Timing of beta oscillatory synchronization and temporal prediction of upcoming stimuli

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ABSTRACT

Modulations of beta oscillatory power serve a predictive role, in preparation of future actions. It is well known that beta amplitude decreases prior to voluntary movements and expected tactile stimuli. Paradoxically, recent studies have reported a beta amplitude increase prior to expected visual and auditory stimuli. Moreover, it has been suggested that, in isochronic stimulus series, the rising beta slope is adjusted to the duration of the interstimulus interval. We investigated the characteristics of such timing related pre-stimulus beta power increases using visual stimulus sequences that were presented at three regular rates (0.61, 0.74 and 0.95 Hz). EEG was recorded from twenty participants while they attended the sequences by performing a clock reading task. Time-frequency analyses showed a consistent pattern of beta modulation: the post-stimulus beta power decrease was followed by a steep increase. Contrary to recent views, we found that the peaks of beta power, for the three presentation rates, were reached at a similar latency post-stimulus, instead of a fixed interval preceding the next stimulus. This demonstrates that, at interstimulus intervals between 1–2 s, beta synchronization slopes are not modulated by timing mechanisms related to prediction of upcoming stimuli. We reconcile the discrepant results by proposing that when shorter interval durations are used, as in previous studies, beta resynchronization is interrupted by the presentation of a new stimulus, making it seem as if beta power peaks prior to upcoming stimuli. We emphasize caution with respect to the notion that the timing of beta synchronization is an expression of predictive timing.

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Introduction

Temporal preparation is fundamental to the planning of movement and the allocation of attention towards relevant sensory input, and consequently leads to behavioral benefits such as faster reaction times, increased movement accuracy and improved perception. The contingent negative variation (CNV) is a neurophysiological signature of temporal preparation that has been known for a long time (Walter et al., 1964). This slow cortical potential of negative polarity builds up over central cortical areas and peaks just before voluntary movements and immediately prior to the expected presentation of a temporally predictable stimulus (Praamstra et al., 2006; Breska and Deouell, 2014).

Similar to the climbing slope of the CNV, oscillatory beta-band (13–30 Hz) power over motor cortical areas gradually decreases prior to voluntary movements and the magnitude of this power reduction (event-related desynchronization; ERD) correlates with the CNV amplitude (Bickel et al., 2012). Likewise, a sensorimotor beta power decrease precedes attended sensory stimuli that are presented at a predictable point in time, even when no immediate motor-response is required (Van Ede et al., 2010, 2011; Bidet-Caulet et al., 2012). It thus appears that sensorimotor beta ERD is another neurophysiological signature of temporally specific neural and behavioral preparation.

Paradoxically, several recent studies have reported a gradual increase of sensorimotor beta power prior to expected external stimuli (Saleh et al., 2010; Fujioka et al., 2012, 2015; Zaepffel et al., 2013). Additionally, there have been various reports of a task-performance benefit for high versus low pre-stimulus beta power in prefrontal and parietal areas (Linkenkaer-Hansen et al., 2004; Donner et al., 2007; Zhang et al., 2008; Kaminski et al., 2012). In recent literature, the pre-stimulus beta power increase (event-related synchronization; ERS) has received growing attention and acquired apparent recognition as another signature of neural preparation for expected sensory input (Arnal, 2012; Arnal and Giraud, 2012; Gulberti et al. 2015; Kilavik et al., 2013; Patel and Iversen, 2014; Teki, 2014; Merchant et al., 2015).

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However, actual evidence that the pre-stimulus beta ERS is temporally tuned to upcoming stimuli is limited. The strongest evidence comes from a magnetoencephalography study by Fujioka et al. (2012), who presented participants with auditory tone sequences at three different regular rates, while participants watched a silent movie. The researchers showed that after an initial post-stimulus beta ERD, the subsequent beta ERS adjusted to the interval duration such that the beta amplitude reached its maximum just before the occurrence of the next sound, at all three rates. Given this limited evidence base, many questions remain unanswered, e.g. concerning modality specificity, the range of intervals and effects of attention.

In the present study, we investigate the temporal specificity of the pre-stimulus beta ERS with visual stimuli that are presented at three regular rates. Noteworthy, we use longer inter-stimulus intervals than previous studies on pre-stimulus beta ERS. By means of a delayed response paradigm we ensure that beta oscillatory effects associated with temporal attention are not contaminated by movement-related beta power decreases (Kilavik et al., 2013). The results reveal that the time-course of the beta power increase is, at the stimulation rates that we used, not modified by implicitly induced anticipatory timing. The results thus question the generality of previous claims that the timing of beta oscillatory synchronization reflects temporal anticipation.

Materials and methods

Participants

Initially, ten healthy participants of late middle age (age 55–66 years; 4 females; 1 left-handed) were included in the study. When the beta-ERS results in this group did not display temporal anticipation effects, we additionally recruited ten healthy, younger participants (age 19–29 years; 4 females; 2 left-handed). We will report the grand-average results of all twenty subjects, unless mentioned otherwise. None of the participants reported any past or present neurological problems. All participants received financial compensation and provided written informed consent according to local institutional guidelines (Committee on Research Involving Human Subjects, region Arnhem–Nijmegen, The Netherlands).

Experiment setup

Fig. 1 gives a schematic representation of the task. The task has some resemblance with the spatial association task used by Saleh et al. (2010), which has shown to elicit robust pre-stimulus beta ERS. Participants were seated at 1 m distance from a screen with a gray clock image (4.5° visual angle) on a black background. At a fixed presentation rate, clock hands and centrally displayed numbers appeared simultaneously for a duration of 150 ms. Stimuli were presented in series consisting of thirteen consecutive stimuli, preceded by three warning cues. The three warning cues served to prime participants to the regular rhythm of stimulus presentation and these three visual cues were accompanied by simultaneous auditory tones in order to help induce a sense of rhythm (Grahn et al., 2011). Within one series, the onset to onset stimulus interval (stimulus-onset asynchrony; SOA) had a fixed duration of either 1050, 1350 or 1650 ms.

The first clock stimulus in each series always displayed a matching ('congruent') number and clock hand, and was not analyzed. The other twelve clock stimuli contained the twelve different clock-hands in randomized order, such that each hand (direction) appeared once. At random places the corresponding numbers in the center were changed to form incongruent stimuli. The number of incongruent stimuli per series varied between zero and seven, but did not exceed four in 90% of the series. Participants had to count the number of times that the center digit did not correspond with the direction of the clock hand (the 'incongruent' stimuli). At the end of each series, participants verbally reported their count, which the experimenter entered into
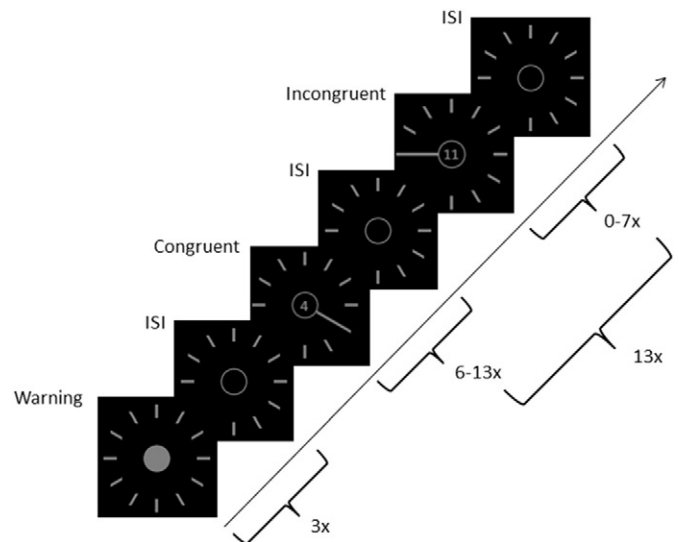

Fig. 1. Schematic representation of a stimulus sequence. Stimuli of 150 ms duration (warning, congruent or incongruent) were followed by a fixed interstimulus interval (ISI). Depending on the presentation block the ISI was 1500, 1200 or 900 ms). Blank clock images remained on screen during the intervals. Three warning cues preceded thirteen clock stimuli. One sequence contained up to seven randomly placed incongruent stimuli, in which the centrally displayed number did not match the clock hand. The remaining clock stimuli were congruent. Participants' task was to count the number of incongruent clock stimuli in the sequence.

the computer. A correct score was shown to the participants as visual feedback on the computer screen, so as to encourage their performance.

Ten series of the same interval duration were grouped to form one block. There were nine blocks in total, i.e. three blocks per SOA. The blocks were presented in a fixed order of the respective SOAs: 1650, 1350, 1050, 1350, 1050, 1650, 1050, 1650 and 1350 ms. In between every two blocks participants had a break for as long as they needed. Total duration of the experiment was approximately 1 h (excluding preparations). For the presentation of the stimuli we used the Psychophysics Toolbox (Brainard, 1997) for Matlab (Mathworks, Nantucket, Massachusetts, USA).

EEG recording and data preprocessing

The electroencephalogram (EEG) was recorded continuously with a 128 channel Biosemi ActiveTwo system and Ag/AgCl-electrodes that were placed according to the 10–5 electrode system (Oostenveld and Praamstra, 2001) using a nylon cap. Two additional electrodes were placed at the left and right mastoid. EEG signals were amplified, filtered with an anti-aliasing filter and digitally sampled at 512 Hz. Offline data processing was performed using the FieldTrip Toolbox (Oostenveld et al., 2011).

The continuous signals were segmented into epochs containing one entire series (twelve consecutive stimuli and subsequent intervals). An additional 500 ms at the beginning and end of each series prevented filter (ringing) artifacts. Only series that were answered correctly by the participants were analyzed.

The 128 channels were initially referenced to an averaged left and right mastoid reference. Line noise was reduced using a discrete Fourier transform filter at 50, 100 and 150 Hz. Slow drift within the series was removed with a 1 Hz high-pass filter. Channels with excessive noise were visually identified and rejected (they were interpolated at a later processing stage). In no subject did we reject more than ten channels. Parts of series were annotated (for later removal) and replaced by zeros of the same length if they contained transient, high amplitude artifacts over multiple channels (i.e. caused by swallowing or coughing, but eye-blinks were exempted). Electrode-pop artifacts (Barlow, 1986) were automatically detected by tracking sudden amplitude changes in