



## Dynamic phase alignment of ongoing auditory cortex oscillations

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### ABSTRACT

Neural oscillations can synchronize to external rhythmic stimuli, as for example in speech and music. While previous studies have mainly focused on elucidating the fundamental concept of neural entrainment, less is known about the time course of entrainment. In this human electroencephalography (EEG) study, we unravel the temporal evolution of neural entrainment by contrasting short and long periods of rhythmic stimulation. Listeners had to detect short silent gaps that were systematically distributed with respect to the phase of a 3 Hz frequency-modulated tone. We found that gap detection performance was modulated by the stimulus stream with a consistent stimulus phase across participants for short and long stimulation. Electrophysiological analysis confirmed neural entrainment effects at 3 Hz and the 6 Hz harmonic for both short and long stimulation lengths. 3 Hz source level analysis revealed that longer stimulation resulted in a phase shift of a participant's neural phase relative to the stimulus phase. Phase coupling increased over the first second of stimulation, but no effects for phase coupling strength were observed over time. The dynamic evolution of phase alignment suggests that the brain attunes to external rhythmic stimulation by adapting the brain's internal representation of incoming environmental stimuli.

### Introduction

Many environmental stimuli, such as speech and music are characterized by their temporal regularity. It has been shown that the brain can extract this temporal structure by aligning its low-frequency oscillations to the rhythm of the input stream (Besle et al., 2011; Lakatos et al., 2008; Schroeder and Lakatos, 2009). This neural entrainment has been confirmed for strictly rhythmic stimulation (Henry and Obleser, 2012) as well as for quasi-rhythmic stimulation (Herrmann et al., 2016) in the auditory and visual modality (Henry et al., 2014; Notbohm et al., 2016; Stupacher et al., 2016).

Since environmental stimuli are naturally evolving and changing over time, our brain needs to continuously track incoming information to keep internal representations up to date. This temporal information of a stimulus has been shown to be encoded by the phase of the neural oscillation (Besle et al., 2011; Chakravarthi and VanRullen, 2012; Kösem et al., 2014; ten Oever and Sack, 2015). On relatively short time scales (~1 s) shifts in brain phase were observed to attended targets in a selective attention paradigm (Besle et al., 2011). Further, Kösem et al.

(2014) observed that shifts in event timing resulted in a phase shift of auditory cortex oscillations, indicating that entrainment is not a passive neural response, but rather that the neural oscillations are actively adapting to the stimulus. On longer time scales, observations from auditory stream-segregation paradigms suggest that phase coherence increases over the time course of stimulation (~5 s) resulting in improved target detectability (Akram et al., 2014; Elhilali et al., 2009).

From the above studies it becomes apparent that there is a tight link between rhythmic stimulation and behaviour (Hickok et al., 2015). Further, it was suggested that the link between rhythmic stimulation and behaviour is mediated by the neural oscillation (e.g. Henry et al., 2014; Henry and Obleser, 2012). In particular, a tight coupling between stimulus and brain activity has been observed, which is reflected in a constant *stimulus-brain lag* (Keitel et al., 2017). It has been further suggested that neural oscillations drive rather than modulate perception, resulting in perceptual cycles that are critically dependent on the neural phase relative to the stimulus (for a review see: VanRullen, 2016). Consistent with this idea, Henry and Obleser (2012) showed that auditory gap detection performance was best for targets that were presented in the rising

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segment of the neural oscillation. Furthermore, Simon and Wallace (2017) support the notion of preferential processing in the rising segment, indicating a specific *brain-behaviour* phase relationship. Finally, studies investigating behavioural effects of neural entrainment with regard to the stimulus have demonstrated systematic phase-dependent behavioural effects on both target detection and reaction times, that is, *stimulus-behaviour* (Breska and Deouell, 2017; Mathewson et al., 2010; Stefanics et al., 2010). Consequently, a better understanding of the role of neural entrainment requires the investigation of all three relationships that is *stimulus-brain*, *stimulus-behaviour*, and *brain-behaviour* links (Fig. 1A).

While, the fundamental role of neural entrainment in encoding the timing of periodic events has been well established, little is known about the evolution of entrainment over time, and the behavioural consequences such an evolution may have. Neural entrainment to an external stimulus is a dynamic process that is developing over time, where the neural oscillation aligns its phase to the rhythmic input (Pikovsky et al., 2003; Thut et al., 2012, 2011). On the population level, as recordable with electroencephalography (EEG), neural entrainment would show as an increase in amplitude at the frequency of the entrainer (Pikovsky et al., 2003; Thut et al., 2011).

In this human EEG study, we studied the build-up of neural entrainment over a time-course of several seconds. Participants had to detect silent gaps that were inserted in a 3 Hz frequency-modulated tone (cf. Henry and Obleser, 2012) of variable length (short stimulation: 11 cycles, long stimulation: 23 cycles). We predicted that long stimulation would be characterized by a stronger phase coupling between the stimulus and the brain compared to the short stimulation (Fig. 1B). We hypothesized that longer stimulation would lead to behavioural changes compared to short stimulation reflected as higher accuracies and stronger behavioural modulation. Besides the strength of the phase coupling over time, we were interested in the phase lag of the neural oscillation relative to the stimulation.

Our results demonstrated a phase-shift in stimulus-brain relationship over time. This supports the idea that the entrained auditory cortex oscillations dynamically align to stimulus streams over time.

## Materials and methods

### Participants

Twenty-five healthy volunteers (11 female;  $M_{age} = 23.5$ ,  $SD = 2.9$ ) participated in the study after providing written informed consent. All participants were right-handed and reported no history of hearing, neurological, or psychiatric disorders. Data of two participants were discarded due to their inability to perform the gap detection task. Participants received financial compensation of 8 EUR per hour. The study was approved by the local ethics committee of the University of Oldenburg and conducted in accordance with the declaration of Helsinki.

### Stimuli

The stimulus duration was 3.67 s (11 cycles) in the short condition and 7.67 s (23 cycles) in the long condition (see Fig. 2A). Each stimulus consisted of a fade in (1 s, 3 cycles), an interval within the gaps occurred (1 s, 3 cycles), 2 cycles (667 ms) allowing the participants to respond (see “response break” Fig. 2A) and a fade out (1 s, 3 cycles). In the long condition an additional four second window (12 cycles) was inserted between fade in and gap interval, to have a longer entrainment period. The signal was faded in and out by using a 1 s Hanning ramp. This was done to avoid evoked brain responses to stimulus onset and offset.

The auditory stimuli were generated with Matlab 2012a (Mathworks Inc. Natick, MA) with a 96000 Hz sampling rate and presented binaurally over EAR-Tone 3A insert earphones (3 M Auditory Systems, Indianapolis, United States) at a comfortable listening level. Stimuli were complex tones that were frequency-modulated at a rate of 3 Hz and a modulation depth of 37.5%. We used three complex carrier signals with differing frequencies (800 Hz, 1000 Hz, and 1200 Hz) to ensure that gap detection performance was not dependent on the carrier frequency. The carrier signals were centred on one of the three frequencies and were comprised of 30 components sampled from a uniform distribution with a 500 Hz range. The onset phase of the stimulus was randomized over trials and could take one of eight values ( $0, \pi/4, \pi/2, 3\pi/4, \pi, 5\pi/4, 3\pi/2, 7\pi/4$ ). All stimuli were root-mean-square amplitude normalized.

In each stimulus, one gap between 10 and 20 ms (the exact gap duration was subject dependent, see section Staircase Procedure) was inserted using a 3 ms Hanning ramp at the onset and offset of the gap. In contrast to Henry and Obleser (2012) only one gap was inserted per trial and was done here to avoid potentially confounding effects of previous gap auditory and motor evoked responses. The gap was centred in 1 of 12 equally spaced phase bins on the 3 Hz frequency-modulated cycle (see Fig. 1; *Gap Locations*). Gaps were inserted after at least one second in the short condition and after five seconds in the long condition and evenly distributed over three cycles to reduce the predictability of gap occurrence within each stimulus.

The resulting stimulus pool consisted of 1728 distinct stimuli: 2 conditions x 12 phase bins x 3 cycles of gap occurrence x 8 onset phases x 3 carrier frequencies. Overall, participants listened to 720 stimuli, 360 stimuli each for the short and long condition. For each condition (short and long) and for each of the 12 phase bins, 30 gaps were presented (10 gaps per cycle in the designated gap time range). Onset phases and complex carrier signals were randomized within each participant on a trial-by-trial basis. Rayleigh  $z$  tests confirmed that onset phases for the three carrier frequencies were uniformly distributed across participants (800 Hz: Rayleigh  $z = 0.008$ ,  $P = 0.11$ ; 1000 Hz:  $z = 0.0006$ ,  $P = 0.86$ ; 1200 Hz:  $z = 0.001$ ,  $P = 0.70$ ).

### Procedure

Each session began with a staircase procedure to individualize the gap duration, and was followed by a practice block for the gap detection task before the main experiment was conducted. Participants were seated in a dimly lit and sound-shielded cabin, approximately 1.7 m in front of the

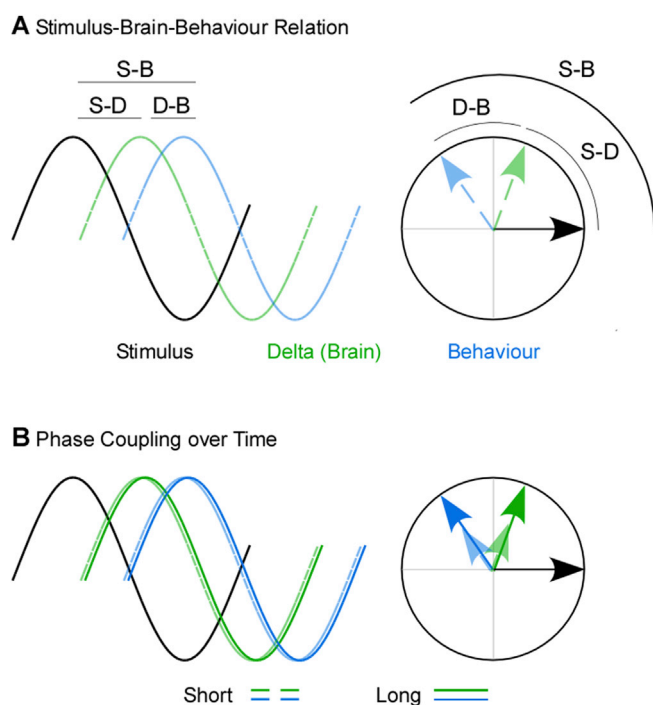


Fig. 1. A) Schematic representation of the stimulus-brain-behaviour relationship (cf. Henry and Obleser, 2012). B) Phase coupling hypothesis: longer stimulation yields a stronger phase coupling over time.

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