Alpha activity reflects individual abilities to adapt to the environment

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ABSTRACT

Recent findings suggest that oscillatory alpha activity (7–13 Hz) is associated with functional inhibition of sensory regions by filtering incoming information. Accordingly the alpha power in visual regions varies in anticipation of upcoming, predictable stimuli which has consequences for visual processing and subsequent behavior. In covert spatial attention studies it has been demonstrated that performance correlates with the adaptation of alpha power in response to explicit spatial cueing. However it remains unknown whether such an adaptation also occurs in response to implicit statistical properties of a task. In a covert attention switching paradigm, we here show evidence that individuals differ on how they adapt to implicit statistical properties of the task. Subjects whose behavioral performance reflects the implicit change in switch trial likelihood show strong adjustment of anticipatory alpha power lateralization. Most importantly, the stronger the behavioral adjustment to the switch trial likelihood was, the stronger the adjustment of anticipatory posterior alpha lateralization. We conclude that anticipatory spatial attention is reflected in the distribution of posterior alpha band power which is predictive of individual detection performance in response to the implicit statistical properties of the task.

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Introduction

When driving down a long and lonesome road, you can probably attend to the road while also talking to your passenger. As you head towards a crowded crossing, you will gradually focus your attention to the traffic and eventually stop talking to your passenger. After having passed the crossing you can allow yourself to again attend to your passenger.

This example illustrates our ability to gradually adjust our attentional resources according to the surrounding. This process is likely to be associated with a gradual engagement and disengagement of brain regions processing respectively relevant or irrelevant for the task at hand. We hypothesize that this redistribution of resources is partly reflected by a differential adjustment of neural oscillations in various brain regions. Recent findings suggest that oscillatory alpha activity (7–13 Hz) plays a role in the distribution of attention resources by functional inhibition of sensory regions. This allows for filtering incoming information (reviewed in Bonnefond and Jensen, 2012; Foxe and Snyder, 2011; Jensen and Mazaheri, 2010; Jensen et al., 2012; Klimesch, 1999, 2012). The main idea is that alpha activity increases in sensory regions associated with suppression of task-irrelevant information, while alpha activity decreases in regions processing the task-relevant information. For instance, recent studies on visual covert attention have

demonstrated that alpha power decreases in the parieto-occipital regions contralateral to the anticipated stimuli whereas alpha activity increases relatively in ipsilateral parieto-occipital regions (Worden et al., 2000). In a visuo-spatial detection task, Thut et al. (2006) demonstrated that the degree of prestimulus hemispheric alpha lateralization correlated with faster target detections. Kelly et al. (2009) and Händel et al. (2011) showed that the strength of prestimulus alpha lateralization is predictive of target discriminability. These studies indicate that hemispheric alpha lateralization correlates with enhanced performance in spatial attention tasks. Finally, Romei et al. (2010) demonstrated that TMS can be applied to entrain alpha oscillations over the parietal cortex ipsi-lateral to the attended direction. Since this entrainment had positive consequences for performance in a spatial attention task, one can argue for a causal inhibitory role of the alpha oscillations.

Two recent studies provided strong evidence for alpha power being under top-down control by demonstrating that prestimulus hemispheric alpha lateralization is influenced by explicit manipulation of the reliability of the spatial cue (i.e. a cue indicating the visual hemifield to covertly attend to). Haegens et al. (2011) conducted a spatial somato-sensory discrimination task in which subjects were explicitly informed about the cue reliability. They found that the reliability of the cue correlated with the prestimulus alpha power lateralization in sensorimotor regions. A related study was performed by Gould et al. (2011) in the visual domain. They found a linear increase in alpha lateralization in visual regions with cue reliability. Furthermore, subjects with a stronger alpha power decrease contralateral to the cue also showed a stronger behavioral cueing effect as reflected in faster reaction times. These two studies show that alpha power in both visual and somatosensory

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regions is modulated by expectations about the likelihood of external events.

In these paradigms attention biasing was manipulated using explicit cues. In real life, however, attention biasing is often modulated by statistical properties of events in the environment. The aim of our current study was to assess whether biases in the allocation of attention due to statistical properties in the environment are reflected in anticipatory alpha-band lateralization. In a visual covert attention paradigm subjects were instructed to detect a stream of targets occurring in one hemifield. However, they had to switch attention to the unattended hemifield when a stimulus change occurred in the unattended side. The likelihood of an attention-switch-stimulus (indicating an attention switch trial) increased with the number of trials following the previous switch; however, the subjects were not explicitly informed about this statistical property. We assessed the individual change in alpha lateralization and switch-trial detection rate with switch-trial likelihood. Our study provides evidence that subjects who adapted their behavior (i.e. switch trial detection rate) according to the statistical properties of the task (switch-trial likelihood) also were the ones who adjusted their hemispheric alpha lateralization accordingly.

Materials and methods

Participants

Twenty healthy subjects with normal or corrected-to-normal vision (mean age: 24 ± (SD) 4 years) participated in the experiment after providing written informed consent according to the Declaration of Helsinki and the local Ethics board. The subjects did not have neurological or psychiatric disorders. The study was approved by the local ethics committee (CMO region Arnhem/Nijmegen).

Stimulus presentation and experimental paradigm

Stimulus presentation was performed using Presentation (Neurobehavioural Systems, Inc.) and a liquid crystal display video projector (SANYO PROxtraX multiverse; refresh rate of 60 Hz), back projecting onto a screen in the magnetically shielded room using two front-silvered mirrors. The distance to the screen as well as the size of the displayed screen size were measured individually for each subject. This allowed us to compute stimulus sizes and distances in visual degrees ensuring the same stimulus properties across subjects.

We developed a covert attention switching paradigm based on the study of van Schouwenburg et al. (2010), see Fig. 1. Squares were flashed on each side and subjects had to report the color of the attended square by a button press. When subjects detected a color change at the unattended side (signaling a *switch trial*), they had to report the color of the unattended square (but not the currently attended square) and switch attention to the unattended side in future trials.

At the beginning of each block, subjects were explicitly cued to which side to attend. From then on, the attended side was determined by stimuli properties alone. A central fixation point was presented during the entire experiment. Colored squares were flashed 1200 ms after the beginning of each trial for about 33 ms (two frames = 2/60Hz). These stimuli were presented with nine degrees eccentricity and two degrees lower than the fixation cross (measured from the fixation cross to the center of the stimuli). The squares were two degrees wide.

Subjects had to report the color of the square on the attended side by pressing a button with their left (for red) or right hand (for blue). On the unattended side, the square was either gray (*repeat trials*) or colored in blue or red (*switch trials*). Subjects had to respond within 2500 ms. After responding, the fixation cross turned gray, indicating that the subject could blink or move the eyes in a 1000 ms period. Then the fixation cross turned white again indicating the start of the next trial. Subjects had to keep attention to one hemifield (*repeat trial*) and report the color of the square on that side until they detected a colored stimulus
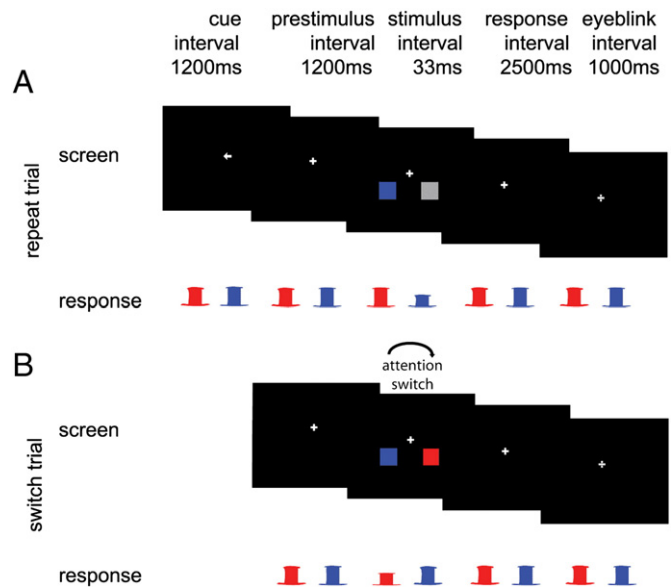

Fig. 1. The paradigm. The attended side was initially indicated by a cue. Subjects had to focus at the fixation cross and by button press indicate the color of the attended squares (left button for red and right button for blue). The 1200 ms prestimulus period was followed by the colored stimuli flashed for 33 ms. Subjects had to respond within 2500 ms. If there was a color change in the square of the unattended hemifield, attention had to switch to that direction ('switch-trial'). After the response there was a 1000 ms window for eye blinking. A Example of an explicit cue followed by a repeat trial. The subject had to covertly attend to the left and subsequently report the color of the stimuli by pressing the corresponding button (here: blue, right button). B Example of a switch trial. In the previous repeat trials, the subject had to attend to the left, because of the initially shown spatial cue. Upon stimulus presentation, the subject correctly switched attention and indicated so by reporting the color of the stimulus at the formerly unattended side (here: right, red color). If the subject responded according to the formerly attended side (here: left, blue), the switch trial would repeat up to four times. Repetitions of switch trials were removed from the analysis. If the subject did not switch after the fourth consecutive switch trial, another explicit spatial cue pointing to the formerly unattended side was presented (here: a rightward pointing arrow).

in the unattended hemifield (switch stimulus). A trial which includes a switch stimulus is called a *switch trial*. The switch stimulus was detected if the color of the unattended target was correctly reported (*detected switch trial*). Subjects then had to keep attending the formerly unattended hemifield until a next switch trial was detected. If a subject failed to detect the switch stimulus (*undetected switch trial*), it was repeated with a random color (blue or red) up to four times. We focused the analysis on the first switch trials, i.e. dismissed switch trials immediately following an *undetected switch trial*.

The probability of a switch trial was increasing with the number of trials since the last switch trial (see Fig. 2). The number of trials between switches was precomputed, so that the sequence of trials was as similar as possible across different subjects (on average 4.5 trials). We call the number of trials from the last switch trial *Inter-Switch Trial Number* (ISTN). A number of *detected repeat trials* were required to trigger a switch trial. When a subject made a wrong response to a repeat trial, the trial number from the last switch trial was reset. Thus a number of consecutive correct responses to repeat trials were needed to trigger a switch trial. This ensured that subjects did not only attend the supposedly unattended side throughout the experiment. The number of response errors to repeat trials was, however, very low (<10%, see also Section 3.1 Behavioral Performance). Our setup resulted in a linear increase in switch trial likelihood with ISTN (see Fig. 2). Subjects were given a break of at least 2.5 s after every 15th *detected switch trial*. After each break, an explicit spatial cue indicated the initially attended side. Additional explicit spatial cues were provided after four *undetected switch trials* and after four errors to repeat trials in between two switch trials (5.2 ± (SD) 3.9 cues for attention to the left and 5.9 ± (SD) 4.4