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Implicit variations of temporal predictability: Shaping the neural oscillatory and behavioural response

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ABSTRACT

Being able to predict *when* an event will occur (temporal predictability) can help us prepare and time our responses. We here sought to delineate the neural and behavioural corollaries of highly implicit, probabilistic temporal predictability in an auditory foreperiod paradigm. To this end, we measured electroencephalography (EEG) and response times in two independent experiments (total N =46). Unbeknownst to participants, we induced a probabilistic variation of cue-target delays (i.e., foreperiods) in a pitch-discrimination task on a noise-embedded tone: The smaller the standard deviation of the underlying foreperiod distribution, the more predictable the time of target occurrence should be. Both experiments showed that more predictive foreperiods sped up listeners' responses. Crucially, neural signatures of temporal predictability emerged when comparing EEG activity between conditions of varying temporal predictability. First, cue-related P2 evoked responses were less pronounced for cues that implicitly signalled temporal predictability of target occurrence. Second, in both experiments, fronto-central delta (1–4 Hz) phase coherence was found relatively reduced during predictive foreperiods. Concomitantly, in Experiment II, the most predictive condition yielded a central alpha (7–12 Hz) power increase just before the most likely time point of tone onset, likely reflecting improved temporal orienting of attention. In sum, neural oscillations in anticipation of, and response times to a target show that humans are susceptible to even strictly implicit, probabilistic temporal regularities.

1. Introduction

The input to our senses has temporal structure. This structure can be a rhythm like in speech or music or an informative duration as when thunder followings lightening. Extracting this temporal structure can help predict the temporal occurrence of new input and prepare a response. Previous research has shown that the processing of sensory stimuli can be facilitated by temporal predictability, resulting in faster response times (Bueti et al., 2010; Cravo, Rohenkohl et al., 2011; Janssen and Shadlen, 2005; Rohenkohl et al., 2011; Rohenkohl and Nobre, 2011; Stefanics et al., 2010; Tomassini et al., 2016), as well as enhanced detection or discrimination performance (Cravo et al., 2013; Herrmann et al., 2016; Rohenkohl et al., 2012; Wilsch et al., 2014; Wright and Fitzgerald, 2004).

A common way to induce temporal predictability is by manipulating the time interval between cue and target in a trial-based design, i.e. the foreperiod. Notably, most previous studies used either two discrete foreperiods (e.g. Cravo et al., 2011; but see Tomassini et al., 2016), or participants were made aware of the temporal contingencies by explicit temporal cues (e.g. Stefanics et al., 2010). Thus an overriding aim of the two studies presented here was to test whether temporal predictive processing occurs also in a more naturalistic paradigm, that uses probabilistic distributions of foreperiods, introduced implicitly. There were no temporally informative cues and participants were not informed of the manipulation or relevance of timing. While temporal predictability can of course be studied in any modality, we here chose an auditory pitch discrimination task and measured response times and electroencephalographic (EEG) activity to assess the behavioural and neural mechanisms of temporally predictive processing.

What are feasible hypotheses on a neural level when listeners are faced only with such probabilistic, highly implicit temporal predictability? Given the short time scale on which temporal predictions most often occur (in the range of hundreds of milliseconds to few seconds), M/EEG studies are most suited to observe underlying mechanisms. Accordingly, various correlates of temporally predictive processing have been revealed. In the time-domain, the best established neural correlate of temporal processing is the contingent negative variation, a slow negative potential that builds up over frontal brain areas during duration estimation (CNV; Herbst et al., 2014; Macar et al., 1999; Walter et al., 1964). Although studies have reported effects of temporal

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predictability on the CNV (Macar and Vidal, 2004; Praamstra and Pope, 2007), it is unclear whether such effects depend on the involvement of explicit timing processes or wheter they could be found in an implicit timing paradigm. Furthermore, temporal predictability affected N1 and P3 components of the event-releated potential in auditory studies (Lange, 2013; Volosin et al., 2016).

In the time-frequency domain, no unique neural substrate has been identified: as recently reviewed by Wiener and Kanai (2016), all established frequency bands of the human EEG (delta, theta, alpha, beta, gamma) have been found to carry information about temporal predictions. On the one hand, the variety of relevant frequency bands might be explained by different stimulation frequencies used in previous studies (either by deliberately presenting rhythmic stimuli, or by inducing a dominant rhythm through the stimulus and inter-stimulus intervals in trial-based studies). On the other hand, the frequencies at which effects are found likely depend on the sensory modality studied, as well as the task used (e.g. response time tasks, detection tasks, discrimination tasks).

Consensus is arising, however, that slow oscillations convey temporally predictive information, both in the delta (0.1–4 Hz) and theta (4–8 Hz) band (Cravo et al., 2013; Herbst and Landau, 2016; Herrmann et al., 2015, 2016; Parker et al., 2014; Stefanics et al., 2010; Wilsch et al., 2015). A putative mechanism governing temporally predictive processing might be the entrainment of these slow frequencies to the temporal structure of the stimulation, such that if the stimulus occurs at the predicted time point the system is in a particular, beneficial state (Schroeder and Lakatos, 2009). Previous evidence would thus predict that neural delta phase should become optimally aligned to occurrence of a relevant target event if participants can predict its onset. This should surface as enhanced delta phase coherence over trials in predictive compared to non-predictive blocks, potentially also for the highly implicit and probabilistic distribution of foreperiods employed here.

Complementary to neural phase alignment of slow oscillations, phasic changes in the power of alpha (8–12 Hz) and beta (15–30 Hz) oscillations reflect temporal predictions. Changes in alpha power have generally been subscribed to orienting of attention, mostly in space (Hanslmayr et al., 2007; Klimesch et al., 2007; Strauß et al., 2014; Wöstmann et al., 2016). Recent studies from the visual domain have shown that attention can also be oriented in time, i.e. to a cued time point, and that this orienting of attention is reflected by reduced alpha power over visual areas (Praamstra and Pope, 2007; Rohenkohl et al., 2012; Rohenkohl and Nobre, 2011). To our knowledge, no study so far has provided a direct link between alpha power and orienting of temporal attention in an auditory task. Changes in beta power have been related to temporal preparation directly, especially in the auditory domain, e.g. by the observation of higher beta power prior to a temporally predictable stimulus (Arnal, 2012; Kononowicz and Rijn, 2015; Todorovic et al., 2015). In sum, we were expecting to find differences in alpha and/or beta power during high (versus low) temporal predictability.

To study the behavioural and neural mechanisms of temporally predictive processing in a strictly implicit, probabilistic setting, we performed two independent experiments using an auditory foreperiod paradigm. Participants were instructed to perform a simple pitch discrimination task, while we implicitly introduced temporal regularities by varying foreperiods – the time interval between a cue and the target tone – between blocks. Foreperiods were drawn from three different probability distributions: a uniform distribution (non-predictive), and two Gaussian distributions with varying standard deviation (weakly and strongly predictive, respectively). The smaller the standard deviation of the probability distribution, the more predictable the foreperiod duration in that condition.

In Experiment I, we presented three blocks in fixed order, to maximize potential condition differences: Non-predictive, strongly predictive, and again non-predictive foreperiods. In Experiment II we chose a more fine-grained approach and employed non-predictive, weakly predictive, and strongly predictive blocks in random order to study how flexibly temporal regularities can be utilized.

We compared EEG activity prior to target onset for intervals with high versus low temporal predictability. Differences in response times across foreperiods and between conditions indicate that temporal predictability was utilized to perform the task. Several signatures of the neural data confirm the utilization of temporal predictability: we found condition differences in the cue- and target-evoked event related potentials, in delta ITC during the foreperiod (albeit in the opposite direction as predicted), and in alpha power prior to the target event (only in Experiment II).

2. Materials and methods

2.1. Participants

A total of 46 healthy participants took part in the two studies: N = 22 in Experiment I (mean age 26 years ± SD 2.9; 14 female, three left-handed, one both-handed), and N = 24 in Experiment II (mean age 23.9 ± SD 2.2 years; 11 female, all right-handed). All participants reported normal hearing and no history of neurological disorders and were naïve with respect to the experimental manipulations. Participants gave informed consent and received payment for the experimental time (7 € per hour). The study procedure was approved by the local ethics committee (University of Leipzig, Leipzig, Germany).

2.2. Stimuli and Paradigm

Two independent EEG experiments were conducted in an electrically shielded sound-attenuated EEG booth. Study setups were similar except for differences reported below. Stimulus presentation and collection of behavioural responses was achieved using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Responses were entered on a custom-built response box, using the fingers of the right hand for the pitch judgement and the fingers of the left hand for a subsequent confidence rating. Auditory stimuli were delivered via headphones (Sennheiser HD 25-SP II) at 50 dB above the individual's sensation level.

Stimuli were pure tones of varying frequencies (duration 50 ms with a 10 ms on- and offset ramp), embedded in low-pass filtered white noise. In Experiment I, sensation level was individually predetermined for a 750-Hz tone presented without noise using the method of limits, and then augmented by 50 dB. Relative to that, noise with a tone-to-noise ratio of −12 dB was then employed. In Experiment II, a similar procedure was performed using the noise to predetermine sensation level instead, and a more adverse tone-to-noise ratio of −16 dB was chosen to render the tone-noise differentiation harder. Since pilot testing had revealed stronger utilization of temporal predictability in more challenging listening situations, we used a more negative signal-to-noise ratio to promote the use of temporal predictability.

Participants had to perform a pitch discrimination task on a single tone, presented in noise: 'was the tone rather high or low?' (for an exemplary trial see Fig. 1a). Target tones varied in individually predetermined steps around a 750-Hz standard, which was itself never presented. The minimal difference in frequency needed to correctly classify a tone as 'high' or 'low' with 71% performance was determined using a staircase procedure individually for each participant. The staircase procedure was performed twice and the average step size was used to present tones one to five times this difference above and below the standard (in logarithmic steps).

The beginning of each trial was indicated by the simultaneous onset of the fixation cross and the noise. After giving their response to the target tone, participants were asked to indicate their confidence about the judgement on a three-point scale. Inter-stimulus intervals (ISI) were drawn from a truncated exponential distribution (mean 1.5 s, truncated