Auditory–motor synchronization facilitates attention allocation

Maren Schmidt-Kassow *, Linda V. Heinemann, Cornelius Abel, Jochen Kaiser

Institute of Medical Psychology, Goethe University, Frankfurt am Main, Heinrich Hoffmann Strasse 10, 60528 Frankfurt, Germany

ABSTRACT

Temporal predictability of auditory events induces larger P300 amplitudes and shorter P300 latencies compared to stimulus presentation with variable onset asynchronies. This suggests that periodic stimuli lead to neuronal entrainment resulting in a more efficient allocation of attentional resources. Simultaneous synchronized motor activity should facilitate the precise temporal encoding of acoustic sequences. Therefore the current event-related potential study investigated whether embodied stimulus encoding enhances the reported effects of stimulus periodicity. We found that simultaneous pedaling on an ergometer compared to a physically passive situation amplified the predictability effect on the P300 component. Furthermore, the temporal variability of cycling behavior correlated positively with both P300 latency and P300 amplitude. These findings indicate that auditory–motor synchronization enhances the attentional processing of periodical auditory stimuli.

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Introduction

According to the influential *dynamic attending theory*, neural oscillations "are capable of entraining to external events and targeting attentional energy to expected points in time" (Large and Jones, 1999). The synchronization of internal attending activity with an external event is a prerequisite of attentive processing (Jones et al., 2002). Accuracy should be greatest when the peak of the attentional pulse coincides with the onset of the relevant event. Indeed it has been shown repeatedly that temporally regularly presented stimuli attract attention and are processed faster and more accurately (Correa et al., 2006; Drake et al., 2000; Jones et al., 2002; Rohenkohl et al., 2011). Hence, stimulus periodicity facilitates the focusing of attention on anticipated points in time, resulting in a more efficient allocation of cognitive resources.

Within the last decade several studies have investigated the influence of stimulus periodicity on processing efficiency as reflected by event-related potentials (ERPs), in particular the P300 component. While the ontology of the P300 is still unknown, Polich (2007) has defined the P300 effect as an index of attentional and memory processing. A larger P300 amplitude should indicate the increased allocation of attentional resources, and the P300 latency should indicate how rapidly attentional resources are allocated. Larger P300 amplitudes and shorter P300 latencies should hence reflect successful memory storage facilitating retrieval and recognition.

Recent electrophysiological studies on the effect of stimulus periodicity on attentive processing have corroborated the findings of the above-mentioned behavioral studies by showing that the

P300 is sensitive to the temporal regularity of the presented stimuli (Correa and Nobre, 2008; Lange, 2010, 2009). Schmidt-Kassow et al. (2009) reported better performance as well as a larger P300 amplitude and shorter peak latency in response to periodically compared to randomly presented tones. Stefanics et al. (2010) showed that attended events presented at time intervals corresponding to the delta frequency range (~1 s) led to entrainment of delta oscillations resulting in faster stimulus processing. Schwartze et al. (2011) have recently provided evidence for an attentional modulation of the effects of stimulus timing on ERPs. Comparing pre-attentive and attention-dependent temporal processing within the same paradigm, they found that stimulus regularity affected attention-dependent components such as the P3b but not pre-attentional components such as the MMN. This result emphasized the interaction between temporal stimulation properties and the allocation of attention during stimulus encoding. At the same time it underscored the value of the P300 as a reliable tool to investigate stimulus-driven attention.

The current experiment assessed whether the effect of stimulus periodicity on stimulus-driven attention can be amplified by embodied stimulus encoding. People spontaneously coordinate motor activity with periodic auditory sequences via head nodding, finger flipping, or foot tapping, and in turn motor activity guides auditory processing (Drake et al., 2000; Phillips-Silver and Trainor, 2007; 2005). We hypothesized that an embodied rhythm leads to an even more precise temporal encoding of the presented stimuli compared to sitting still during encoding. Recently, Su and Poeppel (2012) have shown that body movement actively assisted the extraction of temporal structures in auditory events. In line with this finding, previous neuropsychological studies on rhythm perception have provided evidence for the involvement of motor areas in the perception of auditory rhythms (Bengtsson et al., 2009; Chen et al., 2008; Grahn and Brett, 2007).

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* Corresponding author. Fax: +49 69 6301 7606.
E-mail address: schmidt-kassow@med.uni-frankfurt.de (M. Schmidt-Kassow).

Moreover there is substantial evidence for a common timing mechanism underlying both perception and production of time intervals (Fraisse, 1982; Ivry and Hazeltine, 1995; Keele et al., 1985; Treisman et al., 1994). Besides, motor activity in response to auditory stimuli is modulated by the way people attend to the stimuli (Jones and Boltz, 1989; Jones et al., 1993; Klapp et al., 1985). Based on this evidence Drake et al. (2000) stated that attentional synchrony can be reflected by motor synchrony. We thus inferred that motor synchrony in turn should result in attentional synchrony, i.e. the more accurately motor performance is timed, the more efficiently can attentional resources be employed for task performance.

Here, we used an auditory oddball paradigm to assess whether auditory–motor interaction may amplify the effect of temporal regularity on stimulus encoding. Participants listened to periodic and aperiodic continuous tone sequences and were asked to silently count deviant tones that differed in sound frequency from the standard tones. They did so a) during a physically inactive control condition and b) while pedaling on a cycling ergometer at very low intensity. The latter condition should lead to an even more efficient allocation of attentional resources, facilitating the temporal encoding of the auditory sequence and deviant processing. In the pedaling condition, we monitored the individual variability of auditory–motor synchronization as a possible further determinant of successful attention allocation and stimulus processing.

We hypothesized (1) decreased P300 latency and increased P300 amplitude in response to periodic compared with aperiodic stimuli. This effect should be modulated by auditory–motor synchronization resulting in stronger timing effects for the auditory–motor condition. (2) P300 latency and P300 amplitude should vary as a function of motor variability. Cycling variability was expected to correlate positively with P300 latency and negatively with P300 amplitude.

Materials and methods

Participants

20 right-handed volunteers took part in the study after giving written informed consent following the guidelines of the Ethics Committee of the University of Frankfurt, Medical Faculty. All subjects were undergraduates or doctoral students at the University of Frankfurt. Three participants had to be excluded due to technical problems. The remaining 17 participants (12 females, mean age: 24 years, SD = 3.13) did not report any known neurological dysfunction or hearing deficit. Participants received a remuneration of €10 per hour.

Procedure

The stimulus material consisted of sinusoidal tones of 100 ms duration (sound pressure level 75 dB). Standard tones had a frequency of 600 Hz and deviant tones had a frequency of 660 Hz. In the periodic condition tones were presented at a constant stimulus onset asynchrony (SOA) of 1000 ms. In the aperiodic condition the SOAs varied randomly between 600 and 1400 ms (SOAs were evenly distributed around an average of 1000 ms). These parameters were chosen to allow participants to synchronize their lower limb movements with the acoustic stimuli by a cadence of 60 revolutions per minute (RPM). 60 RPM is a pace that is usually recommended to beginners in fitness centers. At the same time this frequency (1 Hz) corresponds to the optimal repetition rate for human repetitive perceptuo-motor behavior (Will and Berg, 2007). During the pedaling blocks each revolution was recorded by a customized microcontroller (®Arduino, www.arduino.cc) whenever pedals crossed a light barrier which was built into the cycling ergometer (Conditronic 100 PV/ZR-NS, Dynavit, Kaiserslautern, Germany).

Standard tones were presented with a probability of 0.75 and deviants with a probability of 0.25. Each block contained a total of 400–405 auditory stimuli and lasted for about 7 min. Subjects passed two blocks (one periodic and one aperiodic block) during which they cycled at very low intensity (50 W) during stimulus presentation and 2 blocks (one periodic and one aperiodic block) during which they sat still on the ergometer. The order of the 4 experimental blocks (pedaling periodic, PP; pedaling aperiodic, PA; sedentary periodic, SP; sedentary aperiodic, SA) was counterbalanced across participants. Presentation 14.8 (Neurobehavioral Systems, Albany, USA) running on a Windows PC was used to create the pseudorandomized oddball sequences and to present the stimuli via headphones (AKG K271, HARMAN International Industries, Stamford, USA). Pseudorandomization ensured that no more than two deviant events could appear in a row. Participants were instructed to silently count deviant tones and to blink and to move their upper limbs as little as possible.

The recordings took place in an air-conditioned, windowless and quiet room. During stimulation participants faced a white wall to avoid any distractions and were asked to silently count deviant tones.

ERP analysis

EEG was recorded from 61 scalp sites by means of Ag/AgCl electrodes mounted in an elastic cap (Falk Minow Services, Munich, Germany). Fz served as ground and electrodes were referenced on-line to an average reference (recordings were re-referenced to averaged mastoids off-line). Electrode impedances were kept below 7 kΩ. In order to control for eye movements, eight infra- and supraorbitally mounted electrodes were recorded. EEG and EOG signals were digitized online with a sampling frequency of 500 Hz. An anti-aliasing filter of 135 Hz was applied during recording.

After visual inspection of EEG data three excessively noisy data sets were removed, resulting in 14 remaining data sets. EEG data analysis and statistical analysis were carried out in MATLAB (The Mathworks, Natick, USA) with the FieldTrip toolbox for EEG/MEG analysis developed at the Donders Institute for Brain, Cognition, and Behavior (Nijmegen, The Netherlands, (Oostenveld et al., 2011). EEG data were segmented into 1500 ms epochs (from 500 ms before onset of the critical tone up to 1000 ms afterwards). Muscle artifacts of the electrodes were detected by means of thresholding the z-transformed value of the preprocessed raw data. A band-pass filter (80–135 Hz) was applied, Hilbert analytic amplitude extracted and the z-scores calculated. The z-score cutoff was set to 4 across data sets. Furthermore, epochs with amplitudes exceeding 100 μV were excluded from further analysis. To identify eye artifacts, the data underwent independent component analysis (ICA) using the FastICA algorithm implemented in the fieldtrip toolbox. All components were correlated with signals at the vertical EOG channels. The component with the highest correlation was rejected. Prior to the ERP analysis, the original EEG data were filtered with a band pass of 0.3 Hz–20 Hz. Epochs were averaged per participant, condition, and electrode site, with a 200-ms pre-stimulus baseline.

Statistical analysis

ERPs were computed separately for standards and deviants in each condition and averaged across the central region of interest (ROI) electrodes. To determine a reasonable ROI, we evaluated the maximum amplitude across all deviant conditions within the time window of interest described below. Electrodes that showed at least 70% of the maximum activity entered the region of interest. This computation resulted in 13 centrally distributed electrodes that matched P300-related ROIs described of previous work (e.g., (Schwartze et al., 2011) as highlighted in Fig. 1). On average 94.4% (SD = 3.4%) trials per condition entered the statistical analysis.

P300 differences between relevant conditions were tested using a data-driven non-parametric cluster-based permutation procedure