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Inter- and intra-individual variability in alpha peak frequency

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ABSTRACT

Converging electrophysiological evidence suggests that the alpha rhythm plays an important and active role in cognitive processing. Here, we systematically studied variability in posterior alpha peak frequency both between and within subjects. We recorded brain activity using MEG in 51 healthy human subjects under three experimental conditions — rest, passive visual stimulation and an N-back working memory paradigm, using source reconstruction methods to separate alpha activity from parietal and occipital sources. We asked how alpha peak frequency differed within subjects across cognitive conditions and regions of interest, and looked at the distribution of alpha peak frequency between subjects. In both regions we observed an increase of alpha peak frequency from resting state and passive visual stimulation conditions to the N-back paradigm, with a significantly higher alpha peak frequency in the 2-back compared to the 0-back condition. There was a trend for a greater increase in alpha peak frequency during the N-back task in the occipital vs. parietal cortex. The average alpha peak frequency across all subjects, conditions, and regions of interest was 10.3 Hz with a within-subject SD of 0.9 Hz and a between-subject SD of 2.8 Hz. We also measured beta peak frequencies, and except in the parietal cortex during rest, found no indication of a strictly harmonic relationship with alpha peak frequencies. We conclude that alpha peak frequency in posterior regions increases with increasing cognitive demands, and that the alpha rhythm operates across a wider frequency range than the 8–12 Hz band many studies tend to include in their analysis. Thus, using a fixed and limited alpha frequency band might bias results against certain subjects and conditions.

Introduction

The prominent posterior alpha rhythm was first recorded by Hans Berger (1929) and long considered to reflect cortical idling (Adrian and Matthews, 1934; Pfurtscheller et al., 1996). More recently, converging electrophysiological evidence suggests that the alpha rhythm actually plays an important and active role in cognitive processing (Cooper et al., 2003; Jensen and Mazaheri, 2010; Klimesch et al., 2007). In particular, alpha oscillations are proposed to reflect a mechanism of functional inhibition (Foxe and Snyder, 2011; Jensen et al., 2012; Mathewson et al., 2011), regulating the engagement and disengagement of sensory areas depending on task demands.

In support of this idea, several studies have shown that alpha oscillations reflect the focus of attention, both in the visual (Gould et al., 2011; Thut et al., 2006; Worden et al., 2000) and the somatosensory system (Anderson and Ding, 2011; Haegens et al., 2011a; Jones et al., 2010), with consequences for subsequent perceptual performance. Furthermore, alpha activity has been shown to increase with load during working memory (WM) maintenance, presumably in order to facilitate WM retention by preventing interfering inputs (Jensen et al., 2002; Sauseng et al., 2009; Tuladhar et al., 2007).

Alpha peak frequency is known to change with age, increasing up to adulthood and then decreasing with older age (Aurlien et al., 2004; Lindsley, 1939). Inter-subject variability in alpha frequency is to a large degree explained by genetic factors (e.g., Bodenmann et al., 2009), with twin studies showing heritability estimates of about 80% (Smit et al., 2006; Van Beijsterveldt and Van Baal, 2002). Inter-subject differences in alpha peak frequency have been linked to various cognitive measures, including WM performance (reviewed in Klimesch, 1999). Additionally, intra-subject variability in alpha peak frequency has been described, which may reflect different alpha networks kicking in dependent on task demands (Başar, 2012; Klimesch, 1999).

Thus, alpha frequency can be seen both as a 'trait' variable, with inter-subject variability potentially explaining differences in overall cognitive performance, as well as a 'state' variable, with intra-subject variability possibly reflecting fluctuations in moment-to-moment

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performance. Knowing the range within which the posterior alpha rhythm operates, both between and within subjects, will be crucial in order to interpret results from studies that try to explain performance differences in terms of alpha activity modulations.

However, most studies define the alpha rhythm as a fixed narrow band (most commonly 8–12 Hz), and average over spectral activity within that fixed band for all subjects. It has been argued that using the individual alpha frequency (IAF), determined per subject (defined in terms of either peak or 'gravity' frequency), gives a more accurate estimate of alpha modulated activity (Doppelmayr et al., 1998; Klimesch, 1999; although see Smit et al., 2005; Shackman et al., 2010). The reasoning is that because of substantial inter-individual variability in alpha frequency (a mean SD of 1 Hz is reported, cf. Klimesch, 1997), significant portions of alpha power will fall outside a fixed frequency window, and/or activity from neighboring frequencies (i.e., theta or beta) might erroneously be included in the fixed alpha window. Along these same lines, it was suggested that the alpha frequency range should be further subdivided into low- and high-alpha subranges, which may behave differently under certain task conditions (Klimesch et al., 1996, 1998). While adopted by a substantial part of the field, this approach is by no means common practice. Given the emergence of more sensitive analyses of especially alpha phase (e.g., cross-frequency coupling mechanisms, phasic modulation of stimulus processing), optimized individual peak frequency detection might become essential.

Here, we systematically studied how posterior alpha peak frequency varies both between and within subjects. We aimed to establish whether individual alpha peak variability indeed goes beyond the often-used 8–12 Hz fixed band. We recorded brain activity using MEG in 51 healthy human subjects under three experimental conditions — rest, passive visual stimulation and an N-back WM paradigm. Using MEG in combination with source reconstruction methods allowed us to separate alpha activity from parietal and occipital sources, which to the best of our knowledge has not been done before in this context. We asked how alpha peak frequency differed within subjects across cognitive conditions and regions of interest, and looked at the distribution of alpha peak frequency across this relatively large set of subjects. Furthermore, we explored the relation between individual alpha and beta peak frequencies, as a harmonic relationship between the two has been suggested (Carlqvist et al., 2005; Gaarder and Speck, 1967; Klimesch, 2012).

Methods

Participants

Fifty-one healthy right-handed volunteers (27 female, 24 male; mean age 24.2 years; range 19–34) with normal or corrected-to-normal vision participated in this experiment. Ethical approval was obtained from the NHS South Central Berkshire ethics committee (11/SC/0053). Each subject participated in three experimental blocks that were recorded successively: (1) resting state, (2) N-back, (3) visual gratings.

Paradigm

Resting state: 6 min of resting state was recorded while subjects kept their eyes open and fixated on a fixation cross.

Visual gratings (Fig. 1A): stimuli consisting of vertical, stationary, maximum-contrast, 3-cycles-per-degree gratings were presented on a mean luminance background. Ninety stimuli were presented in either the left or right lower visual field. Participants were instructed to maintain fixation on a dot in the middle of the screen for the duration of the experiment. Stimuli were presented for 2 s followed by 2 s of fixation in blocks of five, with each block of five followed by 20-s fixation during which the subjects were allowed to blink.

N-back (Fig. 1B): the N-back paradigm consisted of a 0-back and a 2-back task, seven blocks each, presented in alternating fashion,

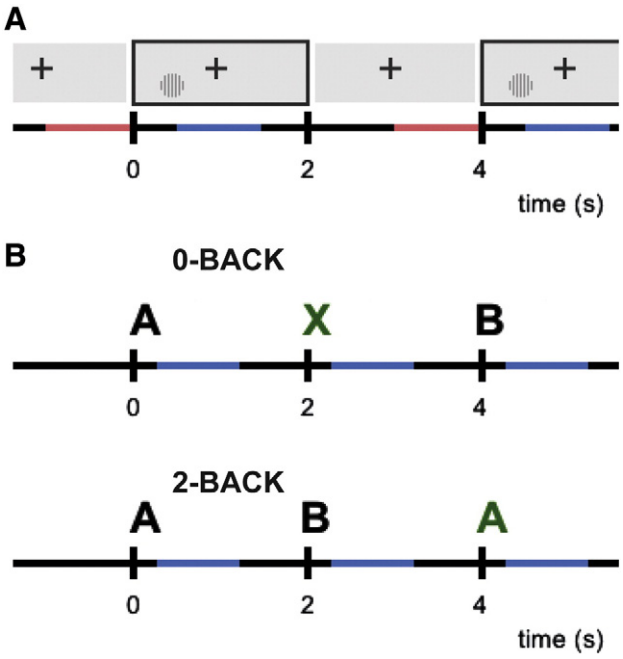

Fig. 1. Experimental paradigm. (A) Visual condition: stimuli consisting of vertical, stationary gratings were presented in either the left or right lower visual field, while participants maintained central fixation. Stimuli were presented for 2 s followed by a 2-s baseline window. Analysis windows (1 s length) are indicated in blue for stimulation and in red for baseline. (B) N-back task: stimuli consisting of letters were presented for 200 ms at 2-s SOA. In the 0-back task (upper panel) the subject had to respond to the letter X. In the 2-back task the subject had to respond if the letter was the same as that of two stimuli back. (Targets are presented in green here for illustrative purposes only.) Analysis windows (1 s length) are indicated in blue on the time axis.

followed by 15-s breaks. Each block consisted of presentation of 15 letters with 200-ms stimulus duration and 2-s SOA, i.e., 1.8-s WM retention/decision period. Each block contained 2–4 targets. In the 0-back task, subjects had to respond by button press to the letter X, while on the 2-back task subjects had to respond when the stimulus was the same as the one two stimuli back.

Data acquisition

Whole-head MEG recordings were acquired at a sampling frequency of 1000 Hz, using an Elekta NeuroMag MEG System. Data from the 204 gradiometers were analyzed. A magnetic digitizer (Polhemus FastTrach 3D) was used to measure the relative positions of four head-position indicator coils and three anatomical landmarks (nasion, left and right auricular points). These coordinates were used for co-registration of the sensor montage to the participant's anatomical magnetic resonance image (MRI), which was acquired using a 3 T Siemens system.

Data analysis

The data were analyzed using custom-build Matlab code, the FieldTrip toolbox for EEG/MEG-analysis (Oostenveld et al., 2011; http://www.ru.nl/neuroimaging/fieldtrip/) and SPM8 (http://www.fil.ion.ucl.ac.uk/spm). The data were down-sampled offline to a sampling frequency of 500 Hz, after applying a 0.5 Hz high-pass filter and a 200 Hz low-pass filter. Bad channels and trials were rejected upon visual inspection. We used independent component analysis (Jung et al., 2000) to identify eye artifacts, which were then projected out of the data.

First, we studied the main effects in each condition by computing sensor level power spectra and whole brain source reconstructions, focusing on alpha activity within the band of 7–14 Hz. Second, we