

Circumstances Matter -

Establishing a Timeline for the Context Effect in Interval Timing

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Abstract

The timing of events is crucial for behaviours and cognitive processes. Research has established that the estimation of intervals is influenced by many factors. The context effect shows that the same duration is underestimated when encountered within a block of short durations and overestimated when encountered within a block of relatively long durations. While these behavioural findings have often been replicated, the underlying neural mechanism as well as the timeline of this phenomenon is not clear. Traditional models of time perception assume that the representation of an interval is blended with memory traces from previous durations after perception. Alternatively, context could already actively influence the perception of a duration. In the current study, participants performed an auditory reproduction task while EEG was recorded. The context effect was introduced by two types of blocks one consisting of short durations and one consisting of long durations. One duration interval was present in both blocks. In an exploratory analysis, we investigated whether timing-related ERP components showed differences based on context and during which phase of a trial (perception, memorization or reproduction) differences are evident in the EEG signal. Behavioural results showed that reproductions depended on the context. The CNV was found to be more negative for the overlapping duration in the short context during the perception and reproduction phase. With EEG decoding analysis it was possible to distinguish the context of a trial during the perception and memorization stage. These results suggest that the context already affects the perception stage of an interval. This indicates that timing models not only need to implement a memory process but also consider the effect of previous durations on perception.

Keywords: interval timing, auditory reproduction, context effect, CNV, decoding

Circumstances Matter - Establishing a Timeline for the Context Effect in Interval Timing

Time and its Perception

Timing and the perception of time has received an increased amount of attention in the recent years. It has been established that timing mechanisms are vital for behaviours such as movement and speech but also for the planning of actions (Bangert, Reuter-Lorenz, & Seidler, 2010; Eagleman, Tse, Buonomano, Janssen, Nobre, & Holcombe, 2005). However, when it comes to estimating intervals involving just a couple of seconds there are differences between subjective and veridical time. Several studies have investigated under which circumstances humans fail to estimate an interval correctly and whether there may be patterns in our inaccuracy. It has been shown that there are large individual differences in timing tasks but nevertheless, there are still predictable systematic biases (Corcoran et al., 2018). Intrinsic factors, such as the current mood of the participant (Tipples, 2008) as well as psychiatric disorders, brain damage (Moreira, Pinto, Almeida, & Barbosa, 2016) and drugs (Tinklenberg, Roth, & Kopell, 1976; Wittmann, Leland, Churan, & Paulus, 2007) can systematically evoke effects on accuracy across individuals in timing tasks. External factors, that is, the characteristics of the stimulus used in the task, can influence the perception of durations, too. Such external factors are the magnitude of a stimulus (i.e. size, amount), its modality or the presented speed which as they increase, lead to overestimations of durations (Kanai & Watanabe, 2006; Mioni, Zakay, & Grondin, 2015; Xuan et al., 2007). Results of this research are laws of timing and other well established biases.

Another phenomenon that has consistently been found in interval timing tasks is Vierordt's law. Vierordt's law suggests that relatively short durations are in general overestimated and an underestimation occurs for relatively long durations (example in Figure 1; Gu & Meck, 2011).

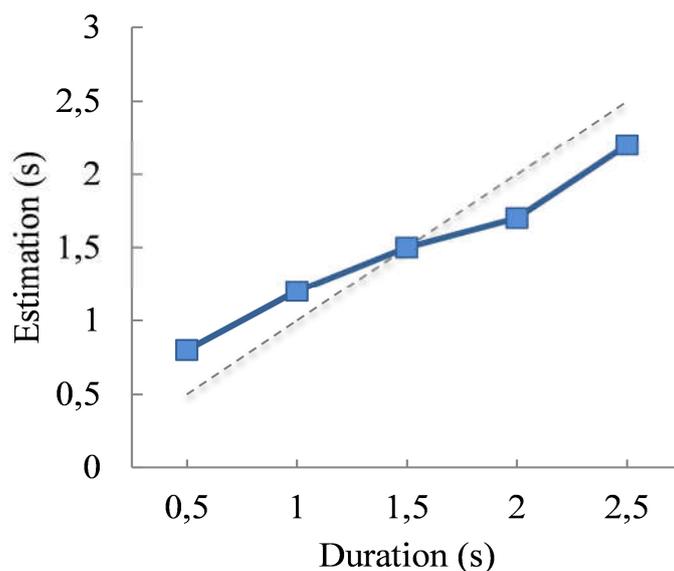


Figure 1. A simplified example of Vierordt's law. Estimations are shown in blue; the dashed line represents veridical time. In general, short durations are overestimated whereas long durations are underestimated.

Furthermore, this law presents the basis of a phenomenon called the context effect, as it predicts that the same interval is underestimated if presented in a block with relatively short durations, and overestimated when presented in a block with relatively long durations (Jazayeri & Shadlen, 2010).

Explaining Timing Behaviour

The first attempts to explain the behavioural observations in timing tasks emerged in the late 1970s. One of the most influential theories of timing till today is the scalar expectancy theory (SET) published by Gibbon (Gibbon, 1977). The SET proposes a linear relationship between the duration and its estimation as well as between the variability of the estimation and the length of the duration. Based on this, SET (or internal clock models) were developed (Bangert et al., 2010; Creelman, 1962; Gibbon, Church, & Meck, 1984; Treisman et al., 1990). These models consist of several processes that are involved in estimating time interval. The first process involves a pacemaker-accumulator component. The pacemaker emits steady pulses, and when a switch that is controlled by attention closes, these pulses are

counted by an accumulator. The amount of pulses is stored in working memory and updated as long as the switch is closed. When the switch opens again, the accumulator stops counting and the last duration that is stored in working memory reflects the perceived duration of an interval. The final mechanism of an internal clock model involves the retrieval of the perceived duration and a decision-making process (comparing a stored duration in working memory with durations in the reference memory). When trying to explain the observed biases, it has been suggested, that the activation level of attention to a specific duration is associated with its perceived length (Block, & Zakay, 1996; Casini & Macar, 1997) as it was shown that paying attention to time increases the perceived duration (Politi, Martin, van Wassenhove, 2018). The variability in temporal judgments between individuals could therefore be assigned to differences in the level of attention towards a target duration as this mechanism ultimately controls the switch. The clock is sped up, or slowed down based on allocated attention, and therefore a different quantity of pulses is accumulated. Still, the context effect shows that the attention allocation or clock speed are not the only factors that influence subjective timing due to the fact that the same exact stimuli would need to elicit differences in attention. What could be a possible different factor for the context effect?

A study investigating whether there are differences in judgments for different modalities (auditory vs. visual stimuli) was conducted by Penney and colleagues (Penney, Gibbon, & Meck, 2000). When the two stimulus modalities were presented during the same trial simultaneously but their onsets were asynchronous, visual stimuli were judged as shorter than auditory ones. The effect did not occur when only a single modality was presented during the trial. When relating their results to the SET models, the authors suggest, that during a temporal bisection task, the duration present in the accumulator is compared to the to be remembered intervals, which is already stored in reference memory. They further concluded that the two modalities affect the clock speed differently (i.e., leading to different

accumulation times) and when these modalities are combined in working memory to a single duration, the decision making process is occasionally dominated by the auditory modality. Gu and Meck (2011) also showed that this distortion of memory-mixing occurs when multiple durations are presented. It has been suggested that a carryover of memory traces from previous durations to the current estimation is occurring (Gu & Meck, 2011; Jazayeri & Shadlen, 2010; Taylor & Lupker, 2001). Additionally, some authors have proposed a model involving a temporal reference memory, which assumes that the representation of an interval in reference memory is based on a combination of several recently encountered durations (Taatgen & van Rijn, 2011).

The timeline of the context effect is still in question. Traditional SET/internal clock models predict that the accumulator reflects the objective time and that attention allocation is the cause of estimation inaccuracy. Alternatively, it can also be suggested that a blending of previously remembered intervals affects the estimation, ultimately placing the source of this bias at a later time point, namely the memorization process.

Timing in the Brain

Through the development of neuroimaging methods such as the electroencephalography (EEG) and (functional) Magnetic Resonance Imaging (fMRI), the building of cognitive models has improved. It is possible to develop models of better quality that are able to explain observed behaviours and are neurobiologically plausible.

Event-Related Potentials. There are several event-related potentials (ERPs) that have been associated with timing processes (for a review, see Ng, & Penney, 2014). The contingent negative variation (CNV) is one of the most described ERP components in timing tasks. Originally, it has been identified as a marker of expectancy (Walter, Cooper, Aldridge, McCallum, & Winter, 1963). In the late 90's, the hypothesis emerged, that the CNV may reflect the accumulator as described in internal clock models (Macar, Vidal, & Casini, 1999).

Macar and colleagues (1999) presented the first empirical evidence for their hypothesis. In their study, participants were required to reproduce a 2.5s interval manually. They found that the amplitude of the CNV decreased (became more negative) with shorter estimations in their reproduction task at FCz (in the 10-20 system) corresponding to the supplementary motor area (SMA; see figure 2).

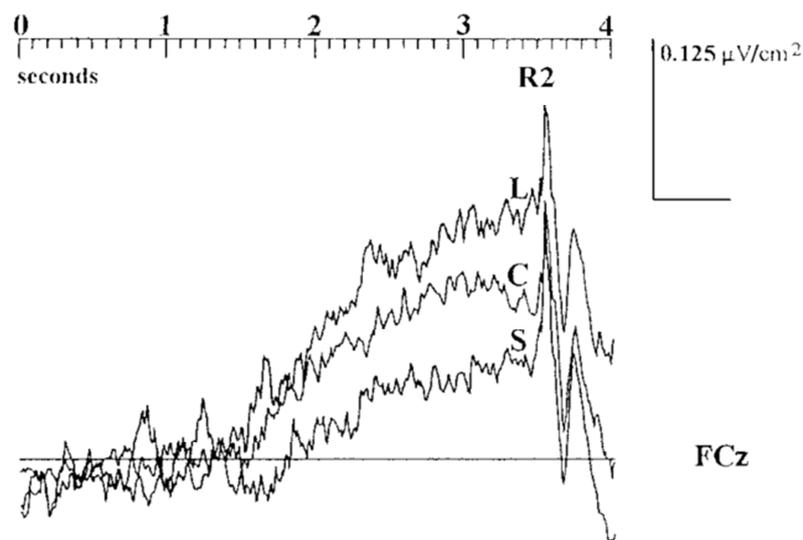


Figure 2. EEG recording at FCz, obtained during the target interval. Backward recording was time-locked of the target to the second trigger press of the reproduction task. Participant's accuracy is indicated by L (too long), C (correct), S (too short). The amplitude is more negative for longer reproductions than for shorter reproductions. Retrieved from Macar & Vidal (1999).

This suggests that durations are reflected in the CNV amplitude prior to a response. Findings were reproduced for shorter durations, too (Bendixen, Grimm, & Schröger, 2005). Additionally, it was found that the resolution of the CNV was in line with the length of a memorized interval in a temporal comparison task (Macar, & Vidal, 2003). The CNV peak was at the target interval and resolved if the current duration was longer. The authors suggested that the resolution may resemble a memory trace of the target duration which then leads to a decision in the comparison task. However, this study already showed that the CNV and its association with the accumulator are not as clear as hoped. Several studies have failed to replicate the original findings (Kononowicz, & van Rijn, 2011; Ng, & Penney, 2014).

Studies showed a habituation effect of the CNV (Kononowicz, & van Rijn, 2011), and it was also presented that timing in the brain can continue after the CNV had already deflected (Kononowicz, & van Rijn, 2014), refuting the pacemaker-accumulator and CNV hypothesis. Kononowicz and Penney (2016) suggest that the CNV may resemble a preparatory process in timing tasks.

To summarize, there is still a large debate about what the role of the SMA and its measured electrical activity (CNV) in timing tasks is. Some authors suggest that the activity is associated with the decision-making and preparation process of comparing memorized intervals (Kononowicz, & Penney, 2016; Pfeuty, Ragot, & Pouthas, 2003) whereas others link its activity to the accumulation of a duration (Bendixen et al., 2005; Macar, Vidal, & Casini, 1999). It is not clear during which process the CNV may be involved in the estimation of an interval. If the CNV resembles the perceived accumulation instead of an interval differences should be observable during the perception phase. In case it represents the objective duration then no differences should be visible during this phase. If the CNV resembles the decision-making process or the preparation for action, then differences would be expected during the phase of a task where the duration is estimated. Therefore, investigating the CNV in relation to the context effect could bring about more information about the role of this ERP and the timeline of the emergence of the context effect.

Decoding of Brain States. A rather new approach to investigate brain processes is that of decoding, a method more commonly used in fMRI analysis. Wolff and colleagues used this strategy to decode on neural hidden states from EEG data (Wolff, Jochim, Akyürek, & Stokes, 2017). They were interested in investigating how working memory holds items and whether it is possible to uncover them in the absence of attention. The authors used a multivariate pattern analysis in order to reveal ‘hidden’ memory items that are in the subconscious by ‘pinging’ the brain, and were successful. In general, the decoding procedure

of brain activation tests whether the patterns of brain activation are different between the two experimental conditions. The analysis involves first the training of a classifier, using a portion of the data (training data). The classifier learns when a certain pattern of brain activation is associated with a specific condition. Secondly, the trained classifier is used to predict the conditions of the rest of the data (test data). If the prediction rate is above chance, the classifier can successfully distinguish the conditions and there is indeed a difference in activation patterns. Crucially, this information can further be used to infer at which time point and at which electrode location the differences can be observed by repeating the decoding process several times.

The Current Study

The here discussed explorative research attempts to shed light on the underlying mechanisms and the timeline of the context effect. During which processes does the context effect emerge in the brain when performing a reproduction task? Can we find typical timing ERP markers such as the CNV and what could it reflect in this paradigm?

Participants will perform an auditory temporal reproduction task while EEG is recorded. They will hear a tone and have to reproduce the duration of that tone so that it is equal to the former. It is expected that an identical duration will be estimated shorter in a block consisting of relatively short durations (short context) and longer when encountered in a block with relatively long durations (long durations). Crucially, one interval will appear in both contexts (overlapping interval). In line with this and previous EEG studies (Bendixen et al., 2005; Macar et al., 1999) the CNV is expected to be more negative for the overlapping duration in the short context than in the long context.

Concerning the timeline of the context effect, a multivariate decoding analysis will be performed. Aside from the possible influence on memory processes that have been suggested, it can also be speculated that processes such as the perception of the presented duration as

well as the decision stage could potentially be influenced by previously encountered durations. Therefore, it is expected that it is possible to categorize the overlapping duration into the two conditions solely based on the EEG signal during the perception stage of the task as well as the memorization stage. Due to the expected behavioural difference, it is also hypothesized that we are able to distinguish the context of the overlapping duration during the reproduction stage.

Models of time perception typically include components such as an accumulator that is counting the passage of time (i.e., the perception of an interval) and a decision-making process (i.e., the reproduction of an interval), however, due to the introduction of context effects, also memory processes need to be accounted for in a successful model (Bangert et al., 2010). The context effect is not a big focus in timing research. Timing tasks are usually done in a very artificial setting, potentially resulting in behavioural results that do not relate to mechanisms in real-life. The context effect resembles a bias that could potentially be closer to ‘real-life’ timing than others, as in real-life also several durations are usually timed at once (e.g. when driving a car). Therefore, understanding the context effect in terms of its timeline and its underlying neural mechanisms may help improve models of timing in general and lead to an increased understanding of ‘realistic’ timing in humans.

Materials and Methods

Participants

For the current electroencephalographic study 27 participants were recruited (22 females; age range 18 - 33 years with $M = 21.333$, $SD = 3.783$ years) through the 1st-year SONA psychology student participant pool and the paid participant pool of the University of Groningen. Their participation was voluntary and they were compensated with course credits or monetary compensation (€ 14). The study was approved by the Psychology Ethical Committee of the University of Groningen (17141-S-NE). Written informed consent was

obtained from each participant before EEG cap preparation and testing. Additionally, participants were given information about the EEG procedure one day prior the experiment was scheduled to take place. After the experiment, students were debriefed about the aim of the study.

Materials and Apparatus

The paradigm of the task constitutes an auditory interval reproduction experiment. The experiment took place in the EEG laboratory of the Psychology faculty basement. Participants performed the task in a room separated from the experimenter by a noise-cancelling door. Communication between participant and researcher was possible through an intercom. Participants were also visible through a video camera. The monitor used during the experiment was a 27 inch monitor with a 1920x1080 resolution at 60 Hz (ProLite G27773HS, Iiyama). For the auditory stimuli, stereo over-ear headphones were used (HD 280 Pro, Sennheiser). The back trigger buttons of a Gamepad (SideWinder Plug & Play Game Pad, Microsoft Corporation) were used to record responses.

Auditory Reproduction Task. In the auditory reproduction task, participants were required to replicate a previously heard duration by terminating a current tone. The experiment was programmed in Matlab (The MathWorks Inc., Version R2014b) using the Psychophysics Toolbox 3.0.12 extension (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). The task involved two conditions, a short context condition (set A, with durations of 0.625s, 0.75s and 0.9s) and a long context condition (set B, with durations of 0.9s, 1.08s and 1.296s). Crucially, there was an overlapping duration in both contexts (0.9s). Representative of the duration, filled auditory stimuli, that is, a continuous tone with sharp on- and offsets were used. The tone was a 440Hz sine wave produced in Matlab.

EEG Data Acquisition. EEG signals were recorded from 62 Ag/AgCl electrodes (a list of all channels can be found in Appendix A), placed in accordance with the 10 to 20

International System of Electrode Placement (Wave Guard, 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 for the horizontal recording and from the top and bottom of the left eye for the vertical recording. Impedances were below $5\text{k}\Omega$ prior experiment start. The signal was amplified using the Refa 74-channel stationary system by TMSi (Type Refa8-64e4b4a). Besides the built in anti-aliasing filter no online filtering was applied. Data was collected at a sampling frequency of 512 Hz.

To mark the stimulus onsets as well as the response on- and offsets during the experiment for later analysis a custom made trigger box was used. The trigger signal was implemented in the amplifier as an additional analogue channel.

Procedure. Prior to EEG cap preparation, students received a sheet containing information about EEG cap preparation and signed the informed consent. After EEG cap preparation, participants were seated in the EEG lab in front of the monitor. The experimenter checked the impedance of the EEG signal and they were reduced to be $< 5\text{k}\Omega$. Participants were instructed to sit comfortably, blink only between trials (during the ITI) and not move during the experiment. Descriptives (age, gender, and handedness) were recorded prior the start of the task.

The experiment included four blocks, and both conditions were presented twice. Each block consisted of 30 trials of each duration of a set (A or B) presented in random order. This amounted to a total of 90 trials for each block, and 360 trials for the experiment of which 120 trials were of the overlapping duration. The hand needed for reproduction was switched halfway through the experiment (after two blocks) and the set (A or B) was switched after each block. Block order was counterbalanced across participants and breaks were provided between blocks.

When starting the experiment participants were given instructions about the task on screen and they performed two practice trials of durations that were outside the range of the durations of both sets (0.4s & 2s). Prior to each experimental block, participants were notified with which hand (i.e. which gamepad button) they were required to terminate the duration as well as informed about the set of block they will be doing (set A or set B). In the beginning of the first trial of a block, a fixation cross was presented for 0.5s. It was then replaced by a ‘!’ and participants heard a tone of one of the durations from the previously defined set. This is the perception phase of the trial. The memorization phase followed for an inter-stimulus interval of 1.5s, where a ‘?’ was presented. Subsequently, the tone started again until the participant terminated it with a button press of the to be used hand, forming the reproduction phase. If no button was pressed the trial was terminated after six seconds automatically. The inter-trial interval (ITI) during which a fixation cross was displayed again, was a random rational value drawn from a discrete uniform distribution between 2 -3s (therefore averaging an ITI of 2.5s across participants). An example of a trial can be found in Figure 3. Once the students had finished the replication task, the cap and electrodes were removed. Finally, they received a debriefing form, and potential questions were answered.

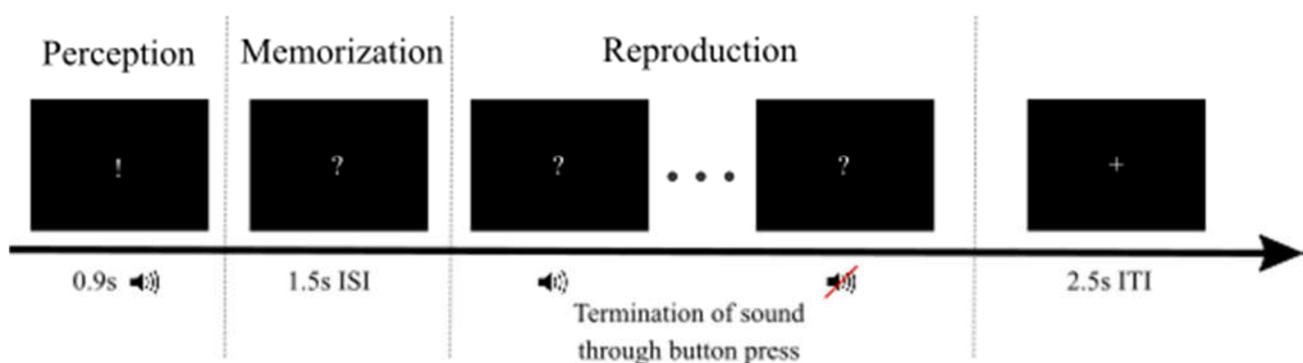


Figure 3. Example trial of a 0.9s duration in the middle of a block. The loudspeakers symbolize the presentation of the sound. The trial can be divided into three phases: perception, memorization and reproduction.

Data Analysis Plan

For all data processing and analysis, Matlab scripts and functions were used (The MathWorks Inc., Version 2016a) if not further specified.

Behavioural data. To test whether there is a difference in the reproduced estimates of the overlapping duration (0.9s) depending on the context, a paired-sample t-test was calculated using the average estimates over trials of the 0.9s duration in the short duration and the average estimates of the 0.9s duration in the long context.

EEG data. EEG pre-processing and ERP analysis were performed using the FieldTrip toolbox for EEG/MEG-analysis (Oostenveld, Fries, Maris & Schoffelen, 2011; <http://www.ru.nl/neuroimaging/fieldtrip>).

pre-processing. Data was re-referenced to the averaged mastoids (M1 & M2 channels). Data was filtered using a Butterworth infinite impulse response (IIR) band-pass filter with a high-frequency pass of 0.01 Hz and low frequency pass of 80 Hz. The filter order was 3. Subsequently, the signal of the trigger channel was used to create the epochs of a trial (stimulus presentation, response onset, response offset). The prestimulus phase was 1s and the poststimulus phase was 6s.

independent component analysis. In order to detect artefacts, an independent component analysis (ICA) was performed. Prior the analysis, EOG channels (horizontal & vertical) were removed from the dataset. The settings for the ICA were kept at default and using the 'runica' method. This implies that the data was decomposed using an infomax ICA algorithm and a natural gradient. The ICA computes the topography and timecourses of the components. Since there were 62 channels, 62 components were computed. These were then visually inspected by the researcher using the topographical images and the timecourses for each trial. Components showing eye movements such as saccades or blinks and noisy single

electrode signals were removed from the dataset (11 on average). Subsequently, epochs were redefined so that the prestimulus phase was 0.5s and poststimulus phase was 4.5s.

artefact rejection. All trials that exceeded an amplitude range of 120 mV were removed from the dataset. If the artefact rejection resulted in more than 20% of all trials, the components were inspected again. Due to the fact that the overlapping duration (0.9s) is of interest for the ERP and decoding analysis, it was ensured that no more than 20% of these were removed (10.8% on average (3.6% of all duration trials)).

event-related potentials. In order to investigate the ERPs of the data, the EEG signal of all trials was timelocked to stimulus onset. The resulting data was then baseline corrected using the average EEG signal in the 200ms window prior to stimulus onset. The channels of interest for ERP inspection was a fronto-central electrode cluster involving Cz, FC1, FCz and FC2 which has been found to be relevant for timing processes in different contexts (see Kononowicz & van Rijn, 2014). Thus, the average signal of these electrodes was used for the ERPs.

multivariate decoding. A machine learning algorithm was used to investigate, whether the context of the presented duration could be predicted by the EEG signal. The scripts for the multivariate pattern analysis used here, were adapted from M. Wolff and M. Stokes (see Wolff et al., 2017). The analysis was performed on the pre-processed and cleaned EEG data. The decoding procedure tests whether patterns of brain activation are different between the two experimental conditions (short or long context). The analysis involved first the training of a classifier using a portion (80%) of the data (training data). The classifier learned when a certain pattern of brain activation is associated with a specific condition (short or long context). Secondly, the trained classifier is used to predict the conditions of the rest of the data (test data).

The decoding procedure was done for each participant separately. Firstly, epochs of the trials involving the overlapping duration were defined. It was of interest whether the perception and memorization phase could be decoded (predefined by the ‘!’ and ‘?’ during the task). Therefore, a trial was ranging from 100ms prior stimulus onset until 2.4 poststimulus (i.e. the response onset; when the second tone started for reproduction) to avoid decoding the reproduction phase of the task. In contrast to the multivariate pattern analysis done by Wolff et al. (2017), a moving average was used to act as a baseline and averaging of the data. This means that for each trial, the data from the time points within a 100ms window moving window were averaged and subtracted from the data. The window was moved along the signal with a pre-specified amount of 50 data samples (in steps of 5).

Prior decoding the data was split into eight partitions by means of ‘k-fold cross-validation’. The data of the training partitions were then averaged over the two conditions and a covariance matrix was computed. Subsequently decoding was done at each time point using the covariance matrix. The pair-wise Mahalanobis distance between the average of the training data and the test data was calculated. A trial was classified to belong to the condition for which the distance difference was smallest. This decoding procedure was then repeated for 50 simulation cycles to make the results more stable. The resulting distance differences of each trial to the stimulus pattern were then averaged to make inferences about the accuracy of the decoding and a permutation test was done to test whether and where the decoding was significant. The results were plotted as a function of time across participants.

Results

Behavioural Data

To examine whether the context manipulation worked, the averages and standard deviations of estimations for each of the two sets of intervals were calculated for every participant over trials (see Table 1). In general, participants overestimated all the durations they needed to reproduce. Furthermore, there is a difference in the reproduction estimates of the overlapping duration of 0.9s, in that the interval in the short context was estimated as shorter than in the long context.

Table 1

Average reproduction estimates of the different durations for both contexts.

Context	Duration	Mean (SD)
Short	0.625s	0.769 (0.079)
Short	0.75s	0.888 (0.078)
Short	0.9s	0.998 (0.076)
Long	0.9s	1.069 (0.084)
Long	1.08s	1.205 (0.074)
Long	1.296s	1.333 (0.092)

To investigate whether this difference in the overlapping duration is significant, a paired-sample t-test was calculated using the average estimates across participants of the 0.9s duration in the short duration and the average estimates of the 0.9s duration in the long context. The estimation of the 0.9s duration proved to be significantly larger in the long

context than in the short context at the $\alpha = 0.05$ level ($t(26) = -5.229, p = < .001, 95\% \text{ CI} [-0.099 -0.043]$), see also Figure 4.

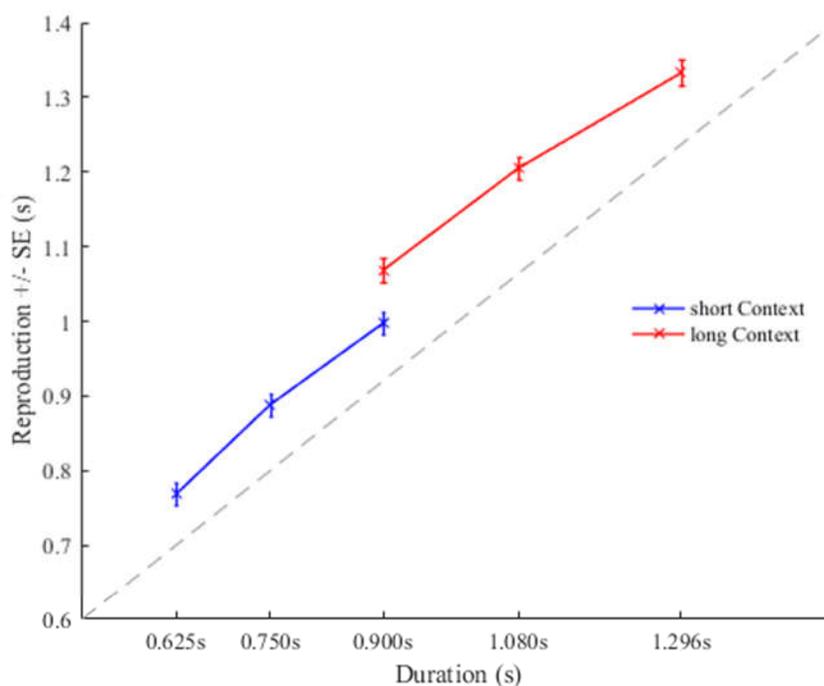


Figure 4. Behavioural results of the auditory reproduction task. Average reproduction estimates over trials and participants for all durations in both contexts.

EEG Data

Due to noisy signals, EEG data from 2 participants were excluded from subsequent analyses. The final sample comprised EEG data from 25.

Event-Related Potentials. The obtained waveform of the averaged activity at the fronto-central cluster locations (Cz, FC1, FCz, FC2) for the different durations and contexts is depicted in figure 5. Just after stimulus onset a typical ERP for auditory tasks can be observed, the N1P2. This ERP does not show any differences in amplitude or waveform based on the different durations and lasts approximately 300ms. The N1P2 is followed by the CNV. While the amplitude is approximately equal across durations, the time point of deflection of this component is approximately equal to the end point of the presented duration.

Furthermore, the positive peak after resolution increases with durations, more so for the short context durations than for the long context.

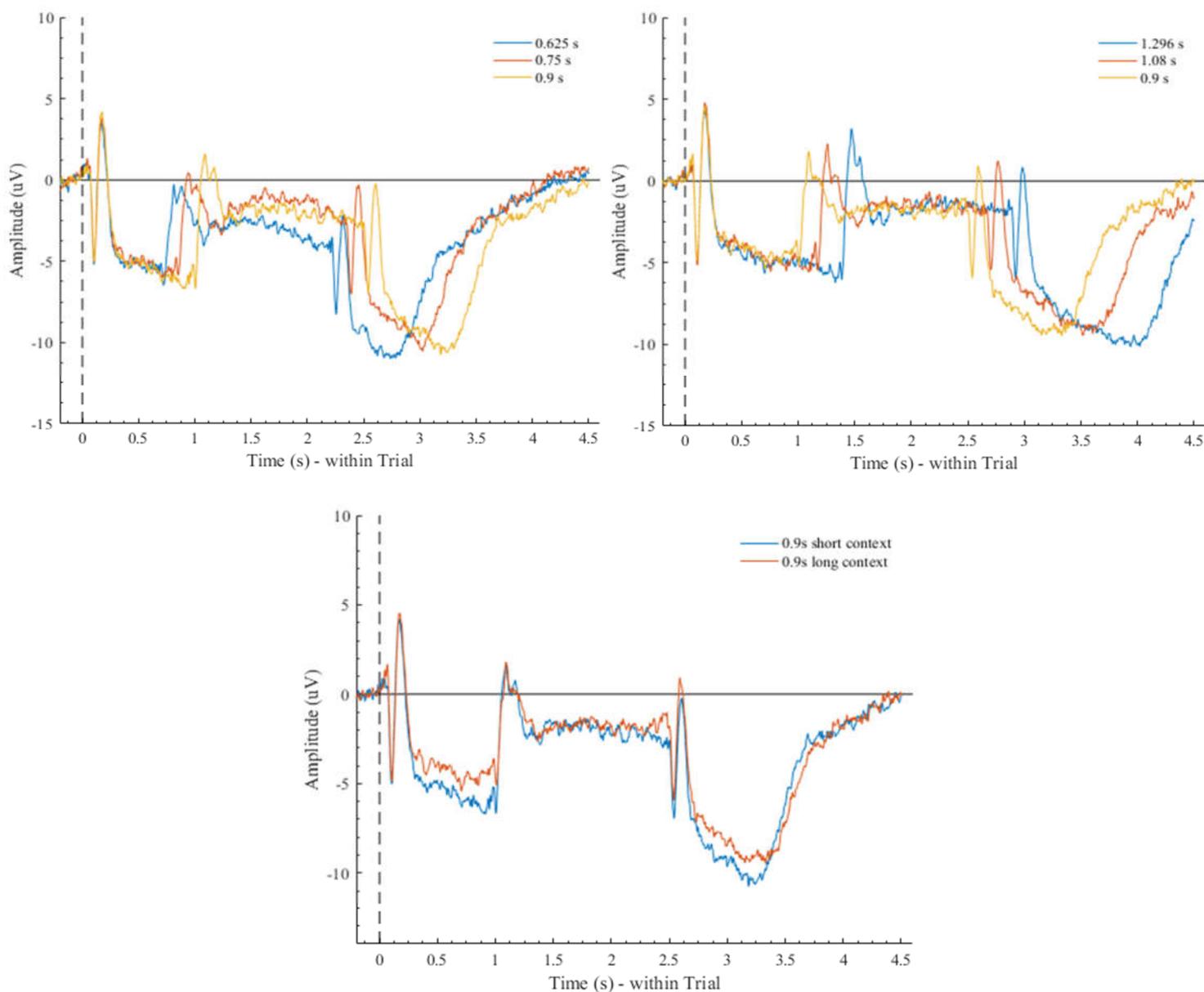


Figure 5. Averaged activity of the fronto-central electrodes (Cz, FC1, FCz, FC2) for the short context condition (left), the long context condition (right) and for the overlapping duration (bottom). EEG data has been baseline corrected at 200ms prior stimulus onset (the vertical dashed line).

When looking at the activity of the fronto-central cluster for the 0.9s durations for both contexts we can observe that during the perception phase (0s-0.9s, see Figure 6.1) the N1P2 component at interval onset shows little to no difference depending on the context. The

following CNV is, as expected, more negative in the short context than in the long context.

The resolution is again very similar for both contexts, namely around the 1s mark.

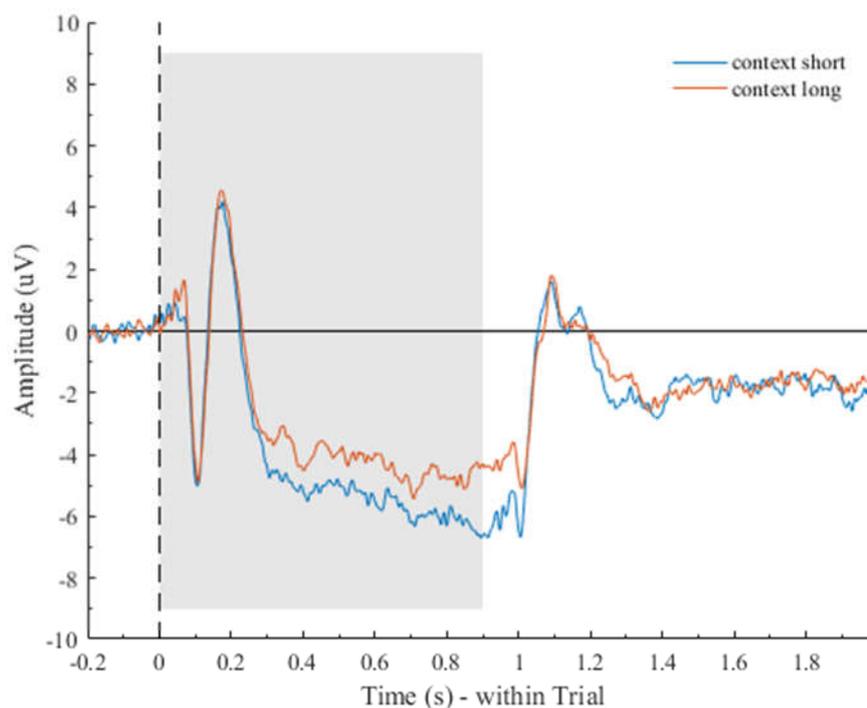


Figure 6.1 Averaged activity of fronto-central electrodes (Cz, FC1, FCz, FC2) for the 0.9s duration in both contexts for the perception phase. EEG data has been baseline corrected at 200ms prior stimulus onset (vertical dashed line). The grey box indicates the length of the 0.9s duration.

During the reproduction phase (Figure 6.2) the overall waveform it is more negative than in the perception phase. Additionally, the N1P2 shows the same pattern as before, there is no difference between contexts. The CNV amplitude prior to resolution, is more negative in the short context than in the long context. At the 3.4s mark, which would be 0.9s after the onset of the reproduction tone, the CNV in the short context deflects earlier. This is in line with the shorter reproductions in this context. The deflection is more extended and lasts until the ITI (starting on average at 3.5s) compared to the perception phase.

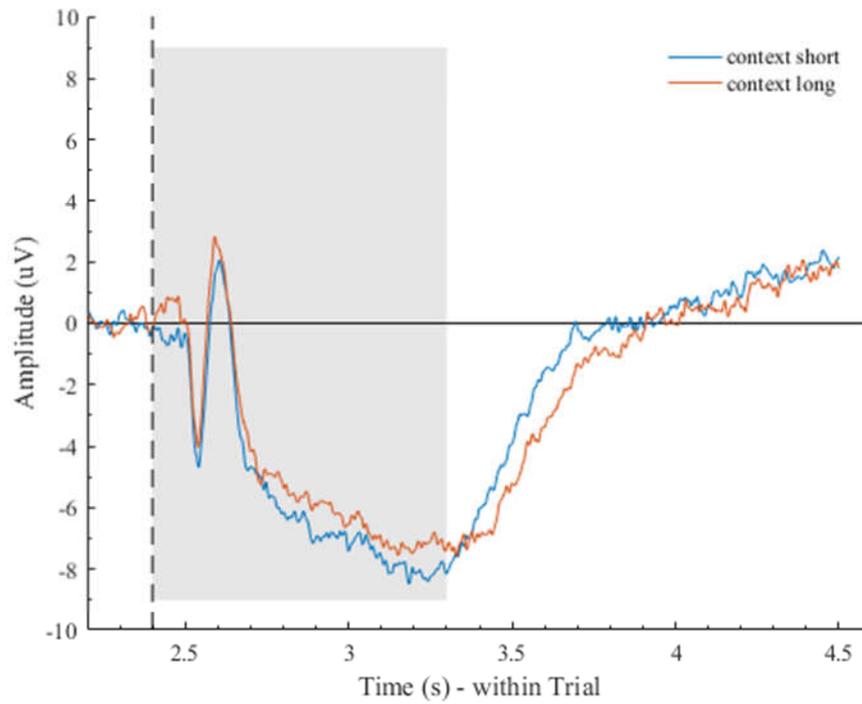


Figure 6.2. Averaged activity of the fronto-central electrodes (Cz, FC1, FCz, FC2) for the 0.9s duration in both contexts for the reproduction phase. EEG data has been baseline corrected at 200ms prior reproduction sound onset (vertical dashed line). The grey box indicates the length of a 0.9s duration.

Multivariate Pattern Analysis. The decoding procedure involved the overlapping interval to decode its context. The results for all channels and averaged across participants is summarized in Figure 7. In the beginning of the perception phase (0s–0.2s within the trial) it is possible to significantly distinguish a 0.9s trial between the two contexts based on the EEG signal. The memorization phase can also be decoded; here the duration is almost twice as long for successful decoding (1s-1.35s within the trial).

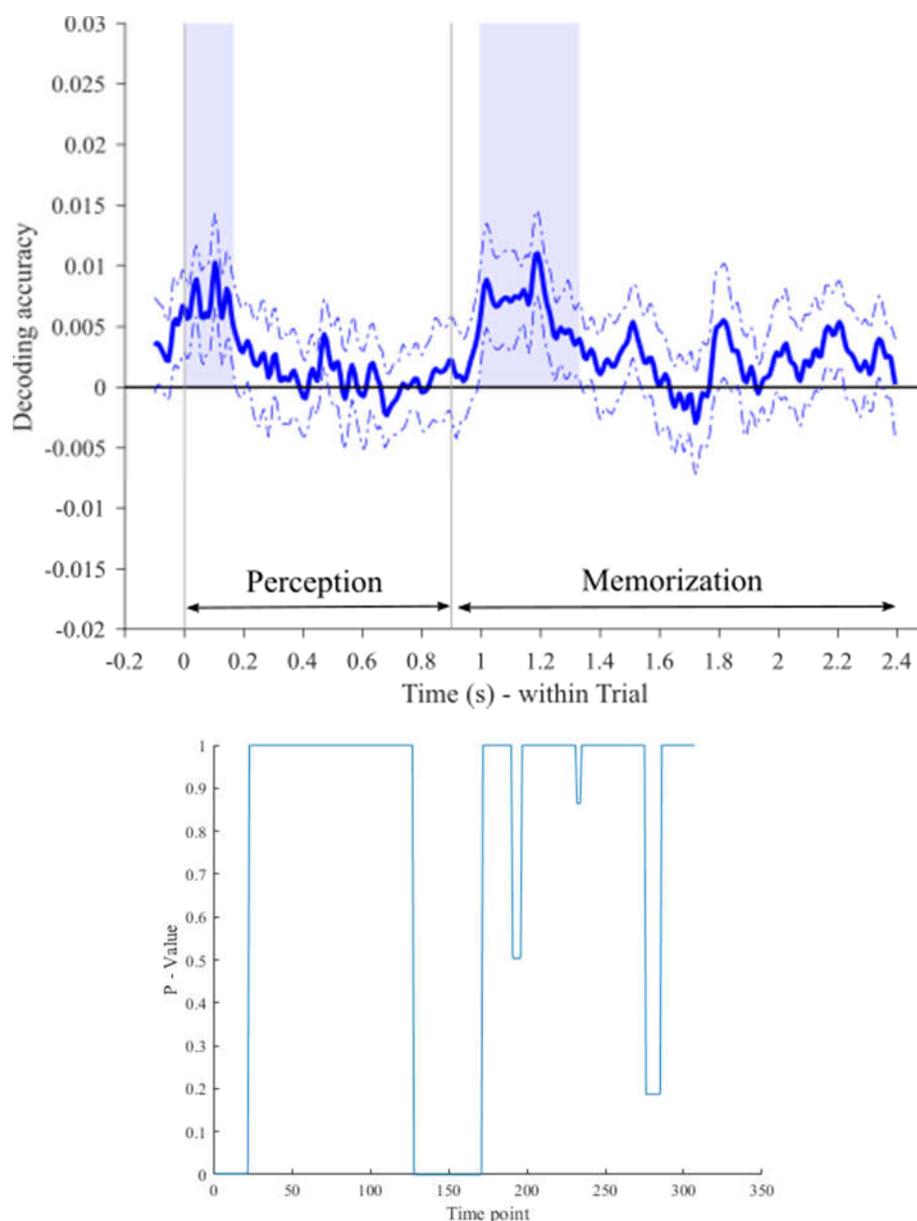


Figure 7. Decoding accuracy for the EEG signal during the perception and memorization phase using all electrodes (top). Positive values on the y-axis correspond to decoding success that is above chance level. The bold blue line indicates the decoding accuracy. The dashed lines indicate the confidence interval. The blue boxes indicate significant decoding success based on the p-values of the permutation test (bottom).

To investigate whether it is also possible to decode the reproduction phase successfully and to see whether the CNV cluster would be sufficient to decode the context effect, the MVPA was run again for the whole trial using all electrodes as well as the CNV cluster channels. The decoding accuracy during the whole trial, including the reproduction phase, is illustrated in Figure 8. Even though decoding accuracy increased during the reproduction phase, the permutation test showed that it was not significantly different from chance level.

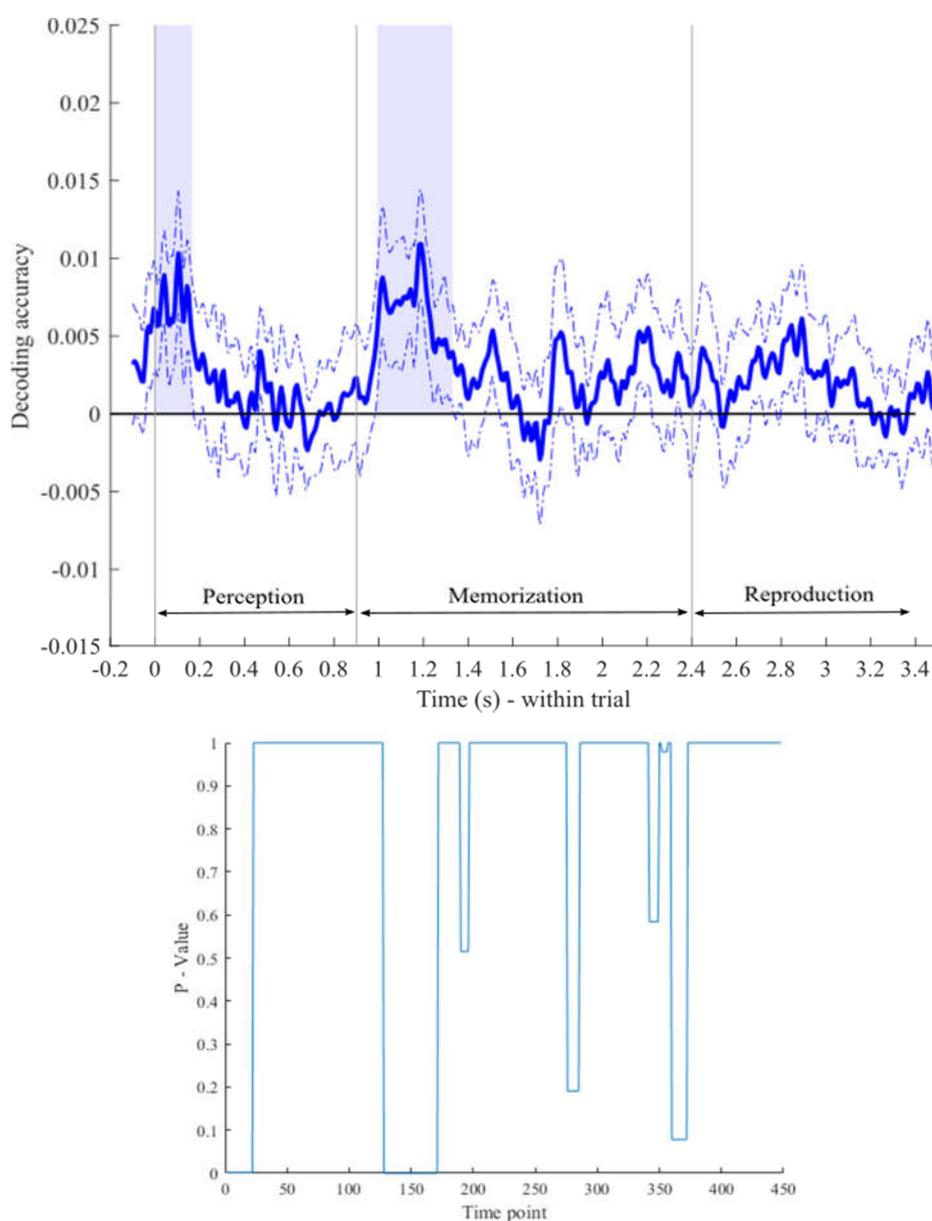


Figure 8. Decoding accuracy for the EEG signal during the whole trial using all electrodes (top). Positive values on the y-axis correspond to decoding success that is above chance level. The bold blue line indicates the decoding accuracy above chance level. The dashed lines indicate the confidence interval. The blue boxes indicate significant decoding success based on the p-values of the permutation test (bottom).

When only using the fronto-central cluster channels for the MVPA, it was only possible to distinguish between conditions during the memorization phase (Figure 9). Also here, the decoding accuracy increased in the reproduction phase (around 2.6s within the trial) but it did not pass the significant threshold.

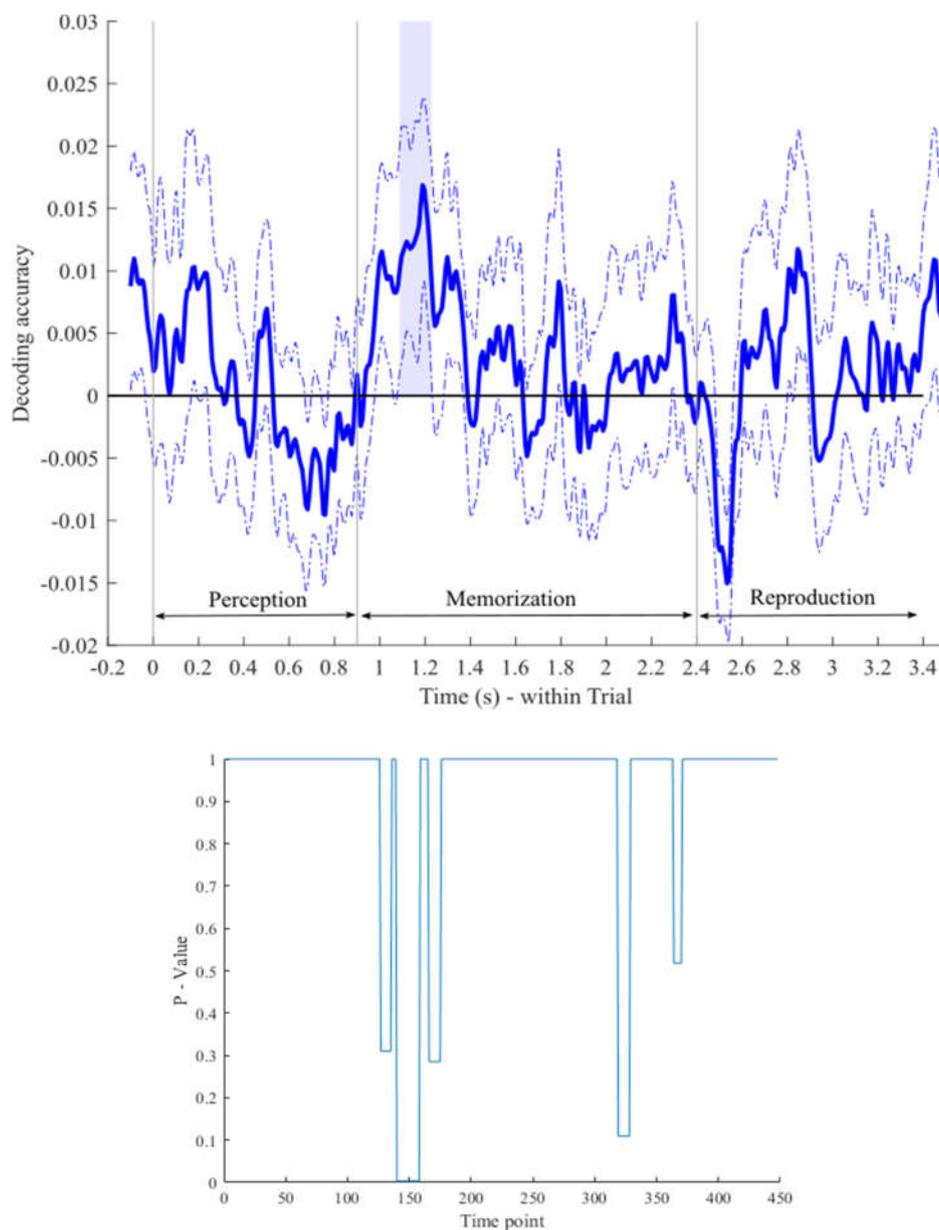


Figure 9. Decoding accuracy for the EEG signal during the whole trial using the cluster channels (top). Positive values on the y-axis correspond to decoding success that is above chance level. The bold blue line indicates the decoding accuracy above chance level. The dashed lines indicate the confidence interval. The blue boxes indicate significant decoding success based on the p-values of the permutation test (bottom).

Discussion

The purpose of this study was to investigate the timeline of the context effect in interval timing. Participants reproduced previously heard durations in an auditory timing task. There were two conditions, one where short durations were presented and another where relatively long durations were presented. Crucially, one duration was presented in both conditions (0.9s). The physically identical interval is consistently over- or underestimated depending on temporal context, also in the current study. Hence, examining the overlapping interval in more detail can tell us more about the context effect and its timeline. The focus of the analysis here, was on the EEG data recorded during this overlapping interval to gain knowledge about the context effect on a neurobiological level, through investigating differences in brain activity (ERPs). In particular, it was expected that besides the behavioural context effect, a more negative CNV would be found in the short context compared to the long context. Furthermore, we investigated whether we could decode the context of a trial during the perception, memorization and reproduction phase.

Establishing a Timeline for the Context Effect

The CNV, an ERP typically found in timing tasks (van Rijn et al., 2011) was present in the data. According to expectations, the time course of this component was correlated with the end of the presented duration (for all durations). As the intervals became longer, the deflection of the CNV started at a later time point. Looking at the context dependent CNV, that is the CNV during the 0.9s duration, it was evident that the CNV was more negative for the short context than for the long context during the perception phase. Additionally, the typical CNV resolution occurred during the memorization phase. It needs to be kept in mind that at the observed time point of the CNV no response was required from the participants. This suggests that the CNV amplitude and time course may be related to the perceived passage of time, as suggested in previous research (Bendixen et al., 2005; Macar et al., 1999).

Furthermore, this indicates that the context actively influences timing-related brain activity during perception of an interval since the CNV already showed differences during this phase.

When looking at the reproduction phase, the same difference between the two conditions of the overlapping duration can be found explaining the significant difference in estimations in the behavioural data. A more negative CNV and earlier deflection during the reproduction phase lead to shorter estimations. In contrast to the perception phase, the amplitude of the waveform was in general more negative. Additionally, the time course of the resolution of the ERP was more extended than during the perception phase and the typical deflection was missing. The occurrence of the CNV and its difference in amplitude depending on the context suggests, that it may be related to the preparation for motor action. The starting point of the resolution occurred earlier for the short context compared to the long context where shorter estimations were found. This would also be in accordance with other findings (Kononowicz & Penney, 2016). It needs to be kept in mind however, that the results of the ERP analysis were purely visual and no statistical testing was done on the context-dependent differences.

The CNV may have more than one function in a timing task, as it is elicited during two very different phases: during the passive perception phase and during the more active reproduction phase. It may on the one hand represent the passage of time during perception as its amplitude is related to the reproduced duration. On the other, it may also function as a preparation for action signal due to the earlier deflection and the more negative amplitude in the short context compared to the long context during the reproduction phase. The CNV results further indicate that the context effect is evident in timing components already during the perception phase of the trial. When using the fronto-central cluster for the decoding analysis, only part of the memorization phase could be successfully decoded. In contrast, the decoding results when using all channels suggest that the context is already biasing the

perception stage of an interval. However, as it was also possible to decode the beginning of the memorization stage, memorization processes also play a role in the occurrence of the context effect.

The fact that it was not possible to distinguish a trial during the perception phase based on the activity of this CNV cluster and the observed context-dependent difference in amplitude can also be interpreted as evidence against the hypothesis that the CNV represents the objective accumulator as suggested by some of the previous research (Bendixen et al., 2005; Macar et al., 1999). While these locations are important for timing processes in general and also seem to be involved in the memorization of duration (not reflected in the CNV), they are not sufficient to fully explain the context effect. To investigate the contribution of different channels in more detail, a channel-wise decoding analysis would be beneficial. The resulting contributions of different channels to the decoding success could then be used to find indications which electrode locations are most important to classify a trial in a specific phase. From that, further inferences could be made about the locations that are involved in the context effect.

Surprisingly, it was not possible to sufficiently decode the context of trial during the reproduction phase. As the decoding accuracy slightly increased in this phase it could be possible that due to the limited sample size and number of trials in this study no effect was found. On the other hand, it could also indicate that the decision-making process may not be as relevant for the context effect as expected. Perhaps when using a different paradigm, where durations have to be directly compared, results would be different.

While the SET models attempt to explain differences in estimations through the speeding up and slowing down of the pacemaker by the allocation of attention, it seems doubtful that this would be the reason for the differences in estimations for the same exact duration in different contexts. The stimuli of the overlapping duration had the exact same

characteristics in both conditions. As an alternative, it could be speculated that memory traces of previous durations are blending in with the current presented interval during its perception.

The context effect is a bias immensely relevant for real-life timing. It encompasses the possible influence of multiple durations, which is a crucial contrast to the usual artificial timing tasks used. However, this study is still making use of artificial means, by using stimuli with sharp on- and offsets, which may further limit the generalization of the results to everyday tasks.

Conclusion

The current study established that already the perception of a duration is influenced by the context, suggesting that the context not only affects our timing behaviour but also actively influences the way time is perceived. Based on the obtained results, models of time perception need to not only focus on the perception of the duration but also on the memorization process. All three phases seem to be relevant for the here studied temporal phenomenon to emerge in one way or another. The accumulation of time is already distorted during the perception of an interval and this bias is then memorized and ultimately influences the reproduction. This suggests that accumulator models need to be combined with the idea of the past traces in memory. Furthermore, the CNV cluster locations may not be sufficient to explain the context effect. For future research it would be of interest to investigate the amount of contribution of the different locations to the context effect in the three phases to get an idea which brain regions are relevant in this phenomenon. Alternatively, investigating the question of how the content of the initial perception of a duration is transferred into memory and whether this is directly related to the behavioural outcome would be beneficial for modelling purposes. Finally, as it was assumed that the perception stage entails the encoding of a duration and the reproduction stage the decoding of the duration it cannot be said with certainty that this is indeed the case. It would be therefore of interest to investigate which

processes underlie these three phases and whether specific ERPs could be related to them.

Answering these questions would further improve models of time perception and help us understand timing in humans.

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Appendix A

List of scalp sites used for EEG recording

'FP1'	'FT7'	'T8'	'P8'
'FPz'	'FC5'	'TP7'	'PO7'
'FP2'	'FC3'	'CP5'	'PO3'
'AF7'	'FC1'	'CP3'	'POz'
'AF3'	'FCz'	'CP1'	'PO4'
'AFz'	'FC2'	'CPz'	'PO8'
'AF4'	'FC4'	'CP2'	'O1'
'AF8'	'FC6'	'CP4'	'Oz'
'F7'	'FT8'	'CP6'	'O2'
'F5'	'T7'	'P7'	'PO9'
'F3'	'C5'	'P5'	'PO10'
'F1'	'C3'	'P3'	
'Fz'	'C1'	'P1'	
'F2'	'Cz'	'Pz'	
'F4'	'C2'	'P2'	
'F6'	'C4'	'P4'	
'F8'	'C6'	'P6'	