



## Dissociation of formal and temporal predictability in early auditory evoked potentials

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### ABSTRACT

Perceived regularity among events in the environment allows predictions regarding the “when” and the “what” dimensions of future events. In this context, one crucial question concerns the impact and the potentially optimizing effect, of regular temporal structure on the processing of “what”, or formal, information. The current study addresses this issue by investigating whether temporal and formal structure interact during early stages of sensory processing, and by relating the respective findings to the concept of a predictive bias in brain function. Analyses were performed on two components of the auditory event-related-potential of the electroencephalogram, namely the P50 and the N100. Oddball sequences consisting of frequent standard and infrequent deviant sinusoidal tones were presented with either regular or irregular temporal structure in pre-attentive and attentive experimental settings (Schwartz, Rothermich, Schmidt-Kassow, & Kotz, 2011). Temporal regularity effects on pre-attentive and attentive processing of deviance. *Biological Psychology*, 87, 146–151). The results confirm that the P50 and the N100 amplitudes reliably encode formal and temporal predictability. Similar patterns of results obtained with pre-attentive and attentive task instructions, as well as the absence of a significant interaction of formal and temporal structure suggest that the P50 response may be interpreted as an automatic marker of predictability, whereas the N100 may represent a more complex marker, in which formal and temporal structure start interacting as a function of attention.

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### 1. Introduction

The ability to predict the type and the timing of upcoming events is essential for efficient adaptation to continuous changes in the environment. Prediction implies projecting a previously established representation of some regular relation among events to future events. While inherently temporal, this process pertains just as much to the formal structure of events, defined as perceived changes, for example, of the color or the sound of objects in the environment, as it concerns their temporal structure. Yet, independent of each other, regularity in either dimension affords predictability and establishes a basis for predictive behavior, which has to rely on sensory mechanisms for regularity-encoding (Costa-Faidella, Baldeweg, Grimm, & Escera, 2011). However, questions arise as to how and why temporal regularity is encoded, and whether this occurs independently of formal regularity-encoding.

By varying formal and temporal predictability independent of each other in attentive experimental settings, it has been shown that both, the latency and the amplitude of the P3b component of the event-related-potential (ERP) of the electroencephalogram

(EEG) vary as a function of temporal predictability (Lange, 2009; Minuissi, Wilding, Coull, & Nobre, 1999). The P3b amplitude typically increases with higher stimulus discriminability, while its latency increases with lower stimulus discriminability (Linden, 2005). Accordingly, the amplitude of the P3b is larger and its latency is shorter in response to a sensory object that is temporally predictable (Schmidt-Kassow, Schubotz, & Kotz, 2009; Schwartz, Rothermich, Schmidt-Kassow, & Kotz, 2011). At the cognitive level, the P3b has been interpreted as reflecting the restructuring of a mental model of the environment in response to deviance (Donchin, 1981; Polich & Criado, 2006). As such, the P3b is part of a complex ‘processing cascade’ that involves attentional and memory mechanisms (Polich, 2007). However, while such findings support the notion of a modulatory effect of temporal predictability, the P3b is but one of several components within a sequence of partly overlapping, partly successive, lower- and higher level processes associated with the perception of change, or deviation—each with its own temporal dimension. Hence, additional markers have to be considered to gain better understanding of the interplay of formal and temporal predictability. This may lead to a more detailed picture of sensory processing within the general concept of a predictive bias in brain function (Bar, 2007; Bubic, von Cramon, & Schubotz, 2010; Friston, 2010; Raichle, 2010), particularly in the auditory domain (Bendixen, Prinz, Horváth, Trujillo-Barreto, &

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Schröger, 2008; Bendixen, SanMiguel, & Schröger, 2012; Schwartz, Tavano, Schröger, & Kotz, 2012; Winkler, Denham, & Nelken, 2009).

The most basic benefit that may arise from this predictive bias is probably an increased efficiency in allocating the brain's energy resources, as expressed, for example, in the free-energy principle that is central to the influential 'predictive coding' framework (Friston, 2010; Raichle, 2010). According to the free-energy principle, adaptive systems such as the human brain strive to reach equilibrium with the environment by maximizing expectations about events in the environment (Friston, Thornton, & Clark, 2012). A high degree of predictability in formal and temporal structure bears the potential to maximize expectations, thereby also optimizing cognitive processing, for example, via stable and effortless synchronization of oscillations guiding the stimulus-driven allocation of attention in time (Barnes & Jones, 2000; Large & Jones, 1999).

The high temporal resolution of the EEG offers a means to dissociate between short-latency, mid-latency, and long-latency markers of formal and temporal predictability within the sub-second range. Furthermore, it allows consideration of the effects of predictability on well-established ERP components associated with different pre-attentive and attentive perceptual processes, starting with lower-level, potentially automatic processing stages, and advancing to higher-level controlled processing stages. This, in turn, allows speculation about which specific processes may actually benefit from predictability in formal and/or temporal structure. In this context, auditory change (deviance) processing is an extensively investigated multi-stage process that comprises sensory as well as cognitive aspects. It is conceptualized as an instance of surprise. In the framework of predictive coding, the minimization of surprise is equivalent to the maximization of expectations (Friston et al., 2012).

A number of ERP components reflect auditory deviance processing, most prominently long-latency responses in the hundreds-of-milliseconds range such as mismatch negativity (MMN) and P3b (Näätänen, Paavilainen, Rinne, & Alho, 2007; Polich, 2007). However, more recent animal and human findings confirm deviance processing within the first 50 ms after stimulus onset, a timescale that spans brainstem and thalamic levels of auditory processing (Grimm & Escera, 2012; Slabu, Escera, Grimm, & Costa-Faidella, 2010). In the following, we will focus on two auditory ERP components that can be considered intermediate—the P50 and the N100. Analysis of these components and contrasts in three dimensions, i.e., task-directed attention, formal predictability, and temporal predictability, provide the opportunity to investigate the potential modulation of these early stages of auditory processing as a function of temporal predictability. The approach complements previous results (Schwartz et al., 2011), showing MMN-indifference and P3b differentiation with temporal predictability. More specifically, the paradigm allows the following questions to be addressed: (1) Is early auditory processing sensitive to formal and temporal predictability alike, (2) Do the two dimensions interact? and, (3) Is regularity-encoding at these early stages comparable for pre-attentive and attentive task instructions?

Principally, both, the P50 and the N100 component of the auditory ERP are indicative of predictive processes. The P50 has been primarily investigated as a marker of sensory gating, particularly in schizophrenia, reflecting suppression in response to repetitive stimulation (gating out) relative to changing stimulation (gating in, e.g., Marshall, Bar-Haim, & Fox, 2004; Moura, Triñanes-Pego, & Carrillo-de-la-Peña, 2010; Pratt, Starr, Michalewski, Bleich, & Mittelman, 2008). This P50 repetition-suppression is typically observed in response to a second stimulus in paired-stimulus paradigms with relatively long inter-pair-intervals in the seconds-range, although shorter intervals yield comparable results (Rentzsch, Gomez-Carrillo de Castro, Neuhaus, Jockers-Scherübl, & Gallinat, 2008). Recordings of intracranial evoked potentials point towards a

role of temporo-parietal (BA 2 and 22) as well as prefrontal areas (BA 6 and 24) in sensory gating (Grunwald et al., 2003). Similarly, the N100 is linked to stimulus suppression, e.g., when comparing self-initiated and externally-initiated sounds (Baess, Jacobson, & Schröger, 2008; Knolle, Schröger, Baess, & Kotz, 2012). In general terms, ERP-suppression may represent the neural correlate of priming (Grill-Spector, Henson, & Martin, 2006). However, how does priming based on formal structure relate to priming based on temporal structure? One may expect an impact of both, formal and temporal predictability on the P50 and N100 and furthermore, a potential influence of temporal predictability on the quality of the processing of formal structure. Hence, we hypothesized that varying formal and temporal predictability independently should lead to a modulation of the P50 and N100, indicating an inverse relation between ERP amplitude and predictability. In other words, ERP responses should be smaller for standard events presented with predictable temporal structure (maximized expectation) relative to deviant events presented with predictable temporal structure as well as standard events and deviant events presented with unpredictable temporal structure (minimized expectation). Furthermore, considering that auditory deviance processing evolves in time and across several processing stages, we hypothesized that earlier processing stages (P50) may co-vary with later processing stages (N100). This should be confirmed by correlations of ERP amplitudes and latencies. Finally, varying task demands (pre-attentive and attentive task instructions), should reveal whether formal and temporal regularity-encoding at early stages of auditory processing can be considered automatic or whether they differ as a function of task demands.

## 2. Methods

Parameters for data acquisition and analysis of long-latency ERP components are described in detail elsewhere (Schwartz et al., 2011). Here we focus on P50 and N100 only. The EEG was recorded with a standard 10–20 international system 64-channel setup, a mastoid reference, and ground placed on the sternum. The study comprised two experimental sessions. A pre-attentive session, in which participants ( $N=24$ , 12 female) were listening to auditory oddball sequences while watching a silent video, and an attentive session on a consecutive day, in which participants silently counted deviant tones while fixating an asterisk on a computer screen. Oddball sequences consisted of 512 standard (300 ms, 10 ms rise and fall, 600 Hz), and 128 deviant (300 ms, 10 ms rise and fall, 660 Hz) sinusoidal tones (ratio 4:1) presented within either regular or irregular temporal structure (Fig. 1). Pseudo-randomization ensured that four standard tones were presented at the beginning of each sequence, and that no more than two deviants followed each other in a row.

Raw data from each participant were filtered prior to all subsequent analyses. A broad range of band-pass-filter settings has been used for P50 analyses in previous studies narrowing the critical band to 10–50 Hz (for a review see Patterson et al., 2008). However, for the combined analyses of the P50 and N100, we used a 5–75 Hz filter, as a more narrow filter would interfere with the analysis of the N100. Automatic rejection, followed by manual rejection of artifacts as well as epochs for all tones following a deviant tone was performed for epochs lasting from  $-75$  ms to 175 ms relative to stimulus onset. Statistical analyses were conducted in the following time-windows: 50–85 ms (P50) and 100–145 ms (N100) in six regions of interest (ROIs): frontal (left: AF7, AF3, F9, F7, F5, F3; right: AF8, AF4, F10, F8, F6, F4) central (left: T7, C5, C3, TP7, CP5, CP3; right: T8, C6, C4, TP8, CP6, CP4), and parietal (left: P7, P5, P3, PO7, PO3, O1; right: P8, P6, P4, PO8, PO4, O2). A separate ROI contained only midline electrodes (FZ, FCZ, CZ, CPZ, PZ, POZ). Correlation analyses were conducted using peak-amplitude and peak-latency measures for maxima across midline-electrodes, i.e., data obtained from FCZ for the P50 and from CZ for the N100 component.

## 3. Results

Precision in the counting task was at 97.78% for regular, and 98.04% for irregular sequences suggesting that the participants paid attention to the stimulus sequences. Visual inspection of the ERPs reveals a dissociation of the P50 and N100 components as a function of formal and temporal predictability (Fig. 2A). The ERP

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