Attention and entrainment: P3b varies as a function of temporal predictability

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Recently, it has been shown that feature discrimination in temporally regular rhythms results in enhanced performance compared with feature discrimination in temporally irregular rhythms. In this study, we investigated the influence of temporal predictability on attentional processing. We show that temporal predictability of a sequence results in a decreased peak latency of the P3b compared with temporally random sequences. The present findings clearly illustrate that temporal predictability results in faster processing of deviant stimuli. NeuroReport 20: 31-36 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

P3b is a widely discussed event-related potential (ERP) associated with selective attention. This positivity is usually elicited 300-500 ms after the onset of the critical stimulus and has its maximum over central and parietal electrode sites. In most cases, the component has been investigated in simple oddball paradigms [1,2]. Functional explanations concerning the P3b are manifold: the P3b has been related to updating working memory [3], surprise in response to a less frequent stimulus [4], target versus standard discrimination [5], or as a reflection of rehearsal strategy [6]. In a detailed review, Polich [7] describes the P3b as a neural signature of mechanisms required to change the mental model of an environment to respond appropriately [8].

Usually, auditory as well as visual sequences in the classic oddball paradigm are based on highly predictable interstimulus intervals allowing maximal prediction of when the next event in a sequence will occur. This is comparable with perceptual studies investigating feature discrimination in isochronous (i.e. temporally predictable) and irregular temporal rhythms that show rapid temporal entrainment of information processing [9,10]. Entrainment is a process, in which two (or more) autonomous oscillators (oscillators are generators of periodic vibrations) synchronize and interact with each other [11]. Thus, entrainment is the tendency to synchronize with another event. If this process is successful, it results in perfect synchronization. According to the Dynamic Attending Theory (DAT) suggested by Large and Jones [12], the brain produces self-sustained oscillations and temporal structured patterns when rhythmically stimulated. Such oscillation is synchronizing with an external rhythmic signal resulting in entrainment. Thus, stimuli (e.g. deviants) that occur at expected time points are preferably and effectively processed. This results in enhanced perceptual judgement in trials within regular rhythms and at the concrete point in time where the event is expected [9,10,13,14].

Some ERP experiments investigated the influence of temporal predictability on the allocation of attention [15,16]. These studies showed that both the visually and the auditory-evoked P3b vary as a function of temporal expectancy. Deviant stimuli that occur at temporal predictable points in time result in a significantly earlier P3b than deviants at unexpected points in time. In both studies participants, however, built up expectancies in response to the previously seen or heard stimulus (e.g. stimulus A was always followed by a long pause, whereas stimulus B was always followed by a short pause). Thus, they did not synchronize with a given stimulus but explicitly predicted the time point of each following event.

In this study, we investigated the influence of entrainment or synchronization on attentional processing as revealed in the P3b component. In the classic oddball paradigm isochronous tone sequences are utilized. To address the question whether the P3b is sensitive to entrainment or not we designed P3b paradigm that is temporally more complex. Hence, we compared stimulus sequences that were temporally isochronous, chunked, or completely random. Lakatos et al. [17] pointed out that in cases, in which the brain cannot detect an inherent rhythm in a stimulus stream, a continuous processing mode should be initiated while stimuli, which are presented rhythmically and at predictable points in time led to neural oscillations entraining to the structure of an attended stimulus stream. Accordingly, we manipulated temporal predictability in the P3 oddball paradigm. In doing so, we aimed to induce entrainment at a low level (the onset of each tone), or a slightly higher level (the onset of a chunk, i.e. groups of three successive tones) in comparison with randomly occurring tones that should not result in entrainment at all.

We hypothesize that if the initially mentioned DAT can model our data, the time-to-peak latency of the P3b should vary as a function of entrainment. In this context Polich [7] pointed out that the timing of the P3b is 'negatively correlated with processing efficiency in normal individuals'. Thus, we hypothesize that predictable timing leads to more efficient processing through entrainment, and thus to the shortest time-to-peak latency.

As we direct participant's attention to the deviant stimuli, we expected an N2b effect in addition to the P3b. The N2b is inter alia connected with expectancy violations (e.g. Ref. [18,19]) and with the identification of a stimulus as a deviant (e.g. Ref. [20]). This component is enhanced with increasing stimulus deviation. We thus expect an N2b, but the focus of interest lies on the P3b and its sensitivity to entrainment.

Methods

Participants

Thirty-six right-handed native speakers of German with unimpaired hearing (18 females) aged 21-33 years (mean = 25.1; SD = 2.7) participated. The experiment was conducted with the understanding and the written consent of each participant. They were paid a small compensatory fee. None of them had any neurological impairment. The ethics committee of the University of Leipzig approved the experiment.

Materials

We used a 3×2 within-subjects design (factor 'timing' = isochronous, chunked, random; factor 'condition' = ordered, violated). Ninety-six tone sequences were presented in three different timing conditions, that is, isochronous, chunked, and random timing. In isochronous timing the interval between two successive tones remained constant (250 ms). In chunked timing three successive tones were grouped together by lengthening the interval between the third tone in one group and the first tone of the following group (750 ms instead). In random timing the interstimulus interval among all tones was completely variable.

Each of the 96 trials consisted of a 12-tone hypersequence being composed of three synthetically generated violin tones (123, 130, and 146 Hz). These three tones formed a hypersequence that they build a pattern that was repeated three times. In the last sequence of three tones the pattern either changed (violated condition) or remained the same (ordered condition; Fig. 1).

At the end of each 12-tone hypersequence, participants decided whether the hypersequence they listened to was ordered (i.e. consequent repetition of the first three tones) or violated (changed pattern of the last three tones). Sequences changed from trial to trial. Half of the trials were incorrect.

The three different timing conditions (isochronous, chunk, random) were presented blockwise and the order of the conditions was counterbalanced across participants.

Electrophysiological recording

The EEG was recorded from 28 scalp sites by means of Ag/AgCl electrodes mounted in an elastic cap (Electro-Cap Inc., Eaton, Ohio, USA; no date) according to the 10-20 International System [21]. The sternum served as ground, the left mastoid as online reference (recordings were re-referenced to averaged mastoids offline). Electrode impedances were kept below $3 k\Omega$. To control eye movements, a horizontal and a vertical electrooculography was recorded. An antialiasing filter of 135 Hz was applied during recording. Sampling rate was 250 Hz.

Data analyses

Individual EEG recordings were scanned for artefacts such as electrode drifting, amplifier blocking, muscle artefacts, eye movements, or blinks by means of a rejection algorithm as well as on the basis of visual inspection 200 ms before onset of the critical tone up to 1500 ms after the critical tone. Trials were averaged per participant, condition, and electrode site, using a baseline from -200 to 100 ms. For graphical display only, data were filtered offline with a 7 Hz low-pass filter. All statistical evaluations were carried out on antialiasing filtered ERP data.

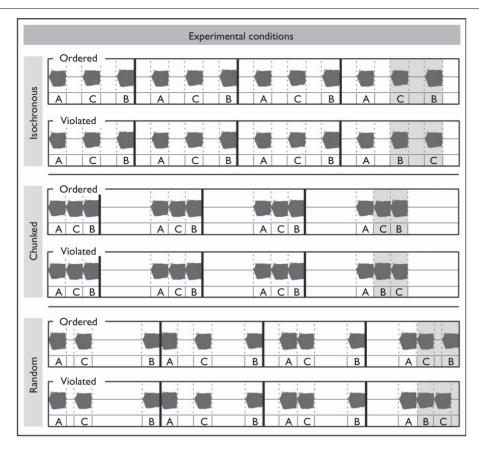
Results

Behavioral data

We ran two analyses of variance (ANOVAs) including the within-subject factors condition and timing to evaluate reaction times and error rates. Concerning error rates, the omnibus ANOVA resulted in a main effect of timing (isochronous: 3%; chunk: 1.5%; random: 10.1%; [F(2,66) = 19.59, P < 0.001]. Step-down analyses revealed significant differences between random compared with isochronous [F(1,33) = 21.23, P < 0.001] and random compared with chunked timing (F(1,33) = 20.16,P < 0.001). A significant difference between isochronous and chunked timing was also observed [F(1,33) = 5.41,P < 0.03]. The Bonferroni's corrected α value was 0.03.

With respect to reaction times, statistical analysis revealed a main effect condition [ordered: 380.7 ms;

Fig. 1



Overview of the experimental conditions. A-C indicate different tone pitches. Gray shadings mark critical parts of the signal. Bold lines indicate the end of a sequence.

violated: 361.9 ms; F(1,33) = 6.21, P < 0.03] and a main effect timing [isochronous: 358.6 ms; chunk: 367.3 ms; random: 387.9 ms; F(2,66) = 4.82, P < 0.03]. Post-hoc comparisons of all levels of timing yielded a significant difference between random compared with the isochronous timing [F(1,33) = 7.70, P < 0.001] and random compared with chunked timing [F(1,33) = 5.03, P < 0.03].

Event-related potentials

Deviations of the sequence-ending final tone in all timing conditions (isochronous, chunk, random) resulted in a biphasic pattern that consisted of an N2b-like component and a P3b (Fig. 2). The N2b was widely distributed while the P3b had its maximum at parietal sites. On the basis of a 50-ms timeline analysis, two time windows were statistically analyzed: 150-300 ms (N2b) and 350-800 ms (P3b). Different subsets of electrodes were analyzed as regions of interest and labeled as follows: left anterior (F7, F3, FT7, FC3), right anterior (F8, F4, FT8, FC4), right posterior (CP6, P4, P8, O2), and left posterior (CP5, P3, P7, O1).

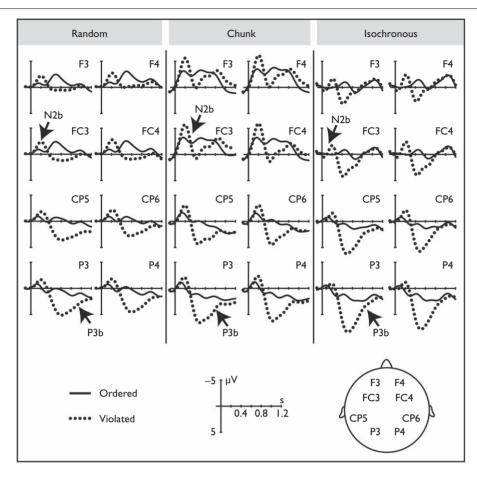
The Greenhouse–Geisser correction [22] was applied when evaluating effects with more than one degree of freedom.

Only those significant results that correlated with a critical experimental factor are reported in the following. To evaluate effect sizes we computed omega-square (Ω^2) , that is, the coefficient of determination that represents the proportion of variance in the dependent variable accounted for by the independent variable (interpreted in a similar manner as r^2). As we have used a within-subject design, Ω^2 values greater than 0.26 are defined as large effects, Ω^2 values from 0.048 to 0.26 are defined as medium effects, and Ω^2 values from 0.019 to 0.048 are small effects (cf. [23]).

N2b

The N2b was quantified by an ANOVA with four withinsubject factors, namely condition (correct/incorrect), timing (random/isochronous/chunk), hemisphere (left/ right), and region (frontal/parietal). This ANOVA resulted in a significant main effect of condition [F(1,33) = 149.35], P < 0.001], as well as an interaction of condition \times hemisphere \times region [F(1,33) = 6.35, P < 0.05]. Step-down analyses by the factor region revealed a condition effect in the parietal region [F(1,33) = 69.27, P < 0.001], and an interaction of condition × hemisphere in the frontal region

Fig. 2



N2b and P3b elicited by the critical tone in the random, chunk, and isochronous timing condition. Waveforms show the average for the ordered and the violated condition from 200 ms before the critical tone up to 1200 ms.

[F(1,33) = 7.96, P < 0.01]. Resolving this interaction (condition × hemisphere) by the factor hemisphere resulted in a significant condition effect in both the hemispheres [left: F(1,33) = 62.91, P < 0.001, $\Omega^2 = 0.65$; right: F(1,33) = 104.16, P < 0.001, $\Omega^2 = 0.75$].

Hence, the results support a widely distributed N2b that was slightly larger at right frontal than left frontal electrode sites.

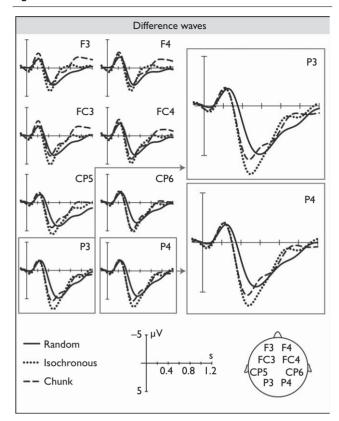
P₃b

The P3b effect was quantified with the same four withinsubject factors (timing, condition, hemisphere, and region). The omnibus ANOVA revealed a main effect of condition [F(1,33) = 90.33, P < 0.001], an interaction between the factors condition and region [F(1,33) = 55.10, P < 0.001],as well as an interaction between the factors condition, timing and region [F(1,33) = 6.18, P < 0.05]. Resolving the interactions by the factor region showed a significant condition effect for both regions [frontal: F(1,33) = 42.04, P < 0.001, $\Omega^2 = 0.55$; parietal: F(1,33) = 109.13, P < 0.001, $\Omega^2 = 0.76$], however, the effect was stronger at parietal electrode sites. Furthermore, we found a significant interaction condition × timing at parietal electrode sites [F(1.33) = 3.94, P < 0.03]. Post-hoc analyses yielded a significant condition effects in all timing conditions [random: F(1,33) = 45.42, P < 0.001, $\Omega^2 = 0.56$; isochronous: F(1,33) = 83.64, P < 0.001, $\Omega^2 = 0.71$; chunk: F(1,33) = 99.19, P < 0.001, $\Omega^2 = 0.74$ indicating larger effects for the temporal predictable conditions.

To look into potential latency differences in the P3b, a component peak analysis was conducted. Visual inspection indicated that the P3b peaked earlier in the isochronous condition compared with the chunk and random condition (Fig. 3). The omnibus ANOVA including the same within-subject factors as described above applied a time-to-peak latency as a dependent variable.

Results revealed a main effect of timing [F(2,66) = 14.38,P < 0.001]. Post-hoc comparisons for the three levels of timing yielded significant differences between isochronous

Fig. 3



N2b and P3b component elicited by the critical tone in the random, chunk, and isochronous timing condition. Waveforms show the difference of the ordered and the violated condition from 200 ms earlier to the critical tone up to 1200 ms.

(mean = 520 ms) and chunked (mean = 581 ms) timing [F(1.33) = 6.63, P < 0.03], between isochronous and random (mean = 640 ms) timing [F(1,33) = 39.34, P < 0.001], as well as between the chunked and the random timing [F(1,33) = 6.06, P < 0.03].

Thus, the amplitude of the P3b peaked earliest in the isochronous condition followed by the chunked (+61 ms) and the random (+159 ms) condition.

In summary, we report a significant P3b effect in all timing conditions maximally distributed over parietal electrode sites. Although the amplitude size of the P3b did not vary as a function of timing, the time-to-peak latency revealed peak latency differences because of temporal predictability.

Discussion

We investigated whether the P3b associated with stimulus-related attention is sensitive to entrainment. For this purpose, we used tone sequences the succession of which was based on a simple sequence established by the first three tones of a tonal unit and manipulated the temporal predictability of the tones by using three different presentation conditions (isochronous, chunked, random).

Our results not only show larger P3b amplitude for the temporal predictable conditions compared with the random condition, but also reveal that the peak latency of the P3b varies as a function of synchronization. The peak latency of P3b was systematically enhanced by increasing temporal variability. Time-to-peak latency was shortest in the isochronous timing condition and the longest in the random timing condition. Hence, it shows that timing variability influences the latency of the P3b. These results are in line with the results of Lakatos et al. [17] who suggested that attention enforces entrainment of neuronal oscillations when the brain detects a regular rhythm in a stimulus stream. This in turn accelerates the detection of a deviant stimulus as reflected in the latency of the P3b. Consequently, deviant events that occur at expected time points are preferably processed. This fits well with predictions of the DAT. In the random condition, that is, in absence of an external rhythmic signal, the phase and period of such oscillations should drift around. Indeed, we found no indication of entrainment. Instead, performance was less accurate and the latency of the P3b was enhanced compared with other conditions. In contrast, temporal predictability as in the chunked and in the isochronous condition results in better performance and shorter latencies. This should be a consequence of entrainment as the attentional focus lies on these specific time points where the deviant occurs. Thus, our results fit the assumption that those stimuli that occur at expected time points are more effectively processed.

Besides the P3b effect an N2b was elicited. The N2b has been linked to consciously identify a stimulus as a deviant [20,24]. In this experiment, participants were able to extract a simple rule on the basis of the repeated threetone sequences. On the basis of this rule they have certain expectancies about which tone may occur next. In the incorrect trials, the observed N2b should therefore reflect the detection of this unfulfilled expectancy [18,19].

Conclusion

To conclude, we found a correlation of entrainment and peak latency of the P3b, that is, the more temporally predictable the stimulus, the shorter the latency of the P3b. Our results show that entrainment maximally enhances efficient stimulus processing.

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