Behavioral and Neurophysiological Correlates of Interval Timing

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1 General Introduction

> “We are surrounded by the clocks on our wrists, smartphones, cars, appliances, walls, and computers. But it turns out that we are not only surrounded by clocks, we are also filled with them.”
>
> Dean Buonomano, *Your Brain is a Time Machine*

Timing is a fundamental mental ability which underlies the primary cognitive and perceptual functions of the brain. This ability enables the organisms to determine *when* an event occurs and *how long* it lasts. For example, while we get ready for work in the morning, we have the striking ability to keep track of the passage of time of our every behavior or action. There is almost an inner “sense” for how long time has been spent in the shower or preparing breakfast, when the bus will be arriving at the bus station or when we should leave home. Our subjective timing is not only limited to such conscious experiences, but also holds an essential role in more unconscious or automatic processes such as perception or motor performances (Coull et al., 2011).

Temporal prediction, that is, the time interval in which an organism expects an event to occur, is one of the key mechanisms affecting perception and action (Barnes & Jones, 2000; Nobre et al., 2007). Perceptual studies varying temporal uncertainties have shown that visual detection performances, e.g., for luminance and orientation, increase with higher temporal certainties (Lasley & Cohn, 1981; Westheimer & Ley, 1996). Similarly, studies using attentional orientation tasks have reported that detection and discrimination performances are faster and more accurate when temporal expectations are cued to the moment when stimuli would appear (Correa et al., 2004; Coull & Nobre, 1998). Moreover, in addition to predicting onset and offsets of events, the delay in between those markers as well as their orders, the brain can also measure elapsed time. The time keeping ability at the sub-second to several seconds range, known as *interval timing*, is required for the perception and production of accurate motor responses, speech, rhythm and music (Matell & Meck, 2000; Patel, 2003). This is illustrated by the studies researching the individuals with Parkinson’s disease (PD), i.e., a disorder related to the dysfunctioning dopamine system in the basal ganglia, an area also responsible for interval timing (Buhusi & Meck, 2005; Gu et al., 2016; Merchant et al., 2008). The patients with PD have been reported to have difficulties in movement production and coordination, keeping up with rhythmic motor responses and speech production (Gu et al., 2016; O’Boyle et al., 1996; Volkmann, 1992). Overall, interval timing has been suggested to be essential and inevitable for attention, perception, action and cognition (Matell & Meck, 2000).

Despite the importance of interval timing ability, it still holds very systematic biases. Sensory environments built up through trial history and expectations derived from the recent past are the two common factors affecting subjective judgments of time (Bausenhart et al., 2014; Dyjas et al., 2014; Lejeune & Wearden, 2009). The former phenomenon which is termed as *central tendency bias* implies that the perceptual judgements are influenced by the statistical structure of the past events (Gu & Meck, 2011). Likewise, responses to current stimuli are biased towards the preceding stimulus, indicating *serial dependence* characteristics in timing (Cicchini et al., 2018). Over the half a century, these biases have been studied extensively (Helson, 1948; Parducci, 1965). Helson (1948)'s adaptation-level theory and Parducci (1965)'s range-frequency theory have defined the biases in terms of the sample range which is the current stimulus drawn from while providing no explanation why they occur initially. Bayesian models of timing stand out for a more recent interpretation of the contextual biases (Jazayeri & Shadlen, 2010; Miyazaki et al., 2005). They suggest that the brain monitors the uncertainty of a sensory measurement and adapts its estimation based on the statistics of the sensory environment (Jazayeri & Shadlen, 2010). Since then, Bayesian analysis has long been used to provide insights on many contextual factors (Burr et al., 2013; Gu et al., 2016; Shi et al., 2013). However, there are still some key questions which cannot be answered using classical Bayesian approaches. For instance, classical models do not consider the temporal order of the tested intervals while integrating the sensory temporal input with prior history. In fact, we observe differential time estimation results with the change of target interval orders while keeping the statistical properties of the input the same (the details are described in Chapter 2). Moreover, there is a gap between the Bayesian descriptions and their implementations in the brain.

The following part (1.1) reviews general systematic biases observed during interval timing and introduces influential cognitive frameworks of interval timing process. Then, the second part of the introduction (1.2) describes the typical temporal distortions related to the features of sensory environments and their potential neural underpinnings. The third part (1.3) details the Bayesian models of time and describes how the Bayesian frameworks might be implemented in the brain. The final part (1.4) details the aim of the current dissertation. Chapters 2, 4 and 5 report three studies performed to address the effects of temporal characteristics on the subjective experience of the passage of time, while Chapter 3 describes a short review on the neural signatures of interval timing. Chapter 6 discusses the findings of the empirical work and evaluates the short review.

1.1 Psychophysical Laws of Time and Timing in the Brain

There are quantitative relationships between the physical world and their percept. Over the last decades, psychophysical studies have tried to identify the specific conditions where physical stimuli give rise to constant perceptual outcomes. Previous research has explained these lawful relationships using statistical and cognitive models of the time (Paton & Buonomano, 2018). One caveat of the timing models, however, is to primarily use and model the processing of interval timing. Instead of a single isolated stimulus, objects, sounds or actions that we encounter in everyday life are surrounded by other objects or features; thus, the perception of a target input strongly depends on its spatial and temporal context (Schwartz et al., 2007). In this part, I introduce psychophysical laws of interval timing and how they are explained using neuro-cognitive and statistical models.

1.1.1 Stimulus Order Effects

Performance on stimulus judgments depends on the stimulus presentation order. The discovery of the order effects can be traced back to early work of Fechner (1860). In his influential work *Elemente Der Psychophysik*, he reports two constant errors during two stimuli comparison performance: time-order errors ("Zeitfehler") and space-order errors ("Raumfehler") which are observed depending on the stimulus temporal position (if presented as the first or the second) and spatial position (if presented on the right or left of the visual field). Later, it has been shown that when the two stimuli are presented consecutively, the perception of the second stimulus is systematically biased as a function of the first stimulus magnitude, known as the *time-order error* (TOE) (Allan & Gibbon, 1994; A. Hellström, 1979; Schab & Crowder, 1988). For example, when participants were asked to compare two intervals which were of equal length, participants underestimated the second interval when the first interval was a short duration (shorter than 500 ms), whereas overestimated when the first interval was a long duration (longer than 700 ms) (Nakajima et al., 2004). This effect has been explained by Woodrow's (1935) interpretation stating that the perception of the first interval shifts towards the standard around the 'indifference interval' (a duration between 500 to 700 ms) and the second interval comparison is being made with a subjectively biased first interval. Since then, TOE is generally measured as the difference between the point of subjective equality (PSE) and the standard first interval (Woodworth & Schlosberg, 1954), where PSE is defined as the magnitude which gives rise to 50% "long" duration judgments of the second interval (A. Hellström, 1979; A. Hellström & Rammsayer, 2004; Å. Hellström & Rammsayer, 2015). Subsequently, a series of work has suggested the effects of stimulus order on the discrimination performance depends on the sensitivity differences between two intervals, termed as *Type B effect* (Ulrich & Vorberg, 2009; Yeshurun et al., 2008).

Timing of sequential entities differs compared to single isolated intervals behaviorally and neurally. For example, the neural encoding mechanism of sequence timing (e.g., basal ganglia) has been suggested to differ from those of single interval timing (e.g., cerebellum) (Grahn, 2009; R. Ivry, 1993; Teki et al., 2011). Yet, stimulus order effects are also found in a series of time intervals. When a train of short time intervals are presented consecutively, the last duration is underestimated, an effect known as *time-shrinking illusion* (Hoopen et al., 1993; Nakajima, Ten Hoopen, et al., 1992) and this has been explained within the Bayesian framework stating that the perceived duration of a single target is biased towards the sequence mean (Burr et al., 2013).

1.1.2 Regression and Range Effects

A few years after Fechner's book *Elemente Der Psychophysik (1860)*, Vierordt published *Der Zeitsinn nach Versuchen (1868)* as a seminal work on time perception investigations using psychophysical methods developed until then. One of the main findings from that work is known as Vierordt's law, also referred to as *the regression effect* and *central tendency bias*. It is an observed effect when the subjective judgment of a given interval is biased towards the mean interval (Vierordt, 1868)**,** leading to underestimation of large magnitudes while overestimation of small magnitudes. This effect was evident in many studies showing that the sensory measurement is not only the outcome of the current input but is also influenced by the statistics of the previously experienced stimuli (Gu & Meck, 2011; Lejeune & Wearden, 2009; Penney et al., 2000; Taatgen & van Rijn, 2011). The nature of this effect depends on many factors such as individual differences, sensory modality and stimulus set properties. For instance, expert musicians who are known to be more precise at time perception compared to non-musicians, show less central tendency biases than the control group in temporal reproduction performance (Aagten-Murphy et al., 2014). Moreover, patients with PD who are with dysfunctional dopaminergic regulations in the striatum, resulting in disturbances in interval timing, show stronger central tendency biases than the healthy control group (Malapani et al., 1998). More than a half a century has passed since researchers discovered the differences in time estimations for the different sensory modalities (Goldstone et al., 1959; Maier et al., 1961). It is established that auditory stimuli are more precisely encoded compared to visual stimuli, e.g., sounds are judged longer than the lights when presented for the same amount of time. Therefore, a stronger central tendency bias is observed for visual compared to auditory stimuli. For instance, the study of Cicchini et al. (2012) showed that expert musicians (string musicians) and the non-musician control group had central tendency bias for the visual stimuli only, while no bias was observed for the auditory stimuli, including the control group. The regression bias is also known to be more pronounced for larger sample intervals as compared to shorter sample intervals, known as the *range effect* (Jazayeri & Shadlen, 2010).

1.1.3 Scalar Variability and Internal Clock Mechanism

When subjective judgements of time intervals are being researched in humans and other animals, a consistent feature, referred to as *scalar variability*, is being noticed (Gibbon, 1977). Similar to Weber's law (Fechner, 1860), which is a common psychophysical law followed by many sensory dimensions such as brightness, loudness and motion detection, the standard deviation of participants' time estimations are being observed to increase linearly as the target intervals increase in magnitude (Gallistel & Gibbon, 2000; Rakitin et al., 1998). Since then, the scalar variability in the time domain is being reported in numerous behavioral responses and neural activations (Hinton & Meck, 2004; Malapani & Fairhurst, 2002; Meck, 2003; Meck & Malapani, 2004; Wearden & Grindrod, 2003).

The explanation of this phenomenon roots in the noise emerging in the internal clock system (Treisman, 1963). It has been so long that the question of how the brain achieves its time perception has puzzled scientists. Time, in contrast to the other sensory dimensions, does not have a sensory system devoted to it. Nevertheless, the brain is surprisingly accurate at discrimination durations varying in a few milliseconds (Rammsayer & Lima, 1991) and at sensorimotor synchronization with regular beats (Mates et al., 1994). Yet, the neural basis of timing abilities and time perception is still not known. It has been extensively discussed if the processing of time is achieved with the dedicated, clock-like neural mechanisms or is a consequence of other cognitive processes (R. B. Ivry & Schlerf, 2008). One group of theories suggest that the brain keeps track of time with a *dedicated internal clock mechanism*, e.g., Scalar Expectancy Theory (SET), Striatal Beat-Frequency (SBF). For example, based on

SET, there is a three-stage information processing system where initially, a passage of time index is accumulated in the central clock as “pulses” (resembling the ticks in a physical clock), stored in the memory and retrieved when a comparison is needed during the decision stage (Gibbon et al., 1984). Although SET has been a remarkable model of internal timing for years, it has been criticized to suffer from reasonable neurobiological underpinnings (van Rijn et al., 2014). Matell and Meck’s (2004) SBF model, providing a neurobiological mechanism for the dedicated internal clock, assumes that the oscillations of the group of neurons in the cortex and thalamus reset at the stimulus onsets and the concurrent firing activity of these neurons are detected by the striatum. Dedicated models of time have been supported considering the fact that we can transfer and compare our time estimation of one sensory modality to another (Grondin & Rousseau, 1991; Ulrich et al., 2006). On the other hand, strong evidence against the dedicated models with a centralized internal clock mechanism comes from studies indicating modality-specific timing and local distortions in sensory modalities (Bueti et al., 2008).

Second group of theories of timing, which can be referred to as *intrinsic clock models*, suggest that timing is a consequence of inherent neural dynamics (R. B. Ivry & Schlerf, 2008). According to intrinsic clock models, the time perception is an outcome of the perceptual tasks which are inherently temporal in nature (Paton & Buonomano, 2018). Therefore, they propose no explicit clock mechanism like in pacemaker-accumulation theory (Gibbon et al., 1984) or synchronous oscillations of population neurons (Matell & Meck, 2004). For example, the temporal context model (TCM) of Shankar and Howard (2010) suggests that time perception of a stimulus depends on how it is represented in episodic memory. Dedicated timing models described above are being criticized due to the fact that the proposed mechanism needs to be restarted at every event (Addyman et al., 2016). Memory models of the timing, e.g., the TCM and Gaussian Activation Model of Interval Timing (French et al., 2014), can successfully overcome this resetting problem. Based on these models, timing of all events is encoded by the principles of the memory traces with the temporal representations of each event depending on memory decays (French et al., 2014).

1.1.4 Timing within the Bayesian Framework

The development of theories and models of timing initiates a framework to explain how the brain processes time. Traditional timing models such as the pacemaker accumulator model (Gibbon et al., 1984) suggest algorithms to account for subjective timing behavior, while the models with biological implementations offer explanations on how timing takes place in neural circuits (Paton & Buonomano, 2018). On the other hand, from the computational perspective, Bayesian framework has been successful to elucidate the questions whether and how the brain acts on the psychophysical laws, or systematic temporal distortions, to improve timing performance. Recent studies using Bayesian inference provide a lawful explanation to these questions (Jazayeri & Shadlen, 2010; Shi et al., 2013). Under the Bayesian approach, the observer takes into account two sources of information while making time estimations. First, the likelihood function of the statistics of the sensory measurement is involved. Second, the prior probability distribution function of the past intervals that the observer encountered is included in the final estimate. The idea of this approach is that the information about the time estimations are noisy and they are improved via integrating the prior knowledge.

Bayesian estimation models successfully account for the central tendency bias (Jazayeri & Shadlen, 2010), and serial dependency effects (Cicchini & Burr, 2018). However, they do not consider temporal order effects of the target intervals. There are recent studies which examined the effect of the structure of target interval presentations (Glasauer & Shi, 2019a, 2021a). However, these studies researched the presentation order effects across an experimental session, i.e., from trial to trial, whereas the temporal order effects within a trial on the observed time estimations still lacked a thorough exploration. In **Chapter 2**, I describe an experiment in which we manipulated the orders of target intervals embedded in temporal patterns while keeping the statistics and the range of the probe intervals the same.

1.2 Context Effects in Time Estimation

It is well established that time estimations are influenced by previously experienced intervals. Since the discovery of Vierordt's central tendency bias (1868) and Fechner's time-order biases (1860), there has been a large body of work on the timing focusing on temporal context effects. The term "temporal context" describes sample intervals that are presented and stored in memory over the course of an exposure, i.e., in an experiment. Behavioral studies suggest a distribution-dependent characteristics during time estimations (Wearden, 1991; 1995) and a reliance on the ensemble perception principles (Zhu et al., 2021). But until now, it is not clear how we achieve temporal context integration into the current estimate. This is better investigated using measures with high temporal resolutions such as the scalp-recorded electroencephalography (EEG) and event-related potentials

(ERPs) (Luck, 2005). In this part, I describe the common temporal context effects and how they are explained using both behavioral and neurophysiological evidence.

1.2.1 Distribution dependency

Traditional studies on temporal context commonly involve the use of perceptual duration-categorisation tasks such as temporal generalization and bisection (Penney & Cheng, 2018). Duration categorisation paradigms test the perception of a given interval and provide the relationship between the tested intervals and their percentage of a correct response. Typically, the shortest and longest durations of the target intervals (also known as anchors or standards) are presented with a feedback in the training phase, and later, the classification of the intermediate durations are examined in the testing phase (Church & Deluty, 1977). The early works of Allan and Gibbon (1991) and Wearden (1991) have suggested that the perception of the intermediate target intervals are affected by the geometric mean of the anchor durations. Following this argument, the distribution of all target intervals, including both anchors and intermediate intervals, have been shown to have an effect on the categorisation (Brown et al., 2005; Penney et al., 2014). For example, as Brown et al. (2005)'s temporal range-frequency account has pointed out, the perception of target durations changes even though the mean of anchor durations stays the same. Instead, Brown et al. (2005) suggested that the range position of a target (i.e., how far it is from the anchors) and its rank order (i.e., the second or the sixth) holds a significance on the perceptual judgments. Building upon this, Zhu and her colleagues (2021) proposed an ensemble-distribution account, stating that categorisation judgments are based on the ensemble statistics (mean and variance) of the set of target intervals. In large stimulus sets, how we memorize or assign the weights to the range position or relative rank of each target would be challenging. Thus, Zhu et al. (2021) proposed a categorisation mechanism in which humans make their perceptual decisions by comparing the current stimulus with a memorized standard, i.e. the mean of the target intervals set.

1.2.2 Ensemble perception

When we encounter a crowd of faces, a traffic jam or observe a pile of leaves on the ground, we process, attend or memorize these scenes via several strategies. We either form high-resolution representations at the cost of abandoning some parts of the scenes and selectively attend to the most related part of them (Chun et al., 2011), or form low-resolution representations of these complex scenes to extract the gist of the scenes or its statistical properties (Oliva & Torralba, 2006). The second strategy, which our brain uses to cope with its limitations in sensory mechanisms, involves perceiving the environment in a form of statistical summary representations, known as ensemble perception (Whitney & Yamanashi Leib, 2018). It is well established that ensemble perception takes place in the spatial (Whitney & Yamanashi Leib, 2018) and temporal information (Schweickert et al., 2014). For example, previous studies have shown such averaging mechanism in a variety of spatial features, e.g. size (Ariely, 2001b), motion direction (Williams & Sekuler, 1984), orientation (Parkes et al., 2001) and color (de Gardelle & Summerfield, 2011). Likewise, research has shown that the human brain can form mean temporal information (Albrecht et al., 2012; Piazza et al., 2013; Zhu et al., 2021).

1.2.3 Studying time using EEG

With the first known recording of ‘action potential’, that is a peculiar change in the electric properties of a cell (Bernstein, 1868), researchers could take the advantage of using the techniques to measure the electrical activity along the scalp elicited by the neuron firings. Electroencephalography (EEG), given its high temporal resolution nature, has been a cornerstone method to research how the brain achieves timing. Following the dedicated models of time, EEG has been used to seek for mechanisms underlying different stages of temporal processing including the encoding, maintenance and decision-making (Kononowicz, Rijn, et al., 2018). For example, in a study in which researchers assessed the neural correlates of temporal encoding, a heightened negativity waveform over fronto-central electrodes, known as the contingent negative variation (CNV), was observed for longer compared to shorter duration judgments (Herbst et al., 2015). In addition, the large positivity amplitude measured over frontal cortical and the central-parietal regions following 300 to 400 ms after stimulus evaluation, known as P300 or late positive component of timing (LPCt), has been associated with temporal memory and decision-making processes (Ng & Penney, 2014; Nieuwenhuis et al., 2005).

The late offset positivity components such as LPCt, P300 or P3 have been reported repeatedly as the measures of temporal decision-making (Kelly & O’Connell, 2013; Ofir & Landau, 2022a; Polich & Kok, 1995). In their recent findings, Ofir and Landau (2022b) used a temporal accumulation-to-bound model (Balcı & Simen, 2014) and linked the P3 amplitude to the distance to the decision threshold. In **Chapter 3**, I describe a short review in which we review this recent paper (Ofir & Landau, 2022b) on their findings relating temporal decision-making to offset P3 signals and showing contextual modulations on the offset EEG signals.

1.2.4 Neural correlates of temporal context

Finding the neural mechanisms that translate physical time into perceived time has always been a great interest of neuroscience. Therefore, until now, many aspects of subjective timing have been extensively studied using neuroimaging techniques. With the use of Surface Laplacian source localizations and intracranial testings (Ferrandez & Pouthas, 2001; Onoda et al., 2004), the signals targeting the fronto-central electrodes, in the case of CNV and LPCt, are suggested to originate from pre-supplementary motor area (preSMA) and right dorsolateral prefrontal cortex (DLPFC). The preSMA activation during timing is commonly observed in both *perceptual* (the subjective judgments are typically measured in categorical decisions) and *motor timing tasks* (the judgements are measured by self-timed motor responses) (Coull et al., 2016; Coull & Nobre, 2008). There have been studies reporting the distinct neural populations in the preSMA tuned to distinct stimulus durations (Merchant et al., 2013). Along with these findings, there is a growing literature on the EEG markers of the brain timing and contextual modulations targeting the fronto-central regions of the brain.

A recent study investigated the neural basis of central tendency and sequential effects focusing on the CNV and LPCt components and found that CNV activity covaries with the preceding interval as it was shown by increased CNV amplitude with the longer prior durations, whereas the LPCt amplitude linearly increases with the short target intervals (Wiener & Thompson, 2015). Another study investigated the locus of Bayesian computations in timing using EEG and found that CNV, offset P2 and beta power are affected by the previous trial (Damsma et al., 2021). Although there have been studies on the electrophysiological markers of temporal context, the neural basis of the ensemble context modulations on subjective timing is still not known. In **Chapter 4**, I describe a study with two separate experiments in which we manipulated the distribution context of target intervals and used EEG to measure the common neural underpinnings of time such as CNV and offset components, LPCt and P2.

1.3 Bayesian Frameworks of Time

As it has been introduced in the previous sections, the duration estimates of the brain are noisy and susceptible to many contextual biases such as the central tendency or sequential dependence. A line of work has shown that the sensory estimates advances when the current measurement is combined with a prior built over past experiences (Petzschner et al., 2015; Roach et al., 2017). Similar to classic information-processing models, also referred to as internal clock mechanisms, Bayesian models suggest three basic components for temporal processing: the likelihood, the prior probability, and the loss function. These components had been related to the information-processing stages of the internal clock (Shi et al., 2013). Classic information-processing models specify a clock stage for measuring duration and a memory stage for comparing the current measurement in the working memory to a reference duration in the long-term storage. In line with this, Bayesian models make use of the likelihood function which establishes the probability of a given measurement as well as the prior and posterior functions which mark off the probability of the internal reference and its memory representation, respectively. The considerable emphasis on the computational principles in the Bayesian model has brought about the development of numerous models. These models, however, came out with different assumptions (Glasauer & Shi, 2022a; Jazayeri & Shadlen, 2010; Petzschner et al., 2015). In this part, I describe the common Bayesian observer models and how they are studied at the both behavioral and brain level.

1.3.1 Bayesian observer models

Bayesian observer models have been successful to provide theoretical explanations for the subjective timing and the systematic biases and to make quantitative predictions for the contribution of the prior experience. One crucial aspect of using Bayesian models to predict behavior is the selection of likelihood, prior and loss functions. For example, it is argued that choosing a *fixed* prior distribution to explain the perceptual biases would rule out the influences of sequential dependency (Glasauer & Shi, 2022a). *Static prior models* with a fixed prior distribution assume the same prior distribution throughout all trials, while *iterative prior models* use a dynamically updated prior distribution by each trial. In one of the widely recognised works, Jazayeri and Shadlen (2010) accounted for the central tendency bias observed in the temporal reproduction using the classical Bayesian observer approach where the prior knowledge assumption was defined as a fixed stimulus distribution. Since a model with static prior does not include predictions of the sequential dependency, an iterative

Bayesian approach has been proposed where the prior is iteratively updated based on the previously experienced trial (Dyjas et al., 2012; Petzschner & Glasauer, 2011; Taatgen & van Rijn, 2011).

1.3.2 Temporal context driven by priors

Classic Bayesian models, implicitly, assume that people build a single prior during the stimulus exposure. However, we are commonly exposed to sensory environments filled with a variety of stimulus ranges and information coming from different sensory modalities. For example, while locating a chirping bird on a tree branch, the visual cue as well as the auditory cue of that percept will serve as two distinct information sources. In addition to the integration of simultaneously present sensory information from different senses, we can make use of various other sources of information while forming our perception and action. Earlier, Petzschner and colleagues (2012) showed that informing participants by using categorical perceptual cues influence their perceptual reproduction. Specifically, they used two overlapping *short* and *long* stimulus ranges in three experimental sessions: blocked-wised presentation, interleaved presentation, and interleaved presentation in which they provided categorical cues before each trial. Their results indicated that although both interleaved conditions had the same presentation order and stimulus sets, the session with the categorical cue led participants to form two different priors. As a result, participants' reproductions biased towards these two local priors instead of the global prior of the experimental session. On the other hand, the interleaved presentation session without any categorical cue resulted in forming one generalized global prior for two overlapping stimulus ranges. In a later study, Roach and colleagues (2017) showed that generalized prior formation is not limited to overlapping ranges, but can also occur in stimulus ranges which are clearly separated from each other. Interestingly, this generalized prior formation was not observed when the different motor responses were expected from different stimulus ranges. It suggested that individuals might be keeping multiple motor activity specific priors throughout an exposure. Therefore, it remains as an open question which factors are involved in the grouping of complex stimuli environments and how the brain makes use of multiple prior information acquired from separate stimulus groups.

1.3.3 Electrophysiological signatures of context

A long-lasting question puzzling the researchers in neuroscience is to find out how the brain takes the uncertainty into consideration during the processes of perception, memory, decision making, and response. In the search for an answer, there has been numerous research using behavioral measures as well as the neuroimaging techniques to examine the neural mechanisms underlying these processes (Beierholm et al., 2009; Körding & Wolpert, 2004; Vilares et al., 2012). In an attempt to disentangle cognitive processes in timing, Damsma and colleagues (2021) used an interval reproduction task and measured the EEG signals during the perception stage in which no decision or response takes place. They showed that the CNV and offset P2 components were actively shaped by the prior during the *perception* phase of the reproduction task. Given that CNV and P2 waveforms have been suggested to be associated with the neural populations in the supplementary motor area (SMA) (Coull et al., 2016), these findings propose that populations of neurons in the SMA can flexibly adjust to temporal context at the perceptual stage in which no decision or motor preparation is involved.

Wiener and colleagues (2018) examined the brain oscillations EEG data collected in the temporal bisection and found that longer prior target intervals elicited higher beta power at fronto-central electrode (FCz) site in the current trial. Similar to the trial-by-trial shift of the psychometric function towards the prior interval, e.g., longer prior leads to a right-ward shift in the psychometric function, the beta oscillations also reflected a shift depending on the prior. Therefore, the authors suggested that beta oscillations measured at FCz may be tracking the trial-by-trial update of the prior, consistent with the iterative updating models of Bayesian accounts (Petzschner & Glasauer, 2011). Similar findings have been also reported in many studies (Kononowicz & Penney, 2016; Li et al., 2017; van Rijn et al., 2011). However, it remains unclear how the brain performs multi-prior integration. In **Chapter 5**, I describe a study in which we examined the effects of two prior contexts (uni-prior and multi-prior) on temporal reproductions while measuring EEG signals.

1.4 Aim of This Thesis and Research Questions

The goal of the current dissertation is to examine the behavioral and neurophysiological correlates of contextual modulations in interval timing.

In Chapter 2, I describe an experiment in which we manipulated the temporal order of the target intervals using a temporal reproduction task. In early implementation of Bayesian frameworks in the duration estimation behaviors, the presentation order effects were tested throughout an experimental session, i.e. across different trials. Therefore, in this study, we tested the stimulus order effect within a trial by using temporal patterns generated by the same intervals.

In Chapter 3 and 4, I describe two studies in which we review and test the context modulations indexed by the neurophysiological evidence, respectively. Chapter 3 describes a short review on how the brain activity measured by EEG at the offset of stimulus presentation can successfully account for temporal decision-making. Chapter 4 describes two experiments in which we manipulated the sample distributions presented in an experimental session and examined the contextual effects in the behavioral outcome and in the common EEG signatures of time. We measured post-onset signals, as well as, in line with the short review findings, post-offset signals while searching for the contextual signatures.

In Chapter 5, I describe an experiment in which we manipulated the experimental sessions to test the effects of multi-prior integration to the sensory input at the behavioral and neurophysiological levels. It is still an ongoing issue to understand whether and if so, how the multi-priors contribute to the sensory decisions. Therefore, in this study, we used a duration reproduction task along with the EEG to examine the effects of multi-prior sensory environments presented to the participants.

2 Influences of temporal order in temporal reproduction

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2.1 Abstract

Despite the crucial role of complex temporal sequences, such as speech and music, in our everyday lives, our ability to acquire and reproduce these patterns is prone to various contextual biases. In this study, we examined how the temporal order of auditory sequences affects temporal reproduction. Participants were asked to reproduce accelerating, decelerating or random sequences, each consisting of four intervals, by tapping their fingers. Our results showed that the reproduction and the reproduction variability were influenced by the sequential structure and interval orders. The mean reproduced interval was assimilated by the first interval of the sequence, with the lowest mean for decelerating and the highest for accelerating sequences. Additionally, the central tendency bias was affected by the volatility and the last interval of the sequence, resulting in a stronger central tendency in the random and decelerating sequences than the accelerating sequence. Using Bayesian integration between the ensemble mean of the sequence and individual durations and considering the perceptual uncertainty associated with the sequential structure and position, we were able to accurately predict the behavioral results. The findings highlight the critical role of the temporal order of a sequence in temporal pattern reproduction, with the first interval exerting greater influence on mean reproduction and the volatility and the last interval contributing to the perceptual uncertainty of individual intervals and the central tendency bias.

Keywords: time perception, temporal reproduction, temporal order, temporal sequence perception, auditory pattern reproduction

2.2 Introduction

Timing is critical in various everyday experiences, ranging from taking part in social interactions to producing adaptive motor behaviors. Accurate processing of temporal patterns enables us to recognize delicate differences in words and tones in a conversation or to enjoy the orchestrated rhythm in music. Studies have shown that humans are able to discriminate complex rhythmic patterns very well for both visual and auditory presentation (Grahn, 2012; Su & Salazar-López, 2016). In complex real-world scenarios, such as in musical dance, multiple rhythmic cues are important for perceiving the rhythmic structure (London et al., 2016; Wang et al., 2021). Yet, perception of a temporal pattern is subject to various forms of contextual modulation and integration.

In a simple rhythmic form, it has been shown that changes in the rate of auditory clicks can simultaneously assimilate the apparent flicker rate of a flashing light, known as the auditory driving effect (Recanzone, 2003; Shipley, 1964; Welch et al., 1986). This effect is thought to occur due to the influence of the high temporal resolution of the auditory system on the visual system, likely through cross-modal interactions in the brain. The classic time-shrinking illusion, where a train of different intervals assimilate to each other (Nagaike et al., 2016; Nakajima et al., 1992), further demonstrates how intervals can be perceived as shorter or longer based on their preceding intervals, even within the same modality. Studies on rhythm adaptation have also revealed similar effects, such as adapting to faster rhythms leading to shorter perception of the following sequence (Becker & Rasmussen, 2007) and adapting to decelerating rhythms leading to perception of the following isochronous rhythm as accelerating (Li et al., 2022).

Despite extensive research on temporal rhythms, how the precise reproduction of temporal structure in terms of its basic component - time interval - has yet been largely overlooked in the literature. A temporal sequence consists of an ordered set of individual time intervals, and the perception and reproduction of such sequences depend not only on the individual elements, but also on the perception of the rhythm itself, which is heavily affected by temporal order and the relative length of its subcomponents (Matthews, 2013). Reproducing individual elements of a group can be challenging, even without asking for sequential order information. For example, a study of visual size estimation (Ariely, 2001) showed that observers can relatively precisely estimate the average size of a set of circles, but identifying individual items can be difficult. The ability to extract the summary statistics of a set has since been referred to as ensemble perception (for a review, see Whitney & Yamanashi Leib, 2018).

One reason for difficulties in recalling or reproducing an individual item in a set is due to the ensemble perception itself. Ensemble statistics may serve as a prior that could heavily influence the perception of an individual item (Ariely, 2001; Whitney & Yamanashi Leib, 2018). In a recent study, Zhu et al. (2021) manipulated the ensemble distribution of the sample intervals (i.e., the set) in a temporal bisection task, and found that judgments of individual intervals were assimilated to the mean of the probed intervals across trials, manifesting a central tendency effect (Jazayeri & Shadlen, 2010; Laming, 1999). Previous studies on the time-shrinking illusion (Burr et al., 2013; Hasuo et al., 2014; Nagaike et al., 2016; Nakajima et al., 1992) have suggested that such assimilation may occur within a sequence of intervals within a trial. However, these studies only focused on the influence of general ensemble statistics on one target interval, leaving no prediction on the order effect for sequences with the same stimuli but different orders.

The order effect within a trial has mainly been investigated in a simple two-interval comparison. For example, the threshold and the discrimination sensitivity of the two-interval comparison depend on the order of the standard and the comparison, known as time-order error (TOE) (Allan, 1977; Dyjas et al., 2012; Harrison et al., 2017; Hellström, 1985; Ulrich & Vorberg, 2009). The discrimination sensitivity is higher when the standard is presented first. The order effect is not limited to stimuli presented within individual trials: sequential order of stimuli across trials can also systematically alter judgments (Glasauer & Shi, 2019, 2021, 2022; Shi et al., 2022). For example, Glauser and Shi (2021) tested reproduction of the same set of intervals in two different sequential structures: random walk and completely random order. In the random walk condition, the successive intervals show mild fluctuation while remaining similar, analogous to the temperature fluctuations that occur over consecutive days. In contrast, intervals in the completely random order condition were randomly selected, like the random rearrangement of temperature data from a year. Reproduction in a completely random sequence, relative to a random walk sequence, yielded a more pronounced central tendency effect, suggesting that the volatility[1] of the sequence can influence how an interval is reproduced. However, these studies, including the study of Glauser and Shi (2021), have only used single interval reproduction. Timing of isolated intervals (i.e., interval timing) and complex pattern timing are two distinct mechanisms that involve different neural circuits of the brain (Teki et al., 2011), leaving unanswered the question of how the order of a temporal sequence influences the reproduction of the whole sequence.

On these backgrounds, we aimed to investigate the effect of sequential structure, particularly the order (and the volatility) of sequences in temporal reproduction. We hypothesized that the perceived volatility of a sequence may affect the ensemble representation of the sequence, and subsequently influence its reproduction. In addition to the order of intervals, the first and the last intervals in a sequence may also introduce additional primacy and recency effects, respectively (Deese & Kaufman, 1957). Primacy and recency

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[1] Of note, the volatility should not be equated to the variability. Volatility measures the degree of unpredictable changes from one item to the next in a sequence, while the variability measures the dispersion of the sampled stimuli regardless of the sequential structure.

effects are two phenomena related to memory and information processing that describe the tendency for participants to better remember the first and the last item in a list (Silverman, 2010). The first interval is often perceived as longer than subsequent intervals because of the onset saliency of the first interval (Kanai et al., 2006; Rose & Summers, 1995). According to Bayesian inference of timing (e.g., Shi, Church, et al., 2013), perception tends to assimilate towards the more reliable source. As people are better at recalling the endpoints (the first and the last intervals) of a rhythmic pattern (the primacy and recency effects), they are more likely to depend on these endpoints for perceiving and reproducing a rhythm. Consequently, rhythms with more variable endpoints are expected to have a higher central tendency.

To disentangle these effects, we used a temporal reproduction task in which participants were required to reproduce a series of auditory stimuli which were presented in succession in a trial resembling a rhythm production task. Considering the ensemble statistics (mean and variance) effects on stimulus judgements, we used temporal patterns with the same sequence mean and variance values. Temporal patterns we used in this study had decelerating (DS), accelerating (AS) or random (RS) sequence structures, which differed in their volatilities. A decelerating sequence structure denotes a pattern of intervals in descending rhythmic order (from short to long) whereas an accelerating sequence structure has a reserve pattern. For a random temporal pattern, time intervals were presented in a random order excluding decelerating or accelerating structures. Thus, the random temporal pattern had the highest volatility. We expected that sequential volatility and the first and the last intervals would impact on the perceived interval mean and central tendency. Given the primacy effect of the first interval, which receives more attention than subsequent intervals (Kanai & Watanabe, 2006), we hypothesized that the first interval would have a greater impact on the perceived ensemble mean interval. However, we also considered the possibility of the recency effect for the last interval, and thus, conducted analyses on both the first and the last intervals. To preview the main results, we found a general bias in the reproduction of a temporal pattern, which depended on the temporal pattern structure. Intervals in the AS structure were reproduced more precisely than in the RS and DS structures, and the mean interval of the DS were underestimated. Furthermore, the interval reproductions in the RS structure showed higher variability than those in the AS and DS structures.

2.3 Method

Participants

15 participants (seven females, mean age 25.3 years) with normal hearing took part in the experiments at Ludwig Maximilian University (LMU) of Munich. The sample sizes were determined based on the sample sizes of previous similar temporal pattern reproduction studies (Hardy et al., 2018; Laje et al., 2011), in which 11 to 12 participants were recruited. We further increased the sample size to 15 to ensure the statistical power of the study. Written informed consent was received from all participants before the experiments. They received 9 Euro per hour or course credit for their participation. The study protocol was approved by the Ethics Board of the Department of Psychology at LMU Munich. All participants were naive to the purpose of the research.

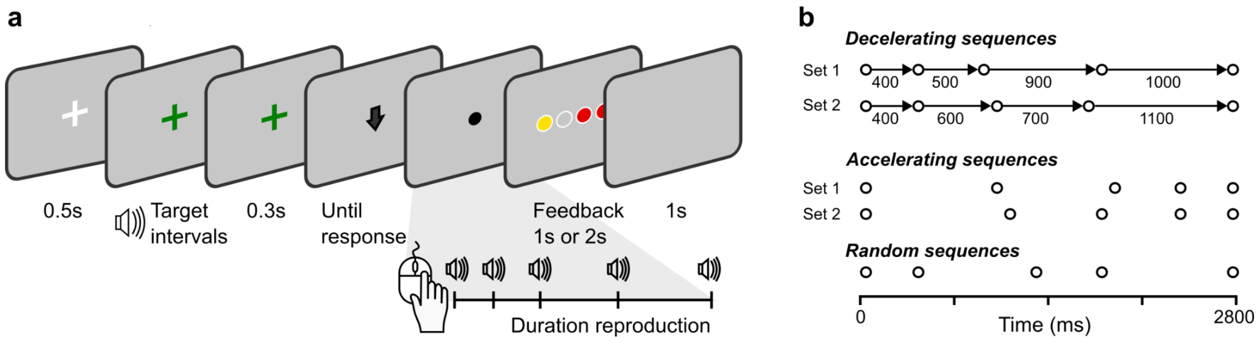

*Fig. 1. Illustration of the experimental design and target intervals. (**a**) Each trial started with a fixation cross presented for 500 ms in the middle of the screen. Participants received five beep sounds marking the four sequential intervals, followed by a 300-ms-long presentation of the fixation cross. Then, they were asked to reproduce the temporal pattern by clicking the mouse. After the reproduction, a feedback was shown to indicate the accuracy of the reproduction (see the main text in Procedure for more details). After a blank period of 1000 ms, the next trial began. (b) Illustration of the temporal patterns used in the experiment. Each circle represents a beep sound. Two sets of intervals were tested in the decelerating (DS) and accelerating (AS) sequences. The AS condition consisted of the same interval sets used in the DS condition but the intervals were in the inverted order, whereas the RS condition consisted of the same intervals randomized (in the illustration, only one possible sequence is shown).*

Apparatus and stimuli

The experiments were conducted in a sound-reduced and moderately lit testing room. Instructions and feedback were presented on a CRT monitor. Auditory stimuli were generated with customized Matlab codes and presented via Sony MDR stereo headphones using the

Psychtoolbox-3 (Kleiner et al., 2007). Responses were acquired via a computer mouse for the reproduction task. In the experiment, three temporal patterns were compared: the decelerating sequence (DS), accelerating sequence (AS) and random sequence (RS). Each sequence had four intervals demarcated by five 'beep' sounds. In each sequence type, we used two interval sets that were randomly shuffled across trials to avoid participants recognizing the four fixed intervals. In the DS condition, two sets of intervals with the same mean (700 ms) and the standard deviation (SD of 294.39 ms) were tested: [400, 500, 900, 1000] ms and [400, 600, 700, 1100] ms, whereas in the AS condition, these two interval sets were in the inverted order (Fig. 1b). In the RS condition, the orders of the sample intervals were randomized, and all-four-intervals ascending or descending orders were excluded to distinguish them from the other two conditions. Thus, in all sequences, the first and the second moments of the ensemble statistics were the same (*M* = 700 ms, *SD* = 294.39 ms).

To present the intervals accurately and precisely, we created sound waves of five brief beeps (20 ms, 1000 Hz, 60 dB) for each stimulus onset asynchrony (SOA) that corresponded to one of the four intervals. The sound wave lasted for a duration of 2.8 seconds.

Procedure

The task was to reproduce a sequence of auditory time intervals, presented within a single trial, using mouse-clicks. As illustrated in Figure 1a, each trial started with a white fixation cross for 500 ms. Next, as the fixation cross turned to green color, participants heard the sequence of five consecutive beeps that demarcated four temporal intervals. The total duration of the intervals was 2.8 seconds, which was immediately followed by a gap of 300 ms. Then a down arrow image appeared on the screen to indicate the reproduction of the temporal pattern could be started. The reproduction was performed by clicking the mouse button five times, each mouse click producing a beep, and attempting to as closely as possible imitate the previously heard sequence of beeps. Each button press initiated a beep for 20 ms (1000 Hz, 60 dB) regardless of the pressing duration. After the reproduction, a feedback display was shown for accuracy. The feedback consisted of four adjacent circles showing how close the participants' reproduction to the veridical interval of each sample interval was. The four disks represented the four sequential intervals from the left to the right, and their colors indicated correspondent reproduced accuracy. The red disk indicated the relative error was 50% longer or shorter than the sample duration, and the yellow disk for the relative error in between [-50%, -15%] or [15%, 50%], the white disk filled with gray color (as it was the same as the background color of gray) for the relative error in between [-15%, 15%]. To encourage participants to reproduce the intervals accurately, the duration of the feedback display was contingent on the accuracy. If more than three reproduced intervals were in ‘red’ or ‘yellow’, the feedback display lasted for two seconds, otherwise, it was shown only for one second. After a one-second blank screen, the next trial started. Participants received one practice block of 44 trials prior to the main experiment to familiarize them with the task, which was discarded in the formal analysis. The main experiment consisted of six blocks, with 44 trials in each block, and 264 trials in total. The orders of the trials were randomized for each participant.

Statistical Analyses and modeling

All statistical tests were carried out in either Python or JASP. The latter was used for Bayesian analyses of variance (ANOVAs) with default settings (i.e., r-scale fixed effects = 0.5, r-scale random effects = 1, r-scale covariates = 0.354) to provide a more rigid criteria required for hypothesis testing (Kass & Raftery, 1995; Rouder et al., 2009). All Bayes factors reported for the main effects and interactions were calculated using “inclusion” Bayes factors across matched models. Additionally, outliers were excluded from all the statistical analyses below. These outliers were defined as trials on which the reproduced interval mean of the stimulus sequence was higher or lower than two times the standard deviation of the sequence mean, which accounted for approximately 3% of all trials.

As demonstrated in behavioral results below, the mean reproduced interval was influenced by the first probe interval. Therefore, in our model, we assumed the mean prior (μ_e) of the sequence is a weighted average of the first probe interval (D_1) and the mean of the tested intervals (700 ms):

$$\mu_e = \alpha \cdot D_1 + 700 \cdot (1 - \alpha).$$

with the weight α being determined by the variability of the stimulus distribution and measurement noise. Since duration estimates often follow Weber's law (Shi, Church, et al., 2013), the sensory variability and the prior variability are determined by Weber fractions (wf_s and wf_p respectively). In addition, we assumed the perceived volatility of the sequence may scale the sensory uncertainty. To be more precise, the variability (σ_i) of a given interval D_i has a volatility factor k_j, which depends on the sequence type j,

$$\sigma_i^2 = k_j (w f_s \cdot D_i)^2.$$

The reproduction pattern (R_i) is then modeled as Bayesian integration between the ensemble mean μ_e and individual duration D_i (Jazayeri & Shadlen, 2010; Ren et al., 2021; Shi, Church, et al., 2013):

$$R_i = (1 - w)\,\mu_e + w\,D_i,$$

where weight $w \propto 1/\sigma_i^2$, the reproduction variance $\sigma_r^2 = \frac{(\sigma_i^2 \cdot \sigma_e^2)}{(\sigma_i^2 + \sigma_e^2)}$, and $\sigma_e = w f_p \cdot \mu_e$.

Based on these assumptions, we fitted the model to the observed data and estimated duration reproduction patterns for each participant. The model was implemented using PyMC3 (Salvatier et al., 2016). To demonstrate the robustness and predictiveness of the model, we first fit the model with the structured sequences (i.e., AS and DS) and then use those fitted parameters (excluding the sequence scaling factor *k*) for the RS condition. We also assessed the model's goodness using coefficients of determination (R^2) between the predicted and observed data.

2.4 Results

Effects of the temporal pattern on the central tendency bias

The central tendency bias is a phenomenon, showing that intervals shorter than the pattern mean interval are overestimated and intervals longer than the pattern mean are underestimated. To measure this bias, a linear regression was conducted between sample intervals and reproduced intervals (as shown by the lines in Fig. 2). As depicted in Figure 2, all three sequence types exhibited the central tendency bias, with reproduction slopes less than one (*M* = 0.8, 0.526, 0.53 for the AS, DS and RS respectively). Among the three conditions, DS and RS caused a higher central tendency bias, while the AS condition had the lowest bias.

The results of a two-way repeated-measures ANOVA on the regression slopes revealed significant main effects of sequence type, $F(2, 28) = 16.92$, $p < .001$, $\eta_p^2 = .55$, $BF > 100$, and interval set, $F(1, 14) = 57.93$, $p < .001$, $\eta_p^2 = .81$, $BF > 100$. Post-hoc Bonferroni-corrected *t*-tests revealed that AS (*M* = 0.80) had a steeper slope (i.e., less central tendency) compared to RS (*M* = 0.53, $t(14) = 6.50$, $p < .001$, $BF > 100$) and DS (*M* = 0.526, *t*(14) = 3.85, *p* < .01, *BF* = 23.95). However, there were no significant differences between the RS and DS conditions (*t*(14) = 0.09, *p* = .93, *BF* = 0.26). The significant difference between the two interval sets suggests that the separation of individual intervals may also affect reproduction (as seen by the horizontal gaps among points in Fig. 2). An interaction between interval set and sequence type was also observed, $F(2, 28) = 4.00$, $p = .03$, $\eta_p^2 = .22$, *BF* = 0.51. However, the small BF value suggests that this interaction should not be over-interpreted.

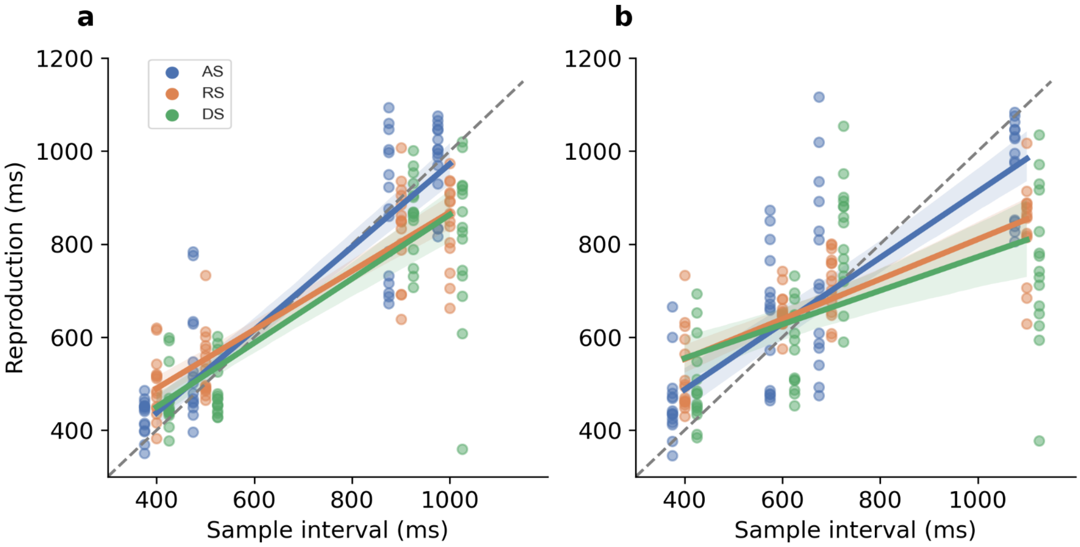

Fig. 2 The slope of the reproduction lines varied as a function of stimuli sequences. The AS condition (blue) had a significantly steeper reproduction line than the RS (orange) and the DS (green) conditions. The DS condition showed the most deviations from the equal reproduction line for which the subjective reproduction would be identical to the sample intervals (diagonal dashed lines) towards the means of the temporal patterns (700 ms). Each dot on a column of sample intervals corresponds to the data point of one single participant. Dots shifted gradually by conditions for illustration purposes. (a) Reproductions of interval set 1: type of pattern created using 400, 500, 900 and 1000 ms intervals. (b) Reproductions of interval set 2: type of pattern created using 400, 600, 700 and 1100 ms intervals.

Influences of the first and last intervals

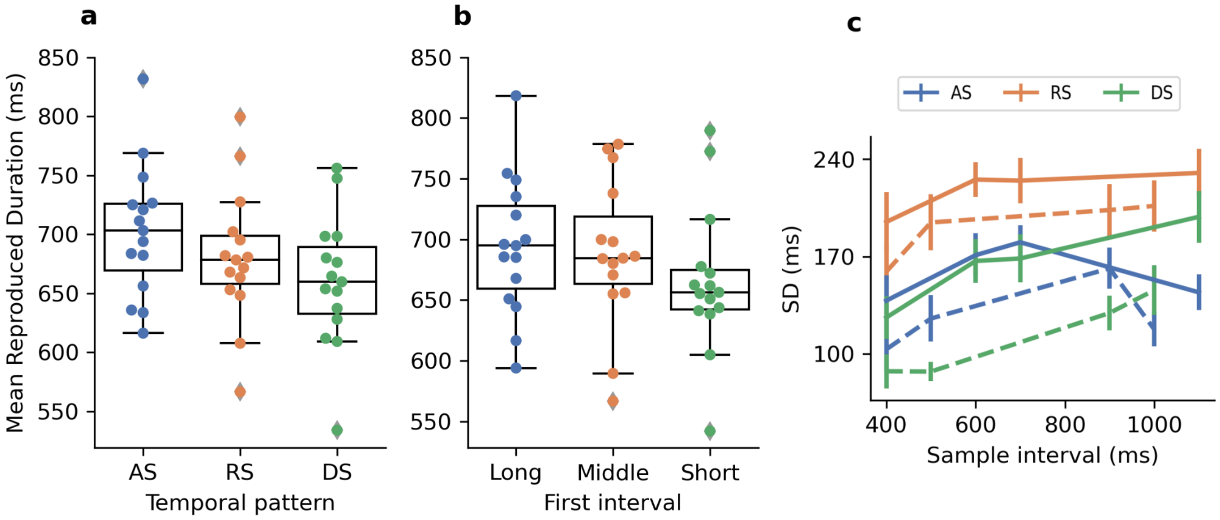

Fig. 3. (a) Boxplots of the mean reproduction of sequence intervals (AS: accelerating sequences; RS: random sequences; DS: decelerating sequences). The dots depict the mean reproductions of one participant for one sequence type, averaged over interval set 1 and set 2.. (b) Boxplots of the mean reproduction of sequence intervals in the RS, divided into three categories based on the time interval in the initial position (Long: first interval longer than 700 ms; Middle: first interval of 700 ms; Short: first interval shorter than 700 ms). The dots depict the mean reproductions of one participant for one sequence type, averaged across both interval sets. (c) Standard deviation of reproductions in the AS (blue), RS (orange) and DS (green) conditions. Solid lines represent the type of pattern created using 400, 600, 700 and 1100 ms, and dashed lines represent the type of pattern created using 400, 500, 900 and 1000 ms.

Figure 3a shows that the average reproduction of intervals decreases from AS, to RS, and to DS. A repeated-measures ANOVA showed that the mean reproduced interval was significantly affected by sequence type, $F(2, 28) = 18.08$, $p < .001$, $\eta_p^2 = .56$, $BF > 100$. The post-hoc Bonferroni-corrected t-tests revealed the mean reproduced intervals differed significantly from each other ($ts > 3.2$, $p \leq .02$, $BFs > 8.0$), with AS having the highest mean ($M = 702$ ms, $SD = 56$ ms), DS having the lowest mean ($M = 660$ ms, $SD = 55$ ms), and RS falling in between ($M = 660$ ms, $SD = 55$ ms).

Since the AS had the longest interval and the DS the shortest interval in the first position, the differential mean reproduced intervals may stem from anchoring to the first interval or the directionality of the sequence. To test this hypothesis, we further analyzed the reproduced intervals in the random sets based on the first interval being the short (<700 ms), middle (700 ms) or long (>700 ms) sample interval in the stimuli sequence. Figure 3b shows a similar pattern to Figure 3a, with the mean reproduced interval decreasing as a function of decreasing first interval duration (*long*: *M* = 694 ms, *SD* = 57 ms; *middle*: *M* = 689 ms, *SD* = 61 ms; *short*: *M* = 666 ms, *SD* = 60 ms). The mean reproduced interval significantly differed based on the first stimulus magnitude in the random sequences, *F*(2, 28) = 7.78, p = .002, η_p^2 = .36, *BF* = 16.79. Post-hoc Bonferroni-corrected *t*-tests revealed that the *short* yielded significantly lower reproduced intervals compared to the *long* and the *middle* (*t*s > 2.59, $p \leq$ .02, *BF >3*.0), while no difference between the long and middle (*t*(14) = 0.94, p = .36, *BF* = 0.38). The results suggest that the mean reproduction may be influenced by the first interval, rather than the sequential structure.

We conducted a similar analysis for the last interval in random sets by dividing them into three categories based on their last interval being short (<700 ms), middle (700 ms), or long (>700 ms). However, the analysis on the mean reproduced interval did not reveal any significant difference (*F*(2, 28) = 1.20, p = .32, η_p^2= .08, *BF* = 0.38). Instead, we found the central tendency effects were different among three categories, *F*(1, 14) = 13.25, p = .002, η_p^2 =. 49, *BF* > 100 . The mean slopes were 0.62, 0.50, and 0.31 for random sets ending with a *short*, *middle*, and *long* interval, respectively. Post hoc Bonferroni-corrected *t*-tests revealed that the slopes significantly differed from each other (*t*s > 2.94, *p*s < 0.33, *BF*s > 11). The central tendency was least prominent for random sets ending with a short interval and most pronounced for sets ending with a long interval, suggesting that the last interval may influence the perceived variability of the sequence and subsequently influence the central tendency. The impact of the last interval on the central tendency effect was similar to the structured AS and DS sequences (see Fig. 2).

Variance of time estimation

To test if the type of sequential structure affects the reproduction variability, we estimated the standard deviation of reproduced durations for the three types of sequences, separately for each interval (Fig. 3c). A two-way repeated-measures ANOVA showed that the SDs of the reproduced durations were significantly influenced by both sequence type, *F*(2, 28) = 48.31, p < .001, η_p^2 = 0.78, *BF* > 100, and sample interval, *F*(6, 84) = 16.29, p < .001, η_p^2 = 0.54, *BF* > 100. Post hoc *t*-tests revealed that the reproduction variability was significantly higher for RS ($M = 204.79$) than for AS ($M = 142.66$) and DS ($M = 138.72$), ts > 7.4, ps < .001, BFs > 100. However, there was no significant difference in variability between AS and DS, $t(14) = 0.81$, $p = .43$, $BF = 0.35$. The interaction between the sequence type and durations was also significant, $F(12, 168) = 3.46$, $p < .001$, $\eta_p^2 = 0.20$, $BF = 32.83$, partly due to the same interval having different positions in different sequences. The largest variability in the RS reproduction, significantly greater than the AS and DS reproduction, suggesting that the motor execution uncertainty was greatly influenced by the volatility. This was likely caused by unfamiliarity of executing irregular tapping.

Estimates and prediction of the model

Using the model we illustrated in the Method section, we estimated the model parameters and its prediction of interval reproduction. The Weber fractions of the sensory input and the mean prior (and associated SDs) were 0.18 ± 0.09 and 0.35 ± 0.03 respectively. The weight of the first interval was 0.195 ± 0.07, suggesting the first interval partially yet significantly influenced the mean prior. The volatility scaling factors were 2 ± 1.2 and 2.4 ± 1.4 for the AS and DS sequences, respectively, which is consistent with observed data showing the length of last interval may influence the perceived variability. With those parameters obtained from the AD and DS, the fitted volatility scaling for the RS sequence was 2.13 ± 0.17, in a similar range as the AS and DS conditions. Figure 4a shows the model predicted mean reproductions (the solid lines) vs. the mean behavioral data (the dashed lines). To evaluate the overall performance of the model, we run linear regression analysis between the predicted and observed reproductions for each sequential type. The mean coefficient of determination, R^2, of the linear regressions were relatively high, 0.80, 0.62 and 0.91 for AS, DS and RS, respectively, which indicates the model in a good agreement with the observed data.

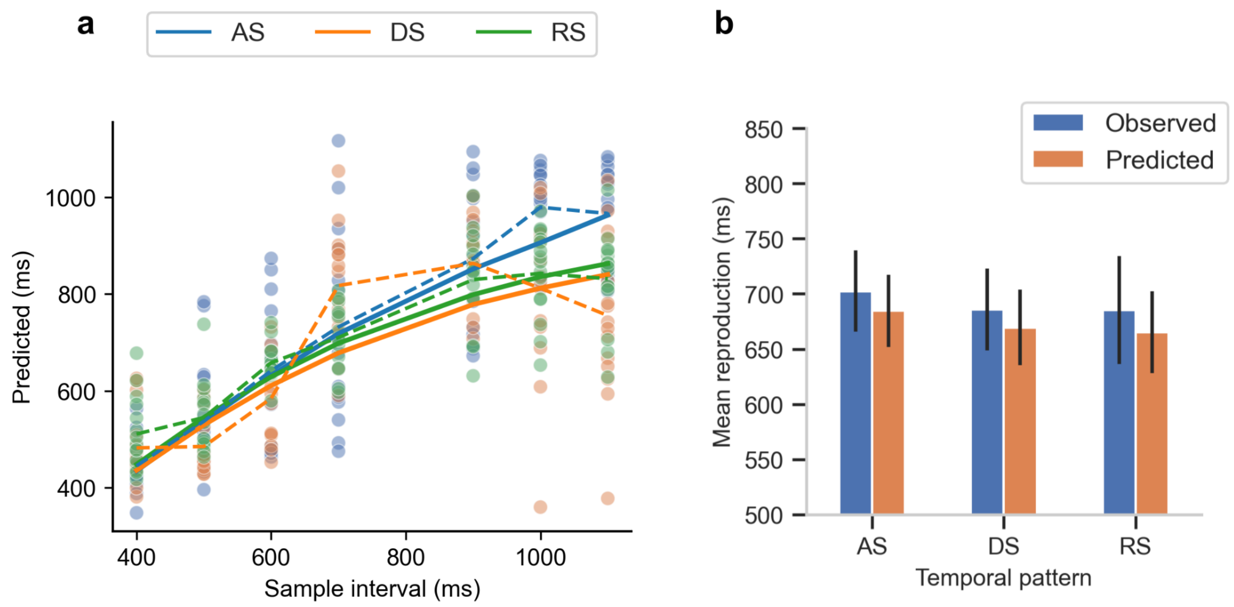

Fig. 4. (a) Predicted reproduction durations of the model are plotted against sample intervals and the observed reproduction durations. Dots represent the observed data and dashed lines represent the averaged observed data across participants. Solid lines represent the predicted reproduction by the model. (b) Observed and predicted mean reproduction of the sequences as a function of sequence condition. Error bars depict one standard error.

The model also successfully predicted the order of the means and SDs of reproduced durations across three sequences: the predicted mean and SD for the AS was 684.9 ± 127.0 ms (observed = 702.5 ± 142.6 ms), for the DS 669.5 ± 132.7 ms (observed = 685.7 ± 143.8 ms), and for the RS 665.0 ± 143.9 ms (observed = 685.3 ± 190.1 ms). However, the model generated some minor undershot (as shown in Fig. 4b). The undershot likely originated from the model assumption. The model considered only the integration of the first interval and the veridical mean interval of 700 ms for the mean prior. As shown in previous research (Shi, Ganzenmüller, et al., 2013; Wearden et al., 1998), auditory intervals are often overestimated, thus assuming a veridical mean interval of 700 ms is likely the primary source of this undershot.

2.5 Discussion

The aim of this study was to investigate the effect of the sequential order of durations on temporal reproduction. The main findings were that, even when the sample intervals in the sequences were the same in terms of mean and variance, (i) the mean reproduced interval of a sequence was shorter with a sequence starting with a *short* relative to a long interval; (ii) the central tendency was more pronounced for sequences ending with *long* intervals; (iii) timing precision depended on the sequence structure, and the structured DS and AS were reproduced more precisely than the RS. Based on those findings, we proposed a pattern timing model that assumes the mean reproduction is a weighted average of the sample durations, with weights determined by their perceptual reliability. The central tendency arises from Bayesian integration of the ensemble prior and individual intervals. Our model was able to predict the observed behavioral temporal reproductions accurately.

Objects, sounds or actions that we encounter in everyday life are surrounded with other objects or features and how we perceive a target strongly depends on its spatial and temporal context (Schwartz et al., 2007). Several model frameworks, including Bayesian estimation models, have been developed to capture central tendency biases arising from trial history in time perception (Cicchini et al., 2012; Dyjas et al., 2012; Jazayeri & Shadlen, 2010). While standard Bayesian models can account for the central tendency biases by integrating the mean prior with sensory inputs (e.g., Jazayeri & Shadlen, 2010), they *fail* to consider the temporal order effects of probe stimuli, and hence fall short in explaining the findings observed in our study. Recent studies by Glasauer and Shi (2019, 2021, 2022) have investigated effects of sequential order of trials on magnitude reproductions. They found that high relative to low volatile sequences produced a stronger central tendency, despite the stimuli being the same but differing in their sequence. Using an iterative Bayesian updating model, they were able to predict the differential central tendency effects and the sequential effects (depending on the previous stimulus) among different sequences. It is worth noting, however, that their studies focused on cross-trial sequential effects on an isolated trial rather than the temporal pattern within a short sequence. To the best of our knowledge, our study is the first to examine the order of sequence influences on the reproduction of temporal patterns.

It is essential to differentiate between individual interval and temporal pattern timing (Hardy & Buonomano, 2016), because interval timing refers to the timing of single durations, whereas pattern timing involves timing relationships among subintervals. When processing auditory interval patterns, assessing the statistical information of patterns is necessary in processes like speech and music (Paton & Buonomano, 2018). Previous research has shown that humans can extract the mean frequency of a tone sequence (Piazza et al., 2013) and statistical information of tone sequences can affect performance, such as speech categorization (Holt, 2006). In contrast to interval timing, it could be argued that participants adopt alternative weighting schemes to process the subintervals of a pattern in pattern timing.

For example, the first interval might engage more attention than subsequent intervals, as the onset often dilates time (Kanai & Watanabe, 2006; Rose & Summers, 1995). Indeed, the present study showed that the first interval in the sequence had a greater impact on the mean reproduced interval. And the pattern timing model also took this into account by adding the weight of the first interval. Thus, our results emphasize that not only the statistical summary but also the order of individual durations in a temporal pattern contributes to the timing of those patterns.

Our study found that the central tendency bias in reproductions varied depending on the sequence structure. The AS had the lowest central tendency bias, while the DS and RS had similar and higher biases. The analysis of the last interval showed that sequences ending with a *long* interval had a higher central central tendency bias. According to Weber's law, the variability increases as the interval increases. Therefore, the findings suggest that the perceptual variability of a sequence was affected not only by its volatility but also by the recency effect - the variability of the last interval. Since the DS sequences had the longest ending interval, the perceived variability of the sequence was overestimated, reaching a comparable level to that of the RS. It should be noted that perceptual variability is different from reproduction variability. Our analysis of the reproduction variability unequivocally showed that the RS had the highest reproduction variability, indicating the volatility of a sequence, not just its physical variance, contributed to observed reproduction variability.

Previous research on central tendency bias (Jazayeri & Shadlen, 2010; Petzschner et al., 2015; Shi, Church, et al., 2013) only considered the dispersion of the sampled intervals, while our study took sequential volatility into account. Our findings highlight the significance of considering sequence order in temporal reproduction. Our temporal pattern model, which included simple volatility scaling, accurately captured the order of variability across the three types of sequences. However, our model did not consider how volatility affects the uncertainty of motor reproduction, such as motor execution of irregular sequences. Future research on how sequential structure influences motor uncertainty could provide further insights into the reproduction of temporal patterns.

In sum, the current study highlights how the sequential structure of a temporal pattern influences listeners' perceived ensemble mean and volatility, reflected by the average reproduced interval and the central tendency bias of duration sequences. The mean reproduction is largely influenced by the initial interval (i.e., onset dilation), while the central tendency effect is influenced by the volatility of the sequence. Moreover, timing precision of same durations differ depending on sequential structure, as it was shown by the lower precision of the random sequence than the structured ascending or descending sequences.

Data availability

The data supporting the findings of this study and the statistical analysis code used in the manuscript are available at https://github.com/msenselab/temporal_patterns.

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3 Temporal decision making: it is all about context

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3.1 Summary

Is there sufficient evidence to make a decision, or has enough time passed to justify making a decision? According to Ofir and Landau (2022), these two questions are closely related: brain activity measured by EEG at the offset of stimulus presentation predicts the behavioral temporal decision, being influenced by the current context, and reflecting the relative distance to a decision threshold which is also context-dependent.

3.2 Outlook

During a lunch break, you open a cup of instant noodles, pour hot water over the noodles, cover, and wait. Time to open depends on your desired noodle softness and the sense of passage of time. Too early, noodles not ready. Too late, noodles too soft. Using a classic temporal bisection task, Ofir and Landau (2022) studied this type of time-based decision to understand the neurophysiological basis of interval timing and how it relates to the cumulative decision process.

In a temporal bisection task, participants are first presented with two references: the shortest and the longest durations. After familiarization, they are asked to classify durations that fall between the two references as ‘short’ or ‘long’. Ofir and Landau (2022) measured electroencephalography (EEG) brain activity while participants performed this task. Similar to previous studies (for a review, O’Connell & Kelly, 2021), they found a decision-related large positive deflection in a group of frontocentral electrodes at 300 to 500 ms after stimulus offset, known as the offset P300 or P3b. As stimulus duration increased, the amplitude of the offset P3b decreased linearly when the duration was close to the ‘short’ reference, but leveled off when the duration was close to the ‘long’ reference. Ofir and Landau (2022) interpreted this offset amplitude as the distance to the decision boundary in a temporal accumulation-to-bound model (Balcı & Simen, 2014). A bisection decision of ‘short’ can be made when the presentation finishes before a decision threshold - the mean duration between the ‘short’ and ‘long’ references. No further trigger for the ‘long’ decision is needed when the presentation time passes the mean duration. Linking the P3b amplitude to the distance to the decision boundary, Ofir and Landau (2022) could predict behavioral bisection performance accurately.

Interestingly, the pattern was similar for the short- and long-range durations. In their Experiment 3, participants performed the bisection task in two separate blocks: one with the sub-second (0.2–0.8 s) range and the other supra-second (1–2 s) range. Short durations in both blocks, albeit differently in their absolute magnitude, elicited a similar large amplitude of the stimulus offset P3b (e.g., 0.2 s in the short block, and 1 s in the long block). This suggests the activation of the offset P3 does not reflect an absolute accumulation, but is rather context-dependent, relative to the decision threshold set in that block. It is well-established that time estimation is susceptible to various background contexts, such as stimulus spacing and ensemble statistics (Zhu et al., 2021). Even with the same shortest and longest references, the mean duration of the two references is perceived as longer when more short durations are probed. But it is perceived as shorter when more long durations are sampled. The temporal bisection decision does not merely compare to the short and long references. Rather, the decision process considers the ensemble mean of the sampled durations as the decision boundary. The findings of Ofir and Landau (2022), consistent with the temporal context modulation, showed that the amplitude of offset P3b was determined by the relative distance to the ensemble mean of the probed range - a critical decision threshold. For example, as the longest duration in the short-range block, the 0.8-s target interval already passed the decision threshold, eliciting a low P3b amplitude. In contrast, larger than the 0.8-s interval in the short context, the shortest 1-s target interval induced the highest activation of the P3b in the long-range block. These results demonstrated that the offset EEG activities, along with the behavioral responses, were context-dependent.

Contexts set our expectations. For example, we expect to wait a short amount of time for a traffic light to turn green than for a bus to arrive. These expectations influence our decision-making processes, as shown by Ofir and Landau (2022). Five minutes would be unexpected when waiting for a traffic light signal, but perfectly normal when waiting for a bus. In the temporal bisection task, a short stimulus duration would be more surprising than a long stimulus duration, because the decision process is likely already completed when the duration is longer than the average. Earlier research has found that the latency of the offset positivity components, such as the P300 or P3b, is positively correlated with participants' reaction times (O'Connell & Kelly, 2021). A higher level of offset activity leads to a longer response time. The reaction time findings, along with the characteristic build-up of the P300, suggest that P300 activity may reflect the intensity of decision-making process (O'Connell & Kelly, 2021), which could also be interpreted as a surprise response to the stimulus offset, as Ofir and Landau (2022) noted. Therefore, it is necessary to further differentiate the nature of the surprise response and temporal accumulation in the offset positivity.

It is worth noting that the interpretation of the offset P3b as reflecting temporal evidence is specific to the context of a prospective timing task, where the decision threshold is predetermined and the critical event is immediately monitored upon the stimulus onset. In many everyday timing tasks, we may not know what our decision threshold is or we may not be constantly monitoring every event. For instance, we may not realize we have overcooked noodles or missed an appointment until after the fact, when our attention returns to the event and we are surprised at having missed the decision threshold. This type of retrospective timing differs from the prospective timing process (Shi, Gu, et al., 2022). In prospective timing tasks, judgments of time involve active monitoring of the passage of time, which could be predicted by the classical pacemaker-accumulator model or the drift-diffusion process (Balcı & Simen, 2014). The drift-diffusion model, for example, proposed that the interval timing process is governed by two competing Poisson processes (one excitatory and one inhibitory). The ratio of these processes determines the rate at which an accumulator increases, and this accumulator is continuously monitored if it reaches a predetermined threshold. However, when we judge the duration of a past event retrospectively, we rely on relationships between past events stored in our episodic memory. It is unlikely that each past event would trigger a diffusion process, as this would be inefficient in terms of cognitive resources. Shi et al. (2022) proposed that retrospective timing may rely on oscillatory patterns with computational accessibility to timestamp individual past events, rather than using individual accumulation processes. Estimating the duration of a past event involves reading out oscillatory patterns that are associated with the onset and offset of the event. Therefore, prospective and retrospective time differ in terms of both the timing process and the source of surprise. Results from a prospective temporal bisection task may not be applicable to retrospective timing. Future studies that compare prospective and retrospective timing may help to determine whether the offset P3b activation is a result of the cumulative process or a signature of surprise, or both.

In sum, Ofir and Landau (2022b) established a clear connection between neural activity related to decision-making and behavioral performance in a temporal bisection task, showing that the stimulus offset activation is related to the relative distance to the decision boundary in the accumulation-to-bound process. The temporal decision is context-dependent, and so is the conclusion drawn from it - we should be cautious on generalizing the relation between the offset activity and the temporal accumulation. Future research that builds on the findings of Ofir and Landau (2022) by using different timing paradigms, such as retrospective versus prospective judgments, would differentiate the nature of the surprise response and temporal accumulation, and further enrich our understanding of neural mechanisms underlying the timing process.

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4 Electrophysiological Signatures of Temporal Context in the Bisection Task

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4.1 Abstract

Despite relatively accurate time judgment, subjective time is susceptible to various contexts, such as sample spacing and frequency. Several electroencephalographic (EEG) components have been linked to timing, including the contingent negative variation (CNV), offset P2, and late positive component of timing (LPCt). However, the specific role of these components in the contextual modulation of perceived time remains unclear. In this study, we conducted two temporal bisection experiments, where participants had to judge if a test duration was close to a short or long standard. Unbeknownst to participants, the sample spacing (Experiment 1) and frequency (Experiment 2) were altered to create short and long contexts while keeping the test range and standards the same in different sessions. The results showed that the bisection threshold shifted toward the ensemble mean and that CNV and LPCt were sensitive to context modulation. Compared to the long context, the CNV climbing rate increased in the short context, and the amplitude and latency of the LPCt were reduced. These findings suggest the CNV represents an expectancy wave for upcoming decision-making, while LPCt reflects the decision-making process, both influenced by the temporal context.

Keywords: time perception, EEG, temporal bisection, CNV, P2, LPCt

4.2 Introduction

Processing the vast amount of information that surrounds us can be challenging, as our sensory organs have limited processing capacity (Wolfe, 1994), and more so, our memory and attentional resources (Cavanagh & Alvarez, 2005). To tackle limitations, our brain has developed ensemble perception (Whitney & Yamanashi Leib, 2018), a method for quickly understanding the essence of a scene by extracting statistical information, such as the mean and variance, from its features. For example, we can quickly determine the average size of apples in a supermarket by just glancing at them, without a need to process each individual apple in detail. We use similar forms of ensemble perception to process basic features, such as the average motion, orientations, and colors (Albrecht et al., 2012; Ariely, 2001b; de Gardelle & Summerfield, 2011; Parkes et al., 2001; Piazza et al., 2013; Williams & Sekuler, 1984), as well as sequential durations (Zhu et al., 2021). There are two types of ensemble representations: spatial (Whitney & Yamanashi Leib, 2018) and temporal (Jones & McAuley, 2005; Schweickert et al., 2014). Spatial ensemble representation involves a group of similar objects that are presented simultaneously, while temporal ensemble representation involves processing a sequence of stimuli over time.

When serving as context, both types of ensemble statistics can influence judgments of individual items (Ariely, 2001b; Zhu et al., 2021). For instance, a temporal bisection task to judge if a probe duration is close to a fixed 'short' or 'long' anchor is thought to rely only on the probe's distance to the standards. However, studies have shown that sampling durations can affect our judgment of related durations (Allan, 2002; Penney & Cheng, 2018; Wearden & Ferrara, 1995). The transition between the short and long durations, known as the bisection point, is often influenced by the mean of the sample durations (Zhu et al., 2021). This form of bias, known as *the spacing effect,* occurs when distances among sampled durations are uneven (Wearden & Ferrara, 1995), and *the range effect,* occurs when the spread of the sample set influences its individual durations (Droit-Volet & Wearden, 2001; Penney et al., 2014; Wearden & Ferrara, 1996). While the behavioral effects of the temporal contextual modulation are now better understood (Zhu et al., 2021), the neural mechanisms governing common temporal context effects are not yet fully understood, although some recent research has shed light on this topic (Damsma et al., 2021; Wiener et al., 2018; Wiener & Thompson, 2015).

Recent EEG studies have identified several event-related potentials (ERP) associated with time processing and contextual modulation (Lindbergh & Kieffaber, 2013; Ng et al., 2011; Wiener & Thompson, 2015). For example, in a bisection task, the contingent negative variation (CNV) - a negative polarity waveform that appears in the supplementary motor area (SMA) - has been found to increase in negativity as the interval progresses and levels off when the duration exceeds the geometric mean of the short and long anchors (Ng et al., 2011; van Rijn et al., 2011; Wiener & Thompson, 2015). Additionally, post-interval positivity ERPs, which appear in the range between 200 to 600 ms after the stimulus offset in the same electrode clusters as CNV after the stimulus offset, have been found to vary with duration judgments and temporal decisions (Damsma et al., 2021; Ofir & Landau, 2022b). The early positivity component P2, peaking around 200 ms after the stimulus, has been suggested to be linked with perceived duration length (Kononowicz & van Rijn, 2011), although the relationship between P2 and the probe duration remains unclear (Kononowicz & van Rijn, 2014; Lindbergh & Kieffaber, 2013). The late positivity components, P3, P3b, or late positive component related to timing (LPCt), measured around 300 - 600 ms after the stimulus, have been related to temporal decision-making (Bannier et al., 2019; Lindbergh & Kieffaber, 2013;

Paul et al., 2011). For example, Ofir and Landau (2022b) revealed that the offset-evoked P3 was negatively correlated with the stimulus duration in a bisection task, and its amplitude decreased as the stimulus duration increased. Using a drift-diffusion model, Ofir and Landau (2022b) could predict behavioral performance by assuming that the amplitude of the offset-P3 reflects the proximity of the temporal accumulation to the decision boundary (i.e., the bisection point). Likewise, LPCt has also been found to vary with the probe duration, with larger positive amplitudes being associated with shorter durations (Wiener & Thompson, 2015). Given that LPCt or P3 is measured after the duration offset, higher peaks for the short compared to long intervals are interpreted as a sign that decisions for short intervals are more demanding, as the decision process remains active and unresolved at the offset of a short presentation (Lindbergh & Kieffaber, 2013).

Early studies primarily focused on those ERP components on temporal accumulation (e.g., Macar et al., 1999), which did not take contextual modulation into account. More recent studies have shown those ERP components are also sensitive to temporal contexts. Wiener and Thompson (2015) have shown that both the CNV and LPCt covaried with the duration presented in the prior trial. Damsma et al. (2021) asked participants to reproduce intervals drawn from two different but overlapping ranges (the short and the long). When the same interval was reproduced in the short-range compared to the long-range session, the reproduction elicited higher amplitudes of CNV and offset P2. Furthermore, the amplitudes of the CNV and the offset P2 decreased as the prior interval increased. By probing a bisection task in sub-second and supra-second ranges separately, Ofir and Landau (2022b) found that the offset P3 amplitude resembled a similar pattern in the two ranges, highlighting the nature of contextual modulation (Baykan & Shi, 2022).

Decisions in a bisection task can be made *during* stimulus presentation without waiting until the end, as it becomes clear whether a duration is short or long once the elapsed time passes the bisection point between the short and the long. But a decision in a reproduction task can only be made during the late reproduction phase, after the full presentation of the duration. As a result, ERP components related to different timing tasks - bisection or reproduction - may reflect different temporal cognitive processes depending on the task being applied (Gontier et al., 2009; Kononowicz & van Rijn, 2014; van Rijn et al., 2011).

It is important to note that the aforementioned EEG studies primarily focused on neural activities during the probe itself. While some studies have discussed contextual modulation (e.g., Ofir & Landau, 2022b), the contexts are often vastly different (e.g., sampling from different ranges of durations, such as subseconds vs. super-seconds). None of these studies have examined *ensemble contexts* within the same range of durations, but with different duration spacing or sample frequencies. Neurophysiological mechanisms underlying such *ensemble contexts* are not yet fully understood. To address this issue, we designed two experiments using the bisection task with manipulations of sampled durations. In both experiments, the short standard was 400 ms, the long standard 1600 ms. Participants had to judge whether a probe duration was close to the short standard or the long standard. Unbeknown to participants, the sampled durations in Experiment 1 were positively skewed in one session and negatively skewed in the other, while in Experiment 2 there were high frequencies of short samples in one session and long samples in the other. Based on previous findings (Ng et al., 2011; Wiener & Thompson, 2015), we expected the CNV peak latencies would correlate to the internal decision criterion of the bisection task, where peak latencies would be earlier in short compared to long contexts, but would plateau after the ensemble mean duration. According to literature (Kononowicz & van Rijn, 2014; Tarantino et al., 2010), which suggests that the P2 amplitude is linked to the stimulus magnitude, we hypothesized that the P2 amplitude would increase with target interval increases and be more positive in short relative to long contexts. To distinguish the late positivity components, e.g. LPCt, from the P2 component, we inserted a 300 ms blank interval after the stimulus offset in Experiment 2, examining the relationship between the LPCt amplitude and the target interval.

4.3 Experiment 1

In Experiment 1, we manipulated the temporal context using the positively skewed (PS, more short durations) and negatively skewed (NS, more long durations) sample distributions, based on our previous work (Zhu et al., 2021). Behaviorally, we expected the same outcome as the previous study - intermediate durations would be more likely to be judged as “long” in the PS than the NS context.

4.3.1 Method

Participants

20 participants with no hearing impairment took part in Experiment 1 in exchange for a monetary reward or course credit at LMU Munich. The sample size was calculated based on

the effect size of a similar temporal bisection study (Zhu et al., 2021) with $\eta_g = .26$, and the assumption of $\alpha = .05$ and power $1 - \beta = .95$, which required a sample size of 16 participants. To be safe for EEG analysis, we increased the sample size to 20. All participants provided written informed consent before their participation. One participant was excluded in the formal analysis because of excessive eye and body movement artifacts. Thus, the final sample in Experiment included 19 participants (10 females, mean age 27.2 years, *SD* = 4.2 years), who were naive to the purpose of the study. The study was approved by the Ethics Board of the Department of Psychology at LMU Munich.

Stimuli and Procedure

The auditory stimuli were generated using the PsychoProtAudio library and presented through loudspeakers (Logitech Z130) using the Psychtoolbox 3 (Kleiner et al., 2007). Instructions and feedback text were displayed on a CRT monitor.

Participants sat in a sound-attenuated, moderately lit test room. Prior to the formal experiment, participants received a practice block consisting of 5 presentations of the short and long standards (400 and 1600 ms) to familiarize themselves with the standards. During the practice, participants made “short” or “long” judgments and received feedback on whether they were correct or incorrect. In the formal test, each trial started with a visual fixation and a brief beep (20 ms, 1000 Hz, 60 dB), followed by a 500 ms blank display, signaling the start of a new trial. A white-noise stimulus (60 dB) was then presented for a given duration chosen from the experimental stimulus sets (see below). Immediately after the sound presentation, a question mark appeared, prompting participants to respond by pressing the right or left arrow keys on the keyboard using two index fingers, indicating if the presented sound was close to the short or the long, respectively (Fig. 1a).

There were two sessions with each session of 336 trials (six blocks of 56 trials each). Two sessions had different duration sets: the positively skewed (PS) duration set consists of [400, 504, 636, 800, 1008, 1270, 1600] ms, the negatively skewed (NS) duration set [400, 730, 992, 1200, 1366, 1496, 1600] ms (Fig. 1b). The ensemble mean of the NS was 223 ms longer than the ensemble mean of the PS context. Each duration was randomly tested 48 times. The order of sessions was counterbalanced across participants (before the outlier exclusion).

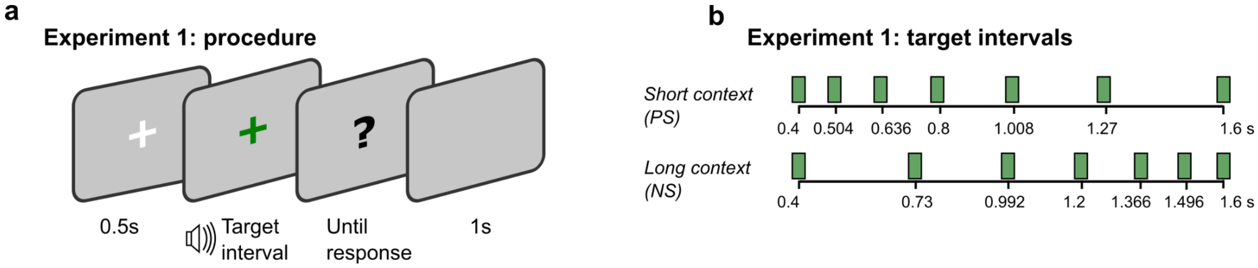

Figure 1. a) *Each trial started with fixation-cross for 500 ms. It was followed by a target interval presentation. Right after the presentation, a question mark appeared, prompting participants to respond. The inter-trial-interval was 1000 ms.* ***b)*** *The target intervals used in Experiment 1. In the short context session (PS), intervals were logarithmically spaced between 400 ms and 1600 ms and the intervals were mirrored in the long context session (NS). Each target interval was presented 48 times during the session.*

EEG acquisition and analysis methods

Electrical brain activity was recorded from 64 scalp locations (actiCAP system; Brain Products, Munich, Germany) using the BrainVision Recorder software (Brain Products GmbH, Munich, Germany) and a BrainAmp amplifier (DC to 250 Hz) at the sampling rate of 1000 Hz. During the experiment, the impedances of all electrodes were kept below 10 kΩ. The electrode FCz was used as an online reference and was re-referencing to temporal-parietal electrodes offline (TP9 and TP10).

The EEG data were analyzed using BrainVisionAnalyzer 2.0 software, with a bandpass filter of 0.1 to 70 Hz. Artifacts caused by eye blinks, eye movements, and muscle noises were removed using independent component analysis (ICA) and visual identification. Before segmentation, the continuous EEG data were inspected automatically using the raw data inspection procedure in the analyzer software and were bandpass-filtered from 0.1 to 30 Hz.

ERP components

All ERP components reported here were calculated for each participant, target interval, and temporal context. The onset-locked ERP data for CNV analyses were baselined to the average voltage 200 ms prior to the stimulus onset, using six clustered frontocentral electrodes FCz, FC1, FC2, C1, C2 and Cz (Kononowicz & van Rijn, 2014; Ng et al., 2011). To examine the evolving velocity of the CNV negativity over time, we conducted linear regression in the time window from the end of post-onset P2 (250 ms) to the start of the CNV

(800 ms) as per previous literature (Ng et al., 2011) and obtained slopes for individual participants in each condition. We extracted the CNV peak latencies as the minimum (most negative) amplitude from stimuli onsets to the longest duration offset (i.e., 1600 ms) for each target interval in each context. We defined the mean CNV amplitude of each target interval as the average waveform in the interval starting from the late negativity onset (250 ms after the onset) and having a length of the stimulus duration (Kruijne et al., 2021). The stimulus offset P2s were calculated using the same frontocentral electrodes as used for the CNV analysis (Damsma et al., 2021). The offset-locked ERP data for P2 analyses were baselined to the 100 ms time window surrounding the stimulus offset (50 ms preceding and 50 ms following the offset) (Kononowicz & van Rijn, 2014). We extracted the P2 peak latencies as the maximum (most positive) amplitude within the 0 - 500 ms duration offset window. We defined the mean P2 amplitude of each target interval as the average waveform between 140 and 300 ms after the stimulus offset (Kononowicz & van Rijn, 2014).

Data analysis

Psychometric functions were estimated using the logistic function with the Quickpsy package in R (Linares & López-Moliner, 2016), the point of subjective equality (PSE) was then calculated at the threshold of 50%, and the just noticeable difference (JND) as the difference between the thresholds at 50% and 75%. Mean PSEs and JNDs were compared using repeated-measures analysis of variance (ANOVA), if necessary, with additional Bayes factor (BF) analyses to provide a more rigorous assessment of the null hypothesis (Rouder et al., 2009). For analysis of the EEG components, we applied a linear mixed model, which can accommodate the covariant factor (duration) in addition to the fixed effects addressed by ANOVA. Mixed models are robust to violations of sphericity and do not inflate Type I errors (Singmann & Kellen, 2019). The p-values reported for mixed models were calculated using the Kenward-Roger approximation.

4.3.2 Results

Behavioral results

Figure 2 illustrates the averaged psychometric functions, mean PSEs, and JNDs. The mean PSE (± standard error, *SE*) for the short-context PS session was significantly shorter (888.7 ± 45.9 ms) than the long-context NS session (958.9 ± 46 ms), $F(1,\ 18) = 6.90$, $p = .017$, $\eta_g^2 = .033$, $BF = 3.04$ (see also Table 1). In other words, the same duration (e.g., 1 sec) was perceived as longer in the short relative to the long context. The sensitivities of the bisection, measured by JNDs, were comparable between two sessions, $F(1, 18) = 2.44$, $p = .14$, $\eta_g^2 = .010$, $BF = 0.74$, indicating the spacing of the target intervals did not change the discrimination sensitivity. Thus, The behavioral results are in line with the previous findings (Zhu et al., 2021).

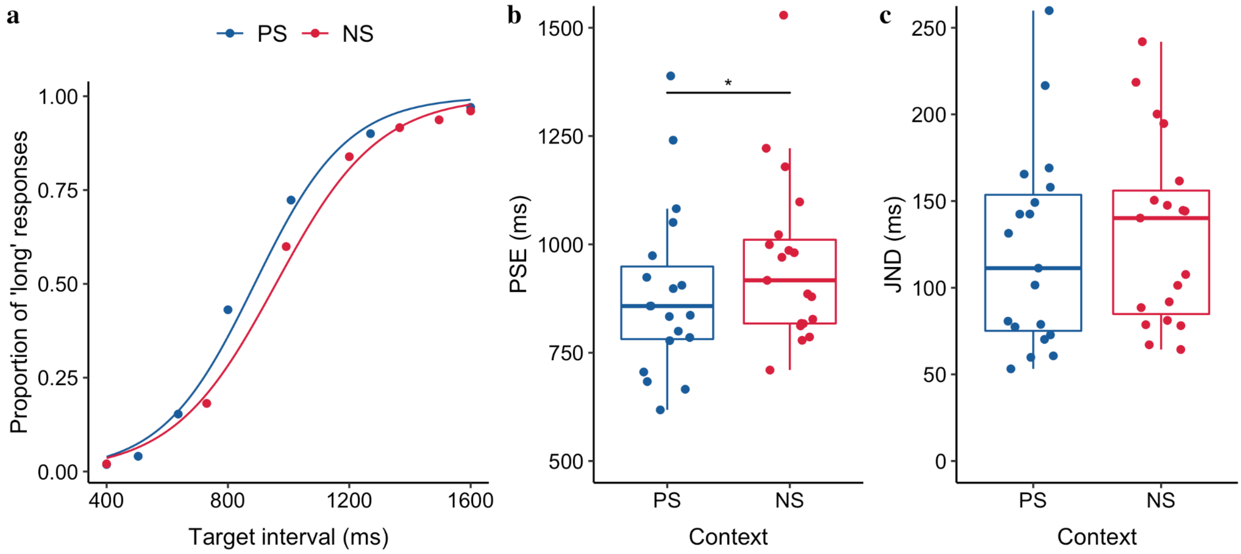

Figure 2. ***(a)*** *The averaged proportion of 'long' responses (scatter dots) and the fitted psychometric curves over 19 participants, separated for the positively (PS) and negatively skewed (NS), stimulus-spacing conditions.* ***(b)*** *Boxplots of the points of subjective equality (PSEs) of the duration judgments for the PS and NS sessions (* p < .05). The dots depict individual PSEs. The lower and upper tips of the vertical lines correspond to the minimum and maximum values, the box the interquartile range (between 25% and 75%), and the horizontal line the median.* ***(c)*** *Boxplots of JND of the duration judgments for the PS and NS sessions. The dots depict individual JNDs.*

Electrophysiological Results

Contingent negative variation (CNV)

Table 1. Mean ERPs and Behavioral PSEs and JNDs

		CNV				Behavioral	
Experiment	Context	Climbing Rate (μV/s)	Peak latency (ms)	Peak amplitude (μV)	Mean amplitude (μV)	PSE (ms)	JND (ms)
1: Spacing	Short (PS)	**-23**	**773.2**	-6.1	-1.47	**888.7**	121.1
	Long (NS)	**-20**	**875.9**	-5.6	-1.17	**958.9**	131.7
2: Frequency	Short (DF)	**-19**	942.8	**-5.4**	-0.78	**749.3**	**96.3**
	Long (AF)	**-17**	876.6	**-4.5**	-0.27	**951.2**	**121.1**

Note. The data are grouped by temporal contexts in both Experiments 1 and 2. Bold values indicate a significant difference between the two contexts.

Figure 3 illustrates the CNV activities in the short PS (a) and long NS contexts (d), showing the negativity changes over time for different target intervals. To characterize the CNV components, we looked into its formation rate, peak latency, amplitude, and the mean latency. Given the negative ballistic deflation of the activities after P2, we used linear regression to estimate the rate (i.e., slope) at which the CNV was forming within the time window from 250 (after P2) to 650 ms (the start of the CNV). The mean values are listed in Table 1.

We found the rate was significantly negative for both the PS context (−23 ± 1.9 μV/s, 95% CI = [−27 to −19] μV/s, t (18) = −12.24, $p < .001$) and the NS context (−20 ± 1.6 μV/s, 95% CI = [−24 to −17] μV/s, t (18) = −13.12, $p < .001$), but significantly smaller in the PS compared to the NS, $F(1, 18) = 9.03$, $p = .01$, $\eta_g^2 = .03$, $BF = 5.53$, indicating a faster temporal accumulation in general for durations in the PS relative to the NS session, consistent with the prior research (Macar & Vidal, 2004). Moreover, the CNV peaked significantly earlier for the short context PS relative to the long context NS (773.2 ms vs. 875.9 ms, $F(1, 18) = 4.99$, $p =$

0.04, $\eta_g^2 = 0.08$, *BF* = 2.17), but only numerically higher in amplitude for the PS relative to the NS (-6.1 μV vs. -5.6 μV, *F*(1, 18) = 3.61, *p* = 0.07, $\eta_g^2 = 0.01$, *BF* = 1.12).

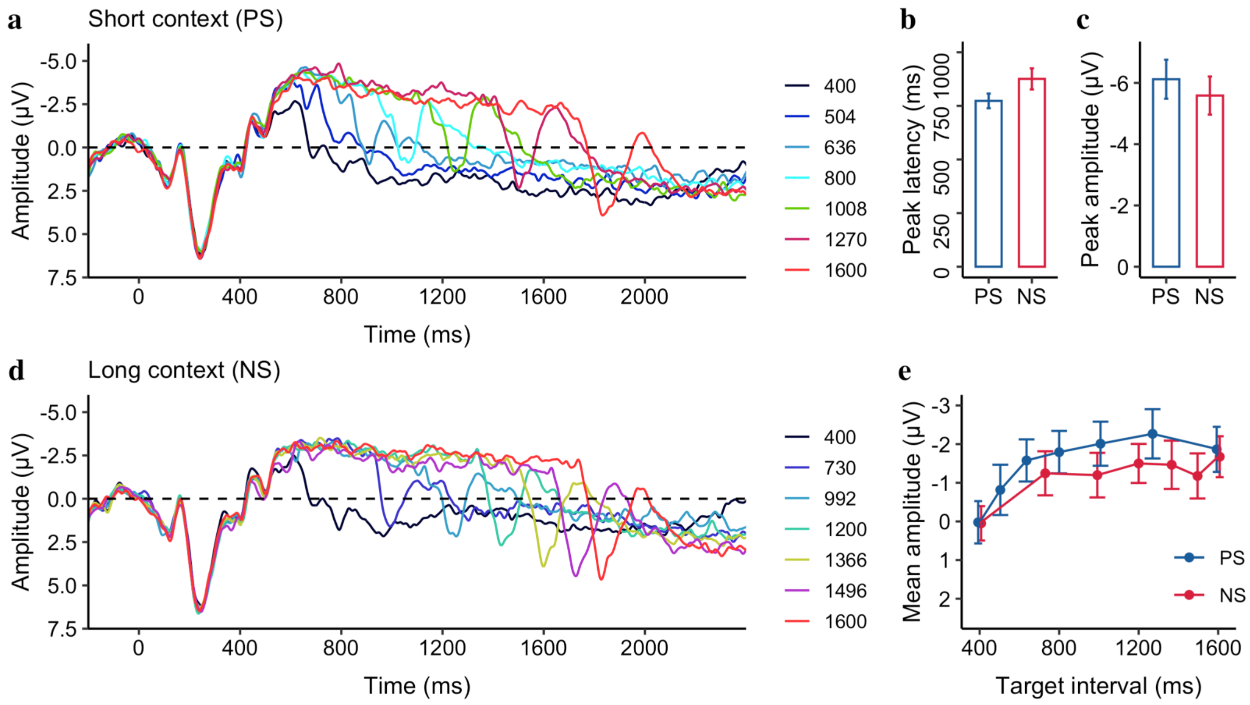

Figure 3. *Grand average of the ERP waveforms over the medial frontal electrodes (FCz, FC1, FC2, C1, C2, and Cz), separated for different target intervals, separated for (**a**) the short (PS) and (**d**) the long (NS) contexts. The mean CNV peak latency (**b**) and amplitude (**c**) of the target intervals, separated for the PS and NS conditions. (**e**) The mean CNV amplitude as a function of the target interval, separated for the PS and NS conditions. Error bars represent the standard error of the mean.*

As research has shown the mean amplitude of CNV to be correlated with the sample duration (Macar et al., 1999; Pfeuty et al., 2003, 2005), we estimated the mean amplitude separately for individual durations, as depicted in Fig. 3e. We then applied a linear mixed model to the mean CNV amplitude, with the Context as the fixed effect and Duration a covariant effect. The mixed model showed that the mean negativity increased by 1.23 μ*V* per second of Duration (*b* = -1.23, *CI* = [-1.72, -0.73], *p* < .001). However, there was no significant difference between the short and long contexts (*p* = .53) and no significant interaction between the Duration and Context (*p* = .31).

Offset P2

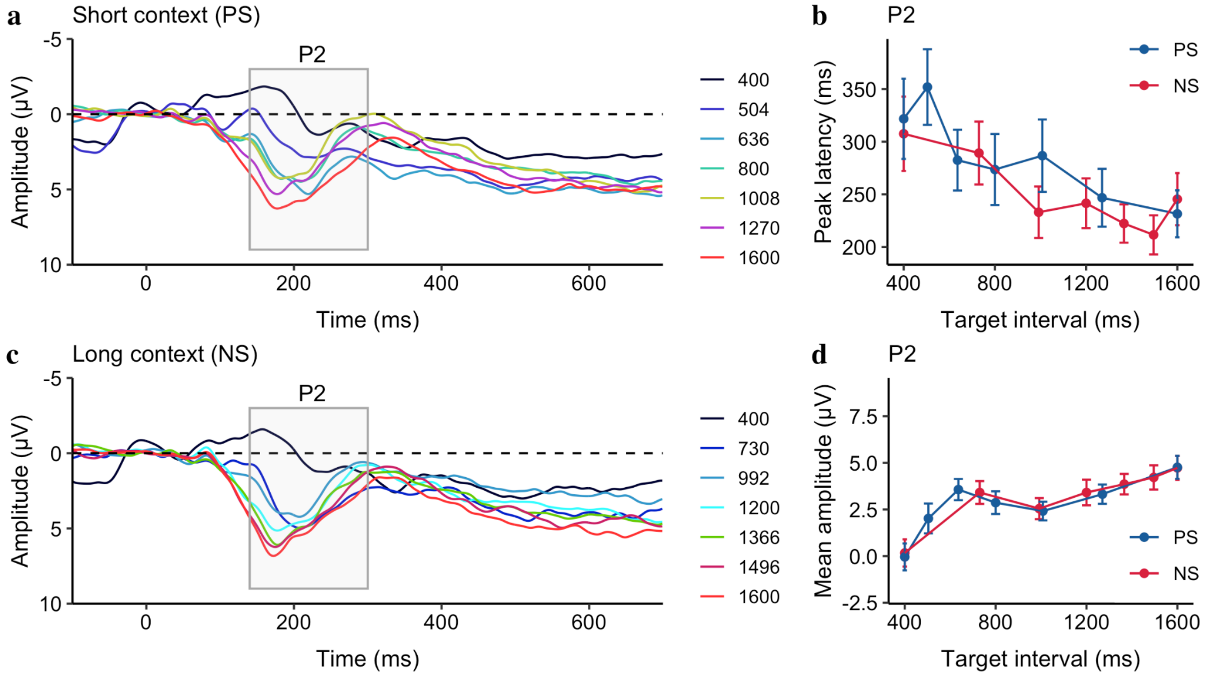

Figure 4. *Grand average of the ERP waveforms over the medial frontal electrodes (FCz, FC1, FC2, C1, C2, and Cz), separated for different target intervals, separated for the PS (**a**) and the NS conditions (**c**). (**b**) Mean P2 peak latency and (**d**) mean P2 amplitude as a function of the target interval, separated for the PS (blue) and NS (red) contexts. Error bars represent the standard error of the correspondent mean.*

Figures 4a and 4c depict the ERP waveforms over the medial frontal electrodes relative to the offset of the stimuli for the short and long contexts, showing a positive peak around 200 ms after the stimuli offset that correlates with the target interval. Figures 4b and 4d show the peak latency and mean amplitude of the offset P2 as a linear trend of the target interval, separated for the PS and NS contexts: The latency decreases, but the amplitude increases as the target interval increases, while there was not much difference between the two contexts. A linear mixed model with the Context as the fixed effect and Duration as a covariant effect was applied to the offset P2 peak latency, which revealed that the peak latency decreased by 78 ms/s of Duration (*CI* = [-144.92, -10.38], *p* = .026). But the peak latency showed no significant difference between the PS and NS Context (*p* = .28). Moreover, there was no significant interaction between Duration and Context (*p* = .58). Similar linear mixed model applied to the Offset P2 mean amplitudes (Fig. 4d) revealed a significant main effect of Duration (*b* = 2.90, *CI* = [1.98, 3.81], *p* < .001). Again, there was no significant Context (*p* = .28) and no interaction between the Duration and Context (*p* =

.41). The findings indicate that while the offset P2 was responsive to the target interval, it was insensitive to variation of ensemble contexts.

4.3.3 Discussion

Experiment 1 replicated previous research (Wearden & Ferrara, 1995; Zhu et al., 2021), confirming that temporal bisection is subjective to the target spacing. Intervals in the short context (PS), relative to the long context (NS), tended to be judged longer, indicating that participants not merely compared the probe duration to the short or long standards (which were the same in both contexts), but also took into account the spacing of the sample durations.

Experiment 1 revealed that the mean amplitude of CNV was linked to the target duration. As the duration increased, so did the mean amplitude. Figure 3e also shows that the mean amplitude leveled off at middle durations (800 to 1200 ms), which is in line with previous research (Macar & Vidal, 2003; Ng et al., 2011) that found CNV plateaued at the geometric mean of the short and long intervals in the bisection task. The findings support that CNV stands for temporal expectation (Amit et al., 2019; Praamstra et al., 2006). Some researchers have suggested that the CNV amplitude is subjective to the context. For example, adapting to shorter durations would lead to an increase in the amplitude of CNV, while adapting to longer durations would decrease the amplitude of the CNV (Li et al., 2017). Here we found the mean (or peak) amplitude of the CNV was higher for the short context (PS) than for the long context (NS), but the difference did not reach statistical significance. On the other hand, we did find that the latency of the CNV was earlier for the short context relative to the long context, which aligns with previous research showing a faster development of the CNV activity for short than long target durations (Pfeuty et al., 2005). However, as Kononowicz and Penney (2016) have suggested, timing isn’t the only factor contributing to the CNV. More complex processes, such as preparation for an upcoming event, could play a role. Therefore, in some cases, the CNV may not truly reflect the temporal interval itself, as revealed in a previous study that CNV-like negativity simply disappears for intervals longer than 4 seconds (Elbert et al., 1991).

Additionally, the offset P2, a common component associated with temporal accumulation as reported previously (Kononowicz & van Rijn, 2014; Tarantino et al., 2010), had a negative correlation with the target interval, which is consistent with previous findings (Kononowicz & van Rijn, 2014). This can be explained by the predictive coding account

(Friston & Kiebel, 2009; Kononowicz & van Rijn, 2014; Rao & Ballard, 1999), because short intervals that stopped before the decision threshold (i.e., the bisection point) led to larger ‘prediction errors’ than long intervals, resulting in early P2 latencies. This is also in line with the previous studies showing that short durations lead to longer reaction times (e.g., Bannier et al., 2019). However, the offset P2 was not affected by the spacing modulation, which is in contrast to previous reports that the late positive component of timing (LCPt), peaking at around 300 ms post-offset (later than P2), can be influenced by the task difficulty (Paul et al., 2011), the prior trial duration (Wiener & Thompson, 2015), or the sample set (Ofir & Landau, 2022b).

It’s worth noting that previous studies that used bisection or duration comparison tasks often employed durations longer than 800 ms (e.g., Ng et al., 2011), meaning that the expectation of a binary decision would not occur earlier than 500 ms, at which point the CNV is just emerging (as seen in Figure 3). Here we used two short intervals (400 ms, 504 ms), which caused the offset of CNV to happen earlier for preparing action, leading to some distortion of the offset P2 component (as seen in Figure 4), making the comparison of P2 across durations less ideal. Given this, to separate the decision-making process from temporal encoding in a bisection task, we added a 300 ms gap before prompting a decision in Experiment 2. In addition, to generalize the contextual modulation, we applied ensemble context instead of sample spacing.

4.4 Experiment 2

4.4.1 Method

Participants

20 participants with no hearing impairment took part in Experiment 2 in return for a monetary incentive or course credit at LMU Munich. The sample size was the same as in Experiment 1. All participants were naive to the purpose of the study and gave written informed consent before the formal experiment. The study was approved by the Ethics Board of the Department of Psychology at LMU Munich.

Because of the excessive eye or body movement artifacts during EEG recording, three participants were excluded from further analyses. Thus, the results of 17 participants (6 females, mean age 27.3 years, *SD* = 3.5 years) were reported here.

Stimuli and Procedure

The experimental setup was the same as in Experiment 1, with the following two exceptions: first, a 300-ms blank was inserted between the stimulus offset and the question mark (prompting for a response), providing a decision time buffer for short durations (Fig. 5a); second, two sessions had the same equal-spaced duration set of [400, 600, 800, 1000, 1200, 1400, 1600] ms, but sampled with different frequencies (Fig. 5b). In one session, the above durations were tested [12, 24, 36, 48, 60, 72, 84] times, respectively. We referred to this session as the ascending frequency (AF) session. In the other descending frequency (DF) session, the same durations were tested [84, 72, 60, 48, 36, 24, 12] times, respectively. Within each session, the durations were randomly selected with the respective frequency. The order of sessions was counterbalanced among participants (before the outlier exclusion).

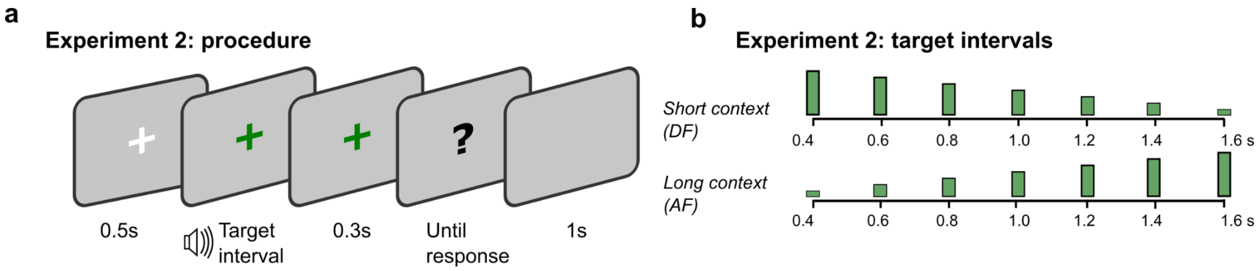

Figure 5. ***a)*** *Each trial started with a fixation cross for 500 ms, followed by a target interval presentation. 300ms after the presentation, a question mark was presented, prompting participants to respond. The inter-trial interval was 1000 ms.* ***b)*** *Target intervals used in Experiment 2. In the short context session (DF), equally spaced intervals between 400 ms and 1600 ms were presented 84, 72, 60, 48, 36, 24, and 12 times during the session, whereas the presentation frequencies were mirrored in the long context session (AF).*

ERP components

In addition to the analyses of the CNV slopes, latencies, and amplitudes, we compared the CNV activities between two sessions for the intermediate target intervals (800, 1000, and 1200 ms), where the temporal context greatly modulated the bisection decision. The LPCt components were estimated on the same frontocentral electrodes as the CNV analysis (Damsma et al., 2021), but baselined relative to the 100 ms time window surrounding the onset of the question mark (50 ms preceding and following the question mark) (Kononowicz & van Rijn, 2014). We extracted the LPCt peak latencies as the maximum (most positive) amplitude within the 500 ms window starting from the question mark and calculated the LPCt mean amplitudes by averaging waveform between 300 and 500 ms after the stimulus offset (Bueno & Cravo, 2021; Ofir & Landau, 2022b).

4.4.2 Results

Behavioral results

Figure 6a illustrates the averaged proportion of long responses and corresponding estimated psychometric functions. The mean PSE (±*SE*) was 749.3 ± 33.86 ms for the DF session, significantly shorter than the AF session (951.2 ± 49.91 ms), $F(1, 16) = 27.72$, $p < .001$, $\eta_g^2 = .27$, $BF > 100$, indicating the durations in the DF session were perceived longer than the same duration in the AF session. Thus, the finding is consistent with the previous study (Zhu et al., 2021). Moreover, the mean JND (±*SE*) was 96.3 ± 6.69 ms for the DF session, significantly smaller than the AF session (119.8 ± 12.09 ms), $F(1, 16) = 8.82$, $p = .01$, $\eta_g^2 = .01$, $BF = 5.22$, showing that the sensitivity of the bisection was higher in the AF compared to the DF session.

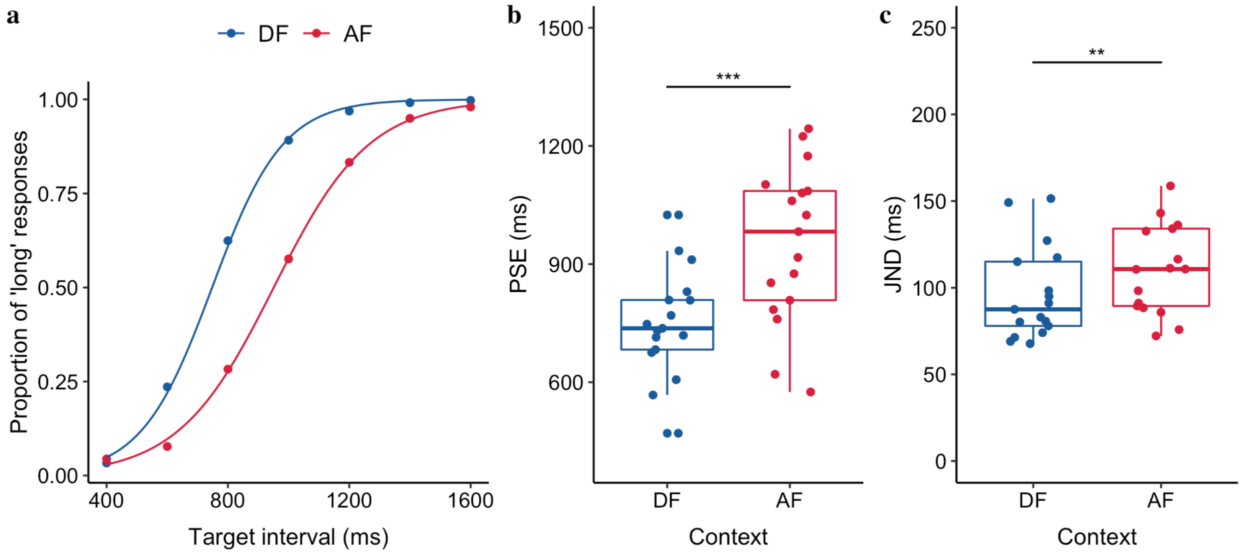

Figure 6. a) *Bisection functions (proportions of "long" responses plotted against the target durations, and fitted psychometric curves) averaged across 17 participants for the two, descending (DF) and ascending frequency (AF) distributions.* ***b)*** *Boxplots of PSE of the duration judgments for the DF and AF sessions (*** p < .001). The dots depict individual PSEs estimated from individual participants. The lower and upper tips of the vertical lines correspond to the minimum and maximum values, the box represents the interquartile range (between 25% and 75%), and the horizontal line represents the median.* ***c)*** *Boxplots of JND of the duration judgments for the DF and AF sessions (** p < .01). The dots depict individual JNDs of individual participants.*

Electrophysiological results

The CNV

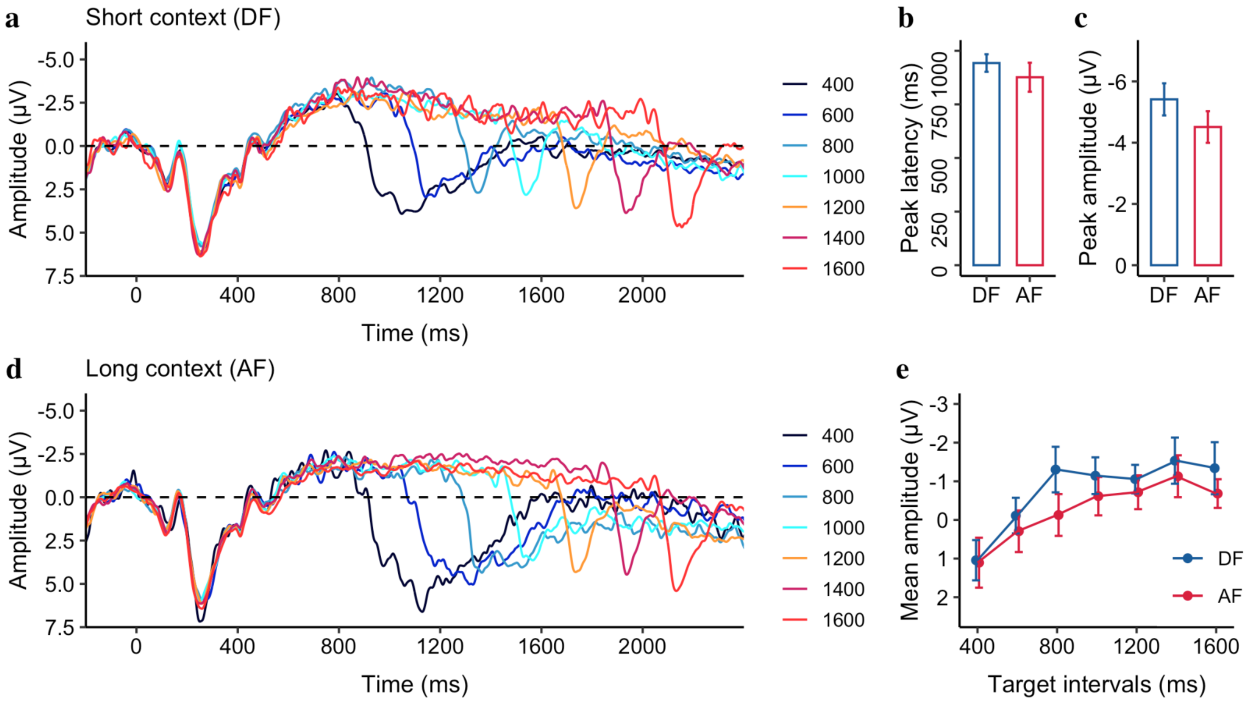

Figure 7. *Grand average of the ERP waveforms over the medial frontal electrodes (FCz, FC1, FC2, C1, C2, and Cz) relative to the onset of stimuli, separate for* ***(a)*** *the short (DF) and* ***(d)*** *the long (AF) contexts. The mean CNV peak latency* ***(b)*** *and amplitude* ***(c)*** *of the target intervals, separated for the DF and AF conditions.* ***(e)*** *The mean CNV amplitude as a function of the target interval, separated for the DF and AF conditions. Error bars represent the standard error of the mean.*

Figure 7 illustrates the CNV activities both in the short DF (a) and long AF (d) contexts, showing that the negativity changes over time for different target intervals. Just like in Experiment 1, to characterize the CNV component, we looked into its formation rate, peak latency, amplitude, and mean latency. Given the negative ballistic deflation of the activities after P2, we used linear regression to estimate the rate (i.e., slope) at which the CNV was forming within the time window from 250 (after P2) to 650 ms (the start of the CNV). The mean values are listed in Table 1.

We found the slope was significantly negative for both the DF context [−19 ± 1.5 µV/s, 95% CI = [−22, −15] µV/s, t (16) = −12.57, $p < .001$] and the AF context [−17 ± 1.5 µV/s, 95% CI = [−20 to −14] µV/s, t (16) = −11.37, $p < .001$], but significantly smaller in the

DF compared to AF context, $F(1, 16) = 5.76$, $p = .03$, $\eta_g^2 = .018$, $BF = 2.14$, indicating a faster temporal accumulation in general for durations in the DF relative to the AF session, consistent with the previous research (Macar & Vidal, 2004). Moreover, the CNV peak amplitudes were significantly higher (-5.4 µV vs. -4.5 µV) for the short context (DF) relative to the long context (AF), $F(1, 16) = 5.89$, $p = 0.03$, $\eta_g^2 = 0.05$, $BF = 2.22$), but with a comparable latency (942.8 ms vs. 876.6 ms, $F(1, 16) = 0.85$, $p = 0.37$, $\eta_g^2 = 0.03$, $BF = 0.49$).

Next, we applied a linear mixed model to the mean CNV amplitude, with the Context as the fixed effect and Duration as a covariant, which showed that the mean negativity amplitude increased by 1.66 µ*V* for each second increased in Duration ($b = -1.66$, $CI = [-2.35, -0.96]$, $p < .001$), demonstrating again that the CNV amplitude is correlated to the target interval. However, there was no significant Context ($p = .47$) or interaction between the Duration and Context ($p = .71$).

Late positive component of timing (LPCt)

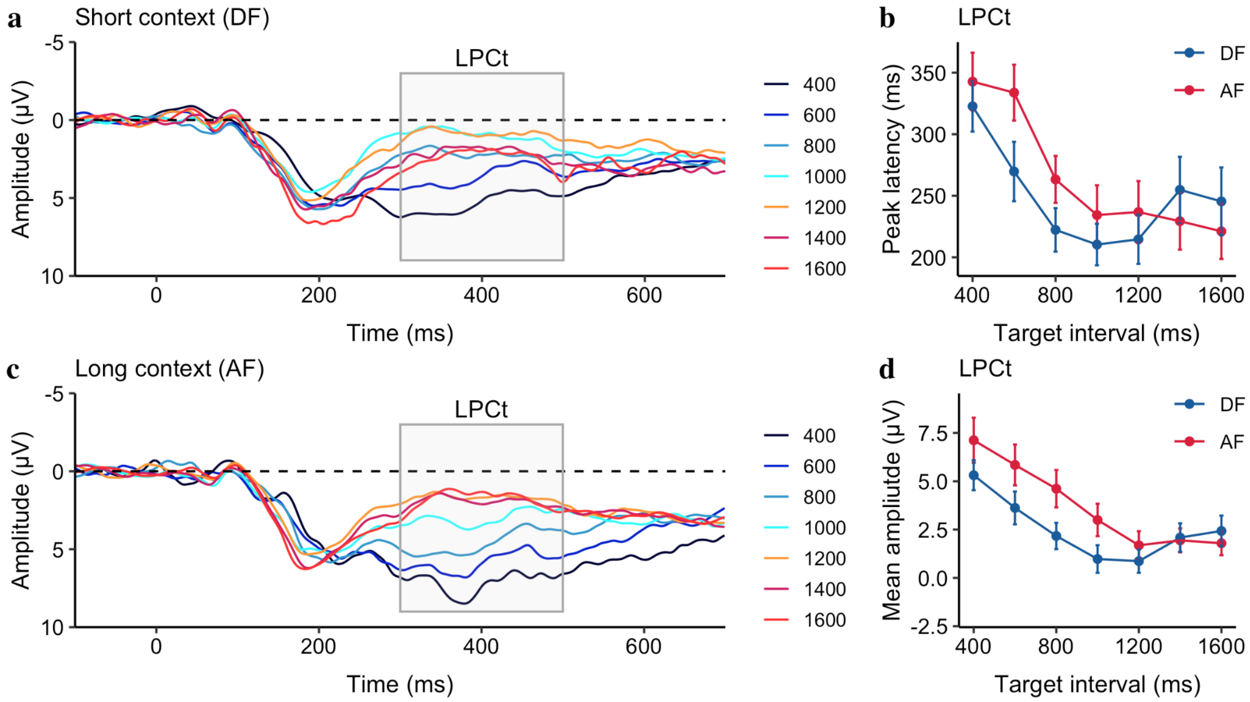

Figure 8. *Grand average of the ERP waveforms over the medial frontal electrodes (FCz, FC1, FC2, C1, C2, and Cz) relative to the stimulus offset in the DF* ***(a)*** *and the AF conditions* ***(c)****.* ***b)*** *Mean LPCt peak latency and* ***(d)*** *mean LPCt amplitude as a function of the target interval, separated for the DF (blue) and AF (red) contexts. Error bars represent the standard error of the correspondent mean.*

Next, we looked into the later positivity components, such as P2 and LPCt, in the window of [0, 500] ms. Unlike Experiment 1, we failed to find any significant difference in the P2 component (the mean amplitudes were 4.2 ± 0.5 and 4.4 ± 0.6 for the DF and AF, respectively, $p = 0.28$. There was no significant difference among different target intervals, $p = 0.99$), but as seen in Figure 8, there were visible differences in the late time window. Thus we focused on the analysis of the LPCt component. The averaged LPCt peak latencies (± standard error, *SE*) were 248.6 ± 14.03 ms and 265.9 ± 11.87 ms for the DF and AF context, respectively (Fig. 8b). Same as in CNV analysis, we applied a linear mixed model to the LPCt peak latency, with the Context as the fixed effect and Duration as a covariant effect. The mixed model showed significant effects of Context ($b = 38$ ms, $CI = [13, 63]$, $p = .003$), Duration ($b = -77$ ms/s, $CI = [-133, -22]$, $p = .009$) and the Duration × Context interaction ($b = -30$, $CI = [-53, -6]$, $p = .013$). The LPCt peaked earlier for the short DF than the long AF context, and the latency decreased as the duration increased (Table 1). The interaction was likely owing to the comparable peak latencies between the two contexts for the long but not for the short durations (see Figure 8b).

For better comparison with the literature (Bueno & Cravo, 2021; Ofir & Landau, 2022b), we extracted the mean LPCt amplitude from the time window of [300, 500] ms. A similar linear mixed model on the LPCt mean amplitude (see Fig. 8d) revealed similar results: significant effects of Duration ($b = -3.55$, $CI = [-5.13, -1.97]$, $p < .001$), Context ($b = 1.83$, $CI = [1.09, 2.58]$, $p < .001$) and the Duration × Context interaction ($b = -1.22$, $CI = [-1.92, -0.53]$, $p < .001$). The mean amplitude was larger for the long AF than for the short DF context (Table 1). As seen in Figure 8d, the interaction was caused by different amplitudes for the short durations but plateaued at a similar level for the long durations.

Cross-experiment comparisons

To gain a better understanding of the temporal encoding process reflected in the CNV and the decision-making process reflected in the offset P2 and LPCt, we further compared the results of our two experiments for short (400 ms), intermediate (around 1000 ms), and long (1600 ms) durations (as shown in Figure 9 a, b, and c). Visual inspection shows that the CNV peaked earlier in Experiment 1 compared to Experiment 2. More interestingly, even when the duration was the same, the offset late positivity was delayed by about 300 ms, suggesting that the late positive component is not solely dependent on the offset of the duration, but also on the onset of the response (the onset of the question mark that prompts for response). Moreover, the late positivity component did not fully emerge for the short duration (400 ms) in Experiment 1, largely owing to the disruption of the ongoing CNV with immediate prompting for a response.

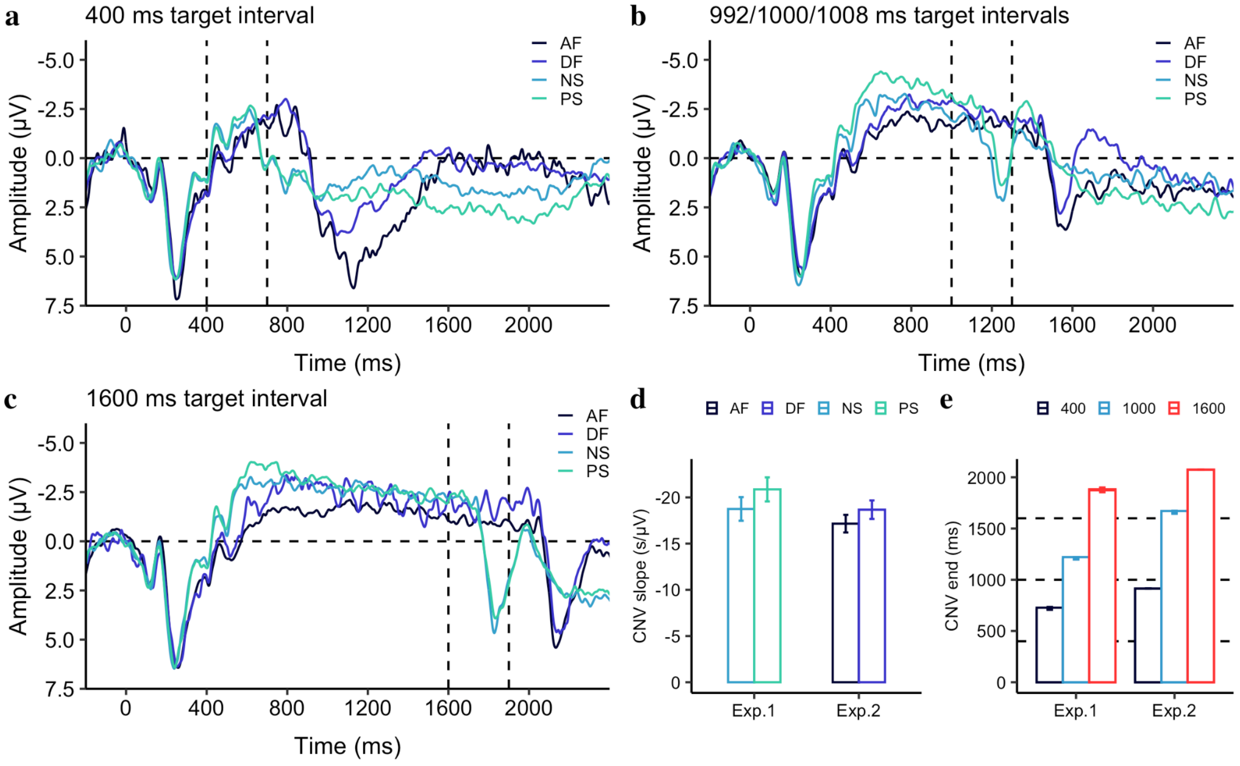

*Figure 9. The grand average of the ERP waveforms over the medial frontal electrodes (FCz, FC1, FC2, C1, C2, and Cz) relative to the stimulus onset are depicted for the shortest **(a)**, intermediate **(b),** and the longest **(c)** target intervals for the temporal contexts used in Experiment 1 and 2. Light blue and light green lines depict the long (NS) and short (PS) contexts of Experiment 1. Black and dark blue lines depict the long (AF) and short (DF) contexts of Experiment 2. The first vertical dashed line marks the offset cue (the question mark presentation) in Experiment 1, while the second vertical dashed line marks the offset cue in Experiment 2. **d)** The CNV slope, measured in the interval from 250 ms to 650 ms after stimulus onset. Error bars show the standard error of the mean. **e)** The CNV end, measured by the crossing point of the negativity waveform from negative to positive. Black and red colors depict the shortest and longest intervals (400 and 1600 ms) in both experiments, while the blue color depicts the intermediate durations of 992, 1000, and 1008 ms used in the experiments. For ease of visualization, they were depicted by the same color and label (1000 ms). Error bars show the standard error of the mean.*

The mean slope of the CNV, measured within the interval from 250 to 650 ms, collapsed for these three intervals, was −22 ± 1.1 µV/s for the short PS and −19 ± 1.0 µV/s for the long NS in Experiment 1, while in Experiment 2, the mean slope was −19 ± 1.0 µV/s for the short DF and −17 ± 1.0 μV/s for the long AF. A linear mixed model was used to analyze the CNV slopes, with Experiment as the fixed effect and Context as the covariant effect. A linear mixed model was used to analyze the CNV slopes, with Experiment as the fixed effect and Context as the covariant effect. The analysis showed that there was a significant effect of Context ($b = 1.14$, $CI = [0.04, 2.24]$, $p = .042$), and Experiment ($b = 2.60$, $CI = [0.92, 4.28]$, $p = .003$), while there was no interaction between Experiment and Context ($p = 0.64$).

To determine when the offset of the CNV and the onset of late positivity begin, we examined the crossing latency, which is the point at which the CNV waveform changes from negative to positive after 650 ms from the onset. We found significant differences in crossing latency between the two experiments, despite using the same probe duration (all *p*s < .001): 703 vs. 914 ms for the 400-ms target interval, 1210 vs. 1628 ms for the 1000-ms target interval, and 1860 vs. 2074 ms for the 1600-ms target interval for Experiments 1 and 2, respectively. This suggests that the CNV is not solely based on the target duration, but also reflects the expectancy of the temporal period before the decision.

4.4.3 Discussion

Similar to the results of Experiment 1, we found that the mean CNV amplitude increased as the target interval increased. A comparison with Experiment 1, however, revealed the CNV is not solely based on the target interval, but also depends on the period before the decision is prompted. Interestingly, we found the rate of the CNV formation and the peak amplitude of the CNV were dependent on the context. Combining the analysis of Experiments 1 and 2 revealed that the rate of the CNV is a robust indicator of context modulation. Specifically, the short context resulted in a faster rate of CNV formation, meaning the CNV began earlier in the short context compared to the long context. Our results are consistent with the notion that CNV activity reflects not only the temporal accumulator of an internal timing mechanism (Macar et al., 1999) but also temporal anticipation (Elbert et al., 1991; Ng et al., 2011), particularly for the forthcoming decision-making (Kononowicz & Penney, 2016).

Interestingly, the offset late positivity component was more distinct in Experiment 2 than in Experiment 1, even for the short durations such as 400 ms, when we inserted a 300 ms gap before prompting for action. This suggests that the late positive component may better reflect the decision process when the CNV is fully evolved. As seen in LPCt, the mean amplitude negatively correlated with the target interval, similar to the recent findings of Ofir and Landau (2022b), who reported that the offset response amplitude decreases as the interval increases, but levels off after the interval passes the bisection point. The late offset positivity components such as LPCt, P300, or P3 have been suggested as indicators of decision-making at post-perceptual stages (Baykan & Shi, 2022; Kelly & O'Connell, 2013; Ofir & Landau, 2022b; Polich & Kok, 1995). For a bisection task, the decision could be made before the stimulus offset when the interval presentation passes the bisection point, as the uncertainty of the response ('long') is greatly reduced for long intervals compared to short intervals. For the short intervals, the online monitoring of the passage of time and comparison to the bisection point remain active (Lindbergh & Kieffaber, 2013). Thus, as suggested by Ofir and Landau (2022), the amplitude of the late positivity may reflect the distance from the decision threshold.

Most importantly, we observed contextual modulation of the late positivity LPCt component: higher amplitude but later latency for the long AF than the short DF context. Given that LPCt amplitude negatively correlated with the target duration, a higher amplitude in the long context (AF) indicates that intervals were perceived shorter as compared to the same duration in the short context (DF), closely reflecting the behavioral results.

4.5 General Discussion (Chapter 4)

The aim of this study was to examine the timing-related ERP components to gain a deeper understanding of neural mechanisms underlying the impact of ensemble contexts on temporal judgments. Results showed that ensemble contexts, both temporal spacing and sample distribution, modulated perceived time intervals, consistent with previous studies (Penney et al., 2014; Wearden & Ferrara, 1995; Zhu et al., 2021). The PSE was biased towards the mean of the ensemble distribution, with short contexts lowering the PSE, resulting in more likely to respond "long" to the target intervals in short relative to long contexts. EEG analysis also revealed context effects on the slope of contingent negative variation (CNV) and the latency and amplitude of the late post-offset positivity related to timing (LPCt), which are commonly associated with expectancy and decision processes of timing.

The CNV

In both experiments, we saw sustained negativity, known as CNV, emerging after the onset P2, peaking between 600-800 ms, and dissolving at the end of the stimulus presentation. The CNV has been considered a strong signal for temporal processing, and early studies have suggested that its evolving slope and amplitude reflect the passage of time (Macar & Besson, 1985; Macar & Vitton, 1982). Our results showed that long durations elicited longer sustained negativities compared to short durations. However, the CNV represents more than just timing. For example, comparing brain activity between two experiments, the sustained negativity elicited by the same duration was nearly 300 ms longer in Experiment 2 than in Experiment 1, due to the 300-ms blank period before the cue display for response in Experiment 2. This modulation of response delay by the cue display supports the early proposal that the dissolving of the CNV may also indicate readiness to act quickly (Loveless & Sanford, 1974; Näätänen, 1970).

Kononowicz and Penney (2016) have recently echoed this idea that the CNV is not just about timing, but also influenced by more complex cognitive processes, such as anticipation and expectation, as well as response preparation (Kononowicz, Van Rijn, et al., 2018; Kononowicz & Penney, 2016; van Rijn et al., 2011). For example, in a study where participants were cued to respond as quickly (speed trial) or accurately (accuracy trials), the CNV amplitude was more negative in speed trials than in accuracy trials (Boehm et al., 2014), suggesting that CNV amplitude may reflect changes in participants' response caution favoring quick decision making. Similarly, Ng et al. (2011) showed that CNV activity for the current long interval leveled off after passing a memorized internal criterion (around the geometric mean of sample intervals). In both experiments, our results also showed that the mean CNV amplitude increased with increasing target interval, leveling off around the middle intervals (Figures 3 and 7), suggesting that the CNV amplitude is closely tied to the expected decision criterion.

Another key finding is the contextual modulation of the climbing rate of CNV. In both experiments, the short context led to faster CNV formation compared to the long context. Since the CNV rate was already determined at the beginning of the presentation when the length of the stimulus was unknown, it reflects the general expectation of how long the decision interval (the ensemble mean of the sample distribution) may arrive in a given block. Thus, the rate difference between short and long contexts indicates whether the internal decision interval shifts earlier or later. While we observed context differences in peak latency in Experiment 1 and peak amplitude in Experiment 2, as well as some numerical differences in the mean CNV amplitude, the effects were not consistently significant across both experiments.

Together, our results suggest that CNV reflects the readiness or expectation to respond to an incoming stimulus (Boehm et al., 2014; Kononowicz & Penney, 2016; Ng et al., 2011), and the rate of initial CNV formation is a good indicator of context modulation of the decision threshold.

The offset positivity components (P2 and LPCt)

After prompting for a response, we saw an offset positivity waveform, peaking at 200-400 ms and lasting for over 600 ms after the stimulus presentation. This offset positivity is known as P2 (Kononowicz & van Rijn, 2014; Tarantino et al., 2010), P3/P3b (Ofir & Landau, 2022b), or LPCt (Paul et al., 2011; Wiener & Thompson, 2015) depending on studies. Depending on the timing of the response cue, either immediately after the duration stimulus or after a 300-ms gap, we observed an offset P2 (no gap) or LPCt (with a gap) that were related to the temporal decision. Short intervals, relative to long intervals, elicited delayed latency for both P2 and LPCt, and higher amplitudes for LPCt.

The early findings of time-related offset P2 came from the duration comparison studies that compared a probe interval either shorter or longer than the standard interval (Kononowicz & van Rijn, 2014; Tarantino et al., 2010) - shorter intervals elicited higher amplitudes and long latencies. Using the bisection task, we only found the latency dependent on duration in Experiment 1. When a decision was requested immediately after the duration presentation, the P2 amplitude was likely influenced by ongoing CNV activity for the short intervals (e.g., 400 and 504 ms). As the between-experiment comparison showed that when the decision response was delayed for 300 ms (Experiment 2), the late positivity was better evolved. However, we did not find any duration-related modulation in P2. Instead, the late positivity component LPCt had a strong relationship with test durations in the decision-making stage.

Late positive components, such as LPCt or P3/P3b in prior research have been measured relative to the response (Bannier et al., 2019; Wiener & Thompson, 2015) or the stimulus offset (Gontier et al., 2009; Tarantino et al., 2010) with prefrontal (Gontier et al., 2008; Paul et al., 2011) or centroparietal electrode sites (Bannier et al., 2019). The late post-positivity has been linked to the involvement of post-perceptual processes (Lindbergh & Kieffaber, 2013), similar to the idea that task difficulty is involved in decision processes (Gontier et al., 2009; Paul et al., 2011). For long durations, memory and decision-making processes would be already finished at the offset, whereas for short durations, these processes would still be ongoing. This means that compared to long durations, short durations resulted in higher LPCt amplitudes and longer latencies. In this study, LPCt was measured over prefrontal electrodes relative to the onset of the response cue, 300 ms after the test duration offset. The results showed that LPCt amplitude and peak latency decreased as the target interval increased and leveled off around intermediate durations, a pattern similar to a recent study (Ofir & Landau, 2022b), which found that the amplitude of the late positivity correlated with the distance to the decision boundary in a drift-diffusion model (DDM). According to the DDM, the uncertainty of temporal bisection depends on the distance between the accumulated time to the decision boundary - bisection threshold. Short intervals with large uncertainty elicited high LPCt amplitudes, while long intervals with less uncertainty resulted in low amplitudes. Our findings are thus consistent with this interpretation. More interestingly, LPCt was found to be context-dependent, with short contexts leading to earlier peak latencies and lower amplitudes compared to long contexts, indicating that the decision boundary was set lower for the short context and, thus, the distance to the boundary was generally shorter.

Context-dependent modulation

Both CNV and LPCt signals have been shown to depend on contextual modulation. Climbing of CNV activity was faster, and the amplitude and latency of LPCt were lower for short contexts compared to long contexts. Previous studies have shown temporal context can impact CNV in different ways (Damsma et al., 2021; Wiener & Thompson, 2015). For instance, in a reproduction task, Wiener and Thompson (2015) found that the CNV amplitude of a current trial was linearly shifted by the duration of the previous interval, with larger negative amplitudes for longer prior durations. In Experiment 1, we also found that the long context (NS) induced larger CNV amplitudes compared to the short context (PS). However, this was not the case in Experiment 2, where the short context (DF) elicited numerically higher amplitude than the long context (AF). This suggests that the CNV amplitude is more sensitive to short-term (e.g., inter-trial duration changes) rather than long-term (e.g., session-wise changes) context modulation. In contrast to the CNV amplitude, the rate of CNV formation was faster for short contexts compared to long contexts in both experiments. The CNV and climbing neuronal activity are believed to have a close relationship (Pfeuty et al., 2005), and the formation of CNV indicates how the brain encodes the timing of an upcoming event. In this study, the rate of CNV reflected the expectation of the decision threshold, which was influenced by the ensemble context.

The climbing CNV activity develops early in the perceptual encoding stage, which is tied to the memory representation of the internal criterion. In contrast, the formation of LPCt occurs during the decision stage, reflecting the comparison process of the perceived duration and the internal criterion. In this study, we showed that context affects the uncertainty of the comparison by altering the PSE towards the ensemble mean. This reduces the uncertainty of bisection for the short context in general as the test duration reaches the threshold earlier in the short relative to the long context. As a result, the amplitude and latency of the LPCt decrease. It is worth noting that the context-dependence of the amplitude and latency of the LPCt has been documented in previous research. For example, Ofir and Landau (2022) found that the late positivity remains similar in both short-range (subsecond) and long-range (supra-second) bisection tasks, even though the duration considered “short” in the long-range is longer than all durations in the short-range.

Conclusion

In this study, we found that ensemble context, both sample spacing and frequency, impacted the bisection task, shifting the bisection point towards the ensemble mean. Temporal context modulation was also evident in the changes in ERPs related to interval timing. In the short context, compared to the long context, the CNV climbing rate increased, and the amplitude and latency of the LPCt were reduced. Both CNV and LPCt were linked to the given test duration, but were not limited to absolute durations. Our findings, consistent with the previous studies (Baykan & Shi, 2022; Boehm et al., 2014; Ofir & Landau, 2022b), indicate that the CNV represents an expectancy wave for upcoming decision-making, while LPCt reflects the decision-making process, both CNV and LPCt influenced by the temporal context.

Data availability

The data supporting the findings of this study and the code of the statistical analysis used in the manuscript are available at DOI: 10.12751/g-node.7snfwg.

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5 Exploring Range Effects in the Temporal Reproduction Using the EEG Signatures of Time

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5.1 Abstract

Human time estimates are influenced by temporal statistics of the surrounding stimuli. Previous studies showed that subjective timing is biased towards the mean of sample distribution, known as prior. When target intervals from different ranges are presented in separate blocks, humans form distinct priors. Although forming separate priors for such sample ranges leads to accurate perceptual outcomes, when these ranges are presented mixed in an experimental session, individuals form a single generalized prior. Through combination of behavioral and electroencephalographic (EEG) measures, we examined how uni- vs. multi-prior environments influence temporal reproduction of different interval ranges. Participants reproduced the target intervals in two prior context conditions: *blocked-range (BR)*, consisting of either lower or upper range intervals in a block, and *interleaved-range (IR)*, including both lower and upper range intervals within a block. The results showed that the reproductions in the IR context were biased towards the single context prior while in the BR context, they were biased towards the priors of each respective interval range. EEG analysis revealed that prior context modulates the CNV buildup and its amplitude during perception, with higher amplitude in the BR than the IR context. In addition, interval range influences the CNV buildup during reproduction, with faster buildup for the lower relative to the upper range intervals.

Keywords: time perception; range effect; context effect; EEG; CNV

5.2 Introduction

Temporal estimation is crucial to everyday activities, from conscious decision-making to spoken language and physical functions. Despite its importance in many activities and behaviors, subjective duration estimation is not always precise. A well-known context effect referred to as central tendency bias or regression effect is a systematic overestimation of short durations and underestimation of long durations when embedded in a temporal context (Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009). This phenomenon has been shown to be modulated by a variety of context components such as range, mean and variance (Lewis & Miall, 2009; Wearden & Ferrara, 1996; Wearden & Lejeune, 2008; Zhu et al., 2021).

However, the neurophysiological mechanism underlying the contextual modulations still needs more exploration.

The features of the stimulus distribution being judged influence the perception and action. For example, the mean and variance of the sample interval distributions have been shown to affect the duration estimates and their sensitivities, respectively (Zhu et al., 2021). Furthermore, when the range of experimental durations (i.e., the ratio between the longest and shortest duration) has been manipulated, the central tendency bias was shown to differ (Brown et al., 2005). Higher central tendency bias occurs with a wider sample interval range. One way of enhancing the noisy sensory estimations is to integrate those estimations with the sensory environment statistics, i.e., our knowledge about previously encountered stimuli. Previous research using the Bayesian framework has shown that humans can integrate the sensory information (referred to as the likelihood) into prior knowledge (referred to as the prior) in timing decisions (Cicchini et al., 2012; Jazayeri & Shadlen, 2010; Shi et al., 2013). According to the Bayesian observer accounts, the assimilation towards the temporal context statistics is a natural outcome of the integration process of the sensory input with the prior (Shi et al., 2013). Bayesian models of timing have successfully provided theoretical support for the common temporal contextual effects.

Classical Bayesian models, implicitly, assume a single prior integration to the sensory representations (Gu et al., 2016; Jazayeri & Shadlen, 2010; Roach et al., 2017; Shi et al., 2013). Humans can estimate the sampled range with a single prior approximation when intervals are randomly sampled from the same range (Acerbi et al., 2012). Several studies have reported that people can form separate priors when intervals from different ranges are presented in separate blocks or presented in the same block but with a distinct separation cue (Gu et al., 2016; Petzschner et al., 2012; Roach et al., 2017). For example, Petzschner et al. (2012) showed that presenting two overlapping short and long stimulus ranges in an interleaved way gives rise to a single prior formation for two different stimulus ranges. On the other hand, if participants receive a categorical cue before each trial starts, this leads to forming two separate priors for these overlapping stimulus ranges. Roach et al. (2017) showed that individuals can form separate priors for short and long range intervals also when these ranges do not overlap. Their results indicated that people form two separate priors for two not-overlapping interval ranges when the ranges are presented in two different sessions and they form a single generalized prior when the ranges are presented interleaved in an experimental session. As a result of this manipulation, participants underestimate the long range intervals and overestimate the short range intervals in the interleaved session relative to their presentations in the blocked-wise session. When humans form and maintain separate priors for each stimulus range, that leads to more accurate perception for the given stimulus. However, this is also more challenging and costly for an efficient response. Thus, how the brain integrates multi-prior information derived from different sources to the current perception while balancing accuracy and efficiency is not yet fully understood.

The contextual modulations are commonly observed in the event-related potentials (ERPs) such as the contingent negative variation (CNV), P2 and the late positivity component of time (LPCt) and in oscillatory powers (Damsma et al., 2021; Kononowicz et al., 2018; Kononowicz & Penney, 2016; van Rijn et al., 2011; Wiener & Thompson, 2015). For example, previous studies showed that a longer prior duration resulted in more ‘short’ responses, larger CNV amplitudes and higher beta power of the current trial in the bisection task (Wiener et al., 2018; Wiener & Thompson, 2015). The CNV buildup or the accumulation has been previously thought to reflect temporal anticipation and expectation (Pfeuty et al., 2005; Praamstra et al., 2006). Higher CNV amplitudes have been related to higher response caution or preparation for favoring quick decision making (Boehm et al., 2014). Similarly, Damsma et al. (2020) found that active anticipation of a target modulates CNV and offset-evoked P2 amplitudes. When individuals expected a shorter interval, the CNV formation rate and amplitude as well as the P2 amplitude increased. The early positivity component P2 has been related to temporal encoding or accumulation (Kononowicz & van Rijn, 2011) but its relation to duration length has been shown to be modulated by temporal context (Damsma et al., 2020). The offset-P3 or LPCt amplitude has been also found to be sensitive to duration and context as its amplitude increases with higher task difficulty (Paul et al., 2011) and shorter stimulus duration (Ofir & Landau, 2022). Taken together, these results demonstrate that CNV, P2 and LPCt activities are related to temporal expectation and the forthcoming decision-making, while beta power indexes the internal criterion to which the current interval is compared (Wiener et al., 2018). Additionally, changes in the low-frequency oscillatory activities such as theta and alpha have been proposed to reflect, respectively, temporal decision making (e.g., decision certainty, post-decision error monitoring) (Cavanagh et al., 2010; Jacobs et al., 2006) and temporal attention (Rohenkohl & Nobre, 2011b).

In the current work, we aimed to examine neurophysiological mechanisms underlying the range effect when tested in uni-prior or multi-prior environments. Earlier studies showed that Bayesian integration takes place even at early stages such as perception rather than reproduction in which memory and decisional processes are involved (Damsma et al., 2020). Therefore, we used a duration reproduction task while measuring EEG signals both in the perception and reproduction phases. Our first goal was to examine how different distribution ranges might affect the EEG signatures of temporal anticipation and decision making. Therefore, in the current study, participants were asked to reproduce *lower* (0.4 s, 0.56 s, and 0.8 s) and *upper* (1.2 s, 1.7 s, and 2.4 s) range intervals. Secondly, we aimed to investigate how processing of separate sample ranges (uni-pior context) and combining two different information sources within an experimental session (multi-prior context) might be apparent in the EEG signatures of temporal context. Accordingly, we tested both interval ranges in two separate context sessions. Each participant started with the *blocked-range (BR)* session in which interval ranges were tested in a blocked manner where lower and upper range intervals were presented in separate blocks. Subsequently, they performed the *interleaved-range (IR)* session in which both *lower* and *upper* interval ranges were tested mixed within a block (referred to as *full range*).

5.3 Method

Participants

27 healthy participants between 21 and 36 years old (13 females, mean age of 26.2 years) with no hearing impairment were recruited for the study. The sample size was the same as in a recent EEG study using the same reproduction task (Damsma et al., 2020). All participants signed informed consent forms prior to the experiment and were paid 9 Euro per hour or course credit for their participation. The study was approved by the Ethics Board of the Department of Psychology at LMU Munich. All participants were naive to the purpose of the study.

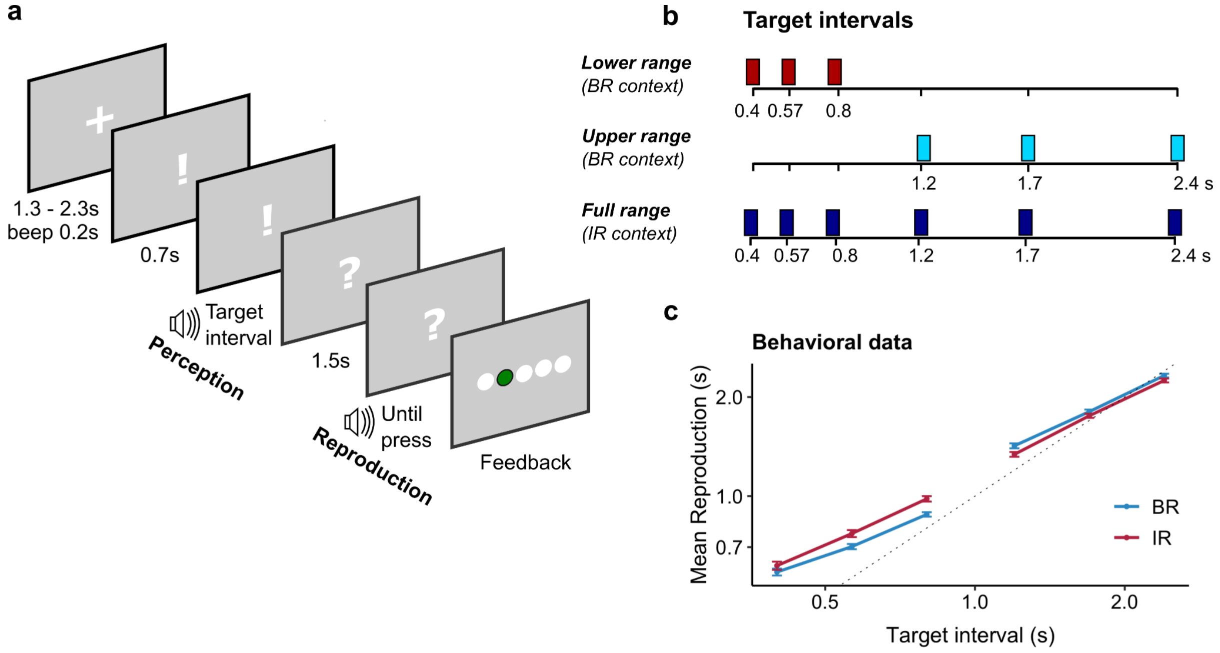

Figure 1. ***a)*** *Illustration of a trial procedure and target stimuli used in the experiment. Participants performed a duration reproduction task in which they heard a tone for a certain duration in the perception phase. After an ISI of 1.5 s, participants were presented with an auditory interval and were asked to mark the offset of that interval.* ***b)*** *The stimuli of lower or upper range blocks consisted of three short or three long durations, respectively. These separate blocks were referred to as the BR context. In the full range blocks, six durations sampled from lower and upper range were presented randomly in the same blocks (referred to as the IR context).* ***c)*** *The reproductions as a function of target interval and session condition: BR (blue) and IR (red). Diagonal dotted line shows the accurate reproduction.*

Stimuli and Procedure

The auditory stimuli were generated using the PsychoPort Audio library as continuous 500 Hz sine wave tones and presented via Sony MDR stereo headphones using the Psychtoolbox 3 (Kleiner et al., 2007). Instructions and feedback text were displayed on a CRT monitor.

Participants performed an auditory interval reproduction task (Figure 1a). Each trial started with a fixation for a random duration, lasting between 1.3 and 2.3 s, immediately followed by an exclamation mark for 0.7 s, which signaled an upcoming tone. The tone was presented for a specific duration (refer to the detailed design in the next paragraph) while the exclamation mark remained on the screen. We refer to this period as the perception phase. Then, the exclamation mark was replaced by a question mark, which appeared for 1.5 s, indicating the start of the reproduction phase. Next, a tone was presented again, with the question mark remaining on the screen. Participants had to terminate the tone when it reached the same duration as the first interval by pressing the spacebar on the keyboard.

The experiment consisted of two sessions: the blocked range (BR) and the interleaved range (IR) contexts. In the BR session, participants were presented with subseconds (0.4, 0.56 and 0.8 s) and super-second intervals (1.2, 1.7 and 2.4 s) in a block-wise manner. Crucially, we kept a gap of 0.4 s between the sub-second and super-second ranges to clearly separate them. The presentation order of the subseconds and supra-seconds blocks was counterbalanced among participants. In the IR session, participants were presented with all possible target intervals, ranging from the subsecond to supra-seconds (0.4, 0.56, 0.8, 1.2, 1.7 and 2.4 s), referred to as the full range in Figure 1b. Every participant began with the BR session to ensure that they were not presented with the full range before the BR session was completed and after a 10-min break, they continued with the IR session.

Prior to the formal experiment, participants performed 5-10 trials until they were familiarized with the task. Each session had 12 blocks with 30 trials each, resulting in a total of 60 repetitions for each target interval.

EEG recording and preprocessing

Electrical brain activity was recorded from 64 scalp locations (actiCAP system; Brain Products GmbH) using the BrainVision Recorder software (Brain Products GmbH) and a BrainAmp amplifier (DC to 250 Hz) at the sampling rate of 1000 Hz. During the experiment, the impedances of all electrodes were kept below 10 kΩ. The EEG data were analyzed using EEGLAB (Delorme & Makeig, 2004). Electrode FCz served as an online reference. Later, the average of the temporal-parietal electrodes (TP9 and TP10) was used in the offline re-referencing. The data was re-sampled to 500 Hz and bandpass-filtered from 0.1 to 70 Hz. Artifacts caused by eye blinks, eye movements, and muscle noises were removed using independent component analysis (ICA). Subsequently, the data were bandpass-filtered from 0.1 to 30 Hz.

ERP components

Figure 2c shows schematically the EEG waveform illustrating its components which we measured. All ERP components reported here, CNV, P2 and LPCt, were measured on the fronto-central electrode cluster by averaging the activity of Fz, FC1, FC2, C1, C2 and Cz electrodes (Kononowicz & van Rijn, 2014; Ng et al., 2011). They were calculated for each participant, target interval and temporal context. EEG data were segmented for CNV analysis relative to stimulus onset (-200 to +3500 ms). The onset-locked data were baselined to the average voltage 200 ms prior to the stimulus onset. We defined the CNV buildup as the average waveform between 300 and 600 ms from the stimulus onset, and the mean CNV amplitude as the interval starting from late negativity onset (300 ms after the stimulus onset) and having a length of the target duration (Kruijne et al., 2021a). For P2 analysis, EEG data were segmented relative to stimulus offset (-100 to +600 ms). The offset-locked data were baselined to the 100 ms time window surrounding the stimulus offset (50 ms preceding and following the stimulus offset) (Damsma et al., 2021). We defined the mean P2 amplitude as the averaged waveform between 200 and 300 ms after the offset. We examined the LPCt by segmenting the averaged waveform relative to the reproduction onset (-1500 to +500 ms). The reproduction-onset-locked data were baselined to the 100 ms time window surrounding the reproduction onset (-50 ms to +50 ms around the onset) and the mean LPCt amplitude was defined as the averaged amplitude in the time window starting 800 ms before the reproduction with a length of 200 ms (-800 ms to -600 ms) (Wiener & Thompson, 2015).

Data analysis

The main behavioral and ERP results were analyzed via linear mixed model analysis using R package *lmerTest* (Kuznetsova et al., 2017) or repeated-measures analysis of variance (ANOVA). Linear mixed models are robust to sphericity violations, do not inflate Type I errors (Singmann & Kellen, 2019) and can accommodate the covariant factor in addition to the fixed effects addressed by ANOVA. The p-values reported for the mixed models were calculated using the Kenward-Roger approximation. ANOVA results were reported with additional Bayes factor (BF) analyses to provide a more rigorous assessment of the null hypothesis (Rouder et al., 2009).

Time-frequency analysis

Time frequency analysis was carried out using MNE-Python (Gramfort et al., 2013). To calculate the oscillatory powers of fronto-central electrodes (Fz, FC1, FC2, C1, C2 and Cz) during the perception and reproduction, we applied to each electrode a Morlet wavelet convolution using the MNE *tfr_morlet* function, frequencies ranging from 4 to 40 Hz, with 3 cycles wavelet width (Wiener et al., 2018). The frequency analysis was applied to each trial before averaging across trials for the given target interval. The absolute power was calculated from the baseline window of 200 ms prior to the stimulus onset. We later averaged the power spectrums over lower and upper range target intervals for each temporal context (BR and IR). The power spectrum differences of the IR and the BR context were tested for significance with a one-sample *t*-test using cluster-based permutation analysis with the MNE *permutation_cluster_1samp_test* function. The significant result of the permutation test reveals whether the given time-frequency points of the temporal context differences are more likely to come from a probability distribution different from a null distribution (a distribution created by randomizing the data). The test identifies the clusters which exceed the critical value of $p < .05$. It is a corrected method for multiple comparisons and identifies the correct region of the significant clusters. We applied cluster-based permutation to the difference between IR and BR sessions at the fronto-central electrode site from 200 to 2600 ms relative to stimulus onset using 1000 permutations. We run separate permutations for theta (4-7 Hz), alpha (8-14 Hz) and beta (15-39 Hz) bands (Kononowicz & van Rijn, 2015).

5.4 Results

Behavioral Results

Figure 1c shows the average reproductions for different intervals. As expected, reproductions in the IR context were biased towards a single context prior while in the BR context, they were biased towards the priors of each respective interval range. The results of the linear mixed model on mean reproduction with fixed factors of Duration, Context, and Range and Duration also as a random factor showed that the reproductions increased with duration ($b = 0.74$, 95% confidence interval $CI = [0.69, 0.78]$, $p < .001$) and interval range ($b = 0.19$, $CI = [0.16, 0.78]$, $p < .001$). We found a significant effect of temporal context, showing that reproductions were shorter in the IR compared to the BR context ($b = -0.04$, $CI = [-0.05, -0.03]$, $p < .001$). In addition, there was a significant interaction between duration and interval range ($b = 0.84$, $CI = [0.06, 0.09]$, $p < .001$), where the lower range intervals in the IR were overestimated (0.79 vs. 0.72 s) and the upper range intervals were underestimated (1.78 vs. 1.85 s) compared to their presentation in the BR context.

Event-related potentials

Perception Phase

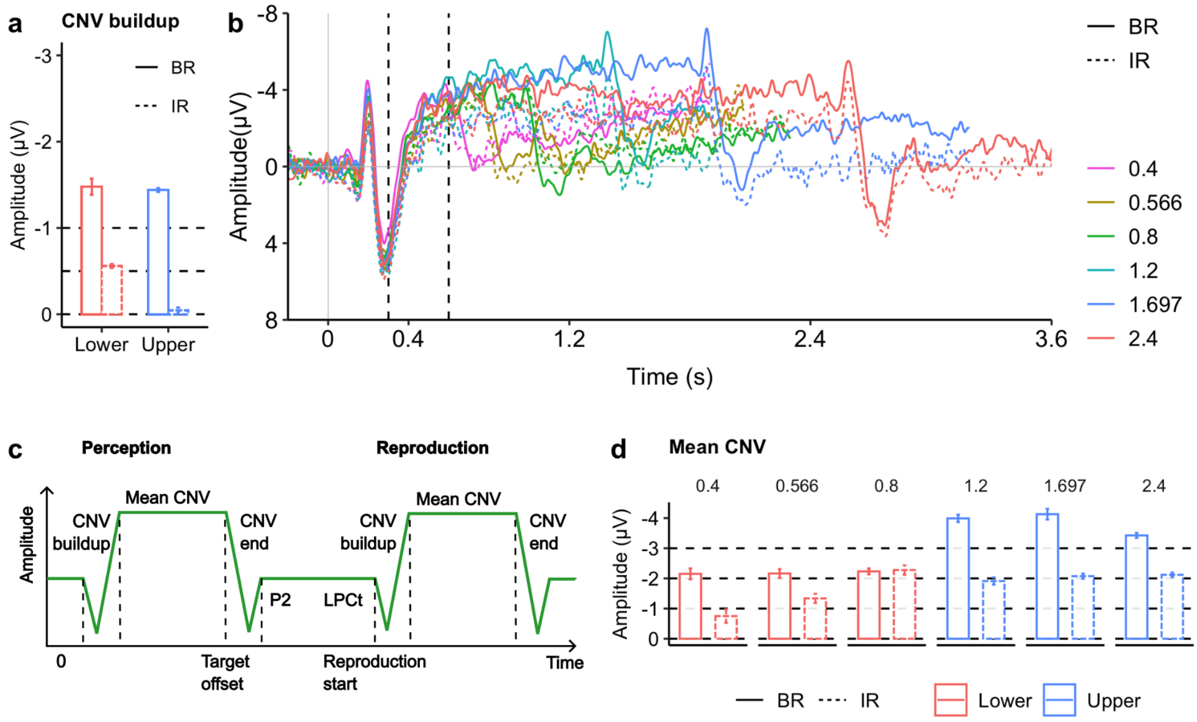

Figure 2. *(**a**) The CNV buildup, measured over the fronto-central electrodes (Fz, FC1, FC2, C1, C2 and Cz) and between 0.3 and 0.6 s. Red represents lower range intervals, blue represents upper range intervals for (**a**) and (**d**). Solid lines depict the BR, dashed lines depict the IR context for (**a**), (**b**) and (**d**). (**b**) Grand average of the ERP waveforms for different target intervals (indicated in seconds) in the perception phase. Each line is plotted for the time window that ends when reproduction starts (1.5 s after the target offset). The vertical dashed lines mark the time window in which CNV buildup was tested. (**c**) The structure of an ERP waveform (see Methods for the details). (**d**) The mean CNV amplitudes during perception.*

Figure 2b illustrates the CNV activity in the perception phase of the BR and IR contexts, showing the negativity changes over the time for different target intervals. During the perception phase, we measured the CNV component by its buildup, mean amplitude and crossing latency, as well as the P2 and the LPCt components. A two-way repeated measures ANOVA on the CNV buildup rate with factors of context (IR and BR) and interval range (Lower, Upper) showed that the CNV rate was faster (−1.5 vs. −0.3 µV/s) in the BR compared to the IR, $F(1, 26) = 16.42$, $p < .001$, $\eta_g^2 = 0.06$, $BF > 100$ (Figure 2a). However, the CNV buildup in the lower and upper range intervals were comparable, $F(1, 26) = 1.68$, $p =$

.21, $\eta_g^2 = 0.01$, *BF* = 0.27, and there was no significant interaction between the condition and interval ranges, $F(1, 26) = 0.51$, $p = .48$, $\eta_g^2 = 0.003$, *BF* = 0.33.

We then applied a linear mixed model to the mean CNV amplitude, with the context and duration as the fixed effects while interval range as the random factor (Figure 2d). The mixed model showed that the average amplitude in the BR context was lower than in the IR context ($b = -0.64$, $CI = [-0.92, -0.36]$, $p < .001$). However, there was no significant effect of duration ($p = .91$), interval range ($p = .05$) or the interaction between context and duration ($p = .34$). We examined the crossing latency of CNV, which is the point at which the CNV waveform changes from negative to positive after the stimulus ends. Our results revealed significant differences in crossing latency for the two prior contexts and the interval length. The mixed model showed that the crossing latency was significantly earlier in the BR than the IR (1.41 vs. 1.47 s), $b = -0.01$, $CI = [-0.02, -0.01]$, $p = .001$, and the latency was significantly delayed as the durations increased ($b = 0.98$, $CI = [0.96, 1.00]$, $p < .001$). The interval range ($p = .11$) and the interaction between context and duration ($p = .35$) were not significant.

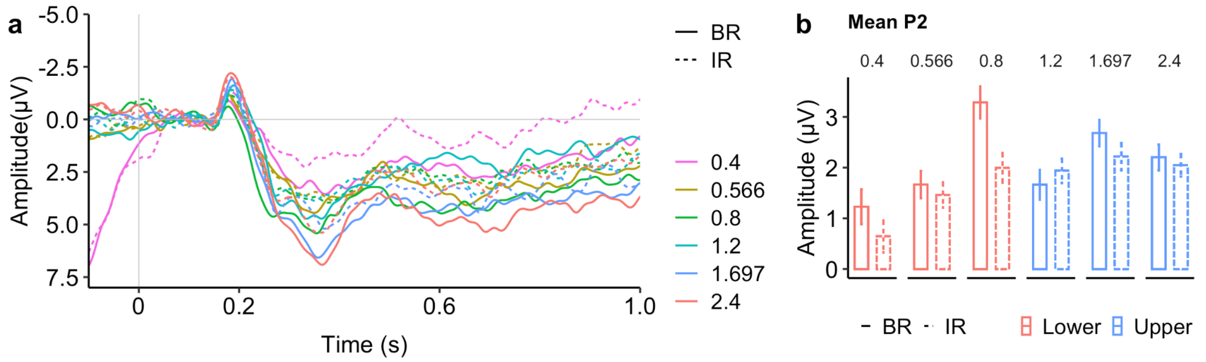

Figure 3. ***(a)*** *Grand average of the ERP waveforms for different target intervals in the target offset. Vertical line shows the perception offset. Solid lines depict the BR, dashed lines depict the IR context.* ***(b)*** *The P2 amplitudes averaged over the time window between 0.2 and 0.3 s relative to perception offset. Red represents lower range intervals, blue represents upper range intervals. Solid lines depict the BR, dashed lines depict the IR context.*

Figure 3a illustrates the averaged amplitude over participants in the perception offset of the BR and IR contexts, showing the positivity changes over the time for different target intervals. We applied a similar linear mixed model to the mean P2 amplitude (Figure 3b). The mixed model showed that the average amplitude in the BR context was higher than in the IR context (2.12 vs. 1.72 μV), *b* = 0.20, *CI* = [0.04, 0.36], *p* = .017. Moreover, there was significantly increasing P2 amplitude for the increasing duration (*b* = 0.63, *CI* = [0.14, 1.12], *p* = .012). The interval range (*p* = .30) and the interaction between context and duration (*p* = .36) were not significant.

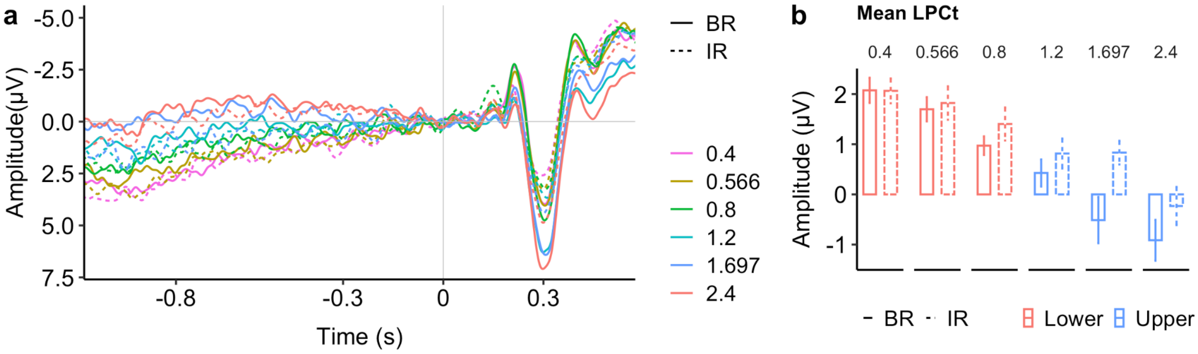

Figure 4. *(**a**) Grand average of the ERP waveforms for different target intervals in the pre-reproduction phase. Vertical line shows the reproduction onset. Solid lines depict the BR, dashed lines depict the IR context. (**b**) The LPCt amplitudes averaged over the time window between -0.8 and -0.6 s relative to reproduction onset. Red represents lower range intervals, blue represents upper range intervals. Solid lines depict the BR, dashed lines depict the IR context.*

Figure 4a illustrates the averaged amplitude over participants in the pre-reproduction phase of the BR and IR contexts, showing the positivity changes over the time for different target intervals. We applied a linear mixed model to the mean LPCt amplitude, with context and interval range as the fixed effects while duration as the random factor (Figure 4b). The mixed model showed that there was a decreasing LPCt amplitude as target duration increased, (*b* = -1.12, *CI* = [-1.96, -0.27], *p* = .01). However, there were no significant effects of context (*p* = .08), interval range (*p* = .60) or interaction between the context and duration (*p* = .27).

Reproduction Phase

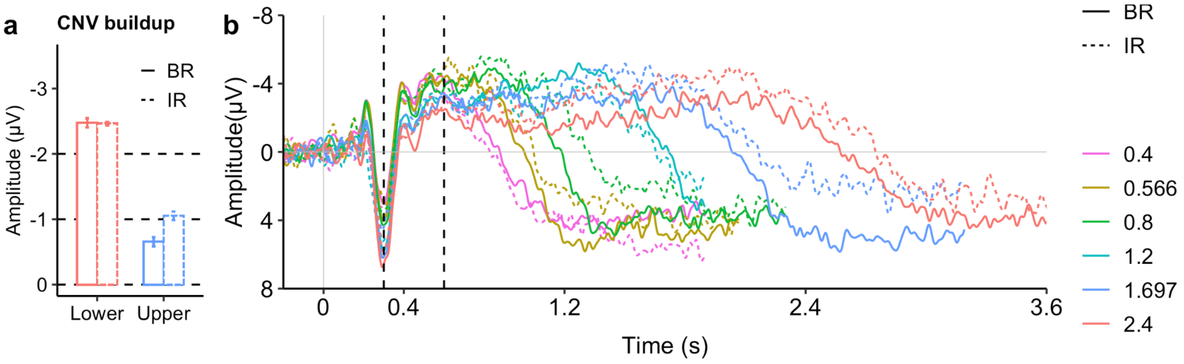

Figure 5. *(**a**) The CNV buildup measured over the fronto-central electrodes (Fz, FC1, FC2, C1, C2 and Cz) and between 0.3 and 0.6 s. Red represents lower range intervals, blue represents upper range intervals. Solid lines depict the BR, dashed lines depict the IR context for (**a**) and (**b**). (**b**) Grand average of the ERP waveforms for different target intervals in the reproduction phase. Each line is plotted for the time window that ends before the start of the next trial. The vertical dashed lines mark the time window in which CNV buildup was measured.*

Figure 5b illustrates the CNV activity in the reproduction phase of the BR and IR context intervals, showing the negativity changes over the time for different target intervals. During the reproduction phase, we measured the CNV component by its buildup, mean amplitude and crossing latency after the reproduction phase starts. A two-way repeated measures ANOVA results showed that the CNV buildup was faster (−2.5 vs. −0.9 μV/s) in the lower compared to the upper range intervals, $F(1, 26) = 16.29$, $p < .001$, $\eta_g^2 = 0.08$, $BF > 100$ (Figure 5a). However, the CNV buildup in the BR and IR contexts were comparable, $F(1, 26) = 0.24$, $p = .63$, $\eta_g^2 = 0.001$, $BF = 0.22$ and there was no significant interaction between the condition and interval ranges, $F(1, 26) = 0.21$, $p = .65$, $\eta_g^2 = 0.001$, $BF = 0.29$.

We then applied a linear mixed model to the mean CNV amplitude, with the context and duration as the fixed effects and the interval range as the random effect. The mixed model showed that the average amplitude in the BR and IR context was comparable ($p = .46$). Moreover, there were no significant effects of interval range ($p = .75$), duration ($p = .45$) or interaction between the context and duration ($p = .23$).

Furthermore, our results revealed significant differences in crossing latency for the two prior contexts and the interval lengths. The mixed model showed that the crossing latency was significantly earlier in the BR than the IR (1.43 vs. 1.47 s), $b = -0.02$, $CI = [-0.03,$

-0.01], *p* = .002, and the latency was significantly delayed as the durations increased (*b* = 0.92, *CI* = [0.89, 0.95], *p* < .001). The interval range (*p* = .10) and the interaction between context and duration (*p* = .33) were not significant.

Time Frequency Results

Perception Phase

We examined the oscillatory power differences between temporal contexts by averaging over lower and upper range intervals for each context (IR and BR). Figure 6 illustrates the power spectrum differences of the averaged lower and upper target intervals when presented in the IR vs. BR being assessed using cluster-based permutation analysis across the theta, alpha and beta bands. The results revealed a significant effect for the alpha and theta bands at the perception phase, while showing no significant effect for the beta band. The significant clusters were observed for the upper range intervals in the alpha band within the 0.57 - 1.73 s (*p* = .001) window, and in the theta band within the 0.63 - 1.78 s (*p* = .003).

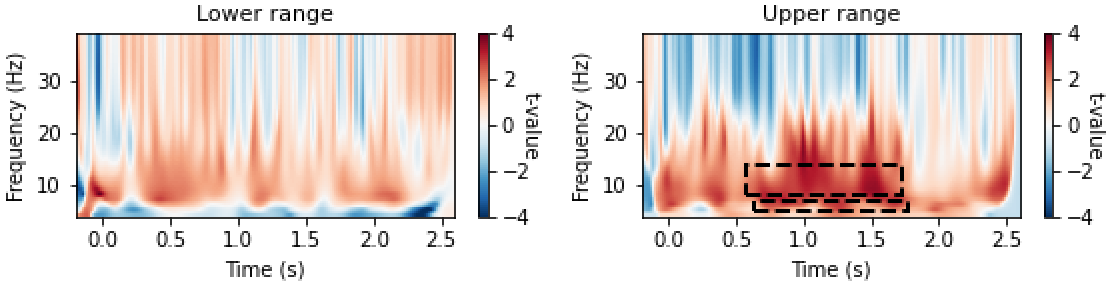

Figure 6. *Time-frequency plot of the t-values for a cluster permutation t-test comparison run over the difference between IR and BR contexts in the perception phase at the fronto-central electrodes (Fz, FC1, FC2, C1, C2 and Cz). Significant clusters in the alpha band (8–14 Hz) and theta band (5–7 Hz) for the upper duration ranges were observed. Dashed rectangles highlight the significant clusters.*

Reproduction Phase

Similar to the perception phase, we examined the oscillatory power differences between temporal contexts by averaging over lower and upper range intervals for each context (IR and BR). Figure 7 illustrates the power spectrum differences of the averaged lower and upper target intervals during the reproduction phase in the IR vs. BR being assessed using cluster-based permutation analysis across the theta, alpha and beta bands. The results only revealed a significant effect for the theta band at the reproduction phase, while showing no significant effect for the beta or alpha bands. The significant clusters were observed in the lower range intervals within the 0.10 - 0.60 s (p = .015) and within the 0.68 - 1.50 s (p = .003) windows.

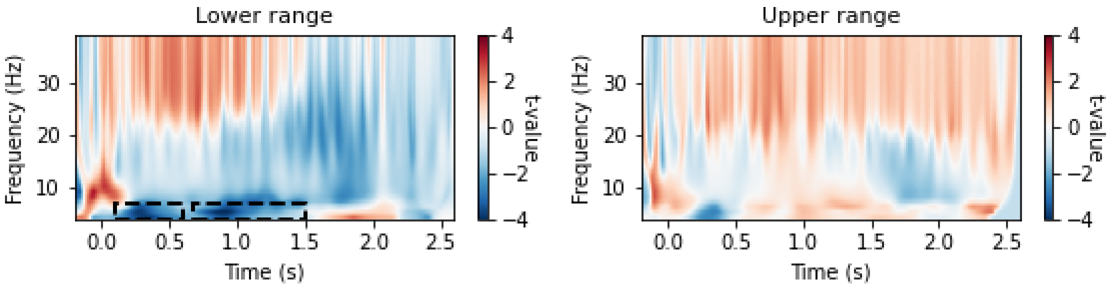

Figure 7. *Time-frequency plot of the t-values for a cluster permutation t-test comparison run over the difference between IR and BR contexts in the reproduction phase at the fronto-central electrodes (Fz, FC1, FC2, C1, C2 and Cz). Significant clusters in the theta band (4 - 7 Hz) for the lower duration ranges were observed. Dashed rectangles highlight the significant clusters.*

5.5 Discussion

The aim of this study was to investigate how the temporal range impacts on duration reproduction by testing duration reproductions in two types of sessions: interleaved session (IR) and blocked sessions (BR). Presentations of sub-second and super-second durations were randomly interleaved in the IR session. In the BR session, they were tested in separate blocks. Behaviorally, we found a general central tendency effect (Lejeune & Wearden, 2009; Shi et al., 2013) in both sessions, manifested by a shallow regression slope (0.74). However, the magnitude of overestimation in sub-seconds and underestimation in super-seconds were more pronounced in the IR session than in the BR session, indicating that the range of the context also influences duration reproduction. EEG findings demonstrated that the effects of temporal context can be detected by event-related potential (ERP) components, such as CNV, P2, and LPCt, as well as the low-frequency oscillatory activities.

The cortical excitability during the perception and reproduction phases represent sensory encoding processes and decision-making together with motor execution processes, respectively. Therefore, ERP components, such as the central negativity component (CNV), a key signature for temporal processing, in the two phases may reflect different underlying processes. The evolving velocity and mean amplitude of the CNV may reflect temporal accumulation, attention, and anticipation to the incoming durations during the perception phase, while they may reflect the memorized standard duration and prior knowledge during the reproduction phase.

ERPs in the perception phase

The CNV and alpha band activity are two commonly used neural markers for measuring temporal expectation and attention (Praamstra et al., 2006; Rohenkohl & Nobre, 2011a; Zanto et al., 2011). In the second study of the thesis (Baykan et al., 2023) which investigated the influences of ensemble context on the temporal bisection task, we observed that long durations elicited longer sustained CNV negativities compared to shorter durations. The present study also confirmed that the sustained CNV correlates with duration. Previous research has shown that the amplitude and climbing rate of the CNV, as well as the alpha power are associated with anticipation and expectation (Kononowicz et al., 2018; Kononowicz & Penney, 2016; van Rijn et al., 2011). We further found that the climbing rate of the CNV was faster for the block-wise (BR) session than the interleaved (IR) session. Moreover, the amplitude of the CNV was larger for the BR relative to the IR context. Recall that the BR session had a narrower range of target durations within each block, the anticipation of incoming stimuli would be expected to increase compared to the IR session, which had a wider range of target durations in each block. These results were consistent with our earlier study on the temporal bisection task (Baykan et al., 2023) in which the climbing rate of the CNV was greater for short relative to long contexts.

We also observed that, similar to CNV, the offset P2 amplitude increased with duration, and the prior context modulated the P2 activity. This observation is consistent with previous studies showing that P2 amplitude positively correlates with stimulus duration (Baykan et al., 2023; Kononowicz & van Rijn, 2011; van Wassenhove & Lecoutre, 2015), as well as active anticipation of a target influences the offset amplitude (Damsma et al., 2020; Pereira et al., 2014). For instance, research has demonstrated that P2 amplitude in the current trial decreased with longer durations presented in the previous trial (Damsma et al., 2020), suggesting that P2 activity at the perception offset is sensitive to temporal context and reflects the perceptual outcome. Similarly, our findings revealed that the range context influenced the offset P2 activity with higher amplitudes in the BR session compared to the IR session, and such context modulation was active throughout the perception phase. P2 activity has been seen as an index of perceptual processes (Kononowicz et al., 2018; van Wassenhove & Lecoutre, 2015). For example, it has been suggested that P2 reflects the sense of physical duration rather than decisional processes (Kruijne et al., 2021b). Given that in the BR context there was a higher temporal anticipation for the incoming stimulus, leading to higher temporal attention, it is possible that the overall sense of physical duration of the target intervals were longer relative to the IR context. According to the Scalar Expectancy Theory (SET) framework, more attention allocation to the target would give rise to more ‘long’ duration perception as a result of more accumulated pacemaker pulses (Lejeune, 1998; Ng et al., 2011). However, the reproductions of the short intervals were not overestimated in the BR session, implying that the decision making processes take place after the perceptual stage which can be measured by late positivity responses such as P3 or LPCt (Kruijne et al., 2021b).

Temporal anticipation has been previously suggested to influence temporal attention by aligning relevant neuronal ensembles beforehand (Nobre & van Ede, 2018). The current experiment revealed this relationship between temporal anticipation and attention to be dependent on the sample stimulus range. Specifically, our findings showed reduced alpha power in the BR context relative to the IR context for the super-second range intervals. This result is likely because anticipation became stronger after the average duration, which was the case in the super-second range. In the BR session all durations were super-seconds, while in the IR session super-second durations were interleaved with sub-second durations. It is possible that the temporal anticipation in the BR session readjusted to the super-second range, while it did not in the IR session, resulting in reduced alpha power in the BR session.

ERPs in the decision-making and reproduction phase

Late positivity components P3 or LPCt have been linked with temporal decision making (Baykan & Shi, 2022; Lindbergh & Kieffaber, 2013; Ofir & Landau, 2022) and have been measured relative to response (Bannier et al., 2019; Wiener & Thompson, 2015) or the stimulus offset (Gontier et al., 2009; Tarantino et al., 2010). Previous studies have shown that the LPCt amplitude covaries with the difficulty of the perceptual task (Gibbons & Stahl, 2008; Paul et al., 2011; Wiener & Thompson, 2015). For example, Bannier et al. (2019) demonstrated that LPCt amplitude averaged over 500-600 ms after stimulus offset was larger in the temporal identification task than the temporal categorisation task requiring fewer cognitive resources. Similarly, Lindbergh et al. (2013) showed that stimulus offset signals are modulated by the subjective judgments with higher positivity amplitudes for the targets judged as “short”.

The LPCt amplitude has been also shown to be affected by the intervals presented in previous trials (Wiener & Thompson, 2015). Short durations presented in the long temporal context reflected larger LPCt relative to their presentations in the short temporal context (Baykan et al., 2023). This has been related to the higher uncertainty of the short intervals embedded in the long context. As it was shown by a recent study (Ofir & Landau, 2022), the LPCt amplitude correlates with the distance between the accumulated time and the decision boundary in a drift-diffusion model (DDM). The DDM posits that information is accumulated until it reaches a decision threshold with a drift rate and the uncertainty of the perception is related to the distance from the accumulated time to a decision boundary. Decision thresholds are set differently in temporal contexts based on their ensemble means. Therefore, the LPCt amplitude elicited by same target intervals when presented in different contexts would be expected to differ.

In our task, we measured LPCt in relation to the onset of the reproduction phase, as we expected the influence of range context and duration in the reproduction task to occur before reproduction. Our results were consistent with previous studies showing that LPCt amplitude decreases as stimulus duration increases (Lindbergh & Kieffaber, 2013; Ofir & Landau, 2022). Although the LPCt amplitude was numerically higher in the IR relative to the BR condition, we did not observe significant range context modulation on the LPCt amplitude. It is worth noting that modulation of LPCt amplitude would be expected depending on varying ensemble context mean (Baykan et al., 2023; Ofir & Landau, 2022). However, in the present study, we used the same sample distribution for the IR and the BR sessions. As shown in behavioral results, the reproduced means of the blocked sub-second and super-second were not centered at their respective actual means but instead were assimilated by the other block’s samples. This suggests that, even when tested sub- and super-seconds separately, observers maintained their global prior with its mean similar to that of the IR session. The lack of substantial difference in ensemble means could be the primary reason why there were no distinct LPCts amplitude differences in the two sessions.

During the reproduction phase, we observed that CNV activity was influenced by the presented stimulus range rather than the prior context. This is consistent with the previous studies showing that the evolving velocity of CNV is influenced by the memorized standard duration (Pfeuty et al., 2005; Praamstra et al., 2006). For example, Pfeuty et al. (2005) found that the CNV slope was steeper when the memorized standard was short and shallower when it was long. Similarly, Praamstra et al. (2006) used a sequence of repeated trials and showed that the CNV slope of the last deviant stimulus onset asynchrony (SOA) is modulated by the repeated standard SOAs after many exposures. The CNV slope of the last stimulus standard was steeper when presented after repeated short SOAs than after repeated long SOAs. As shorter intervals would elicit earlier responses, the CNV would be expected to increase rapidly for short targets during the reproduction. Our results support this explanation, suggesting that the CNV buildup during the reproduction phase reflects the memorized or encoded duration during the perception phase.

Moreover, we observed a decrease in theta power during reproduction for lower range intervals in the IR compared to the BR context. Previous studies have linked theta activity to temporal decision making (Cavanagh et al., 2010; Jacobs et al., 2006). For example, Jacobs et al. (2006) indicated a positive correlation between theta power and decision confidence in a memory retrieval task. Similarly, van Vught et al. (2012) examined the neural correlates of evidence accumulation in decision making and found that theta activity slopes covaried with the drift rate of evidence accumulation. Higher theta power was indicative of higher drift rates of spontaneous neural firing (Smerieri et al., 2010). Our results suggested that the increased theta power in the BR context may indicate higher confidence in decision-making. However, theta power dependencies on context were only observed for lower range intervals, implying that decision confidences are more reliant on shorter intervals.

One noteworthy similarity of the CNV component which we observed during both perception and reproduction was the crossing latency. We examined the resolution of CNV activity by measuring the point at which the CNV amplitude crossed from negative to positive values. This measure showed a positive correlation with the target interval length in both phases. It is worth noting that CNV end latency was also subject to temporal context with earlier latencies in the BR than the IR context. Given that the IR context had a wider range of target intervals, the expectation of an incoming stimulus could be more uncertain. Therefore, our findings suggest that the CNV end indexes the encoded duration to the degree of uncertainty.

Conclusion

We investigated how range and prior context influence the temporal reproduction task. Our results showed that prior context impacted the reproduction outcome by leading to reproduced durations that are biased towards the context mean. Combining behavioral and EEG data, we observed that there was a higher CNV buildup and mean amplitude during perception for the blocked-wise (BR) session, indicating an increased temporal anticipation in this session. In addition, we observed a reduced alpha power in the BR context for the upper range intervals, implying increased temporal attention in those blocks. During reproduction, the CNV buildup increased for lower range intervals regardless of temporal context, reflecting the encoded or memorized target duration. The theta band activity during reproduction was modulated by both temporal context and interval range, with higher theta power observed in the BR session for the lower range intervals, indicating greater confidence for short intervals.

Data availability

The data supporting the findings of this study and the statistical analysis code used in the manuscript are available at: https://gin.g-node.org/msense/EEG_temporal_reproduction.git

5.6 References for Chapter 5

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6 General Discussion

Throughout this dissertation, I described studies in which we investigated and discussed the behavioral and neural correlates of the context modulations in interval timing. We, as humans, estimate durations, make decisions and give responses affected by context. For example, our temporal responses change when the intervals are presented in a different order (Chapter 2). The climbing neural activity measured over fronto-central electrode sites differ when same intervals are embedded in separate temporal contexts (Chapters 3-5). The main objective of this dissertation was to research the potential behavioral and neural correlates of temporal context. Therefore, Chapter 2 studied how temporal order influences subjective timing and Chapter 3-5 focused on whether and if so, how temporal context maps onto the brain signals measured by EEG.

Temporal context modulation is a long-established finding. The range of the given stimuli and the ensemble statistics of the environment influence our timing. For example, Jazayeri and Shadlen (2010) showed that temporal reproductions are drawn towards the mean of the environment. Zhu and colleagues (2021), furthermore, showed that the sensitivity of subjective timing is affected by the variance of the stimulus sets. Although using two sensory environments with the same ensemble statistics (mean and variance), we still observe different subjective timing performances. One reason for this bias is an effect of the stimulus presentation order. Therefore, in the study which I described in Chapter 2, we investigated the stimulus order effects on temporal reproduction. We found that temporal pattern structure and the position of individual intervals influence the mean pattern reproduction and the precision of the reproduced intervals. The mean reproductions were assimilated by the first interval of the pattern. Decelerating patterns (with short intervals in the initial position) had the lowest mean reproductions. Moreover, the volatility of the patterns influenced the central tendency bias and the reproduction precision. Accelerating patterns demonstrated the least central tendency effect. We examined the influences of the last interval of the patterns on perceived volatility. The results showed that sequences ending with *long* intervals had a higher central tendency bias. In addition, the random sequence (with the highest volatility) had lower precision. Bayesian modeling of the temporal patterns, by integrating the pattern mean with the individual durations and assuming that perceptual uncertainty depending on the interval position and pattern structure, could go beyond the literature findings on interval timing and predict the temporal patterns data.

Temporal context modulations can be captured and indexed by neurophysiological evidence. In recent research, this was shown by Wiener and Thompson (2015) where they found that EEG signals elicited by the same target interval have been changing depending on the previous stimulus. Shorter prior durations lead to more “long” duration responses to the current target, as well as less contingent negative variation (CNV) amplitudes measured relative to the stimulus onset. Ofir and Landau (2022b) focused on the stimulus offset related signals while testing for the temporal context signatures. They found that the offset positivity signals correlate with the subjective judgment, with higher amplitude for “short” duration responses, compared to “long”. Importantly, their findings pointed to a relationship between the offset positivity signals and the distance to the decision boundary in the accumulation-to-bound process. In Chapter 3, I described a short report in which we reviewed Ofir and Landau (2022b)’s paper on the offset related signals and their relation to the decision-making. As it was highlighted in this report, temporal context shapes our expectation for an incoming stimulus, which in turn affects the decision-making process. For example, testing sub-second and supra-second intervals in different experimental blocks revealed similar offset amplitudes for the shortest intervals of these blocks (e.g., 0.2 s in the ‘short’ block, and 1 s in the ‘long’ block).

Although the EEG signatures of the common temporal context modulations, such as the central tendency and sequential effects, have been investigated before, the EEG signatures of subjective judgments influenced by ensemble statistics are lacking. Therefore, in the experiments I described in Chapter 4, we tested spacing and ensemble context modulations and measured the common timing EEG components in the bisection task. Our results revealed that the rate of CNV formation is the most robust finding reflecting these contextual effects. Specifically, in both experiments, the CNV formation was faster for the short compared to the long context. The CNV amplitude has been shown to be the more negative for the short than long context, though not significantly. Crucially, we observed that CNV activity continued until a response cue was prompted. In Experiment 1, we presented the response cue immediately after the target duration while in Experiment 2, we presented it 300 ms after the target. This introduced a respective delay in the CNV activity termination, as well. Therefore, our findings suggest that CNV amplitude does not index the target duration itself, but it reflects the readiness for a response. Another crucial finding came from the context modulations in the offset signals. Similar to the previous studies (e.g., Ofir & Landau, 2022b), we observed that the LPCt component was influenced by context and connected to temporal decision-making. Short intervals showed higher LPCt amplitudes than the long intervals. There was also a heightened positivity for the long context, similar to the case where there were more “short” responses during the long context session. Thus, we proposed that CNV indicates the expectation for a response, while LPCt is related to temporal decision-making.

The brain makes use of the prior knowledge while making judgments on a current sensory input. In a multi-prior environment in which multiple sources of prior information are provided, forming and exploiting separate priors for the sensory judgments would be more accurate. On the other hand, maintaining separate priors for different targets would also be costly in terms of an efficient response. The aim of the experiment I described in Chapter 5 was to explore the influence of uni- and multi-prior environments on the reproduction of different interval ranges. We tested lower and upper range intervals presented in the blocked-wise (BR) and interleaved (IR) prior contexts. Our results showed that the CNV and alpha power during the perception phase was affected by the prior context with larger CNV amplitude and decreased alpha power in the BR context relative to the IR context. Consistent with previous research (Praamstra et al., 2006), these findings suggested a possible role of the CNV and alpha power for temporal attention and anticipation during perception. During reproduction, there is a readiness for an incoming motor response. This was reflected by the faster buildup for lower compared to upper range intervals regardless of the temporal context. In addition, there was an increased theta power in the BR compared to the IR context for lower range intervals, suggesting higher temporal decision confidence for shorter intervals in their blocked-wise presentations. One consistent feature of CNV which we observed during both perception and reproduction was the CNV crossing latency with increasing latencies by increasing target durations. The crossing latencies were also subject to the prior context. The IR context had longer CNV end latencies compared to the BR context for both perception and reproduction phases.

6.1 Discussion of results

6.1.1 Order effects in temporal patterns

In everyday life, the stimuli that surround us do not appear as isolated entities but rather occur consecutively. For example, we can make use of the timing differences in the spoken language, music or motor activities. How we perceive, reproduce or act on the basic elements of the sequences of stimuli is still debated. The brain's assumption regarding the individual items of a sequence can be erroneous. One reason for the inaccuracies in recalling the individual items comes from the ensemble perception (Whitney & Yamanashi Leib, 2018). That is, forming an ensemble representation of a group of stimuli presented simultaneously while varying spatially or presented over a course of time. It is possible that the ensemble representation of a stimuli group constitutes a prior while making judgments for single items. Consequently, the perceptual outcome of the same target can change when presented in different contexts.

Temporal context can be defined as the target stimuli presented over the course of an experimental session. However, how we experience a train of stimuli within a trial also has contextual properties. Previously, the order effects on temporal patterns have not been examined extensively. There have been studies to investigate the effects of stimulus presentation order cross-trials (Glasauer & Shi, 2021a, 2022a). In those reproduction studies, high volatile temporal presentation orders, compared to low volatile orders, led to stronger central tendency biases. The stronger central tendency implies more reliance on the sensory environment. For example, if we consider a situation in which things are rapidly changing, we would be more uncertain about our current estimate. Thus, it would be more reasonable to rely on the average of the past observations instead of only relying on the previous observation. However, if we are in a situation in which things are fairly similar to the past experiences, we would be more certain about the current estimate and our environment reliance would be less. Iterative Bayesian models could successfully account for such high and low volatile contextual modulations. Following this, we also applied a Bayesian model to our study described in Chapter 2.

The crucial objective of our study, in Chapter 2, was to find out how the sub-components of a pattern and the pattern structure would weigh in subjective timing. The findings showed that the first interval affects the mean reproduction outcome: the shorter the initial interval, the shorter the mean reproduction. This result is in line with the studies indicating that the first interval engages in more attention (Kanai & Watanabe, 2006; Rose & Summers, 1995). In addition, the last interval of patterns influenced the perceived volatility, hence affecting the central tendency biases. Weber's law states that increasing stimulus magnitude leads to increasing variability of the percept. In this current study, the last interval with high variability has been shown to influence the perceived variability of the entire pattern. This is also consistent with the findings of the recency effect - the tendency of remembering the last item better (Silverman, 2010). Moreover, the pattern structure or the directionality of sequences contributed to the standard deviations in the reproductions. Although all patterns had the same mean and variance, the structure of interval presentation mattered. Rhythm perception is defined by its individual elements as well as the temporal order and relative lengths of its subcomponents (Matthews, 2013). Therefore, perception and reproduction of such sequences are dependent on a relatively complex relationship among its individual durations. Our study results demonstrated the primacy and recency effects on the temporal reproductions, and the proposed model integrating the ensemble prior and individual intervals predicted the behavioral performance accurately. These findings add up to the earlier research which points out the effect of uncertainty of single intervals on the central tendency bias (Jazayeri & Shadlen, 2010; Petzschner et al., 2015) and further highlights the influences of temporal presentation order on perception and reproduction.

6.1.2 EEG signatures of ensemble statistics effects

The stimulus offset signals measured by EEG are thought to be the indicators of temporal decision-making. Ofir and Landau (2022) reported that offset responses correlate with the relative distance of accumulated evidence toward a decision threshold in different modalities and temporal ranges. However, this finding is particular to the prospective timing, as it was discussed in Chapter 3. In *prospective timing*, decision-makers are actively involved in the timing of an event or a duration and track if the estimated duration reaches a decision threshold. Thus, prospective timing involves an attention allocation to timing and a predetermined threshold. In *retrospective timing*, decision-makers make time estimates after an event has already passed. Therefore, they do not necessarily pay attention to timing, instead they are required to retrieve the temporal information from memory. The findings reported by Ofir and Landau (2022b) come from a prospective timing task. Therefore, it was not possible to determine if the offset responses involved any surprise effect. The caveat with the evidence accumulation model used in this work is that it cannot account for retrospective timing in which the stimulus does not have an apparent onset and offset. This is critical because retrospective timing entails the time judgment of past events which involve many memory functions such as storing the events from everyday lives, the so-called episodic memory. Moreover, the authors compared short and long duration contexts (Ofir and Landau, 2022) and found that bisection judgements and the offset amplitudes do not reflect an absolute accumulation. For example, 0.8-s target interval, as the longest duration of the short context, led to more 'long' durations and elicited lower offset amplitudes compared to 1-s, the shortest duration of the long context. The EEG offset responses, along with the behavioral responses, adjusted to the context modulations.

Temporal decisions are shaped by our expectations. Several EEG components (CNV, P2 or LPCt) have been suggested to reflect temporal expectations. As it was reported in Chapter 4, we found that the CNV accumulation rate and LPCt activity index temporal expectancy and decision making processes, respectively. The interpretation of CNV in temporal processing has been controversial. It has been earlier suggested that CNV is a possible signature of temporal accumulation (Macar & Vidal, 2003; Tarantino et al., 2010). However, there have been another line of studies suggesting that CNV is a measure for response readiness, rather than serving as an absolute time tracker of the stimulus (van Rijn et al., 2011). For example, Boehm et al. (2014) showed a larger CNV activity in the trials where participants were cued to respond as quickly (speed trial) compared to trials where they were cued to respond as accurately (accuracy trials), suggesting a role of CNV in response preparation. Contributing to these discussions, we showed in Chapter 4 that CNV activity continued until a response mark was provided even though the target presentation already ended. Therefore, we suggest that our findings support the hypothesis that CNV indexes the time accumulated until a response and/or the readiness for a response rather than the stimulus duration.

The offset positivity components measured in the study described in Chapter 4, P2 and LPCt, had been found to reflect temporal accumulation and decision-making processes. Earlier studies have measured these components over the time window between 200 to 600 ms after the stimulus offset (Kononowicz & van Rijn, 2014; Ofir & Landau, 2022b; Paul et al., 2011; Tarantino et al., 2010; Wiener & Thompson, 2015) based on the task. In our study, we observed an offset positivity peaking around 200 ms at the stimulus offset, the so-called P2, when the stimulus end cue immediately followed the stimulus offset. The P2 amplitude and peak latency were found to be dependent on duration, with higher amplitude and earlier peaks in longer durations. This was consistent with classical interpretation of the P2 component as a temporal accumulation index (Kruijne et al., 2021). On the other hand, the LPCt component, as a late positivity component, has been suggested to occur around 400 ms later than the P2 component (Kononowicz et al. 2018). It has been related to temporal decision making with higher positivities observed in more difficult perceptual tasks (Bannier et al. 2019; Gontier et al. 2009). Sustained LPCt activity after the stimulus offset was observed in Experiment 2 in which the stimulus end cue was presented after a 300-ms gap. Our results align with the interpretation of the LPCt component as a decision making index.

Higher LPCt amplitude was observed for shorter durations. Given that the perceptual decision could be already made during the stimulus presentation for long durations, the LPCt activity is smaller relative to the case of short durations. For the short durations, the decisional processes still continue even after the perception.

6.1.3 EEG signatures of the range effect

Temporal reproduction tasks, in comparison to the bisection or categorisation tasks, can separate the perceptual, decisional and motor execution stages in a behavioral task. Therefore, we used a temporal reproduction task to examine the EEG signatures of the range effect while measuring the brain signals during both the perception and reproduction phases in the study described in Chapter 5. The common time-related ERP component, CNV, indicated different cognitive processes in the perceptual and response stages. As mentioned in the previous sub-section, the CNV has been related to separate stages of temporal processing such as temporal accumulation (Macar & Vidal, 2003; Tarantino et al., 2010) or memory (Ng et al., 2011; Wiener & Thompson, 2015). Our current study demonstrated that CNV buildup and mean amplitude reflect the temporal anticipation of an incoming stimulus in the perception phase. In the blocked-wise (BR) session with a narrow sample range, expectations towards the incoming target were higher as reflected by the larger CNV activity. On the other hand, CNV buildup indexed the memorized target duration in the reproduction phase. Consistent with previous studies (Pfeuty et al., 2005; Praamstra et al., 2006), the CNV buildup was larger for the short memorized durations, implying a readiness for a quicker response.

We further explored the offset-related brain signals, measured by the P2 and LPCt components. P2 component has been earlier associated with perceptual processes (Kononowicz et al., 2018; van Wassenhove & Lecoutre, 2015), while LPCt has been suggested to reflect decisional stages (Ofir & Landau, 2022). The current study results were aligned with these interpretations. Specifically, the P2 amplitude was found to increase by duration and be sensitive to temporal context with higher amplitude in the BR context. The increased P2 activity in the BR context can be related to the increased temporal attention in this session. Scalar Expectancy Theory (SET) posits that more efficient allocation of attention to a stimulus increases the perceived duration by accumulating more pacemaker pulses (Lejeune, 1998; Ng et al., 2011). Therefore, it is likely that higher temporal expectations in the BR session lead to longer duration perceptions. However, we did not observe overestimations of the lower range intervals in the BR session. Thus, the results imply that decision making processes take place at later stages after the perception in the temporal reproduction task. It might be possible to better capture the behavioral performance and reproduction outcomes by measuring late positivity responses such as LPCt. Previous research has linked the LPCt amplitude with the distance between the accumulated time and a decision boundary in an evidence accumulation model (Ofir & Landau, 2022). Decision thresholds are thought to be based on the ensemble mean of temporal context. Our LPCt findings revealed higher amplitudes for shorter durations while showing no context modulation. In the IR and BR contexts, the session means were the same but only the presentation order of the targets differed. The LPCt amplitudes did not demonstrate significant differences between our temporal contexts, likely because the individuals maintained the same ensemble mean in both contexts.

In addition to studying time-locked averaged EEG waveforms (ERPs), another common analysis method used for the EEG data is to examine brain signals depending on their spectral power and its changes over time (time-frequency analysis). In our study described in Chapter 5, we investigated the temporal evolution of the signal frequencies. Our results revealed that temporal attention increased in the BR session compared to the IR session, as indicated by the reduced alpha power during the perception phase. Importantly, this session difference on the alpha power was only apparent for long intervals. Although the larger CNV activity pointed out increased temporal anticipation in the overall BR session, our alpha power findings implied that the influence of temporal anticipation on the temporal attention is dependent on the sample stimuli range. This result is likely due to the stronger temporal anticipation for the target durations longer than the average duration, as in the case of upper range intervals. The upper range intervals are in the supra-second range in the BR session, while they are interleaved with the lower range intervals, hence more adjusted to the sub-second range in the IR session. Therefore, it is possible that temporal anticipation and attention differed based on the perceived average duration of each interval range. In addition, we observed increased theta in the BR session for short intervals relative to the IR session during the reproduction phase. This result, in line with the previous studies (Cavanagh et al., 2010; Jacobs et al., 2006), implied higher decision confidence in the BR session. Given that lower range intervals were interleaved with upper range intervals in the IR session, it is likely that temporal decisions for the short intervals were more uncertain.

6.2 Future directions

When analyzing time-related ERP components, the contextual ERP findings show some inconsistencies. One reason for this is because of the use of different experimental paradigms. For example, a longer prior interval led to higher negativity waveform at the fronto-central electrode cluster in a temporal categorisation task (Wiener and Thompson 2015), while it gave rise to lower negativity waveform in a temporal reproduction task (Damsma et al. 2021). This is because each experimental paradigm has different implicit assumptions and provides different relationships between the stimuli and response. When we examined the same ERP component in these tasks, it is not clear to what extent they reflect the similar cognitive processes. Interval timing does not only involve tracking the passage of time, but also engagements in many other processes such as working memory, attention and decision making. Therefore, future studies are needed to differentiate and compare the neural differences specific to each timing paradigm. For example, one could use retrospective timing paradigms to differentiate the nature of surprise and temporal accumulation because in the retrospective timing paradigm, time estimation is retrieved from the memory and is not necessarily affected by the involvement of attention. Furthermore, linking the ERP and oscillatory processes with internal clock models is challenging considering the fact that internal clock models lack well-established neural support. Therefore, future studies can examine the relationship between EEG signatures of time and more biologically supported mechanisms of an internal clock such as the Striatal Beat Frequency model.

6.3 Conclusions

The interval timing in prospective experimental tasks shows contextual biases. In this dissertation, using a reproduction task, I have shown that the pattern timing is also subject to context modulations (Chapter 2). The directionality of individual durations and the initial interval position in a pattern affect the precision of reproduced intervals and the mean reproduction, respectively. When investigating the temporal context modulations using EEG, the signals measured from fronto-central electrodes, targeting the preSMA brain region, are thought to provide evidence for different temporal processes. For example, there is strong evidence that the latency of stimulus onset-locked signals reflect memory processes (Ng et al., 2011), while the interpretation of the amplitude is more controversial. In this dissertation, I have demonstrated that our experiment findings are more in line with the response readiness or expectation accounts of the onset-locked signal amplitude (Boehm et al., 2014) in the temporal bisection task (Chapter 4). Our findings also point out that stimulus offset-locked signals are related to the temporal decision-making process, consistent with the findings of the recent study (Ofir & Landau, 2022b) which we reviewed in Chapter 3. In addition, we observed that brain signals measured during the perception and reproduction reflect different cognitive processes (Chapter 5). The fronto-central neural activity measured during the perception phase indexes temporal expectation for an incoming stimulus while covarying with the memorized target interval in the reproduction phase. The early offset responses reflect perceptual stages and the late positivity responses are associated with the decision making. This dissertation, overall, demonstrates that temporal order of the individual intervals influences temporal reproductions and EEG signatures of time can be found over the fronto-central electrode sites, although they represent different information processing stages for the temporal bisection and the reproduction tasks.

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Deutsche Zusammenfassung

Timing (Wahrnehmen der Zeit) ist eine grundlegende mentale Fähigkeit, die den primären kognitiven und Wahrnehmungsfunktionen des Gehirns zugrunde liegt. Diese Fähigkeit ermöglicht es den Organismen zu bestimmen, wann ein Ereignis eintritt und wie lange es dauert. Während wir uns zum Beispiel morgens für die Arbeit fertig machen, haben wir die bemerkenswerte Fähigkeit, den Zeitablauf jedes unserer Verhaltensweisen oder Handlungen zu verfolgen. Es gibt fast ein inneres „Gefühl", wie lange wir geduscht oder das Frühstück zubereitet haben, wann der Bus am Busbahnhof ankommt oder wann wir das Haus verlassen sollten. Unser subjektives Timing ist nicht nur auf solche bewussten Erfahrungen beschränkt, sondern spielt auch eine wesentliche Rolle bei eher unbewussten oder automatischen Prozessen wie Wahrnehmung oder motorischen Leistungen (Coull et al., 2011).

Die zeitliche Vorhersage, also das Zeitintervall, in dem ein Organismus das Eintreten eines Ereignisses erwartet, ist einer der Schlüssel Mechanismen, die Wahrnehmung und Handeln beeinflussen (Barnes & Jones, 2000; Nobre et al., 2007). Wahrnehmung Studien mit variierenden zeitlichen Unsicherheiten haben gezeigt, dass visuelle Erkennung Leistungen, z. B. für Leuchtdichte und Orientierung, mit höheren zeitlichen Sicherheiten zunehmen (Lasley & Cohn, 1981; Westheimer & Ley, 1996). In ähnlicher Weise haben Studien mit Aufmerksamkeits Orientierungsaufgaben berichtet, dass Erkennungs- und Unterscheidungsleistungen schneller und genauer sind, wenn zeitliche Erwartungen auf den Moment gerichtet sind, in dem Reize erscheinen würden (Correa et al., 2004; Coull & Nobre, 1998). Außerdem misst das Gehirn nicht nur den Beginn und die Abfolge von Ereignissen, die Verzögerung zwischen diesen Markern und ihre Reihenfolge, sondern auch die verstrichene Zeit. Die Zeitmessung im Bereich von weniger als einer Sekunde bis zu mehreren Sekunden, bekannt als *Intervall-Timing*, ist für die Wahrnehmung und Produktion von genauen motorischen Reaktionen, Sprache, Rhythmus und Musik erforderlich (Matell & Meck, 2000; Patel, 2003). Dies wird durch die Studien veranschaulicht, in denen Personen mit der Parkinson-Krankheit (PD) untersucht wurden, d. h. einer Störung, die mit dem gestörten Dopaminsystem in den Basalganglien zusammenhängt, einem Bereich, der auch für das Intervall-Timing verantwortlich ist (Buhusi & Meck, 2005; Gu et al., 2016; Merchant et al., 2008). Es wurde berichtet, dass Patienten mit Parkinson Schwierigkeiten bei der Bewegung Produktion und -koordination haben, mit rhythmischen motorischen Reaktionen und der Sprachproduktion Schritt halten (Gu et al., 2016; O'Boyle et al., 1996; Volkmann, 1992). Insgesamt wurde vorgeschlagen, dass das Intervall-Timing für Aufmerksamkeit, Wahrnehmung, Handlung und Kognition wesentlich und unvermeidlich ist (Matell & Meck, 2000).

Trotz der Bedeutung der Interval-Timing-Fähigkeit enthält es immer noch sehr systematische Verzerrungen. Sensorische Umgebungen, die durch die Versuchs Geschichte aufgebaut wurden, und Erwartungen, die aus der jüngsten Vergangenheit abgeleitet wurden, sind die beiden gemeinsamen Faktoren, die subjektive Zeit Urteile beeinflussen (Bausenhart et al., 2014; Dyjas et al., 2014; Lejeune & Wearden, 2009). Das erste Phänomen, das als *zentrale Tendenz Verzerrung* bezeichnet wird, impliziert, dass die Wahrnehmung Beurteilungen von der statistischen Struktur vergangener Ereignisse beeinflusst werden (Gu & Meck, 2011). Ebenso sind Reaktionen auf aktuelle Stimuli auf den vorangegangenen Stimulus ausgerichtet, was auf *serielle Abhängigkeit* Merkmale im Timing hinweist (Cicchini et al., 2018). Im Laufe eines halben Jahrhunderts wurden diese Verzerrungen eingehend untersucht (Helson, 1948; Parducci, 1965). Helson (1948)'s Adaptation-Level-Theorie und Parducci (1965)'s Range-Frequency-Theorie haben die Bias in Bezug auf den Sample-Bereich definiert, aus dem der aktuelle Stimulus gezogen wird, ohne eine Erklärung dafür zu liefern, warum sie anfänglich auftreten. Bayesianische Timing-Modelle zeichnen sich durch eine neuere Interpretation der kontextuellen Verzerrungen aus (Jazayeri & Shadlen, 2010; Miyazaki et al., 2005). Sie schlagen vor, dass das Gehirn die Unsicherheit einer sensorischen Messung überwacht und seine Schätzung basierend auf den Statistiken der sensorischen Umgebung anpasst (Jazayeri & Shadlen, 2010). Seitdem wird die Bayessche Analyse seit langem verwendet, um Erkenntnisse über viele Kontextfaktoren zu gewinnen (Burr et al., 2013; Gu et al., 2016; Shi et al., 2013). Es gibt jedoch noch einige Schlüsselfragen, die mit klassischen Bayes'schen Ansätzen nicht beantwortet werden können. Darüber hinaus gibt es eine Lücke zwischen den Bayes'schen Beschreibungen und ihrer Implementierung im Gehirn.

In Kapitel 2 beschreibe ich ein Experiment, bei dem wir die Reihenfolge der Zielintervalle, die in zeitliche Muster eingebettet sind, manipuliert haben, während die Statistik und der Bereich der Prüfintervalle gleich geblieben sind. Bayes'sche Schätzungsmodelle berücksichtigen erfolgreich die Verzerrung der zentralen Tendenz (Jazayeri & Shadlen, 2010) und serielle Abhängigkeitseffekte (Cicchini & Burr, 2018). Sie berücksichtigen jedoch keine zeitlichen Ordnungseffekte der Zielintervalle. Es gibt neuere Studien, die den Effekt der Struktur von Zielintervallpräsentationen untersucht haben (Glasauer & Shi, 2019a, 2021a). Diese Studien untersuchten jedoch die Effekte der

Präsentationsreihenfolge über eine experimentelle Sitzung hinweg, d. h. von Versuch zu Versuch, während die Effekte der zeitlichen Reihenfolge innerhalb eines Versuchs auf die beobachteten Zeitschätzungen noch nicht gründlich erforscht wurden. Wir haben untersucht, wie sich die zeitliche Reihenfolge auf die zeitliche Reproduktion auswirkt. Die Teilnehmer wurden gebeten, entweder beschleunigende, verlangsamende oder zufällige Hörsequenzen, die aus denselben vier Intervallen bestanden, mit Fingertipps zu reproduzieren. Unsere Ergebnisse zeigten, dass die mittlere Reproduktion und die Genauigkeit der reproduzierten Intervalle von der sequenziellen Struktur und ihrer Position abhängt. Das mittlere reproduzierte Intervall wurde durch das erste Intervall der Sequenz assimiliert, wobei es bei der verlangsamenden Sequenz am niedrigsten und bei der beschleunigenden Sequenz am höchsten war. Außerdem war die Verzerrung der zentralen Tendenz von der Volatilität der Sequenz abhängig. Die Zufallssequenz, die eine höhere Volatilität als die strukturierten beschleunigenden und verlangsamenden Sequenzen aufwies, ergab die geringste Genauigkeit der Reproduktionen und eine stärkere Verzerrung der zentralen Tendenz. Mithilfe der Bayes'schen Integration zwischen dem Ensemble-Mittelwert der Sequenz und den individuellen Dauern und unter der Annahme, dass die Wahrnehmungsunsicherheit von der Struktur und der Position der Sequenz abhängt, waren wir in der Lage, die Verhaltensergebnisse vorherzusagen. Wir kommen zu dem Schluss, dass die zeitliche Abfolge einer Sequenz eine entscheidende Rolle bei der Reproduktion zeitlicher Muster spielt, wobei ein höheres Gewicht des ersten Intervalls bei der mittleren Reproduktion und die Volatilität der Sequenz zur Wahrnehmungsunsicherheit einzelner Intervalle und zur Verzerrung der zentralen Tendenz beitragen.

In Kapitel 3 beschreibe ich eine kurze Übersichtsarbeit, in der wir einen kürzlich erschienenen Artikel (Ofir & Landau, 2022b) über ihre Ergebnisse in Bezug auf die zeitliche Entscheidungsfindung in Verbindung mit versetzten P3-Signalen und kontextuellen Modulationen der versetzten EEG-Signale besprechen. Es ist allgemein bekannt, dass Zeiteinschätzungen durch zuvor erlebte Intervalle beeinflusst werden. Der Begriff "zeitlicher Kontext" beschreibt Stichprobenintervalle, die im Verlauf einer Exposition, d. h. eines Experiments, präsentiert und im Gedächtnis gespeichert werden. Verhaltensstudien deuten auf eine verteilungsabhängige Charakteristik bei Zeitschätzungen (Wearden, 1991; 1995) und eine Abhängigkeit von den Prinzipien der Ensemble-Wahrnehmung hin (Zhu et al., 2021). Bislang ist jedoch nicht klar, wie wir die Integration des zeitlichen Kontextes in die aktuelle Schätzung erreichen. Dies lässt sich besser mit zeitlich hochauflösenden Messungen wie der Kopfhaut-Elektroenzephalographie (EEG) und ereigniskorrelierten Potenzialen (ERPs) untersuchen (Luck, 2005). Ofir und Landau (2022b) konzentrierten sich auf die Signale, die mit dem Stimulus-Offset zusammenhängen, während sie auf die Signaturen des zeitlichen Kontexts prüften. Sie fanden heraus, dass sich die Offset-Positivitätssignale als Reaktion auf die subjektive Beurteilung ändern. Antworten von "kurzer" Dauer zeigten im Vergleich zu denen von "langer" Dauer eine höhere Positivitätsamplitude. Wichtig ist, dass ihre Ergebnisse auf eine Beziehung zwischen den Offset-Positivitätssignalen und dem Abstand zur Entscheidungsgrenze im Prozess der Akkumulation bis zur Grenze hinweisen. Darüber hinaus zeigten sie, dass der zeitliche Kontext unsere Erwartung an einen eingehenden Reiz prägt, was wiederum den Entscheidungsprozess beeinflusst. So ergab die Prüfung von Intervallen unter einer Sekunde und über einer Sekunde in verschiedenen Versuchsblöcken ähnliche Offset-Amplituden für die kürzesten Intervalle dieser Blöcke (z. B. 0,2 s im kurzen Block und 1 s im langen Block).

In Kapitel 4 beschreibe ich eine Studie mit zwei separaten Experimenten, in denen wir den Verteilungskontext von Zielintervallen manipulierten und EEG zur Messung der gemeinsamen neuronalen Grundlagen von Zeit wie CNV und Offset-Komponenten, LPCt und P2, verwendeten. In Anlehnung an die speziellen Zeitmodelle wurde das EEG verwendet, um nach Mechanismen zu suchen, die den verschiedenen Phasen der zeitlichen Verarbeitung zugrunde liegen, einschließlich der Kodierung, Aufrechterhaltung und Entscheidungsfindung (Kononowicz, Rijn, et al., 2018). Eine neuere Studie untersuchte die neuronalen Grundlagen der zentralen Tendenz und der sequentiellen Effekte und konzentrierte sich dabei auf die CNV- und LPCt-Komponenten. Dabei wurde festgestellt, dass die CNV-Aktivität mit dem vorangegangenen Intervall kovariiert, was sich in einer erhöhten CNV-Amplitude bei längerer vorheriger Dauer zeigte, während die LPCt-Amplitude bei kurzen Zielintervallen linear zunimmt (Wiener & Thompson, 2015). Eine andere Studie untersuchte den Ort der Bayes'schen Berechnungen im Timing mit Hilfe von EEG und fand heraus, dass CNV, Offset P2 und Beta-Leistung durch den vorherigen Versuch beeinflusst werden (Damsma et al., 2021). Obwohl es Studien zu den elektrophysiologischen Markern des zeitlichen Kontexts gibt, ist die neuronale Grundlage der Modulationen des Ensemblekontexts auf das subjektive Timing noch nicht bekannt. In der aktuellen Studie veränderten wir den Abstand zwischen den Proben (Experiment 1) und die Häufigkeit (Experiment 2), um kurze und lange Kontexte zu erzeugen, während der Testbereich und die Standards in den verschiedenen Sitzungen gleich blieben. Die Ergebnisse zeigten, dass sich die Bisektionsschwelle in Richtung des Ensemble-Mittelwerts verschob und dass CNV und LPCt empfindlich auf die Kontextmodulation reagierten. Im Vergleich zum langen Kontext stieg die CNV-Steigerungsrate im kurzen Kontext an, und die Amplitude und Latenz der LPCt waren geringer. Diese Ergebnisse deuten darauf hin, dass die CNV eine Erwartungswelle für eine bevorstehende Entscheidungsfindung darstellt, während die LPCt den Entscheidungsprozess widerspiegelt, wobei beide durch den zeitlichen Kontext beeinflusst werden.

In Kapitel 5 beschreibe ich eine Studie, in der wir bei der Messung von EEG-Signalen die Auswirkungen zweier vorheriger Kontexte (uni-prior und multi-prior) auf zeitliche Reproduktionen untersucht haben. Die klassischen Bayes'schen Modelle gehen implizit davon aus, dass Menschen während der Stimulusexposition eine einzige Prior aufbauen. Wir sind jedoch in der Regel sensorischen Umgebungen ausgesetzt, die mit einer Vielzahl von Reizen und Informationen aus verschiedenen Sinnesmodalitäten gefüllt sind. Wenn wir zum Beispiel einen zwitschernden Vogel auf einem Ast lokalisieren, dienen sowohl der visuelle als auch der auditive Hinweis auf diese Wahrnehmung als zwei verschiedene Informationsquellen. Neben der Integration gleichzeitig vorhandener sensorischer Informationen aus verschiedenen Sinnen können wir bei der Bildung unserer Wahrnehmung und unseres Handelns auf verschiedene andere Informationsquellen zurückgreifen. Petzschner und Kollegen (2012) haben bereits gezeigt, dass die Information der Teilnehmer durch kategoriale Wahrnehmungshinweise ihre Wahrnehmungsreproduktion beeinflusst. Es bleibt daher eine offene Frage, welche Faktoren bei der Gruppierung komplexer Reizumgebungen eine Rolle spielen und wie das Gehirn mehrere vorherige Informationen aus verschiedenen Reizgruppen nutzt. Durch die Kombination von Verhaltens- und elektroenzephalographischen (EEG) Messungen untersuchten wir die zugrundeliegenden Mechanismen dieser Integration von mehrfachem Vorwissen in Kapitel 5. Die Teilnehmer reproduzierten die Zielintervalle in zwei vorherigen Kontextbedingungen: Blockbereich (BR), bestehend aus entweder kurzen oder langen Intervallen in einem Block, und Interleaved-Bereich (IR), der sowohl kurze als auch lange Intervalle in einem Block enthält. Die Ergebnisse zeigten, dass die Reproduktionen in der IR-Bedingung im Vergleich zur BR-Bedingung in Richtung des Mittelwerts des Gesamtkontexts verzerrt waren. Die EEG-Analyse zeigte, dass die CNV-Amplituden die Reproduktionsleistung direkt nach der Wahrnehmungsphase widerspiegeln. Zusätzlich fanden wir eine erhöhte β-Leistung in der IR-Bedingung während der Wahrnehmungsphase für beide Zielintervallbereiche. Diese Ergebnisse weisen darauf hin, dass der zeitliche Kontext die EEG-Signale in der späten Wahrnehmungsphase der Dauer aktiv beeinflusst, bevor die Reproduktion beginnt.

In dieser Dissertation habe ich anhand einer Reproduktionsaufgabe gezeigt, dass auch das Timing von Mustern kontextabhängig ist. Die Reihenfolge der einzelnen Dauern und die anfängliche Intervallposition in einem Muster wirken sich auf die Genauigkeit der reproduzierten Intervalle bzw. auf die durchschnittliche Reproduktion aus. Bei der Untersuchung der zeitlichen Kontextmodulationen mit Hilfe des EEG wird davon ausgegangen, dass die von fronto-zentralen Elektroden gemessenen Signale, die auf die präSMA-Gehirnregion abzielen, Hinweise auf verschiedene zeitliche Prozesse liefern. So gibt es zum Beispiel deutliche Hinweise darauf, dass die Latenz der stimulus onset-locked Signale Gedächtnisprozesse widerspiegelt (Ng et al., 2011), während die Interpretation der Amplitude umstrittener ist. In dieser Dissertation habe ich gezeigt, dass die Ergebnisse unseres Experiments eher mit den Erklärungen für die Reaktionsbereitschaft oder die Erwartung der Onset-Lock-Signalamplitude übereinstimmen (Boehm et al., 2014). Darüber hinaus weisen unsere Ergebnisse darauf hin, dass Stimulus-Offset-Locked-Signale in hohem Maße mit dem zeitlichen Entscheidungsprozess verbunden sind, was mit den Ergebnissen der kürzlich von uns besprochenen Studie (Ofir & Landau, 2022b) übereinstimmt.

List of Publications

- **Paper (Peer-reviewed)**

Baykan, C., & Shi, Z. (2022). Temporal decision making: it is all about context. *Learning & Behavior*. https://doi.org/10.3758/s13420-022-00568-8

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- **Preprint and in revision**

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