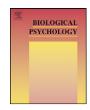
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Temporal regularity effects on pre-attentive and attentive processing of deviance

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ABSTRACT

Temporal regularity allows predicting the temporal locus of future information thereby potentially facilitating cognitive processing. We applied event-related brain potentials (ERPs) to investigate how temporal regularity impacts pre-attentive and attentive processing of deviance in the auditory modality. Participants listened to sequences of sinusoidal tones differing exclusively in pitch. The inter-stimulus interval (ISI) in these sequences was manipulated to convey either isochronous or random temporal structure. In the pre-attentive session, deviance processing was unaffected by the regularity manipulation as evidenced in three event-related-potentials (ERPs): mismatch negativity (MMN), P3a, and reorienting negativity (RON). In the attentive session, the P3b was smaller for deviant tones embedded in irregular temporal structure, while the N2b component remained unaffected. These findings confirm that temporal regularity can reinforce cognitive mechanisms associated with the attentive processing of deviance. Furthermore, they provide evidence for the dynamic allocation of attention in time and dissociable pre-attentive and attention-dependent temporal processing mechanisms.

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1. Introduction

Continuous change is a fundamental characteristic of life. Changes generate temporal structure or events in time, with effective behavior depending in part on the temporal coherence of cognition, action, and these events. The key to temporal coherence is adequate timing, i.e., the ability to be in the right place at the right time. Timing and temporal organization are not only crucial in overt behavior but also in cognitive processes and the allocation of cognitive resources (Fuster, 2001). How do neurocognitive processes cope with the temporal structure of the environment to achieve adequate timing in cognition and action? Adequate timing implies some internal representation of temporal structure. It is unclear though whether temporal structure is processed implicitly, or whether an explicit representation of temporal structure is generated by dedicated temporal processing systems (Buonomano, 2007; Ivry and Schlerf, 2008). Some neurofunctional models suggest that dedicated temporal processing is a function of classical motor systems of which the cerebellum is involved in pre-attentive, short-range, event-based temporal processing, while the basal ganglia engage in attention-dependent, longer-range, interval-based temporal processing (Ivry, 1996; Lewis and Miall, 2003; Spencer et al., 2003; Buhusi and Meck, 2005). A benefit that may arise from the explicit processing and the evaluation of temporal structure is to recognize and prospectively use temporal regularity. This would allow to predict the temporal locus of future events and to allocate attention towards important aspects of information. Expectations and prior knowledge about upcoming information should entail optimized timing in cognition and action even if the use of temporal structure is subconscious and unintentional, i.e., if temporal processing is exogeneous (Nobre et al., 2007; Coull and Nobre, 2008).

The proposed dissociation of pre-attentive and attentiondependent temporal processing systems offers a starting point to further characterize the underlying processes. In this context, important issues concern (1) the moment at which attention affects temporal processing, (2) whether temporal structure can be processed without adopting strategies for estimating time (Grondin, 2001), and (3) how attention is allocated and maintained in the presence of acoustic, and hence inherently temporal, signals. Early on, Bolton (1894) emphasized that attention appears discontinuous and intermittent, and that it manifests in a wave-like form or a series of pulses. Consequently, some form of adaptation deems necessary to align the internal fluctuation of the attentional focus with the temporal structure of external events. With respect to the auditory domain, one important aspect in this interplay could be the bias of the auditory system to search for regularities in sensory input (Winkler et al., 2009). Although continuously changing, the temporal structure of the environment is not arbitrary. Any perceived regularity in temporal structure can indicate a pat-

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tern. Temporal patterns emerge in both the environment and in the allocation of attention (Jones and Boltz, 1989). This transient temporal stability in combination with predictive processing is fundamental for optimal anticipatory timing in cognition and action. This notion is expressed in Dynamic Attending Theory (DAT; Jones and Boltz, 1989; Large and Jones, 1999). DAT proposes that internal attending rhythms synchronize with external event structure. This mechanism may be relevant to dissociate pre-attentive from attention-dependent temporal processing mechanisms. Ongoing processing of relatively stable temporal relations instantiates a repetitive process which can be conceived as an instance of oscillatory activity. Oscillatory activity and interactions between different oscillations caused by appropriate external or internal stimulation constitute another fundamental characteristic of life (Glass, 2001). Their interplay represents an inherent property of both, living things and the activity of attending (Jones and Boltz, 1989). As such, oscillatory mechanisms provide a realistic computational basis to model the "adaptation to change by anticipation" (Fraisse, 1963, p. 18). DAT proposes that one or more attention oscillations entrain to the rate and rhythm of external events (Large and Jones, 1999), i.e., adaptive oscillations lock into the temporal structure of the stimulation, thereby establishing synchronized processing. If confronted with a change in temporal structure, the oscillations adjust their phase and period in order to maintain or to reestablish synchronization. The result of this process is stimulus-driven attending (Barnes and Jones, 2000). DAT provides a framework capable of explaining how temporal structure guides attention on a moment-to-moment basis and temporal dependencies within a pattern, i.e. the possible influence of preceding temporal structure on subsequent temporal processing, and the influence of global temporal context (McAuley and Miller, 2007).

In the current study we used ERPs to investigate the impact of regular and irregular temporal structure on the pre-attentive and attentive processing of deviant events by means of auditory odd-ball sequences. An oddball sequence consists of more (standard) and less (deviant) frequent events, with the deviant event violating some rule established by the standard. Pre-attentive and attentive processing of this deviation is associated with distinct sets of endogenous ERPs. With respect to the former we focus on mismatch negativity (MMN), P3a, and reorienting negativity (RON), and with respect to the latter on N2b and P3b.

In combination, MMN, P3a, and RON form the "distraction potential" (Escera and Corral, 2007). The MMN has a fronto-central scalp distribution and is elicited in response to a discriminable change in auditory stimulation compared to a repetitive aspect of preceding stimuli retained in short-term memory (Näätänen et al., 1978, 2007; Garrido et al., 2009). Usually the MMN peaks around 100-200 ms after the presentation of the deviant event. It reflects pre-attentive processing of sensory information as events in time, including auditory duration discrimination (Näätänen et al., 2004, 2007). The term MMN has largely replaced the classification of this component as a subcomponent of the N2 under the N2a label (Folstein and van Petten, 2008). The P3a is a frontocentrally distributed positive deflection evoked by task-irrelevant salient events (Linden, 2005), whereas the later fronto-central RON reflects restoration of the task-optimal selective attention set following distraction by task-irrelevant events (Schröger and Wolff, 1998). However, although these components are related to the processing of deviant events in the environment they can be elicited independent of each other (Horváth et al., 2008).

With respect to attention-dependent processing we concentrate on another fronto-central N2 subcomponent, the N2b, associated with the attentive detection of a deviant event, and the P3b, which typically peaks around 300 ms after the presentation of a deviant event. Like the P3a, the more centro-parietal P3b is part of the P300 complex (Polich and Criado, 2006; Volpe et al., 2007). However,

each P3a is accompanied by a smaller P3b and vice versa (Linden, 2005). The P3b is commonly related to a task-relevant alteration of a mental model of the environment, a stimulus-driven attention mechanism, and memory processing (Linden, 2005; Polich, 2007).

The goal of the current study was to investigate how the contrast between regular, and therefore highly predictable temporal structure, and irregular temporal structure would modulate the aforementioned ERP components associated with various aspects of the processing of deviance. In line with DAT, regular temporal structure was expected to narrow the attentional focus and to promote synchronization, whereas irregular structure was expected to widen the attentional focus and to promote reactive attending (Jones et al., 2002). We consider the ERP modulation as an index for the quality of stimulus-driven synchronization, the dynamic allocation of attention, and the quality of cognitive processes associated with the processing of deviant events. Specifically, we hypothesize that attention-dependent recognition of temporal regularity and the subsequent use of this information to predict upcoming events results in an enhanced amplitude of the N2b and P3b components in response to deviants embedded in regular temporal structure relative to those embedded in irregular temporal structure. This enhancement should be similar for the pre-attentive processing of deviance, and the distraction potential, i.e., MMN, P3a, and RON, only if the underlying mechanism is also benefits from temporal regularity. Alternatively, if attention-dependent temporal processing is necessary to exploit regularity, pre-attentive temporal processing should not benefit from temporal regularity. In this case the distraction potential should be resistant against the manipulation.

2. Materials and methods

2.1. Participants

Twenty-four right-handed volunteers (12 females) participated in the study. Ages ranged from 19 to 30 years (mean: 24.4; SD: 2.8 years). All participants were students at the University of Leipzig and were recruited via the database of the Max-Planck Institute for Human Cognitive and Brain Sciences in Leipzig. None of the participants reported any neurological dysfunction or a hearing deficit at the time of testing. All participants gave their written informed consent and received a compensatory fee. The study was approved by the Ethics Committee of the University of Leipzig.

2.2. Stimulus presentation, EEG recording, and ERP analysis

The stimulus material consisted of two equidurational (300 ms; 10 ms rise and fall) sinusoidal tones. The tones were used to generate a temporally regular, i.e. isochronous, and a temporally irregular, i.e. random, auditory oddball sequence (Fig. 1). The latter was created by varying the duration of the inter-stimulus-interval (ISI) between individual tones. Whereas the ISI was 600 ms in the isochronous sequence, it was randomly assigned from a range between 200 and 1000 ms (normally distributed around an average 600 ms) in the random sequence. These specific parameters were chosen in order to take into consideration the privileged status of simple integer ratios and intervals lasting about 600 ms (Fraisse, 1982; Essens, 1986; Martin et al., 2007). An average SOA of 900 ms is still within the range of optimal tempo sensitivity (Drake and Botte, 1993), as well as the synchronization range (Fraisse, 1982). The boundary between short-range and attention-dependent longer-range temporal processing mechanisms is commonly associated with values close to 1000 ms (Buhusi and Meck, 2005; Lewis and Miall, 2006). However, the mechanism underlying attention-dependent temporal processing is probably sensitive to intervals ranging from hundreds of milliseconds to seconds (Meck et al.,

The two tones differed in frequency (600 Hz for standards and 660 Hz for deviants). Each oddball sequence comprised 512 standard and 128 deviant tones, corresponding to a total of 640 tones and a standard-to-deviant ratio of 4:1.

Presentation 12.0 (Neurobehavioral Systems) running on a Windows PC was used to create the pseudorandomized oddball sequences and to present the stimuli via two loudspeakers. Pseudorandomization ensured that no more than two deviant events could appear in a row. The 600 ms ISI in the isochronous sequence resulted in a 1:2 ratio for the duration of the filled stimulus intervals and the empty ISI intervals. The order of these sequences was pseudo-randomized across participants. After the presentation of the first sequence, participants were given a 5 min break. The experiment was split into two sessions on two consecutive days. All participants started with the pre-attentive session followed by the attentive session to preclude familiarity effects.

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