Temporal context actively shapes EEG signatures of time perception

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Abstract

Our subjective perception of time is optimized to temporal regularities in the environment. This is illustrated by the central tendency effect: when estimating a range of intervals, short intervals are overestimated whereas long intervals are underestimated to reduce the overall estimation error. Most models of interval timing ascribe this effect to the weighting of the current interval with previous memory traces *after* the interval has been perceived. Alternatively, the *perception* of the duration could already be flexibly tuned to its temporal context. We investigated this hypothesis using an interval reproduction task with a shorter and longer interval range. As expected, reproductions were biased towards the subjective mean of each presented range. EEG analysis showed that temporal context affected neural dynamics during the perception phase. Specifically, longer previous durations decreased CNV and P2 amplitude and increased beta power. In addition, multivariate pattern analysis showed that it is possible to decode context from the transient EEG signal quickly after the onset and offset of the perception phase. Together, these results suggest that temporal context creates dynamic expectations which actively affect the *perception* of duration.

Keywords: time perception; context; Bayesian perception; EEG

Significance Statement

The subjective sense of duration does not arise in isolation, but is informed by previous experiences. This is demonstrated by abundant evidence showing that duration estimates are biased towards previously perceived time intervals. However, it is yet unknown whether this temporal context actively affects perception or asserts its influence in later, post-perceptual stages as proposed by most current formal models of this task. Using an interval reproduction task, we here show that EEG signatures flexibly adapt to the temporal context during perceptual encoding. Furthermore, interval history could be decoded from the transient EEG signal even when the current duration was identical. All in all, our results suggest that context actively influences perception.

Introduction

The way humans experience time is not only driven by the current stimulus, but is also influenced by previous experiences. According to Bayesian observer models, humans integrate noisy sensory representations (the likelihood) with previously learned stimulus statistics (the prior distribution). This is illustrated by the temporal context or central tendency effect: when presented with a range of intervals, short intervals are overestimated and long intervals are underestimated (Jazayeri & Shadlen, 2010). Furthermore, the prior distribution has been shown to be dynamically updated, such that more recent intervals have a greater influence on the current estimate (Dyjas, Bausenhart, & Ulrich, 2012; Taatgen & van Rijn, 2011; Wiener, Thompson, & Branch Coslett, 2014). Although there is abundant behavioral evidence for Bayesian integration in human time perception (Acerbi, Wolpert, & Vijayakumar, 2012; Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Gu, Jurkowski, Lake, Malapani, & Meck, 2015; Hallez, Damsma, Rhodes, van Rijn, & Droit-Volet, 2019; Jazayeri & Shadlen, 2010; Maaß, Riemer, Wolbers, & van Rijn, 2019; Maaß, Schlichting, & van Rijn, 2019; Roach, McGraw, Whitaker, & Heron, 2017; Schlichting et al., 2018; Shi, Church, & Meck, 2013), its temporal locus and neural underpinnings are not yet understood.

Computational models of interval timing often (implicitly) assume that after perception has completed, the noisy interval percept is weighted with previous memory traces representing the prior (e.g., Di Luca & Rhodes, 2016; Jazayeri & Shadlen, 2010; Taatgen & van Rijn, 2011). Alternatively, however, prior experience might actively affect perception, as evidenced by recent behavioral (Cicchini, Mikellidou, & Burr, 2017), fMRI (St. John-Saaltink, Kok, Lau, & De Lange, 2016) and single neuron findings (Sohn, Narain, Meirhaeghe, & Jazayeri, 2019). Specifically, Sohn et al. (2019) showed that neurons in the prefrontal cortex of monkeys exhibited different firing rate patterns based on the prior during interval estimation.

In humans, evidence is now emerging that electroencephalography (EEG) signatures in timing tasks are modulated by recently perceived durations. In a bisection task, longer prior durations led to a larger amplitude of the contingent negative variation (CNV) and increased beta oscillations power (Wiener, Parikh, Krakow, & Coslett, 2018; Wiener & Thompson, 2015). Crucially, however, these studies required an active comparison to the standard interval, in which EEG signatures have

been shown to reflect an adjustment of the decision threshold (Ng, Tobin, & Penney, 2011; see also Boehm, Van Maanen, Forstmann, & van Rijn, 2014). Any context-based changes in these signatures might reflect updating of the comparison process. It is therefore still an open question what the temporal locus of the context effect is: does the prior exert its influence in post-perceptual stages or are purely perceptual processes already affected by previous experiences?

We tested the influence of temporal context in an interval reproduction task, which allowed us to distill EEG signals during the perception phase in which no decision or motor response was required that could yield fallacious conclusions regarding the effect of context effects during perception. Participants reproduced two different interval ranges (the *short* and the *long context*). The ranges shared one interval (the *overlapping interval*), providing a condition in which the physical stimulus was the same, but the temporal context was different. We show that temporal context affects three EEG signatures that have previously been associated with time perception during the perception phase: the CNV and beta oscillations, but also the offset P2, which has recently been shown to predict subjective interval perception better than the CNV (Kononowicz & van Rijn, 2014). A data-driven approach reveals that temporal context can be decoded from transient neural dynamics during the perception phase using multivariate pattern analysis (MVPA). Together, these results show that temporal context actively shapes the perception of duration, falsifying most current formal theories of interval timing.

Materials and Methods

Participants

Twenty-seven healthy adults (22 females; age range 18 - 33 years, $M = 21.33$, $SD = 3.78$ years) participated in the experiment for course credits in the University of Groningen Psychology program or monetary compensation (€ 14). Two participants were excluded from analysis during pre-processing due to excessive artifacts in the EEG data. The study was approved by the Psychology Ethical Committee of the University of Groningen (17141-S-NE). Written informed consent was obtained before the experiment. After the experiment, the participants were debriefed about the aim of the study.

Stimuli and apparatus

Stimuli were presented using the Psychophysics Toolbox 3.0.12 (Brainard, 1997; Kleiner et al., 2007) in Matlab 2014b. Intervals were presented as continuous 440 Hz sine wave tones. These auditory stimuli were presented on Sennheiser HD 280 Pro stereo headphones at a comfortable sound level. Visual stimuli were presented in the center of the screen in Helvetica size 25 in white on a dark grey background using a 27-inch Iiyama ProLite G27773HS monitor with a 1920x1080 resolution at 100 Hz. The index-finger trigger buttons of a gamepad (SideWinder Plug & Play Game Pad, Microsoft Corporation) were used to record responses.

Procedure

Participants performed an auditory interval reproduction task (Figure 1A). Every trial started with a central fixation cross with a uniform random duration between 2 and 3 s. Then, an exclamation mark was presented for 0.7 s. While the exclamation mark stayed on the screen, the auditory interval was presented (the *perception phase*). To signal the next phase, a question mark was presented for 1.5 s. Next, the continuous tone was presented again, which participants had to terminate by pressing a button (the *reproduction phase*). Participants were instructed to match the duration of this second tone to the duration of the first tone as accurately as possible.

The task involved two different interval ranges, the short context (0.625 s, 0.75 s, and 0.9 s) and the long context (0.9 s, 1.08 s, and 1.296 s) (Figure 1A). Crucially, there was an *overlapping interval* that was presented in both contexts (0.9 s). The experiment consisted of four blocks, two of which used intervals of the short context, and two of which used intervals of the long context. Block order was counterbalanced across participants, with the constraint that the context would alternate every block. Within a block, each duration of the short or the long context was presented 30 times, amounting to a total of 90 trials per block and 360 trials over the whole experiment. The presentation order was random, with the constraint that every possible subsequent pair of intervals was presented equally often (i.e., first-order counterbalancing). The hand needed for reproduction was switched after two blocks. Prior to each block, participants were instructed which hand (i.e., which gamepad button) they would use to terminate the duration and which set of intervals would be presented (termed set A and set B for the short and long context, respectively; see also Maaß, Schlichting, et al., 2019), while

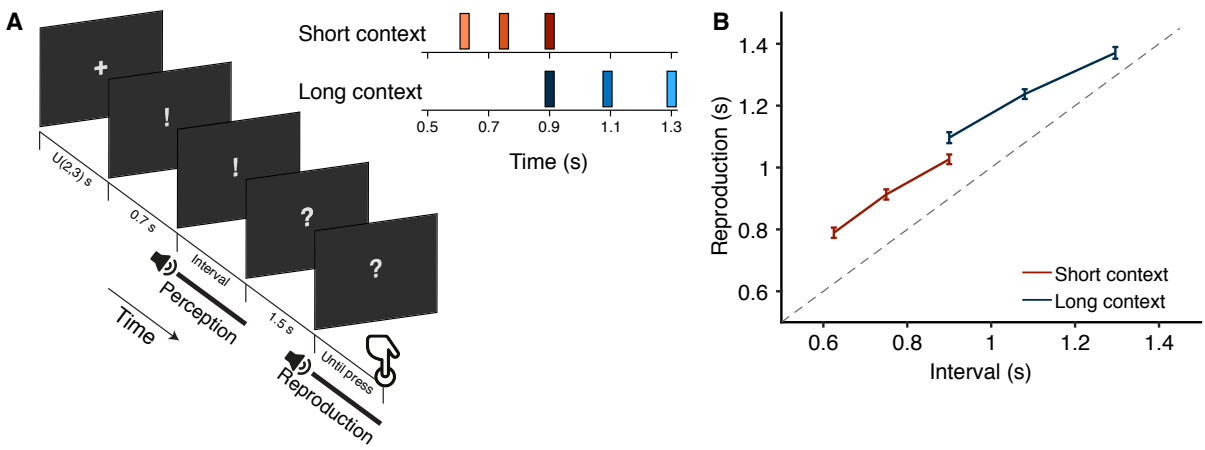

Figure 1. Task and behavioral results. A) Behavioral procedure of the experiment. Participants performed an interval reproduction task in which they heard a tone for a certain duration (*perception phase*). After an ISI of 1.5 s, they were asked to reproduce this duration by pressing a button to indicate the offset of the *reproduction phase*. In separate blocks, the perception phase consisted of three short or three relatively long durations (the *short* and the *long context*, respectively). One interval was presented in both contexts (the *overlapping interval* of 0.9 s). B) Average behavioral reproduction results. Error bars represent the standard error of the mean.

they were not informed about the nature of these sets (i.e., that the sets were associated with interval range). Participants could take self-timed breaks between blocks. Prior to the experiment, participants performed two practice trials with durations outside the range of both context conditions (0.4 s and 2 s). Experiment scripts are available at https://osf.io/sgbjz/.

EEG acquisition

EEG signals were recorded from 62 Ag/AgCl electrodes, placed in accordance with the international 10-20 system (WaveGuard EEG cap, eemagine Medical Imaging Solutions GmbH, Berlin, Germany). The ground electrode was placed onto the left side of the collarbone and the mastoids served as location for the reference electrodes. The electrooculogram (EOG) was recorded from the outer sides of both eyes and from the top and bottom of the left eye. Data was collected at a sampling frequency of 512 Hz using a TMSi Refa 8-64 amplifier. Before the experiment, impedances of all electrodes were reduced to below 5kΩ. Participants were instructed to blink only between trials and not to move during the experiment.

EEG pre-processing

EEG pre-processing was performed using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). EEG data was re-referenced to the averaged mastoids and filtered using a

Butterworth IIR band-pass filter with a high-pass frequency of 0.01 Hz and a low-pass frequency of 80 Hz. Subsequently, trial epochs were created from -1 s until 6 s relative to the onset of the perception phase. Artifacts were corrected using independent component analysis (ICA). Epochs that exceeded an amplitude range of 120 µV were removed from the dataset. On average, 10.72% (SD = 6.10) of the 360 trials were discarded.

Data Analysis

Behavioral analysis. Reproductions lower than 0.1 s and higher than 2 s were excluded from analysis (0.2% of the data). To test whether reproductions were influenced by context, we fitted a linear mixed model (LMM) using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) in R (R Core Team, 2016), including Interval, Context, their interaction and N-1 interval (i.e., the interval in the previous trial) as fixed factors. To facilitate interpretation of the results, Interval and N-1 interval were centered at 0.9 s and the factor Context was recoded using effect coding (-0.5 for short and 0.5 for long context). In addition to the random intercept of Subject, we sequentially added random slope terms and tested whether they improved the model with a likelihood ratio test. We will here report the results of the best fitting model, which included random slopes for Interval and N-1.

ERP analysis. All EEG analyses reported here focused on the perception phase. A brief overview of the EEG results in the reproduction phase is available at https://osf.io/sgbjz/. The CNV and beta signatures in the reproduction phase show trends that are qualitatively similar to the perception phase, although they appear to be less strong.

CNV. The CNV analysis was performed on a fronto-central electrode cluster (FCz, FC1, FC2, and Cz) (cf., Kononowicz & van Rijn, 2014). A 10 Hz Butterworth low-pass filter was applied and the ERP was baselined to the average signal in the 0.1 s window before interval onset. To test the effect of global context during the perception phase, we compared the ERP of the overlapping interval in the short and the long context using a cluster-based permutation test (Maris & Oostenveld, 2007) in the window 0-1.2 s from interval onset. The permutation test assessed whether the difference was different from zero by computing 100.000 permutations using the *t*-statistic, controlling for multiple comparisons with a cluster significance threshold of $p < .05$. To assess the influence of the previous trial (N-1) on CNV, we calculated the average amplitude in the time window that showed CNV

differences in the previously mentioned permutation test (0.3-1.01 s), per participant, context and N-1 for the overlapping interval. Next, we tested a LMM predicting this amplitude, including N-1 and Context as fixed factors, and Subject as a random intercept term.

Offset P2. The P2 analysis focused on the EEG signal at FCz, to which a 1–20 Hz Butterworth bandpass filter was applied to minimize CNV-based contamination (cf., Kononowicz & van Rijn, 2014). The ERP was baselined to the average signal in the 0.1 s window around interval offset (cf., Kononowicz & van Rijn, 2014). P2 peak amplitude was defined as the maximum amplitude between 0.15 and 0.24 s. This window was based on visual inspection of the averaged waveforms. We fitted a LMM predicting P2 amplitude, with Interval, N-1, Context, and the absolute difference between the previous and the current interval as fixed factors, and Subject as a random intercept term. Random slopes did not improve the model fit. We also fitted a model predicting P2 latency with the same factors.

Multivariate pattern analysis. To investigate transient neural dynamics in more detail, we tested whether it is possible to decode global and local context through MVPA of the EEG signal. Following Wolff, Kandemir, Stokes, and Akyürek (2020), we used a sliding window approach in which the EEG fluctuations were pooled over electrodes and time. A window of 50 data points (98 ms) was moved across the signal in steps of 8 ms, separately for each channel. Within the window, the signal was down-sampled to 10 samples (by taking the average over 5 samples) and baseline-corrected by subtracting the mean within the window from all 10 individual samples.

To decode whether an overlapping-interval trial was presented in the short or the long context, the 10 samples per electrode in each time window served as input for 5-fold cross-validation. In each fold, we calculated the Mahalanobis distance (De Maesschalck, Jouan-Rimbaud, & Massart, 2000; Wolff, Jochim, Akyürek, & Stokes, 2017; Wolff et al., 2020) between the test trials and the averaged signal of the short and long context, using the covariance matrix estimated from the training trials with a shrinkage estimator (Ledoit & Wolf, 2004). To make the distance estimates more reliable, the 5-fold cross-validation was repeated 50 times and results were averaged. The eventual decoding distances were smoothed with a Gaussian smoothing kernel (SD = 16 ms). To test whether the

distance between conditions was significantly different from zero, a cluster-based permutation test was performed.

A similar analysis was performed to decode the duration of the previous interval (N-1) from the neural dynamics in the current trial. For the overlapping interval, the Mahalanobis distance between every test trial and the average of the N-1 conditions was calculated. In this way, we aimed to determine whether the distance was higher when the difference between the N-1 condition of the test trial and the other possible N-1 conditions was larger. Next, for every time point, we performed a linear regression on the Mahalanobis distance, using the absolute difference between N-1 conditions and difference between Context as predictors, allowing us to disentangle the effect of sequential and global context on transient neural dynamics. A cluster-based permutation test was performed on the resulting slope values for N-1 and Context, to test whether they deviated from zero (using a one-sided *t*-test).

To investigate which electrodes are most informative in decoding the context of an overlapping interval trial, we performed channel-wise decoding: the procedure to decode global context outlined above was performed separately for every electrode. Topographies were created to show the average decoding accuracy at the different electrodes during time windows in which decoding was significantly higher than zero, as identified by the cluster-based permutation test.

Time-frequency analysis. To assess oscillatory power during the perception phase we performed a time-frequency analysis using a single Hanning taper with an adaptive time window of 6 cycles per frequency in steps of 15 ms for frequencies from 4 to 40 Hz, with the amount of spectral smoothing set to 1. We calculated the absolute power from the baseline window of -0.2-0 s relative to interval onset. Based on earlier work (e.g., Kononowicz & van Rijn, 2015; Wiener et al., 2018), the analysis was focused on the FCz electrode. Similar to the CVN analysis, all time-frequency analyses were performed on the overlapping interval to isolate the effect of context while keeping the actual stimulus constant.

Per participant, for every time-frequency point, we fitted a linear regression model including N-1 (a continuous variable ranging from the shortest to the longest interval in seconds) and Context (short and long context coded as 0 and 1, respectively) as predictors (following an approach similar to

Wiener et al., 2018). For every time-frequency point, this resulted in two slope values, expressing the relative influence of the global context and the previous interval. Next, a one-sample *t*-test against zero was performed for the two slope values at each time-frequency point, which was corrected for multiple comparisons using cluster-based permutation (Maris & Oostenveld, 2007). The statistical testing was performed on the frequency range of 8-30 Hz to include alpha power (8–14 Hz**;** Kononowicz & van Rijn, 2015) and beta power (15–30 Hz; e.g., Haegens et al., 2011; Jenkinson & Brown, 2011; Kononowicz & van Rijn, 2015) during the time window of 0-1.2 s after interval onset.

Results

Behavioral results

Figure 1B shows the average reproductions for the different intervals. The results of the LMM showed that the reproductions increased with duration ($\beta = 0.77$, $t = 24.47$, $p < .001$). We found a significant effect of global context, showing that reproductions were longer in the long compared to the short context ($\beta = 0.046$, $t = 7.16$, $p < .001$). In addition, the increase with duration (i.e., the slope) was lower for the long compared to the short context ($\beta = -0.18$, $t = -7.15$, $p < .001$). Besides the global context effect, reproductions were influenced by the previous trial (N-1) ($\beta = 0.07$, $t = 3.55$, $p = .001$, not depicted).

ERPs

CNV. Figure 2A and 2B show the average fronto-central ERP during the perception phase for the different intervals in the short and the long context, respectively. In addition, Figure 2C shows a direct comparison between the short and the long context of this ERP for the overlapping interval (0.9 s). The cluster-based permutation test showed that the CNV was more negative in the short than in the long context in the time windows 0.30-0.65 s ($p = .004$) and 0.71-1.01 s ($p = .003$). Thus, while the actual interval was the same, CNV amplitude during perception differed depending on the temporal context.

Figure 2D shows the average ERP for the overlapping interval, split for the different previous durations. The LMM results showed that CNV amplitude became less negative with longer previous trials ($\beta = 2.50$, $t = 2.49$, $p = .014$). There was no additional significant effect of context ($\beta = 0.49$, $t =$

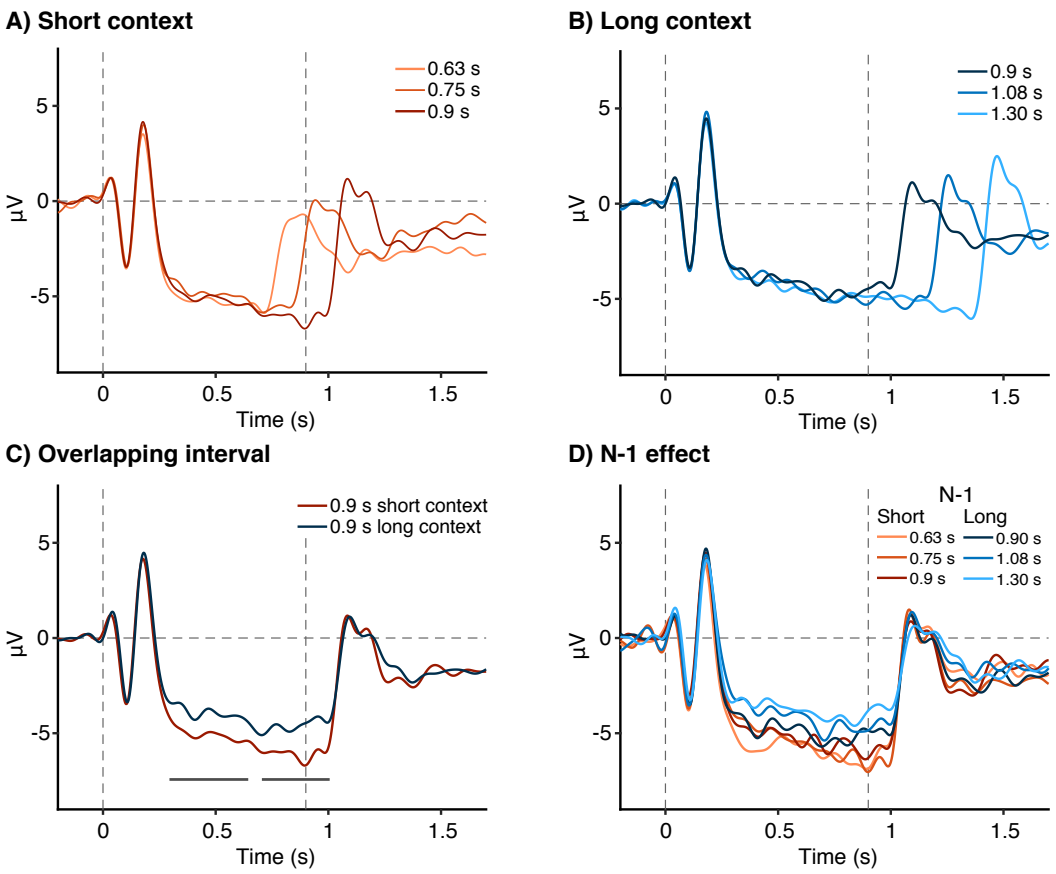

Figure 2. Average ERPs at the fronto-central cluster (FCz, FC1, FC2, and Cz) relative to the onset of the perception phase for the different durations in the short (A) and long (B) context. C) Average ERP of the overlapping interval (0.9 s) in the short and the long context. Grey horizontal bars indicate significant differences according to the cluster-based permutation test. D) Average ERP of the overlapping interval, split up according to the interval in the previous trial (N-1). Red and blue lines show whether the overlapping interval appeared in the short or the long context, respectively. In all panels, vertical grey dashed lines indicate interval onset and offset of the overlapping interval (0.9 s).

1.11, p = .267), suggesting that the global context effect on CNV might be largely driven by the previous trial.

Offset P2.

Amplitude. Figure 3A and 3B shows the offset P2 for the different intervals in the short and the long context. Figure 3C shows the average peak amplitude as a function of interval and context. The LMM showed that the P2 increased with duration (β = 8.22, t = 10.71, p < .001), but that the intercept was significantly lower for the long compared to the short context (β = -1.21, t = -2.86, p = .004). Figure 3E shows the effect of the previous interval (N-1) on P2 amplitude for the overlapping interval. In line with the global context effect, the model showed that the P2 decreased with longer

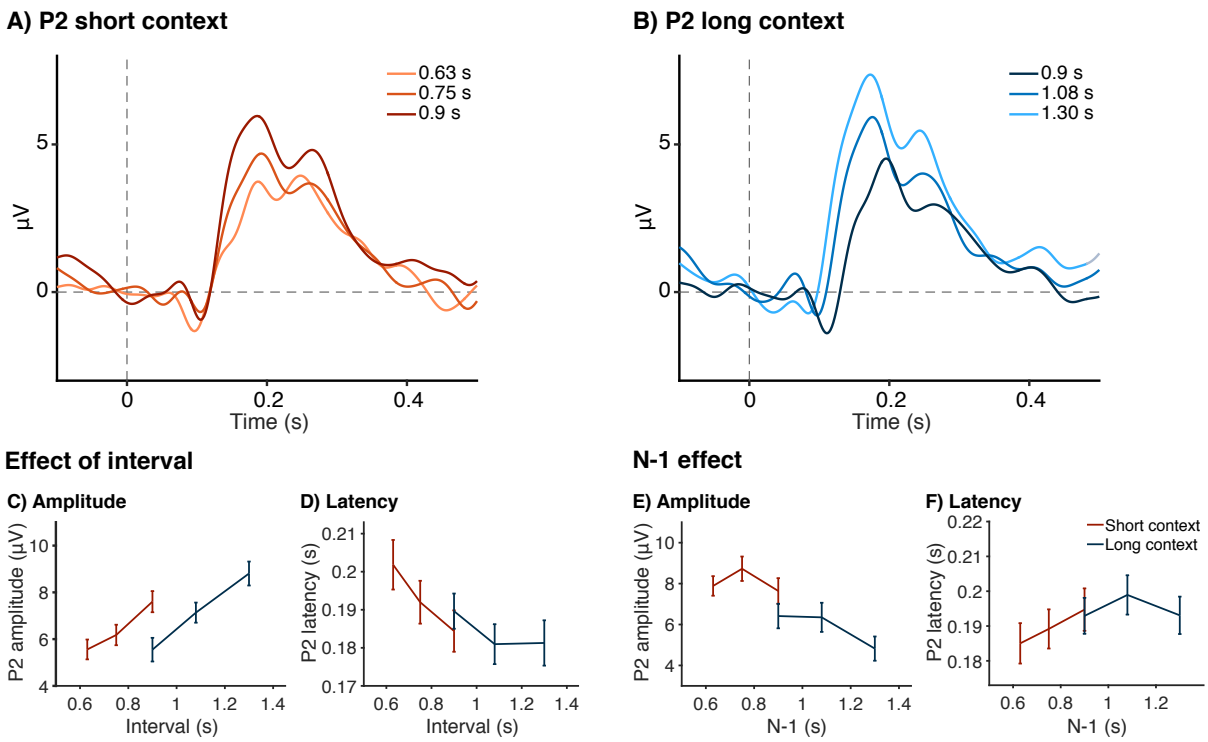

Figure 3. Amplitude and latency of the P2 at the FCz electrode after the offset of the perception phase. A, B) Grand average ERPs baselined at the offset in the short and the long context, respectively. C) Average peak amplitude, calculated as the maximum in the window 0.15-0.24 s after interval offset for every participant and interval. D) Average latency of P2 peak. E, F) Average P2 amplitude and latency for the overlapping interval as a function of the previous interval (N-1). In all figures, error bars represent the standard error of the mean.

previous intervals (β = -2.28, t = -2.97, p = .003). Together, these results show that P2 amplitude reflects the actual duration, as well as the global and local context in which the duration appeared.

Latency. Whereas the P2 latency might seem to decrease with the duration of the current interval in Figure 3D, the model showed that the only significant predictor of latency is the absolute difference between the previous and the current interval (β = -0.05, t = -11.64, p < .001). As can be seen in Figure 3F for the overlapping interval, the latency decreased when the current interval differed more from the previous. The other fixed factors did not reach significance (ps > .483). In summary, whereas P2 amplitude reflects the current duration and the general temporal context, P2 latency codes for the prediction error between the previous and the current interval.

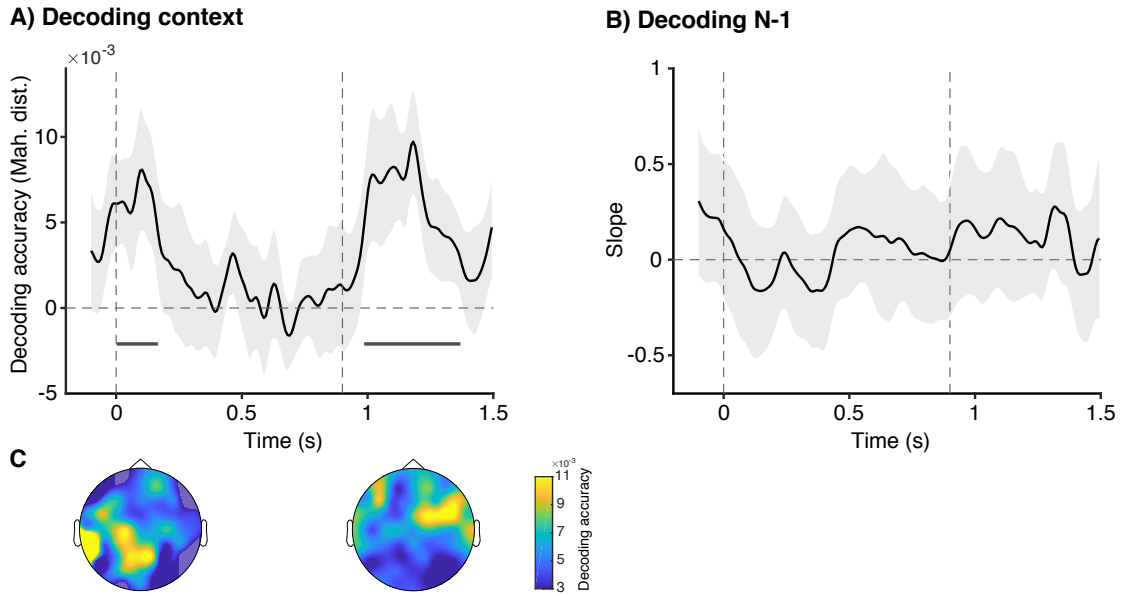

Figure 4. Decoding accuracy relative to the onset of the perception phase. A) Decoding accuracy of context for the overlapping interval as represented by the Mahalanobis distance. Grey horizontal bars indicate a significant difference from zero according to the cluster-based permutation test. Error shading represent 95% CI of the mean. B) Decoding accuracy of N-1 in the overlapping interval, represented by the slope value of the regression of Mahalanobis distance with N-1 and Context as predictors. C) Topographies of channel-wise context decoding accuracy for the overlapping interval, during the first significant cluster in panel A (left) and the second cluster (right). Colors represent the decoding accuracy in Mahalanobis distance.

Multivariate pattern analysis

Figure 4A shows the decoding accuracy for the overlapping interval. The permutation test showed a positive cluster immediately after interval onset (0-0.17 s; $p = .009$) and after interval offset (0.99-1.37 s; $p < .001$). Figure 4C shows the topographies of the channel-wise decoding results during these two clusters, which reflects high parietal and left-lateralized decoding accuracy and high fronto-central and right-lateralized decoding accuracy, respectively. Figure 4B shows the slope value of N-1 in the regression analysis predicting Mahalanobis distance. The permutation test showed that there was no evidence for significant clusters for the slope of N-1 or Context in the regression analysis ($p = .999$), showing that MVPA could not distinguish between N-1 conditions based on the transient EEG signal.

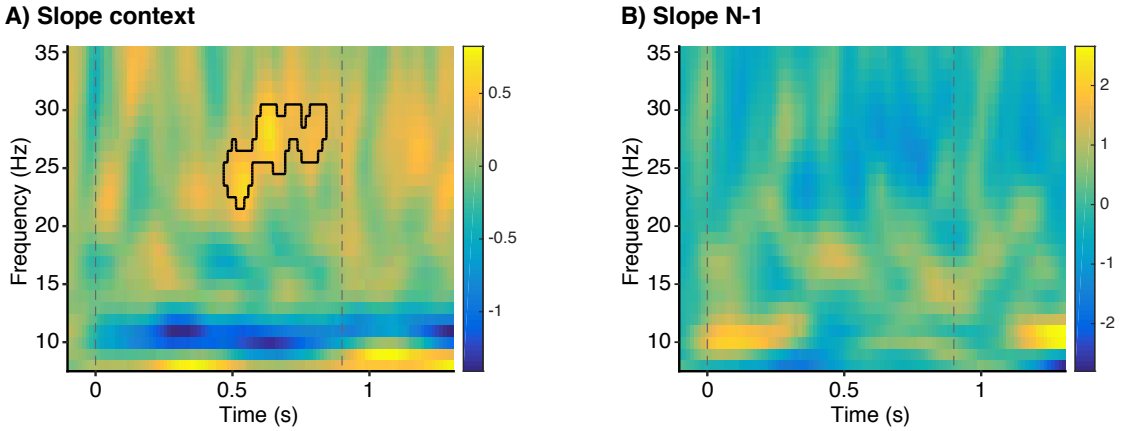

Figure 5. Slope values of regression on frequency power at FCz relative to the onset of the perception phase. A) Slope values of the factor Context (short vs long) in the regression analysis at every time-frequency point. The outlined area marks a significant cluster according to the cluster-based permutation test performed in the time window 0-1.2 s and the frequency window 8-30 Hz. B) Slope values of the factor N-1 in the regression analysis predicting power. There was no evidence for significant clusters. In both panels, vertical dashed grey lines indicate the onset and offset of the perception phase.

Time-frequency analysis

To assess oscillatory power during the perception phase, we calculated a linear regression of frequency power at FCz with global (short vs long) and local context (N-1) as predictors for every time-frequency point during the overlapping interval. Figure 5A shows the slope values representing the effect of global context on the power of the different frequencies over time. We found a positive cluster in the window 0.48-0.84 s after interval onset in the 22-30 Hz frequency range (p = .040), indicating increased beta power in the long context compared to the short context (see the outlined area in Figure 5A). Figure 5B shows the slope values for N-1, for which the permutation test indicated no evidence for a cluster of slopes different from zero. In summary, these results suggest that fronto-central beta power was higher in the long compared to the short context, while there was no evidence for a similar influence of the previous trial.

Discussion

As the temporal locus of Bayesian computations in human time estimation is still unknown, we investigated whether temporal context actively influences neural signatures during the perception of time intervals. Behaviorally, we found that reproductions were biased towards the global temporal context as well as the duration in the previous trial. The EEG results showed that the CNV, the P2 and

beta power, which all have been associated with time perception, were modulated by previously perceived intervals and that context could be decoded from transient brain dynamics at an early stage during perception.

The results indicate that previously perceived durations actively affect EEG signatures during interval estimation, showing that prior experiences act directly on perception. This observation goes against the (implicit) assumption of time perception models that the likelihood is weighted with the prior only after perception. Instead, experiences with the global and recent temporal context actively calibrate cortical dynamics, in which the CNV and beta power may reflect the anticipation of stimulus duration and the P2 component the active evaluation of the interval in the current context. Crucially, by focusing on the perception phase in a reproduction paradigm, this is the first work demonstrating context effects that are not linked to explicit motor preparation or response decisions.

Our findings argue against the idea that the CNV reflects the neural counterpart of the absolute accumulator in pacemaker-accumulator models (Casini & Vidal, 2011; Macar & Besson, 1985; Macar & Vidal, 2004; Macar, Vidal, & Casini, 1999; Macar & Vitton, 1982; Pfeuty, Ragot, & Pouthas, 2005), since no differences based on prior experience would be expected during the perception of an interval. Instead, we found that the CNV during the perception of the overlapping interval was more negative for the short compared to the long context, and for shorter previous durations. This is consistent with anticipation and preparation accounts of the CNV (e.g., Boehm, Van Maanen, Forstmann, & Van Rijn, 2014; Elbert, 1993; Leuthold, Sommer, & Ulrich, 2004; Mento, 2013; Ng et al., 2011): when the interval offset is expected quickly after the offset, the CNV amplitude increases more rapidly. This adaptation is in line with studies showing a faster CNV development for relatively short foreperiods (Miniussi, Wilding, Coull, & Nobre, 1999; Müller-Gethmann, Ulrich, & Rinkenauer, 2003; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004), shorter standard durations in an interval comparison task (Pfeuty et al., 2005) and after adaptation to a shorter interval (Li, Chen, Xiao, Liu, & Huang, 2017). The contextual adjustment of the speed with which the CNV develops suggests that neural populations in the supplementary motor area (SMA), which is typically associated with the CNV (e.g., Coull, Vidal, & Burle, 2016), can perform flexible temporal scaling based on the temporal

context (Remington, Egger, Narain, Wang, & Jazayeri, 2018; Remington, Narain, Hosseini, & Jazayeri, 2018; Sohn et al., 2019), even in the absence of explicit motor preparation. The prior might calibrate the speed of neural dynamics through different initial states at the onset of the perception phase (Remington, Egger, et al., 2018; Sohn et al., 2019), as our multivariate pattern analysis showed that global context can be decoded from EEG dynamics immediately after the onset of the perception phase. Although the precise onset of significant decoding should be interpreted with caution, since the moving window approach and low-pass filtering could smear out the accuracy over time (Grootswagers, Wardle, & Carlson, 2017), these results suggest that temporal context affects the instantaneous neural response to to-be-timed stimuli.

The active anticipation based on context was also indexed by the P2 component. Specifically, P2 amplitude increased with longer current durations, suggesting that it reflects hazard-based expectancy: the probability that the interval offset will occur, given that is has not yet occurred (Nobre, Correa, & Coull, 2007). This in line with previous studies showing that longer ISIs increase P2 amplitude (e.g., Pereira et al., 2014; Röder et al., 2000). Importantly, however, P2 amplitude decreased with longer previous durations, showing that the expectations are updated to the current temporal context, even on a trial-by-trial basis. P2 latency was also sensitive to the local context, but was primarily driven by the absolute difference between the current and previous interval. In this way, latency might be an index of the violation of expectations based on recent experience. These results complement previous studies showing that temporal expectancy modulates ERP amplitude (e.g., Kononowicz & van Rijn, 2014; Li et al., 2017; Todorovic & de Lange, 2012; Todorovic, van Ede, Maris, & de Lange, 2011; Wacongne et al., 2011).

Global context additionally influenced beta power, such that beta power was higher in the long compared to the short context. Higher beta power has been observed when a predictable interval between subsequent stimuli was longer (Praamstra, Kourtis, Hoi, & Oostenveld, 2006) and beta power at interval onset has been shown to predict the produced duration in a given trial: productions were longer when beta power was higher (Kononowicz & van Rijn, 2015). Although beta power has been proposed to reflect motor inhibition (Alegre et al., 2004; Hwang, Ghuman, Manoach, Jones, & Luna, 2014; Kononowicz & van Rijn, 2015; Kühn et al., 2004) and most studies on the link between beta

power and timing have a strong motor component, our results suggest that synchronized beta oscillations also play a role during interval perception after which no immediate motor response is required. This finding complements recent studies showing that the accuracy and precision of time estimates depend on beta (Wiener et al., 2018) and alpha-beta coupling (Kononowicz, Sander, van Rijn, & van Wassenhove, 2019). Additionally, the current global context effect on beta is in line with Wiener et al.'s finding that longer previous durations increased beta power in the current trial. It has to be noted, however, that we found no evidence for similar sequential effects on beta.

Besides the auditory stimuli which participants had to time, the current paradigm also consisted of visual stimuli that indicated the phase of the trial (i.e., perception or reproduction). The general overestimation we found in the behavioral results might potentially be explained by the integration of these visual stimuli in temporal estimation (Shi & Burr, 2016). Future studies might look further into potential modality differences in contextual calibration and their neural underpinnings (Rhodes, Seth, & Roseboom, 2018; Roach et al., 2017). Furthermore, we found no significant decoding corresponding to the windows of CNV differences. This can be explained by the specific decoding method we employed, which focused on transient dynamics, filtering out the stable CNV activity by baselining within a moving window. In addition, decoding might be especially sensitive to stimulus onset and offset, with accuracy peaking shortly afterwards and slowly dropping as the neural synchronization declines (e.g., Wolff et al., 2017, 2020).

A comparison to Wiener and Thompson (2015), who found a larger CNV amplitude for *longer* prior durations, suggests that contextual ERP effects might be dependent on the specific experimental paradigm. In contrast to our reproduction experiment, their bisection task requires an active decision during perception, and the CNV has been shown to reflect this decision process by deflecting or plateauing after the standard interval in memory has been reached (Macar & Vidal, 2004; Ng et al., 2011; Pfeuty, Ragot, & Pouthas, 2003). The difference in task requirement could also explain the different nature of our offset P2 effect compared to Kononowicz and van Rijn (2014). Future studies might directly compare these neural differences in paradigms involving decision, motor or only perceptual timing requirements. Indeed, as we focused on the perception phase in the current study, how the neural differences during perception translate to Bayesian effects in behavior (e.g., the

central tendency effect) remains to be explored further. Potentially, the neural state at the end of the perception phase might set the speed of cortical dynamics during reproduction (Sohn et al., 2019).

In conclusion, our results show that previous durations actively influence flexible neural dynamics during temporal encoding. These findings indicate that previous experiences in memory create expectations that in turn calibrate our perception of the environment. The adaptive influence of prior knowledge on perception could represent a more general Bayesian mechanism of magnitude estimation (Petzschner, Glasauer, & Stephan, 2015), falsifying a class of models that assume discrete, post-perceptual stages in which previous experiences exert their influence.

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