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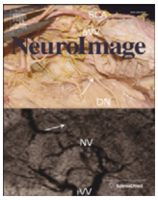

The strength of alpha and beta oscillations parametrically scale with the strength of an illusory auditory percept

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ABSTRACT

Studies investigating the role of oscillatory activity in sensory perception are primarily conducted in the visual domain, while the contribution of oscillatory activity to auditory perception is heavily understudied. The objective of the present study was to investigate macroscopic (EEG) oscillatory brain response patterns that contribute to an auditory (Zwicker tone, ZT) illusion. Three different analysis approaches were chosen: 1) a parametric variation of the ZT illusion intensity via three different notch widths of the ZT-inducing noise; 2) contrasts of high-versus-low-intensity ZT illusion trials, excluding physical stimuli differences; 3) a representational similarity analysis to relate source activity patterns to loudness ratings. Depending on the analysis approach, levels of alpha to beta activity (10–20 Hz) reflected illusion intensity, mainly defined by reduced power levels co-occurring with stronger percepts. Consistent across all analysis approaches, source level analysis implicated auditory cortices as main generators, providing evidence that the activity level in the alpha and beta range – at least in part – contributes to the strength of the illusory auditory percept. This study corroborates the notion that alpha to beta activity in the auditory cortex is linked to functionally similar states, as has been proposed for visual, somatosensory and motor regions. Furthermore, our study provides certain theoretical implications for pathological auditory conscious perception (tinnitus).

Introduction

Different features of brain oscillations make them a prime candidate in regulating sensory perception, such as their proposed outstanding role in mediating neural communication (Buzsáki and Draguhn, 2004; Fries et al., 2001, 2002; Makeig et al., 2002). Furthermore, especially alpha and beta oscillations have been related to rather global cortical excitability states (Jensen and Mazaheri, 2010; Klimesch et al., 2007; Makeig et al., 2002; Pfurtscheller, 2001; Weisz et al., 2011). Studies in the working memory and spatial attention domain imply an alpha increase in task-*irrelevant* brain regions and vice versa for the regions relevant to the task at hand (Sauseng et al., 2009; Thut et al., 2006; Van Der Werf et al., 2008; van Gerven and Jensen, 2009), suggesting that high levels of alpha reflect inhibitory states (Jensen and Mazaheri, 2010).

In essentially all sensory modalities, alpha-to-beta oscillations decrease upon appropriate stimulation (Canolty et al., 2007; Edwards et al., 2009; Gaillard et al., 2009; Siegel et al., 2008; Wyart and Tallon-Baudry, 2009). More importantly, in particular in the visual modality, reduced alpha power has been shown to predispose conscious reports of, for example, near threshold stimuli (Haegens et al., 2011; Hanslmayr et al., 2007; Romei et al., 2008b; van Dijk et al., 2008). There is evidence that beta activity might serve functional inhibition in a similar way (Jensen and Mazaheri, 2010; Müller et al., 2013). Especially with respect to the sensorimotor cortex, several studies have reported beta activity to reflect inhibitory cortical states (Hari and Salmelin, 1997; Jensen et al., 2005; Miller et al., 2010; Schulz et al.,in press). A study by our group also points in this direction, revealing reduced power in the alpha up to the beta range to co-occur with a stronger continuation of hearing music during periods of noise (Müller et al., 2013). To summarize, while some studies (Müller and Weisz, 2012; van Dijk et al., 2010; Weisz et al., 2013) suggest functionally similar roles of alpha-to-beta activity in the auditory modality, the

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role of these oscillations in mediating auditory perception has generally remained under-investigated (Weisz et al., 2011).

The main goal of this study was to investigate whether reduced alpha-to-beta band power is associated with the strength of auditory perception. Some tentative evidence supporting this notion comes from studies on tinnitus (Weisz et al., 2011). Reduced alpha-band power co-occurs with tinnitus and a respective reduction of symptoms can be achieved by increasing alpha power, for instance via neurofeedback (Hartmann et al., 2011; Müller et al., 2013; Weisz et al., 2005, 2007b, 2011). In order to test the relationship between auditory alpha and perception in a more controlled manner, we used the Zwicker tone (ZT) paradigm to induce an auditory illusion (Zwicker, 1964). The ZT illusion can be described as a brief auditory “afterimage” that occurs *following* the presentation of notched filtered white noise.

Studies investigating the possible underlying neural processes giving rise to the ZT illusion (Franosch et al., 2003; Hoke et al., 1996, 1998; Norena et al., 2000) have focused on the attempt to explain cortical mechanisms of the tinnitus pathology. Within this effort, however, none of these works have focused on the role of oscillatory activity. Interestingly, some studies have found evidence for the assumption that the ZT illusion might be caused by relatively reduced lateral inhibition in auditory cortex regions responding to the frequency range surrounding the notch (Franosch et al., 2003; Hoke et al., 1998; Norena et al., 2000). Consequently, the corresponding neurons within the notch will have a higher spontaneous firing rate relative to their neighbors. We hypothesize – in accordance with the notion that auditory cortical alpha/beta activity may play a similar inhibitory role, as reported for other modalities (Weisz et al., 2011) – that a strong ZT illusion (i.e., reduced inhibition) will be paralleled by decreased power in this frequency range as compared to occasions of weak a ZT. In order to obtain multiple lines of evidence, we explored (a) parametric variations of the strength of the illusion via modulation of the notch width (Franosch et al., 2003), (b) fluctuations in illusion strength within a physically identical category and (c) a representational similarity analysis (Connolly et al., 2012; Kriegeskorte et al., 2008) to investigate neural and behavioral similarity patterns.

Materials and methods

Participants

Twelve of the thirteen participants (3 males, 9 females, mean age 24 years) were included in the final analysis. Data from one participant were discarded due to excessive noise in the EEG signal. All participants were right-handed and of normal hearing, as assessed by an Interacoustics AC40 clinical audiometer (Audiometrics, Shreveport, LA). Participants were informed about the experimental procedure and signed a consent form. Following the experimental session, they were paid for their participation. Experimental procedures were approved by the Institutional Review Board of the University of Konstanz.

Stimuli

The fixation cross and rating scale were presented on a computer screen (HANNSG size: diagonal 28 in.). Notched noise stimuli were binaurally presented through stereo headphones (Sennheiser HD pro 180) to induce the ZT illusion. In order to manipulate the loudness of tone illusion in a parametric way, three different notch widths were chosen: .4, .6 and .8 octaves, or, alternatively (in five participants), .6, .8 and 1 octaves wide according to individual ZT detection curves (see below). Because individual notch widths varied across participants, these three different conditions are for practical reasons here referred to as small, intermediate and large notch widths.

Participants were invited twice (or, in four cases, three times) to separate training sessions and the subsequent main experiment. Training was conducted in order to individually determine the optimal ZT notch center frequencies and notch width. These training sessions were divided into three parts: first, different notch center frequencies (1000 Hz, 1412 Hz, 2000 Hz, 2828 Hz, 4000 HZ, 5657 Hz) were randomly presented (notch width: 1 octave) as a series of repetitive noises of one second (ten trials) with 500-millisecond gaps and a duration of five seconds (ten trials), with gaps of two seconds. Notched noise was followed by a white noise control trial and participants had to press a button to indicate if they had perceived a tone illusion solely following notched noise. In the second training session, the best notch center frequency was determined by a two-alternative-forced-choice (2AFC) procedure presenting pairs of different notch center frequencies (duration of 5 s, gap of 2 s). Subjects had to indicate the stronger tone illusion by pressing a button (ten trials per notch center frequency/block).

In the third training session, individual notch widths were chosen according to the individual ZT detection curves of the participants. Eleven different notch widths ranging from 0 to 2 octaves (0, .2, .4, .6, .8, 1, 1.2, 1.4, 1.6, 1.8, 2) were presented (12 trials per notch width) at best notch center frequency (duration 2 s, 500 ms gap). Participants had to indicate whether they had perceived a ZT illusion by pressing a button. In the end, three notch widths elucidating weak, intermediate and strong ZT illusions were selected according to individual detection curves.

Following training, the main experiment was conducted on a separate date, incorporating the individualized stimuli of three notch band widths.

Experimental design and procedure

The manipulation of perceived ZT loudness was realized in a one-factorial design with four factor levels, consisting of three notched noise conditions and an additional behavioral control condition (pure white noise). Acoustic stimuli were simultaneously presented through headphones to both ears (see Stimuli section).

With respect to the main experiment, each notch width condition consisted of 150 trials, with an additional behavioral control condition consisting of 50 trials of pure white noise. Before the experiment started, practice trials with notched noise were presented to participants in order to give examples for each loudness condition.

The order of presentation of the trials was randomized across the experimental session for all conditions. Breaks were introduced every 100 trials, accompanied by short pieces of music played to the subject for relaxation. The beginning of a trial was marked by a black fixation cross that appeared at the center of a white screen, lasting for 1000 ms and representing the inter-trial interval (ITI). The presentation of the noise stimulus (either notched noise or white noise) followed, with a duration of 2000 ms (see Fig. 1A). The fixation cross remained on screen during noise presentation. After the end of noise presentation, the cross remained on screen for another 500 ms. During this time period, participants were able to perceive the ZT illusion. Afterwards, participants were prompted by a question mark that appeared on screen to rate the perceived loudness of the tone illusion from 1 (no tone perceived) to 7 (loudest tone perception) by pressing a button with their right hand. Following the response, the black fixation cross reappeared, marking the next 1000 ms-long inter-trial interval (ITI).

Data acquisition

For the delivery of auditory and visual stimuli, the recording of stimulus marker and responses, the software Presentation (http://www.neurobehaviouralsystems.com) was used. EEG recording was conducted using a 128-electrode cap connected to the ANT acquisition system (Advanced Neuro Technology, ANT, Enschede, Netherlands) digitizing the signal at 2048 Hz. The experiment was conducted in a shielded room. Participants were instructed to sit in a comfortable position.