



Temporal expectations and neural amplitude fluctuations in auditory cortex interactively influence perception



Björn Herrmann^{a,*}, Molly J. Henry^a, Saskia Haegens^{b,c}, Jonas Obleser^{a,d}

^a Max Planck Research Group "Auditory Cognition", Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1A, 04103 Leipzig, Germany

^b Department of Psychiatry, Columbia University College of Physicians and Surgeons, New York, NY 10032, USA

^c Cognitive Neuroscience and Schizophrenia Program, Nathan S. Kline Institute, 140 Old Orangeburg Road, Orangeburg, NY 10962, USA

^d Department of Psychology, University of Lübeck, Ratzeburger Allee 160, 23562 Lübeck, Germany

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ABSTRACT

Alignment of neural oscillations with *temporally regular* input allows listeners to generate temporal expectations. However, it remains unclear how behavior is governed in the context of *temporal variability*: What role do temporal expectations play, and how do they interact with the strength of neural oscillatory activity? Here, human participants detected near-threshold targets in temporally variable acoustic sequences. Temporal expectation strength was estimated using an oscillator model and pre-target neural amplitudes in auditory cortex were extracted from magnetoencephalography signals. Temporal expectations modulated target-detection performance, however, only when neural delta-band amplitudes were large. Thus, slow neural oscillations act to gate influences of temporal expectation on perception. Furthermore, slow amplitude fluctuations governed linear and quadratic influences of auditory alpha-band activity on performance. By fusing a model of temporal expectation with neural oscillatory dynamics, the current findings show that human perception in temporally variable contexts relies on complex interactions between multiple neural frequency bands.

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Introduction

Low-frequency neural oscillations are periodic voltage or field variations of neural populations, and reflect fluctuations in neural excitability (Bishop, 1933; Kayser et al., 2015; Lakatos et al., 2005). Consistent with these cyclic excitability fluctuations, the probability of detecting near-threshold sensory events has been shown to depend on the neural phase into which an event falls (Busch et al., 2009; Busch and VanRullen, 2010; Hanslmayr et al., 2013; Henry and Obleser, 2012; Monto et al., 2008; Ng et al., 2012). For sensory input characterized by temporal regularity, low-frequency neural oscillations synchronize with the pattern of event onsets occurring over time through adjustments of the oscillation's phase and period (i.e., neural entrainment). Neural entrainment brings high-excitability phases into alignment with attended or high-energy portions of the input (Lakatos et al., 2008, 2013; Thut et al., 2011), and is thereby proposed to organize the phase-behavior relation (Henry et al., 2014; Neuling et al., 2012).

Variations in the strength of low-frequency neural oscillations (i.e., amplitude envelope fluctuations) relate to the overall strength of neural excitability fluctuations: High amplitudes correspond to more

drastic fluctuations in excitability than low amplitudes (Fig. 1, Jensen and Mazaheri, 2010). Furthermore, for measurements made at the scalp, neural amplitude is also a reflection of the number of neurons whose excitability fluctuations are temporally synchronized (Musall et al., 2014). In turn, the degree of synchrony among neuronal populations relates to the degree of neural entrainment and thus depends on the degree of temporal regularity in the environmental stimulus (Schroeder and Lakatos, 2009b; Thut et al., 2011).

Temporal regularity in the sensory input gives rise to temporal expectations, meaning that the time of occurrence of an upcoming sensory event can be expected. Conceptually, a sequence's temporal regularity is linked to temporal expectations via oscillatory dynamics (Arnal and Giraud, 2012; Henry and Herrmann, 2014; Schroeder and Lakatos, 2009b). That is, a listener needs an internal model on the basis of which external events can be judged as temporally (un)expected (Jones and Boltz, 1989; McAuley and Jones, 2003). This internal model can be conceptualized as a simple oscillator capable of synchronizing with a stimulus sequence (Canavier, 2015; Large and Jones, 1999). Specifically, the phase of an oscillation synchronized with the external event structure quantifies the timing of an expected event, that is, a temporal expectation (Henry and Herrmann, 2014). In turn, when a stimulus event fails to coincide with the expected event onset, the temporal expectation is violated. Phase can be estimated from measured neural oscillatory activity (Henry et al., 2014; Schroeder and Lakatos, 2009b), which

* Corresponding author at: Brain and Mind Institute, University of Western Ontario, London, Ontario N6A 5B7, Canada.

E-mail address: herrmann.b@gmail.com (B. Herrmann).

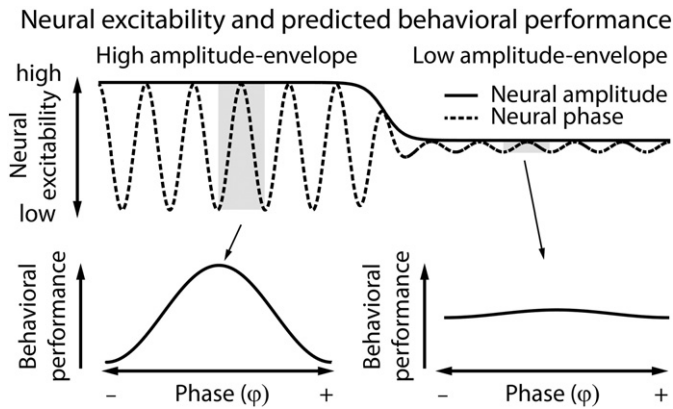


Fig. 1. Neural excitability and predicted behavior. Schematic display of neural excitability fluctuations, the corresponding amplitude envelope changes, and predicted perceptual performance for high and low neural amplitudes as a function of phase/temporal expectation (which was estimated from the oscillator model exemplified in Fig. 2).

emphasizes the relation to neural excitability. However, phase can also be estimated from the external event structure using a mathematical oscillator model (Large and Jones, 1999; McAuley and Jones, 2003), which emphasizes the relation to temporal expectations, and avoids the possibility of poor neural phase estimation for low neural amplitude values (Muthukumaraswamy and Singh, 2011). That is, modeled phase and neural amplitude are estimated independently.

Previous studies investigating the effects of temporal expectations on neural and behavioral responses have reported enhanced perceptual performance in temporally regular compared to irregular stimulation sequences (Cravo et al., 2013; Lange, 2009; Lawrance et al., 2014; Rohenkohl et al., 2012). However, single events in temporally irregular sequences can still be temporally expected to varying degrees based on the local temporal structure (Jones and Yee, 1997). Furthermore, temporal expectations might also be important for perception of natural stimuli such as speech or music (Giraud and Poeppel, 2012; Peelle and Davis, 2013). However, speech and music are not strictly periodic and thus continuously modulate (1) the degree to which low-frequency oscillations are entrained, (2) the strength with which neural excitability fluctuates, and (3) the extent to which temporal expectations can be generated.

In the current magnetoencephalography (MEG) study, we used temporally variable tone sequences to investigate four thus far unanswered questions: (1) Is perceptual performance affected by temporal expectations in stimulus sequences with temporal variation? (2) Do performance effects stemming from variations in the strength of temporal expectations depend on low-frequency neural amplitude (i.e., strength of excitability fluctuations and/or synchrony of neural populations)? (3) Previous studies also reported that amplitude fluctuations, for example, in alpha and beta frequency bands affect perception in temporal context (Arnal et al., 2015; Fujioka et al., 2012; Rohenkohl and Nobre, 2011; Saleh et al., 2010). Thus, we asked: Does perceptual performance in temporally variable tone sequences also depend on neural amplitude variations in non-entrained frequency bands? (4) Finally, recent work has shown complex effects of cross-frequency relations on perceptual performance for phase–phase interactions (Fiebelkorn et al., 2013; Henry et al., 2014) and phase–amplitude coupling (Arnal et al., 2015; Friese et al., 2013). Here we focused on neural amplitude, and asked: Do neural amplitude fluctuations in multiple frequency bands jointly influence performance?

The data revealed a joint influence of temporal expectations and low-frequency neural amplitude variations as well as interactive influences of neural amplitudes in multiple frequency bands on perceptual performance.

Methods and materials

Participants

Twenty adult humans participated in the current MEG study (mean age: 26.2 years, SD: 2.9 years; 10 females). Participants were native speakers of German and were financially compensated for their participation (7 Euros per hour). They did not report any neurological diseases or any hearing problems, and gave written informed consent prior to the experiment. The study was in accordance with the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

Acoustic stimulation and procedure

During the MEG recording, participants were presented with tone sequences containing intensity deviants (target tones; Fig. 2). Non-target tones in the experiment were presented at 50 dB above the individual hearing threshold (i.e., sensation level), which was determined prior to the MEG experiment using the method of limits. Sound intensity of target tones was slightly louder and titrated individually for each participant prior to the experiment to yield on average 65% detection rate (mean target-to-non-target intensity difference: $+2.44 \text{ dB} \pm 0.29 \text{ SD}$; titration was done using similar tone sequences as for the MEG experiment). Note that in the current design, 65% detection rate is far above chance level due to the continuous nature of the sequence.

Tone sequences consisted of 25 1000-Hz sine tones, each 100 ms in duration (5 ms linear rise and fall times). Each sequence contained 2, 3, or 4 target tones at random locations within a sequence and participants were instructed to press a button when they heard a tone that was louder than the others. Responses were considered hits when they occurred within 0.2–1.2 s after target onset. Randomization of target occurrence was constrained such that the first three and the last two tones could never be a target. Furthermore, there were at least three non-target tones between two consecutive targets.

Stimulation frequency was on average 2 Hz ($\pm 0.14 \text{ Hz SD}$), while the exact onset-to-onset intervals were randomly jittered. That is, within each sequence, tones occurred on average every 500 ms, but

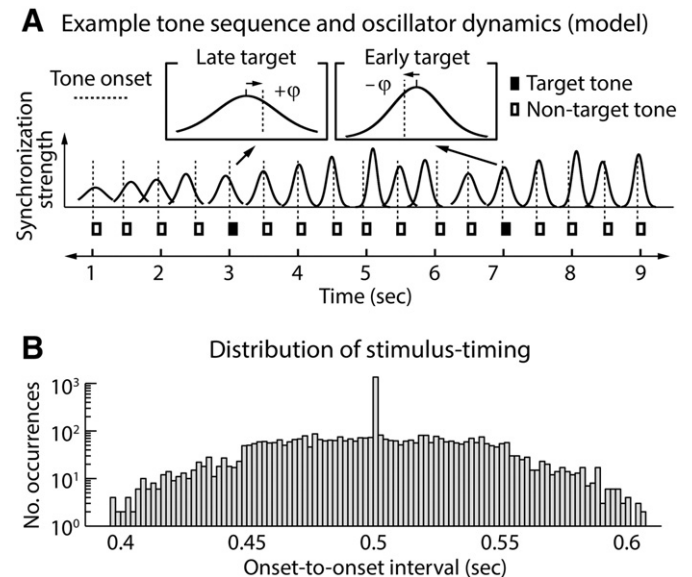


Fig. 2. Experimental stimulation. (A) An example segment of a tone sequence and modeled oscillator dynamics (Large and Jones, 1999). The distance between the peak of the modeled oscillation and the target onset indicates the degree to which a target is temporally expected and is referred to as relative phase (ϕ). Synchronization strength reflects the degree to which the oscillator is entrained by the stimulation. (B) Distribution of onset-to-onset intervals presented to one participant.

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