



## Cortical cross-frequency coupling predicts perceptual outcomes

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### ABSTRACT

Functional networks are comprised of neuronal ensembles bound through synchronization across multiple intrinsic oscillatory frequencies. Various coupled interactions between brain oscillators have been described (e.g., phase-amplitude coupling), but with little evidence that these interactions actually influence perceptual sensitivity. Here, electroencephalographic (EEG) recordings were made during a sustained-attention task to demonstrate that cross-frequency coupling has significant consequences for perceptual outcomes (i.e., whether participants detect a near-threshold visual target). The data reveal that phase-detection relationships at higher frequencies are dependent on the phase of lower frequencies, such that higher frequencies alternate between periods when their phase is either strongly or weakly predictive of visual-target detection. Moreover, the specific higher frequencies and scalp topographies linked to visual-target detection also alternate as a function of lower-frequency phase. Cross-frequency coupling between lower (i.e., delta and theta) and higher frequencies (e.g., low- and high-beta) thus results in dramatic fluctuations of visual-target detection.

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### Introduction

Identical stimulation does not always lead to the same perceptual and behavioral outcomes. The response to a stimulus depends not only on attributes of the stimulus itself (e.g., its intensity), but also on the “neurophysiological context” at the moment when the stimulus occurs (Arieli et al., 1996; Buzsaki and Chrobak, 1995; Lakatos et al., 2009). This neurophysiological context is defined by the brain's intrinsic spatial and temporal dynamics. That is, normal brain function entails the continual synchronization and desynchronization of neuronal ensembles at various oscillatory frequencies. The perceptual outcome of sensory stimulation depends, in part, on which networks (or brain regions) are engaged when a stimulus occurs, as well as on the excitability state of the neurons embedded in those networks (Boly et al., 2007; Busch and VanRullen, 2010; Busch et al., 2009; Haig and Gordon, 1998; Jansen and Brandt, 1991; Kastner et al., 1999; Lange et al., 2011; Mathewson et al., 2009; Monto et al., 2008; O'Connell et al., 2009; Romei et al., 2008; Sadaghiani et al., 2010; Scheeringa et al., 2011; Varela et al., 1981).

Ongoing oscillations in neuronal ensembles reflect fluctuations in local field potentials between high- and low-excitability states, which can be imagined as the peaks and troughs (or phases) of a sine wave. Several studies have now established that the prestimulus phase of cortical oscillations influences perceptual outcomes (Busch et al., 2009; Dugue et al., 2011; Mathewson et al., 2009). During a high-excitability state, when neurons in the sensory cortices are closer to their firing threshold, a near-threshold stimulus is more likely to be detected and selected for further processing (Lakatos et al., 2007, 2009). Moreover, endogenous (or top-down) signals can modulate the phase of cortical oscillations in anticipation of an expected sensory event (Fiebelkorn et al., 2011; Gomez-Ramirez et al., 2011; Lakatos et al., 2007, 2008). For example, phase can be reset in response to an attended temporal cue, such that a subsequent to-be-detected stimulus optimally aligns with a high-excitability state (and is thus more likely to be detected).

Although it is well-established that the prestimulus phase of ongoing oscillations contributes to perceptual outcomes (i.e., whether a near-threshold stimulus is detected), debate remains over the contribution of oscillations at various frequencies. Some recent studies have demonstrated phase-detection relationships at theta and alpha (4–14 Hz) frequencies (Busch et al., 2009; Dugue et al., 2011; Lakatos et al., 2009; Mathewson et al., 2009). Other studies, which focused on the interaction between attention and visual-target detection, have instead emphasized the importance of low-delta (1–2 Hz) frequencies (Besle et al., 2011; Fiebelkorn et al., 2011; Gomez-Ramirez et al., 2011; Lakatos et al., 2008). Here, we hypothesized that the response to a near-threshold visual-target is influenced by an interaction of ongoing oscillations on multiple temporal scales (i.e., cross-frequency coupling between and within the hubs of functional networks). We therefore sought to

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(1) establish which frequencies are most closely tied to visual-target detection and (2) define the temporal and spatial relationships among those frequencies.

## Materials and methods

### Participants

Seven neurologically normal volunteers participated in the experiment (mean age  $30.3 \pm 3.6$  years; 1 female; 1 left-handed), and data from all participants were included in the analyses. The Institutional Review Board of the Albert Einstein College of Medicine approved the experimental procedures. Written informed consent was obtained from all participants prior to data collection, in line with the Declaration of Helsinki.

### Stimuli and task

The experiment was administered in a light- and sound-attenuated chamber using Presentation software version 14.4 (Neurobehavioral Systems, Albany, CA, USA). All stimuli were presented on a  $34.5 \times 55.0$  cm LCD monitor with a 60-Hz refresh rate (ViewSonic, model VP2655wb). Fig. 1 provides a schematic of the experimental task. Participants, who were positioned 70 cm in front of the monitor, were asked to maintain central fixation and report the occurrence of a near-threshold visual target: a sine wave grating (3 cycles per degree) with 16-ms duration, subtending  $2.5^\circ$  of the visual angle in both the vertical and horizontal planes. The visual target was presented  $2^\circ$  below central fixation, and a sound (1000 Hz) with 16-ms duration was presented from a BOSE (Companion 2) speaker positioned directly below the monitor.

After the participant clicked the right mouse button to begin a trial, there was a 3–5 second prestimulus interval, which was followed by a clearly audible sound ( $\sim 65$  dB SPL). The visual stimulus might co-occur with the sound (35%) or it might occur anytime up to 5 s thereafter (45%). Catch trials (20%), where there was a sound presented at the beginning of the trial but no visual target was presented throughout the duration of the trial, were included to estimate false alarms. Participants were directed to click the left mouse button whenever they detected a visual stimulus, regardless of when it occurred. Trials ended either when the participant responded or 6 s after the sound was presented (giving participants enough time to respond to a visual stimulus that occurred at 5 s after the sound). An SR Research EyeLink eye tracker was used to discard all trials with blinks or eye movements.

To maintain vigilance, each participant's time in the experiment was distributed over 2 days. On each day, participants completed 4 blocks, with each block consisting of 120 self-paced trials. After every 20 trials, participants were updated on their behavioral performance. At the end of these mini-blocks, the contrast of the visual target was adjusted to guarantee that overall behavioral performance would be pinned at approximately 50%. That is, if a participant's hit rate in the preceding

mini-block exceeded 60%, the contrast of the visual target was decreased; if a participant's hit rate fell below 40%, or if a participant committed more than two false alarms, the contrast of the visual target was increased. The average hit rates reported in the present manuscript are only based on trials that occurred at least 2.5 s after the auditory cue and therefore might be higher or lower than 50% (Fig. 3).

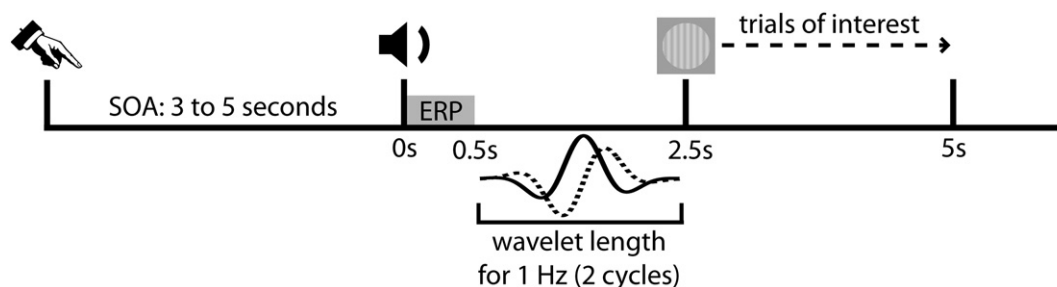
### Electroencephalogram (EEG) recording

Continuous EEG was acquired through the ActiveTwo BioSemi (Amsterdam, the Netherlands) electrode system from 160 scalp electrodes, digitized at 512 Hz with a 31.25 nV quantization resolution. Data were band-passed filtered during acquisition from 0.1 to 100 Hz. With the BioSemi system, every electrode or combination of electrodes can be assigned as the reference, which is done purely in software after acquisition. BioSemi replaces the ground electrodes that are used in conventional systems with two separate electrodes: Common Mode Sense active electrode and Driven Right Leg passive electrode. These two electrodes form a feedback loop, which drives the average potential of the participant as close as possible to the reference voltage of the analog-to-digital converter, thus rendering them references.

### Data processing

EEG data were processed using the FieldTrip toolbox (Donders Institute for Brain, Cognition, and Behaviour, Radboud University Nijmegen, the Netherlands) for MATLAB (The MathWorks, Natick, MA, USA). Here, our goal was to investigate the link between prestimulus phase (at multiple frequencies) and visual-target detection during a sustained-attention task. We therefore needed to obtain an accurate measure of phase on each trial for all frequencies of interest: 1–25, 30, 35, 40, 45, and 50 Hz. Before measuring prestimulus phase, however, we first divided the continuous EEG into epochs, from  $-3$  s prior to the auditory cue to 0.5 s after the visual target was presented. These epochs were detrended, and baseline corrected based on the mean voltage over the entire trial. The EEG data were then filtered using a discrete Fourier transform (DFT) filter to remove 60-Hz line noise. In addition to removing trials with blinks or eye movements based on eye tracking data, an artifact rejection criterion of  $\pm 100$   $\mu$ V was employed at all the electrodes to reject trials with excessive EMG, or other noise transients. Following artifact rejection, the epochs were re-referenced to an average reference (i.e., an average of the activity at all electrodes).

To measure prestimulus phase, we used frequency-specific Morlet wavelets that varied in the number of cycles, from 2 cycles at 1 Hz, 3 cycles at 2 Hz, 4 cycles at 3 Hz, 5 cycles at 4 Hz, 6 cycles at 5 Hz, and 7 cycles for all of the other frequencies. We varied the number of cycles to avoid contamination from the auditory evoked potential that occurred in response to the auditory cue. Each wavelet has a temporal extent based on the frequency and number of cycles. For example, a 1-Hz wavelet with 2 cycles extends for 2 s. To limit the



**Fig. 1.** A schematic of the sustained attention task. Participants reported the occurrence of near-threshold visual targets. The present analysis is restricted to trials when the visual target occurred at least 2.5 s after the auditory cue.

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