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Low-frequency cortical oscillations are modulated by temporal prediction and temporal error coding

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ABSTRACT

Monitoring and updating temporal predictions are critical abilities for adaptive behavior. Here, we investigated whether neural oscillations are related to violation and updating of temporal predictions. Human participants performed an experiment in which they had to generate a target at an expected time point, by pressing a button while taking into account a variable delay between the act and the stimulus occurrence. Our behavioral results showed that participants quickly adapted their temporal predictions in face of an error. Concurrent electrophysiological (EEG) data showed that temporal errors elicited markers that are classically related to error coding. Furthermore, intertrial phase coherence of frontal theta oscillations was modulated by error magnitude, possibly indexing the degree of surprise. Finally, we found that delta phase at stimulus onset was correlated with future behavioral adjustments. Together, our findings suggest that low frequency oscillations play a key role in monitoring and in updating temporal predictions.

1. Introduction

Several environmental events occur regularly in time. We can take advantage of these regularities to generate temporal predictions that can enhance performance (Nobre et al., 2007; Rohenkohl et al., 2012; Vangkilde et al., 2012). For a prediction system to be successful, it is important to keep it constantly updated by monitoring when errors take place and applying the appropriate corrections. However, most temporal prediction studies have focused on situations in which there is an established temporal relation between events and little need for error monitoring and prediction updates.

Although rare in the temporal domain, several studies have investigated how our brain codes other types of prediction errors. In reinforcement learning, negative feedback has been linked to an electroencephalographic component called feedback related negativity (FRN) (Walsh and Anderson, 2012). The FRN is a frontal-central negative deflection in the event-related potential (ERP) that peaks at around 300 ms following a feedback that indicates losses or an error (Walsh and Anderson, 2012). More recently, it has been hypothesized that the FRN could be generated by perturbations in local theta band oscillations (Cavanagh et al., 2010; Cohen et al., 2007). Such perturbations are described as an increase in power and phase coherence in this frequency band in frontocentral regions (Cavanagh et al., 2010). In this view, theta oscillations would serve as a communication mechanism between brain networks, by which errors would alter oscillatory patterns and optimize the communication and the computation of relevant information (Cavanagh and Frank, 2014; Cavanagh et al., 2009). However, whether such mechanism can also be used for temporal error coding is still unknown.

As previously mentioned, the majority of studies that investigate how temporal predictions modulate performance have participants performing a task after the temporal relation between events has been learned. These studies have shown that low-frequency oscillatory brain activity (as delta, from 1 to 4 Hz) can optimize cortical excitability and enhance the processing of stimuli occurring at predicted moments (Cravo et al., 2013, 2011; Lakatos et al., 2008; Schroeder and Lakatos, 2009), as well as impair processing of temporally unexpected stimuli (Stefanics et al., 2010; van den Brink et al., 2014). Importantly, a recent study has shown that similar mechanisms seem to be involved in tasks that require a temporal judgment about the interval itself, and not just the use of the temporal information to form expectations (Arnal et al., 2014). This result supports the hypothesis that neural oscillations might serve as a possible neural mechanism for temporal predictions (Arnal and Giraud, 2012; Morillon and Barbot, 2013).

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Therefore, although oscillatory mechanisms have been proposed to be important in error coding and temporal predictions, it remains largely unknown whether they are used when we need to learn and monitor a temporal prediction. Here, we investigated the neural mechanisms underlying violation and updating of temporal predictions. We developed a behavioral task in which participants had to monitor whether a temporal error had been made. We analyzed ERPs and oscillatory changes evoked by temporal errors in EEG recordings and investigated whether they were linked to theta oscillations. Finally, we looked for correlations between behavioral adjustment and the phase of delta oscillations.

2. Materials and methods

2.1. Participants

Twenty volunteers (18–30 years old; 11 female) gave informed consent to participate in the study. All participants had normal or corrected-to-normal vision and were free from psychological or neurological diseases. The experimental protocol was approved by the University Research Ethics Committee. Three participants did not reach the minimal performance criterion and had their data excluded from the analyses (see below for criterion of exclusion).

2.2. Stimuli and procedures

Stimuli were presented using the Psychtoolbox v.3.0 package (Brainard, 1997) for MATLAB on a 17-inch CRT monitor with a vertical refresh rate of 60 Hz, placed 50 cm in front of the participant. Each trial started with a fixation point. After an interval of 1.5 s, two identical audiovisual cues were presented sequentially separated by an interval of 1 second. These cues consisted of a bulls-eye (3 degrees of visual angle) presented in the center of the screen and an auditory tone (1000 Hz, 70 dB) both presented for 100 ms.

A third stimulus (which we refer to as the target) was an auditory tone (500 Hz, 70 dB) presented for 100 ms. The temporal onset of this target was controlled by the participants. Their main task was to generate the target (tone) at an expected time point by pressing a button while taking into account the inserted delay between their press and the target occurrence. Participants were instructed that the interval between the second cue and the target should be identical to the interval between the first and second cues. Therefore, in order to produce the target at the correct moment, they had to consider the delay between their action and target presentation. Participants were told that the interval between the two cues was constant throughout the experiment, but the exact interval value (1 s) was never mentioned (Fig. 1A).

A delay was inserted between each button press and the occurrence of the target. In the first few trials of each block, the delay between action and target was 50 ms (standard delay). However a new delay between 300 ms and 700 ms was inserted in a given trial within the block and remained fixed for five trials. The change in the action-target delay was intended to cause a temporal prediction violation and have the target appear latter than expected by the participant. Once the new delay had been inserted, participants had to update their temporal model and anticipate their action in order to make the target appear at the appropriate moment in the remaining trials of the block. After five trials with the new delay had been presented, that particular block ended. Thus, each experimental block started with standard delay trials and ended with five new delay trials (Fig. 1B).

Participants were informed that the action-target delay would change in a given trial and remain fixed for five trials, after which the current block would end. Importantly, they could not predict when or by how much the delay would change, as the new delay could be inserted randomly between the 4th and 15th trial in each block. Moreover, a change in delay was made only if participants' absolute errors in the previous three standard delay trials were smaller than 100 ms (i.e., if the target appeared between 900–1100 ms after the second cue). If the participant did not reach this criterion until the 15th standard delay trial, a new delay was inserted in the 16th trial. These two rules inhibited behavioral anticipation to the new delay.

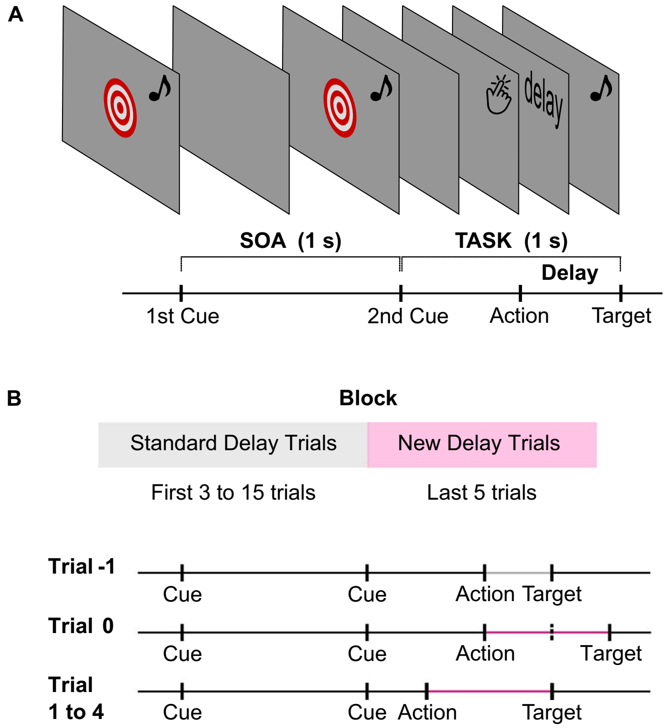

Fig. 1. Schematic illustration of task structure. A) The main task was to generate a third stimulus (target) at an expected time point, by pressing a button while taking into account the delay between the act and target occurrence. Participants were instructed that the interval between the second cue and the target should be identical as the interval between the first and second cues. B) All blocks started with trials where the action-target delay was 50 ms (standard delay trials). At a given trial, a new delay (between 300 ms and 700 ms) was inserted and kept constant for five trials. In trial −1 (before the new delay is inserted), participants are adapted to the delay of 50 ms between their action and outcome and perform the button press at the appropriate moment. In trial 0 (when the new delay is inserted), the outcome comes later than expected. Based on this error, in the following trials (1 to 4) participants have to update their temporal prediction and anticipate their action.

Participants who failed to perform well with the standard delay for more than 10% of the blocks were excluded from the analyses. Blocks in which the participant did not reach the performance criterion until the 15th trial were excluded from both behavioral and EEG analyses. Temporal errors over 1.5 seconds were considered omission errors and removed from subsequent analyses (three trials in total, one omission error for three different participants). Importantly, explicit feedback about the participant's performance was given only at the end of each experimental block. Therefore, no information about errors was shown throughout a block and participants could only extract information about their performance based on their own temporal predictions. Each session consisted of 50 blocks, and lasted between 40 to 60 min. Each block consisted of 8 to 20 trials. Participants underwent two blocks of practice trials before the experimental session began.

2.3. EEG recordings and pre-processing

EEG was recorded continuously from 64 ActiCap Electrodes (Brain Products) at 1000 Hz by a QuickAmp amplifier (Brain Products). All sites were referenced to FCz and grounded to AFz. The electrodes were positioned according to the International 10–10 system. Additional bipolar electrodes registered the electrooculogram (EOG).

EEG pre-processing was carried out using BrainVision Analyzer