



Rhythmic entrainment of slow brain activity preceding leg movements



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ARTICLE INFO

Article history:

Accepted 26 April 2014

Available online 24 May 2014

Keywords:

Beta-oscillations

Contingent negative variation (CNV)

Movement cueing

Timing

Motor preparation

HIGHLIGHTS

- Slow brain potentials and beta-oscillatory power entrain to the rhythm of a task, demonstrating temporal preparation.
- We show here that this is not only the case for upper limb movements, but also for the lower limbs.
- Neurophysiological correlates of leg entrainment are relevant to cueing of gait in Parkinson disease.

ABSTRACT

Objective: The time course of the contingent negative variation (CNV) as well as beta-power are known to entrain to regular task rhythms, revealing implicit anticipatory timing. Thus far, these effects have been established for manual responses only. Here we investigate entrainment preceding leg movements.

Methods: High-density EEG was recorded while participants were standing and responded to series of rhythmically presented arrow stimuli by making brisk leg movements. The standard interval between reaction stimuli differed between series and was either 1500 or 2000 ms. Each series' final interval was 1750 ms, representing a timing perturbation.

Results: Entrainment was manifested in the CNV time course, where the maximum amplitude was reached just before the next stimulus was presented. The pattern of beta-(de)synchronization similarly entrained to the task rhythm. CNV scalp topographies suggested effector dependency of the entrainment-induced CNV.

Conclusion: We demonstrate that lower limb motor control, like upper limb control, readily entrains to a regular task rhythm.

Significance: These findings are relevant to Parkinson's disease (PD), where problems are found in rhythm processing and temporal preparation. Investigation of the neural correlates of leg movement entrainment is important in view of presumed relations between entrainment and cueing of gait in PD.

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1. Introduction

Humans easily adapt to rhythmical patterns in the environment, and use temporal information to predict and prepare for events that are about to occur. In experimental settings, adaptation to the temporal characteristics of a task can be shown at the behavioral (Bertelson and Boons, 1960; Rohenkohl et al., 2012; Rolke and Hofmann, 2007), as well as the neural level

(Nobre et al., 2007; Trillenberg et al., 2000) and involves preparation of the motor system (Müller-Gethmann et al., 2003). Timing is often investigated with tasks that require explicit tracking of time, like comparing interval durations relative to a standard (Macar and Vidal, 2003; Pfeuty et al., 2003, 2005). In such experiments, the time course of the contingent negative variation (CNV, Walter et al., 1964) reveals information on the comparison process of test and standard intervals. In explicit timing tasks, the CNV is therefore thought to reflect a memory trace of the remembered interval (Macar and Vidal, 2003).

Implicit timing, i.e. automatic adaptation to the temporal structure of a task, is supported by similar neurophysiological timing

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mechanisms as found for explicit timing tasks (Praagstra et al., 2006). Praagstra et al. used a serial choice response task with two different SOA (stimulus onset asynchrony) durations (1500 and 2000 ms), keeping the SOA within a series the same. The CNV that developed in the intertrial intervals, between successive reaction stimuli, revealed temporal preparation, because the maximum amplitude was reached just before the next stimulus was presented, independent of SOA duration. Analyses of oscillatory activity showed that beta-activity also adapted to the regular task structure, showing a pattern of contralateral preparatory desynchronization (event-related desynchronization, ERD) followed by synchronization (event-related synchronization, ERS) after the response.

Adjustment of CNV and time course of oscillatory power to regular task patterns are examples of rhythmic entrainment. Slow brain potentials entrain to a rhythm by synchronization of the time course to the regular stream of events. When slow oscillations entrain to the temporal structure of a task, phase resetting occurs, which allows for predictive processing of rhythmically presented input (Lakatos et al., 2008, 2009; Nobre et al., 2007; Schroeder and Lakatos, 2009). Higher frequencies can entrain by means of phase–amplitude coupling to lower frequencies (Canolty and Knight, 2010). It has been suggested that CNVs actually reflect low-frequency cortical oscillations, that are reset by a cue (Cravo et al., 2011; Lakatos et al., 2008; Schroeder and Lakatos, 2009), indicating a direct link between preparatory slow brain potentials and oscillatory activity.

The basal ganglia play an important role in temporal processing (Grahn and Rowe, 2013; Jahanshahi et al., 2006). Praagstra and Pope (2007) studied entrainment in relation to timing functions of the basal ganglia in an investigation of Parkinson's disease (PD) patients, who often demonstrate an abnormal performance in explicit timing tasks (Harrington et al., 1998; Pastor et al., 1992). The authors used a paradigm similar to that of Praagstra et al. (2006) and found that PD patients showed no CNV, while preparatory effects in the alpha and beta-band were attenuated. This deficient entrainment contrasts with observations that PD patients' gait can benefit from cueing with rhythmically presented stimuli, as is often used in rehabilitation (Lim et al., 2005; Nieuwboer et al., 2007; Rochester et al., 2009). While the relevance to cueing was not addressed by Praagstra and Pope (2007), recent research on oscillatory entrainment (Lakatos et al., 2008; Schroeder and Lakatos, 2009), has revealed entrainment as an important mechanism that may contribute to rehabilitation effects of rhythmic cueing. Against this background, we here investigate neurophysiological correlates of rhythmic entrainment of the lower limbs in a healthy population. Specifically, we looked at rhythmic entrainment when people were standing and making leg movements in response to isochronic streams of stimuli.

The investigation of rhythmic entrainment of the lower limbs is also relevant to the question whether the electrophysiological signature of implicit temporal preparation genuinely differs from the preparation in explicit timing tasks. Praagstra et al. (2006) found distinctly lateralized CNV maxima, whereas in explicit timing tasks the CNV is consistently reported to have a midline maximum, pointing to supplementary motor area involvement (Macar et al., 1999; Pfeuty et al., 2003, 2005). With the leg as effector, we expect to reproduce a lateralized CNV distribution, albeit modified by the different representations of upper and lower limb in motor and lateral premotor cortex.

To summarize, the present study investigates whether neurophysiological correlates of motor entrainment, currently only investigated with manual tasks, develop in a similar fashion for the lower limbs. To this end, we adapted existing paradigms to investigate entrainment preceding leg movements, using a choice response task with regular streams of arrow stimuli presented on

a screen. Like in previous experiments (Praagstra et al., 2006; Praagstra and Pope, 2007) we presented series with different SOAs, with the standard SOA being perturbed by a deviant series-final interval. The prediction of similar entrainment for lower and upper limbs entails that the time courses of CNV and beta oscillatory power show an adjustment to the SOA duration.

2. Methods

2.1. Participants

Sixteen subjects (eight male, age 21–54) participated in the experiment. None of the participants had neurological impairments and all had normal or corrected-to-normal vision. All participants were right-handed, according to self-report. Participants gave informed consent and the study was approved by the local ethics committee (CMO region Arnhem/Nijmegen). All participants were students of the Radboud University in Nijmegen and received money or study credits for participation.

2.2. Experimental procedure and stimuli

The experiment consisted of a choice response task with arrows presented on a computer screen (see Fig. 1). Participants were standing in front of the screen and had to respond to arrow stimuli that randomly pointed left or right with equal probability. Participants responded by making a brisk movement with the corresponding leg, by moving the knee quickly forward and back without lifting the foot. Participants were instructed to keep the movement amplitude small, to prevent movement artifacts in the EEG signal.

The experiment consisted of eight blocks of approximately 7.5 min each. Within each block, trials were presented in series of 11, 13, 15, 17, 19 or 21 trials. To examine timing and entrainment properties of the CNV, the experiment manipulated the interval between successive trials, i.e. reaction stimuli. The first experimental manipulation concerned the standard stimulus-onset-asynchrony (SOA), which was either 1500 or 2000 ms and differed between series. A second manipulation concerned the last SOA of each series, which was always 1750 ms, thus creating a long deviant or short deviant, respectively, dependent on the standard SOA in the preceding series. Sequences with long and short SOAs followed each other randomly with pauses of 8 s in between to give participants time to blink. Within series and blocks, left and right pointing arrows were equiprobable. Also the probability of repetitions and alternations of arrow direction was balanced. Between blocks participants could take longer breaks if they wanted. A total of 96 series was presented, equally divided in short

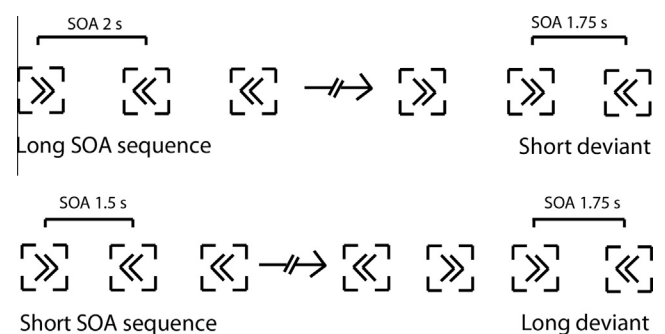


Fig. 1. Experimental paradigm. Arrows randomly pointing left and right were presented in series of 11, 13, 15, 17, 19 or 21 trials. The standard SOA differed randomly between series and was 1.5 or 2 s. The last SOA of a series was always 1.75 s, creating a long or short deviant respectively. The CNV was measured between successive reaction stimuli.

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