



Distinct roles of theta and alpha oscillations in the involuntary capture of goal-directed attention



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ARTICLE INFO

Keywords:

Goal-directed attention
Attentional capture
Neural oscillations
Alpha
Theta

ABSTRACT

Mechanisms of attention assign priority to sensory inputs on the basis of current task goals. Previous studies have shown that lateralized neural oscillations within the alpha (8–14 Hz) range are associated with the voluntary allocation of attention to the contralateral visual field. It is currently unknown, however, whether similar oscillatory signatures instantiate the involuntary capture of spatial attention by goal-relevant stimulus properties. Here we investigated the roles of theta (4–8 Hz), alpha, and beta (14–30 Hz) oscillations in human goal-directed visual attention. Across two experiments, we had participants respond to a brief target of a particular color among heterogeneously colored distractors. Prior to target onset, we cued one location with a lateralized, non-predictive cue that was either target- or non-target-colored. During the behavioral task, we recorded brain activity using electroencephalography (EEG), with the aim of analyzing cue-elicited oscillatory activity. We found that theta oscillations lateralized in response to all cues, and this lateralization was stronger if the cue matched the target color. Alpha oscillations lateralized relatively later, and only in response to target-colored cues, consistent with the capture of spatial attention. Our findings suggest that stimulus induced changes in theta and alpha amplitude reflect task-based modulation of signals by feature-based and spatial attention, respectively.

Introduction

Active search of the visual environment is characterized by spatio-temporal uncertainty. Under such conditions, goal-directed attention allows flexible orienting to potential target stimuli based upon their locations or features. Despite advances in understanding the neural mechanisms of attention (e.g., Corbetta and Shulman, 2002), it remains unclear how goal-directed selection is instantiated in the local circuits that process visual information. Here we examined the role of cortical oscillations (Buzsáki and Draguhn, 2004) in the involuntary capture of goal-directed visual attention, focusing on the theta (4–8 Hz), alpha (8–14 Hz), and beta (14–30 Hz) frequency bands.

To date, there has been no work on the association between cortical oscillations and involuntary capture of goal-directed attention. Previous electroencephalography (EEG) studies of attentional guidance and capture have typically focused on a negativity in the event-related potential (ERP) over occipito-parietal electrodes, at around 200 ms after the onset of a stimulus – the N2pc (Luck and Hillyard, 1994). This component is observed following the presentation of lateralized stimuli possessing a goal-relevant feature, but is attenuated if the stimulus

features are not task relevant (e.g., Eimer and Kiss, 2008; Lien et al., 2008; Noesen et al., 2014). This link to goal relevance has led many authors to conclude that the N2pc reflects the allocation of goal-directed attention (e.g., Eimer, 1996; Eimer and Grubert, 2014; Hickey et al., 2009). However, conflicting empirical results have led to suggestions that the N2pc may reflect other processes, such as the identification of goal relevant features prior to attentional allocation or object individuation (Eimer and Grubert, 2014; Naughtin et al., 2016). Thus, it is currently unclear when goal-directed attention is allocated to a stimulus, and in what part of the EEG signal it is reflected. One promising candidate that has been identified in studies of voluntary attention is the occipito-parietal alpha oscillation.

There is extensive evidence for the involvement of alpha oscillations in voluntary attentional allocation (Foxe and Snyder, 2011). In tasks in which centralized cues direct observers to attend to a location in the left or right hemifield, alpha oscillations measured over occipito-parietal cortex become lateralized such that alpha amplitude is decreased contralateral to the attended side of space (Sauseng et al., 2005; Worden et al., 2000). This alpha lateralization is maintained as long as attention is directed to one side of space (Kelly et al., 2006), the

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magnitude of lateralization tracks the likelihood of targets appearing at the cued location (Bauer et al., 2014; Gould et al., 2011), and predicts subsequent perceptual outcomes (e.g., Händel et al., 2011; Thut et al., 2006). The frequency of lateralized activity can spread up to ~25 Hz (the beta range) in visual attention tasks (e.g., Bauer et al., 2014), but it is currently unclear whether this is simply an extension of the alpha range (Michalareas et al., 2016), or whether this beta activity reflects distinct processes (e.g., Sedley et al., 2016).

Evidence for the involvement of theta oscillations in goal-directed attention is also sparse. Dowdall et al. (2012) had participants perform visual search where targets did or did not “pop out”. Theta power was greater contralateral than ipsilateral to the target location, and this effect was larger for “popout” than for “non-popout” displays. However, as ERPs are strongly represented in the theta range (Klimesch et al., 2004), it is unclear whether this increase in theta amplitude was an indication of theta’s involvement in task-related processing, or simply reflects a spectral representation of the ERP.

Here we examined how oscillations in distinct frequency bands are impacted by the interaction of goal-directed attention with physical characteristics of the environment that elicit involuntary shifts of attention. Across two independent datasets, we show that theta and alpha oscillations are involved in different aspects of goal-directed attention. In contrast, beta oscillations, while showing stimulus induced amplitude changes, were not associated with the goal-directed allocation of spatial attention.

Materials and methods

Overview

We used a well-studied paradigm that provides a precise characterization of the locus of spatial attention (Folk et al., 1992) to investigate the roles of theta, alpha, and beta oscillations in goal-directed attention. Specifically, participants searched for a target of a particular color among heterogeneously colored distractors. Prior to the appearance of the target display we cued one location with a non-predictive cue that was either target- or non-target-colored (Folk and Remington, 1998). Under such conditions, cues possessing behaviorally-relevant stimulus properties – such as the target color – are known to exert a strong and involuntary ‘capturing’ influence on the locus of spatial attention (e.g., Eimer and Kiss, 2008; Folk et al., 1992, 2002; Zivony and Lamy, 2014), even when they occur outside of awareness (Ansorge et al., 2009; Lamy et al., 2014). We recorded brain activity using EEG, with the aim of analyzing oscillatory activity elicited by these task-irrelevant cues.

Participants

Twenty-five individuals participated in Experiment 1 (aged 18–28 years, mean=22.12, SD=2.49, 16 females). A separate group of twenty-four individuals participated in Experiment 2 (aged 18–31 years, mean=22.33, SD=2.92, 10 females). All participants were right-handed, had normal or corrected-to-normal vision, and provided written informed consent prior to participating. One participant was excluded from Experiment 1 due to a technical error that resulted in no EEG data being recorded for that individual. Participants were compensated for their time at a rate of \$10 per hour. The study was approved by The University of Queensland Human Research Ethics Committee.

Behavioral task

We employed a modified spatial cueing paradigm (Fig. 1a; Folk et al., 1992) in which participants were required to identify the orientation of a target letter T of a particular color (red in Experiment 1, counterbalanced across individuals in Experiment 2). Participants fixated a central cross (0.3°×0.3°, 1 pixel thick), sur-

rounded by four placeholder circles (2.2° diameter, 2 pixels thick) placed 7.5° from fixation at the corners of an imaginary square. The placeholder circles and fixation cross were gray (RGB: 160, 160, 160) and were presented on a black background (RGB: 0, 0, 0). The fixation period lasted between 500 and 900 ms (randomly determined) and was followed by a cue period, during which the placeholder circles thickened to 4 pixels and one placeholder changed color for 67 ms (except on no-cue trials, in which the circles thickened, but none changed color; Fig. 1A). Cues were non-predictive of the target location (25% likelihood at each location), and could be red (RGB: 255, 0, 0), green (RGB: 0, 255, 0), blue (RGB: 0, 0, 255), yellow (RGB: 255, 255, 0), or gray (no-cue trials), with equal probability (20% of trials each). The cue display was followed by the fixation display for 133 ms (the inter-stimulus interval [ISI]). Following this, the target display was presented for 100 ms. The target display consisted of the fixation display, with the addition of four “Ts” (0.8°×0.8°, 4 pixels thick) rotated by 90° clockwise (“rightward”) or counterclockwise (“leftward”), one placed centrally in each placeholder location. There were always two leftward and two rightward oriented “Ts” on every trial, each allocated a unique color from the set {red, green, blue, yellow}. In Experiment 1, all participants responded to the orientation of the red “T”. In Experiment 2, target color was counterbalanced such that each participant was randomly allocated a target color from the set {red, green, blue, yellow}. The target display was followed by the fixation display for 1500 ms, during which time participants could make their response to the orientation of the target-colored “T”, pressing the left or right arrow key on the keyboard if the target was rotated to the left or right, respectively.

Stimuli were presented on an NEC Accusync 120 CRT monitor with a resolution of 1024×768 and a refresh rate of 60 Hz. Stimulus presentation was controlled using the Psychophysics Toolbox extension (Brainard, 1997; Kleiner et al., 2007) for MATLAB (MathWorks), running under Windows 7. Viewing distance was maintained at 57 cm with the use of a chinrest. Participants made their responses by pressing either the left or right arrow key on a standard USB keyboard with their right hand.

Each block of the task contained a full factorial crossing of the five cue conditions (red, green, blue, yellow, no-cue), four cue positions (dummy coded for no-cue trials), and four target positions, to give a total of 80 trials per block. All participants completed one block of practice, during which they received feedback at the end of every trial. Feedback consisted of the word “CORRECT” or “WRONG!” presented centrally in white (RGB: 255, 255, 255) 14 point Arial font (3.5°×0.5°) for 300 ms. Incorrect responses were also met with a 1000 Hz tone for 500 ms. During the experiment there was no trial-by-trial feedback, but participants were informed of their accuracy (%) during the self-paced break at the end of every block. Excluding practice, participants completed a total of 1040 trials (13 blocks) each.

EEG recording

Continuous EEG data were recorded using a BioSemi Active Two system (BioSemi), digitized at a rate of 1024 Hz with 24-bit A/D conversion. The 64 active Ag/AgCl scalp electrodes were arranged according to the international standard 10–10 system for electrode placement (Chatrjian et al., 1985), using a nylon head cap. As per BioSemi system design, the Common Mode Sense and Driven Right Leg electrodes served as the ground, and all scalp electrodes were referenced to the Common Mode Sense during recording. Eye movements were monitored online using bipolar horizontal electro-oculographic (EOG) electrodes placed at the outer canthi of each eye, and bipolar vertical EOG electrodes placed above and below the left eye.

EEG analysis

Offline EEG preprocessing was performed with the EEGLAB

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