlap from a target being presented. Importantly, because cue-only trials were randomly interleaved with cue-and-target trials, subjects could not know that no target would be presented on those trials.

When a target was presented, it always followed the cue array, the response to which would overlap the target-evoked response. Thus, to isolate the target-evoked activity from the overlap of activity from the cue array, we subtracted cue-only trials (time-locked to when a target would have occurred but a blank was presented instead) from cue-and-target trials (time-locked to target onset), separately for each cue-awareness condition (Woldorff, 1993). That is, we subtracted aware cue-only trials from aware cue-and-target trials, and unaware cue-only trials from unaware cue-and-target trials. We then separately binned these isolated target responses as a function of validity. We performed the time-locked averaging and plotting of the data using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) and custom scripts in MATLAB (ver. 2013b, The MathWorks, Inc., Natick, MA, USA).

For statistical evaluation of the ERP effects, we first calculated the mean amplitudes across specific time windows and electrode sites, both of which we chose based on previous research, with the following exception: separately for the cue-evoked and target-evoked P1 analyses (time-locked to cue-array onset or to target onset, respectively), we chose the electrode sites where the P1 was maximal, and the time window as ±25 ms around the P1 peak, when collapsing across all conditions. For trials time-locked to cue-array onset, we extracted the P1 between 75 and 125 ms, the VAN between 150 and 250 ms at our occipital electrode sites nearest O1 and O2 and the LP between 300 and 500 ms at our parietal electrode sites nearest P3 and P4 (Koivisto et al., 2009), and assessed them statistically using separate two-tailed paired *t*-tests between the cue-awareness conditions. For cue-only trials, we extracted the N2pc between 180 and 400 ms at posterior electrode sites nearest the 10-10 system electrode locations O1, P3, and PO7 (Harris et al., 2013; Oostenveld & Praamstra, 2001), and assessed it statistically using a rANOVA with the factors laterality and cue awareness. We used two-tailed paired *t*-tests for planned comparisons examining the N2pc separately for the cue-aware and cue-unaware conditions. For the isolated target activity (time-locked to target onset), the P1 peaked somewhat later (~125 ms), perhaps due to

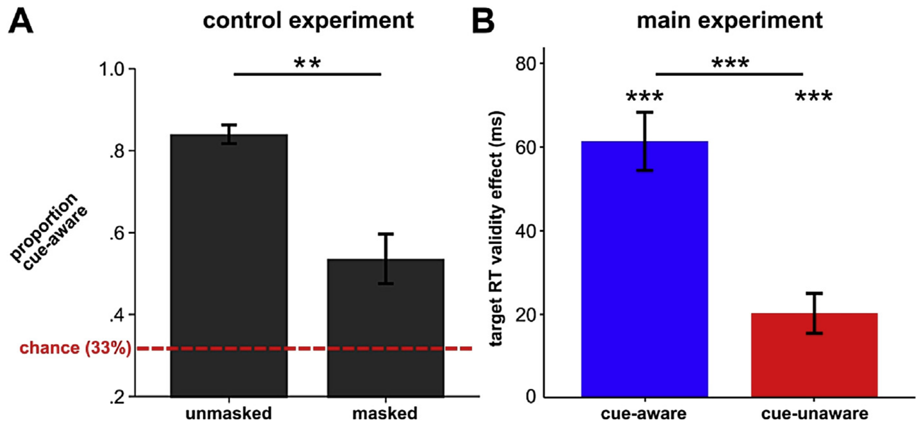

Fig. 2 – Behavioral results. (A) In the control experiment, the mean proportion of cue-aware trials decreased significantly from the unmasked condition to the masked condition. In the main experiment (not shown), the mean proportion of cue-aware trials (50%) was significantly greater than chance (33%). (B) In the main experiment, subjects showed significant target RT validity effects (invalidly minus validly cued targets), both when they were and were not aware of the cue. Vertical bars represent standard error of the mean (SE). $^{**}p < .01$; $^{***}p < .001$.

refractoriness in the response due to the target occurring so soon after the cue array. We thus analyzed the target P1 activity in the time window 100–150 ms using a rANOVA with the factors validity and cue awareness. We used two-tailed paired *t*-tests for planned comparisons examining the P1 validity effect separately for the cue-aware and cue-unaware conditions. We performed the statistical analyses using the RStudio environment (ver. 1.0.136, RStudio, Inc., Boston, MA, USA) for R (ver. 3.3.2, R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Behavior

3.1.1. *Object-substitution masking reduced cue detection performance*

In the control experiment, which included both masked and unmasked conditions, the mean proportion of cue-aware trials decreased from 84% ($SE = 2\%$) in the unmasked condition to 54% ($SE = 6\%$) in the masked condition ($t_9 = -4.48$, $p = .002$; Fig. 2A). This confirmed that we were able to replicate the classic OSM effect on perceptual awareness with our experimental parameters, justifying our focus on the masked condition in the main experiment. In the main experiment, the proportion of cue-aware trials averaged 50% ($SE = 3\%$), giving an approximately equal number of cue-aware and cue-unaware trials for the subjects, on average. The proportion of cue-aware trials was also significantly above chance for the 3AFC cue report (33%; $t_{24} = 6.25$, $p < .001$), demonstrating that subjects were not merely guessing.

3.1.2. *Valid cues enhanced target detection even when subjects were unaware of the cue*

Our behavioral analyses of target detection as a function of validity and cue awareness focused on RT effects. These analyses showed that there was a significant main effect of validity on target-detection RT: subjects were on average 40 ms ($SE = 4$ ms) faster responding to targets following valid ($M = 447$ ms, $SE = 16$ ms) compared to invalid ($M = 487$ ms, $SE = 18$ ms) cues ($F_{1,24} = 100.19$, $p < .001$). There was a significant interaction between validity and cue awareness ($F_{1,24} = 22.36$, $p < .001$), due to the validity effect (invalidly minus validly cued target RTs) being larger in the cue-aware condition (Fig. 2B). Planned comparisons of this validity effect between the cue awareness conditions showed a significant effect on both cue-aware trials ($M = 61$ ms, $SE = 7$ ms; $t_{24} = -8.83$, $p < .001$) and, importantly, cue-unaware trials ($M = 20$ ms, $SE = 5$ ms; $t_{24} = -4.26$, $p < .001$). There was also a significant main effect of cue awareness on target-detection RTs: subjects were on average 63 ms ($SE = 6$ ms) faster responding to targets on cue-unaware trials ($M = 440$ ms, $SE = 16$ ms) compared to cue-aware trials ($M = 503$ ms, $SE = 19$ ms) ($F_{1,24} = 89.37$, $p < .001$). For comparison, target-detection RTs for trials in which no cue was presented (no-cue condition; $M = 457$, $SE = 16$ ms) were similar to (but a bit slower than) cue-unaware trials ($t_{24} = 3.84$, $p < .001$), while they were also significantly faster than cue-aware trials ($t_{24} = -7.06$, $p < .001$). However, within the cue-unaware condition, invalid trials were not statistically different than no-cue trials ($t_{24} = 1.19$, $p = .244$), while valid trials were significantly faster ($t_{24} = 5.65$, $p < .001$).

There was also a significant main effect of validity on target-detection accuracy: subjects were on average 6% ($SE = 1\%$) more accurate responding to targets following valid

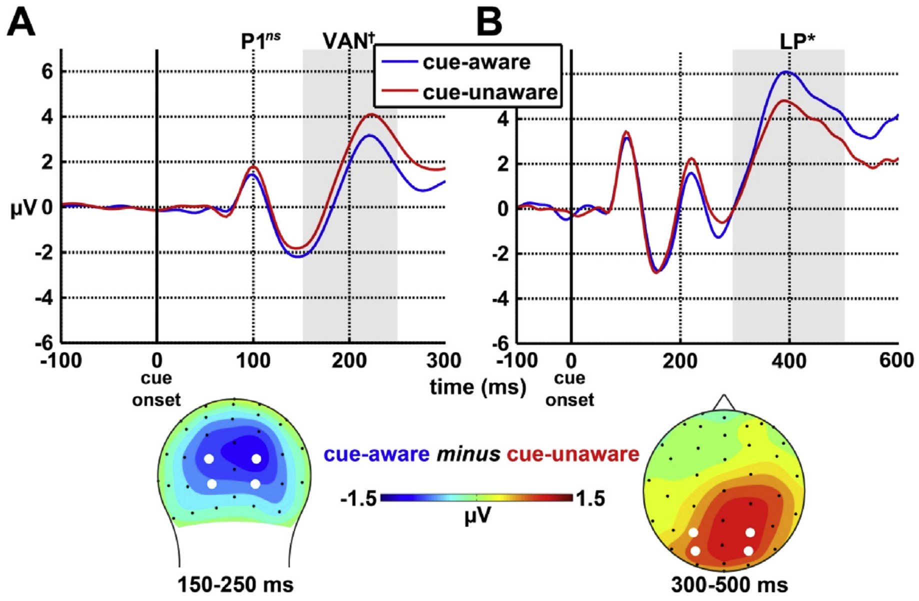

Fig. 3 – Cue processing differed as a function of awareness. (A) No difference was found at the P1 latency (75–125 ms), but there was a trend toward an increased negativity for cue-aware trials from 150 to 250 ms (the VAN). (B) This was followed by a significantly increased positivity for cue-aware trials from 300 to 500 ms (the LP). Scalp topographies for the VAN and LP are plotted below; white circles indicate the channel locations plotted above. Shaded areas indicate measurement time windows. *ns*: not significant; $^{\dagger}p < .08$; $^{*}p < .05$.

(*M* = 94%, *SE* = 1%) compared to invalid (*M* = 88%, *SE* = 1%) cues ($F_{1,24}$ = 34.50, $p < .001$). There was also a significant interaction between validity and cue awareness ($F_{1,24}$ = 15.97, $p < .001$), due to the validity effect being larger in the cue-aware condition. Planned comparisons of this validity effect between the cue awareness conditions showed a significant effect on both cue-aware trials (*M* = 9%, *SE* = 2%; t_{24} = 5.39, $p < .001$) and, importantly, cue-unaware trials (*M* = 3%, *SE* = 1%; t_{24} = 4.07, $p < .001$). There was also a significant main effect of cue awareness on target-detection accuracy: subjects were on average 5% (*SE* = 1%) more accurate responding to targets on cue-unaware trials (*M* = 93%, *SE* = 1%) compared to cue-aware trials (*M* = 88%, *SE* = 1%) ($F_{1,24}$ = 31.22, $p < .001$).

Together, these results are consistent with classic cueing effects in which subjects are faster and more accurate responding to validly compared to invalidly cued targets, and show that this effect was robustly present even when subjects were unaware of the cue.

3.2. *Neural processes (ERPs)*

3.2.1. *Cue processing differed as a function of awareness*

Cue-evoked activity differed significantly as a function of cue awareness in a way that is consistent with previous findings (Fig. 3). There was no evidence of a difference in the cue response at the P1 latency (t_{24} = −.99, p = .334), but there was a trend toward significance for the VAN (cue-aware trials more negative than cue-unaware trials; t_{24} = −1.84, p = .078; Fig. 3A) and a significant LP (cue-aware trials more positive than cue-unaware trials; t_{24} = 2.21, p = .037; Fig. 3B). These findings are consistent with previous literature (Koivisto & Revonsuo, 2010) and theories of how OSM disrupts awareness (Di Lollo et al., 2000; Harris et al., 2013). These results also provide additional support for our use of subjective report to determine awareness of the cue on each trial.

3.2.2. *N2pc elicited only when subjects are aware of the cue*

The N2pc analyses showed a trend toward a significant main effect of laterality: voltages measured at electrodes contralateral to the cue location were more negative than those at ipsilateral electrodes ($F_{1,24}$ = 4.04, p = .056), consistent with the elicitation of the N2pc (Fig. 4). Importantly, there was a significant interaction between laterality and cue awareness ($F_{1,24}$ = 7.23, p = .012), due to the N2pc being substantially larger in the cue-aware condition. Planned comparisons between the awareness conditions revealed a significant N2pc for cue-aware trials (t_{24} = −2.71, p = .012; Fig. 4A), but no evidence of this component for cue-unaware trials (t_{24} = −.13, p = .895; Fig. 4B). In light of the significant behavioral validity effects found in both cue awareness conditions, this finding suggests that a different neural pathway than that which is indexed by the N2pc is responsible for orienting attention in the cue-unaware condition.

3.2.3. *Enhanced early sensory processing for validly cued targets regardless of cue awareness*

The target P1 analyses (Fig. 5) showed a significant main effect of validity: voltages for validly cued targets were significantly more positive than for invalidly cued targets ($F_{1,24}$ = 29.52, $p < .001$). There was also a significant interaction between validity and cue awareness ($F_{1,24}$ = 5.94, p = .023). Planned comparisons revealed a significant P1 validity effect for both cue-aware trials (t_{24} = 4.93, $p < .001$; Fig. 5A) and cue-unaware trials (t_{24} = 3.12, p = .005; Fig. 5B), although the difference was on average .5 μV smaller on cue-unaware trials. Crucially, the presence of a P1 enhancement for validly cued targets in the cue-unaware condition suggests that spatial attention, even

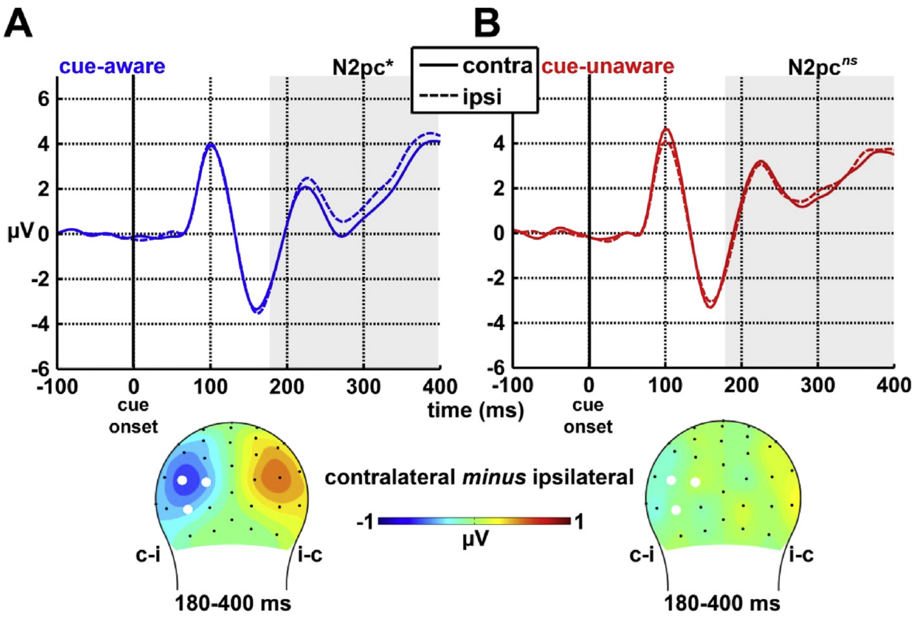

Fig. 4 – Lateralized orienting of attention to the cue. There was a significantly increased negativity at electrode sites contralateral to the cue (N2pc) on cue-aware (A) but not cue-unaware (B) trials. Scalp topographies are plotted below; white circles indicate the channel locations plotted above. c-i: contralateral minus ipsilateral; i-c: ipsilateral minus contralateral. Shaded areas indicate measurement time windows. *ns*: not significant; *$p < .05$.

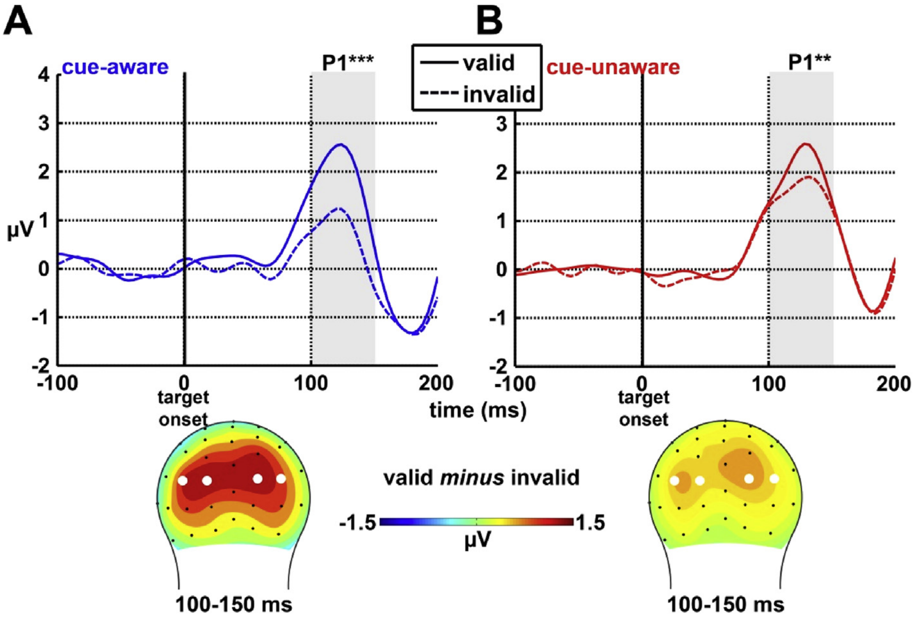

Fig. 5 – Enhanced early sensory processing for validly cued targets regardless of cue awareness. There was a significantly larger P1 (100–150 ms) for validly versus invalidly cued targets for both cue-aware (A) and cue-unaware (B) trials. Scalp topographies are plotted below; white circles indicate the channel locations plotted above. Shaded areas indicate measurement time windows. $^{**}p < .01$; $^{***}p < .001$.

when oriented unconsciously and not indexed by an N2pc, can lead to biased sensory processing for subsequently presented stimuli.

4. Discussion

As part of the larger endeavor investigating the relationship between attention and awareness, the specific goal of this study was to directly compare the mechanisms of spatial attentional orienting with and without perceptual awareness. To do this, we developed a paradigm that combined a classic spatial-cueing task with object-substitution masking to manipulate subjects' awareness of the cues. Our paradigm allowed us to examine the full cascade of attentional processes—the N2pc reflecting attentional orienting to the cue, enhanced target-detection behavior, and, critically, the effect of attention on target sensory processing via an enhanced P1—in the presence and absence of awareness. We found validity effects in both enhanced target detection (faster RTs and better accuracy) and enhanced target-evoked P1s, regardless of cue awareness, although both the behavioral and neural enhancements were larger when subjects were aware of the cue. Interestingly, and contrary to previous findings (Ansorge et al., 2011; Harris et al., 2013; Prime et al., 2011; Woodman & Luck, 2003), we found an N2pc only when subjects were aware of the cue. This finding, in the context of the enhancements to both the sensory processing and behavioral responses to the subsequent targets, suggests that attention was being oriented to subliminal cues, but via a different neural pathway than for supraliminal cues.

We first demonstrated that we could successfully manipulate cue awareness with our experimental parameters. In the control experiment, the rate of cue detection, based on subjects' report at the end of every trial, went from 84% in the unmasked condition to 54% in the masked condition. In the main experiment, which consisted solely of the masked condition, the rate of cue detection was 50%, similar to that for the masked condition in the control experiment. While useful, subjective report is a far from perfect measure, and it is valuable to have converging evidence to add confidence to these reports. We found that the ERP responses to cues differed as a function of awareness: no difference was found at the P1, but there was a trend toward a significantly increased negativity (VAN) followed by a significantly increased positivity (LP) for cue-aware compared to cue-unaware trials. These effects are consistent with previous literature that examined manipulations of stimulus awareness (reviewed in Koivisto & Revonsuo, 2010), as well as the theory that OSM exerts its awareness-disrupting influence not on feedforward sensory processing (P1), but on later feedback/reentrant processing (indexed here by the VAN/LP) (Di Lollo et al., 2000; Harris et al., 2013). In addition, the pattern of behavioral effects (discussed below) adds further confidence to our claim that the processing occurring in the cue-aware and in the cue-unaware conditions were qualitatively different.

Behaviorally, subjects responded faster and more accurately to validly compared to invalidly cued targets in both cue-awareness conditions, replicating previous behavioral results in subliminal cueing (reviewed in Mulckhuyse & Theeuwes, 2010). Both the RT and accuracy validity effects were larger for cue-aware than for cue-unaware trials, a difference that was driven by a significantly greater slowing and decrease in accuracy in invalid cue-aware compared to invalid cue-unaware trials. These effects may reflect a working memory (WM) response conflict (Kiyonaga & Egner, 2014) on cue-aware trials; namely, subjects had to first correctly detect the cue and hold its location in WM (for ~1 s until the appearance of the cue report screen) while correctly responding to the target location, which on invalid trials was opposite the cue location being held in WM. In addition, there was an overall slowing and decrease in accuracy for cue-aware compared to cue-unaware trials, regardless of validity. This can likely be attributed to the dual-task nature of cue-aware trials (responding to both the cue and target); in addition to WM response conflict, such increased cognitive load as a result of the two tasks is known to slow response times and decrease accuracy (Pashler, 1994). Further, RTs in the cue-unaware condition were similar to those in the no-cue condition, and both of these conditions had faster RTs than the cue-aware condition. The pattern of results in these conditions thus argues that there was no such WM conflict or dual-task interference on cue-unaware trials, reinforcing the conclusion that subjects were not aware of the cue.

The N2pc, indexing the lateralized orienting of attention to the cue, was found only when subjects were aware of the cue. This result may seem somewhat surprising given several previous studies reporting an N2pc in response to stimuli in the masked condition of OSM, even when taking subjects' behavior within that condition into account (Harris et al., 2013; Prime et al., 2011; Woodman & Luck, 2003). For several reasons, however, we conclude that not all unconscious attentional orienting is indexed by the N2pc. For one, the task in both Woodman and Luck (2003) and Prime et al. (2011) required subjects to detect a target shape in an array that consisted of bilateral masks (each containing a possible target shape) and 20 distractor shapes, and to press a button indicating that the target shape for that block was either present or absent. Both groups found an N2pc that did not differ significantly for correct responses (target present with "present" response) and incorrect responses (target present with "absent" response). This difference in findings from ours might thus be due to the fact that incorrect responses in their task only indicated that subjects were unable to detect the specific target shape (which required shape discrimination), not whether they detected a target shape at all. In our paradigm, the cue report was a 3AFC with "no" cue as an option; thus cue misses (which we coded as unaware) meant subjects reported that no cue was detected at all, a stronger and more selective criterion for unawareness.

Another potential reason for the discrepant N2pc findings is that our cue array was presented much more briefly (17 ms) than the ones in Woodman and Luck (2003) and Prime et al. (2011) (83 ms), meaning that the to-be-masked stimulus was less salient overall. The experimental parameters in Harris et al. (2013) were more similar to ours, including the stimuli used, the to-be-masked stimulus duration (17 ms), and the 3AFC report used to create the conditions of awareness. Yet, they found N2pc activity for both aware and unaware trials within the masked condition, although it was substantially reduced for unaware trials. The likely difference is that the delayed-offset mask in Harris et al. (2013) was unilateral and stayed on the screen for 500 ms after the offset of the rest of the array; thus, the observed N2pc in that study could be attributable to either the masked target stimulus or the mask itself, and likely stems from a combination of the two. In the current study we eliminated this confound by using bilateral masks, making our stimulus array physically identical on both sides of the vertical midline—except for the cue—and thus ensuring that any lateralized effects could be attributed only to the cue.

Our other findings showing enhancements to both the behavioral detection and sensory processing of the targets strongly suggest that attention had indeed been oriented unconsciously. This pattern of results thus raises the question of how we can have attentional orienting without an accompanying N2pc, the well-replicated cortical index of the shifting and focusing of attention. A plausible explanation is that the attentional orienting in the cue-unaware condition was mediated by a different neural mechanism than that reflected by the N2pc, such as by the subcortical retinotectal pathway (Mulckhuyse & Theeuwes, 2010), and is therefore not indexed by the cortically generated N2pc (Hopf et al., 2000; Luck, 2014). The retinotectal pathway, which proceeds from the retina to the superior colliculus and is then routed via the thalamic pulvinar nucleus to extrastriate and parietal cortices (Blumenfeld, 2010; Kato, Takaura, Ikeda, Yoshida, & Isa, 2011), is integral to oculomotor programming and the rapid orienting of attention (Awh, Armstrong, & Moore, 2006; Kato et al., 2011; Mulckhuyse & Theeuwes, 2010; Van Le et al., 2013). Thus, our rapidly presented, masked cues could plausibly activate this phylogenetically ancient, rapid attentional-orienting circuit—and elicit effects on both subsequent target processing and behavior—without also generating either the cortical N2pc or perceptual awareness of the cue.

Another novel contribution of the present study is that, in addition to measuring the cortical reflection of the orienting of attention to the cue (i.e., the N2pc) and subsequent behavioral target-detection enhancements, we were able to directly examine modulations of early neurosensory processing of the target as a function of both attention (valid versus invalid cueing) and awareness of the cue. As noted above, previous studies have shown that cueing spatial attention leads to enhanced processing for stimuli subsequently presented at the cued location, an effect manifested by larger amplitude P1s (Hillyard & Anllo-Vento, 1998; Hopfinger & Mangun, 1998). We found that the target P1 was robustly enhanced on valid compared to invalid trials in the cue-aware condition, an expected result replicating a myriad of previous reports. Crucially, we also found a cue-induced enhancement of target P1 amplitudes on cue-unaware trials, strongly arguing that unconscious orienting, even when apparently not mediated by a cortical pathway, can modulate the sensory processing of target stimuli. Previous studies have demonstrated the effects of unconscious orienting on behavior (reviewed in Mulckhuyse & Theeuwes, 2010), but these effects could be attributable to modulations at any of several points along the processing cascade from incoming sensory input to behavioral output. Other studies have examined neural indices of attentional orienting as a function of awareness (Ansorge et al., 2011; Harris et al., 2013; Prime et al., 2011; Schettino et al., 2016; Woodman & Luck, 2003), but here we have examined the entire cue-target processing sequence, including the neural and behavioral effects of attention on subsequent stimulus processing. This is a critical point, because a defining function of spatial attention is that it enhances or biases the processing of stimuli at attended locations (e.g., Desimone & Duncan, 1995).

A concern that might be raised regarding the current results is that they could have been biased by the post-hoc exclusion of 14 subjects due to low trial counts within some task conditions (<40 trials in any of the conditions). The low trial counts for these subjects were due both to EEG artifacts ($M = 6\%$ rejected trials) and to behavior that resulted in highly unbalanced bin numbers within those individual subjects. More specifically, the cue-detection rates in the excluded subjects were either substantially higher or substantially lower than the average across subjects, resulting in either one or the other cue-awareness condition having insufficient trials and therefore an unacceptable signal-to-noise ratio. Importantly, however, the exclusion of these 14 subjects seems very unlikely to have biased the results, for two main reasons. First, if we used a less stringent trial-count threshold of at least 20 trials per bin, which results in excluding only 5 subjects (leaving 34 for the final analyses), the results are nearly identical—but with noisier data—and our conclusions would not change. Second, the average cue-detection rate across the excluded subjects (41%) was similar to the average across the included subjects (50%), but with much more extreme individual detection rates (excluded subjects range: 3–93%; included subjects range: 26–79%). Because the group of excluded subjects was not biased toward very low or very high cue-detection rates, it would be very unlikely that their exclusion would have introduced a systematic bias to our results.

Overall, we have demonstrated that attention can be oriented in the absence of awareness and enhance both the neural sensory processing and behavioral detection of subsequently presented stimuli, findings that add to the active literature investigating the relationship between attention and awareness. According to one prominent theoretical perspective, attention is necessary, but not sufficient, for conscious awareness (Cohen, Cavanagh, Chun, & Nakayama, 2012b; Dehaene et al., 2006). Our results further validate and expand upon the claim that attention is not sufficient for awareness, and, although our results do not bear on the necessity of attention for awareness (although see Cohen et al., 2012b; Dehaene et al., 2006), they are nonetheless consistent with this perspective. Under this theoretical view, attention is a construct that describes the way certain assemblies of neural activity are amplified or biased relative to competing assemblies (Desimone & Duncan, 1995), for instance via correlated activity (Cohen & Maunsell, 2009; Ruff & Cohen, 2016; Salinas & Sejnowski, 2001) and/or synchronous oscillations (Buschman & Kastner, 2015; Fries, 2015; Miller & Buschman, 2013; Sejnowski & Paulsen, 2006). Awareness, on the other hand, has been proposed to result from a relatively global, dynamic state of integrated activity and information content in the brain (Dehaene, Charles, King, & Marti, 2014; Oizumi, Albantakis, & Tononi, 2014). According to this view, then, attended representations are amplified and thus relatively biased to become part of this global, dynamic network state (awareness), but these are not identical neural processes.

Funding

This work was supported by NIH grant R01-NS051048 to MGW. The authors declare no competing financial interests.

Acknowledgments

We thank Benjamin Geib, Khoi Vo, Peter Whitehead, and two anonymous reviewers for useful feedback on earlier versions of the manuscript.

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