Adaptive Timing

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general introduction

Everything we do, see, hear and feel exists in time. Timing plays an important role in almost every daily activity, whether it is making coffee, having a conversation with a friend or deciding whether to break before a traffic light turns red. It may even be a determinant in life-or-death situations, for example, when a gazelle makes a well-timed deflective move to escape a hungry predator. It is therefore crucial for humans and other species to be sensitive to the timing of events. When something in the environment happens regularly, it can be highly adaptive to use this regularity to predict not only what will happen, but also when it will happen. In addition, humans are able to estimate and predict how long something lasts, in a process called interval timing. These processes are vital to staying in tune with a dynamically changing world.

Compared to other senses, the study of time perception has proven particularly elusive. Unlike auditory and visual perception, there is no dedicated sense organ for time. Temporal processing involves a distributed network of brain areas, depending on the particular task at hand (Paton & Buonomano, 2018). In addition, the sense of duration has been shown to be highly susceptible to non-temporal factors like emotion (Droit-Volet & Meck, 2007), attention (Matthews & Meck, 2016), movement (Brown, 1995) and experiences in memory (Shi, Church, & Meck, 2013). These temporal biases show that subjective time does not linearly grow with physical time: time perception does not seem to be accomplished by an isolated internal clock. Instead, humans flexibly use clues from their environment as well as previous experiences to estimate time.

Memory seems to be especially important in this regard. After all, when we try to estimate how much time has passed since we turned on the coffee machine, we need to rely on our memory of the past few minutes. In addition, our memory of an experience with the coffee machine last week enables us to predict how long it will take before our coffee is done. The interaction between time perception and memory has recently gained increasing interest in cognitive neuroscience (for reviews, see Matthews & Meck, 2016; Teki, Gu, & Meck, 2017; Van Rijn, 2016). For example, it has been suggested that neural oscillations that support working memory may also code for duration (Gu, Van Rijn, & Meck, 2015). In addition, cells in the entorhinal cortex and the hippocampus that are crucial for episodic memory have been shown to encode the timing of events (Montchal, Reagh, & Yassa, 2019; Tsao et al., 2018). It has also become increasingly clear that previous experiences in memory inform current estimates of time, resulting in predictable biases (Jazayeri & Shadlen, 2010), but also allowing expectations to guide attention to relevant events (Nobre & Van Ede, 2018).

These recent studies show that we are only just beginning to understand the ways in which our sense of time relies on memory processes. Specifically, as we will see, two important issues remain as yet unknown: first, how are time intervals represented in memory, and second, how are these temporal experiences in memory used to optimize attention and duration estimates? This thesis focusses on the interaction between time perception and memory by investigating these questions. But before turning to the empirical studies trying to answer these questions in the next chapters, I will discuss several key models that have been proposed to describe time perception, which I will refer to in later chapters. After that, I will describe what we know so far about the interactions between memory and subjective time and how previous experiences may optimize the timing of attention.

Models of time perception

Over the past few decades, several computational and neurobiological models have been proposed to account for the wide range of timing behaviors that humans exhibit. A major distinction that can be made between these models is whether they assume that time perception is achieved through a dedicated 'internal clock' (*dedicated models*) or that time can be decoded from naturally occurring neural processes that are not dedicated to timing (*intrinsic models*) (Ivry & Schlerf, 2008; Wittmann, 2013).

Dedicated models

Pacemaker-accumulator models. One of the most influential cognitive models of interval timing is the Scalar Expectancy Theory (SET) (Gibbon, 1977; Gibbon, Church, & Meck, 1984). The SET model proposes that we have a dedicated internal clock that consists of a pacemaker that outputs pulses at a regular rate and an accumulator that assembles these pulses over time. In between, the switch component makes sure that the pulses reach the accumulator after a starting signal. The output of the accumulator can be compared to a reference memory in order to make a decision about the currently perceived duration. Overall, the SET model has been successful in accounting for many behavioral interval timing findings (Van Rijn, Gu, & Meck, 2014; Wearden, 2016).

However, pacemaker-accumulator models might suffer from a 'degrees of freedom' problem: there are several parameters that can be flexibly tuned to fit behavioral data, which limits the descriptive and predictive power of the model (Van Rijn et al., 2014). In addition, although the SET model does not make any assumptions about its neurobiological implementation, researchers have made an effort to map the components and mechanisms of SET to brain mechanisms. This has proven to be a difficult task (Van Rijn et al., 2014). For example, ramping activity in the supplementary motor area (the contingent negative variation, CNV) observed during timing tasks has been linked to the accumulator component of the SET model. However, this interpretation of the CNV is hard to disentangle from alternative interpretations, such as the idea that the CNV reflects expectations or motor preparation building up over time. It might in that sense be related to time perception, but not the sought-after implementation of the accumulator (as we will also demonstrate in Chapter 5). In the same way, researchers have been unable to locate neural mechanisms corresponding to other components of the SET model (Van Rijn et al., 2014). This might not be a problem specific to SET, as it has been noted that the neural basis of most computational models is as of yet unknown (Hass & Durstewitz, 2014).

Given the strong interactions between time perception and non-temporal factors, it has recently become more and more clear that time perception should be studied in the context of other domains (Matthews & Meck, 2016). Therefore, efforts have been made to integrate dedicated timing models with other cognitive components (Taatgen, Van Rijn, & Anderson, 2007; Van Rijn et al., 2014). For example, a pacemaker-accumulator timing module based on SET has been integrated into the Adaptive Control of Thought-Rational (ACT-R) architecture (Taatgen et al., 2007). In this way, the timing model could be studied in interaction with other functions, such as memory and motor modules. The advantage of this approach is that these modules come with their own set of established mechanisms (such as a forgetting rate in the memory module), predicting behavior that otherwise needs to be accounted for by explicit manipulations of internal clock components.

Oscillator models. As an alternative to SET, the striatal beat-frequency (SBF) model offers an internal clock model that is inspired by neurobiological mechanisms (Matell & Meck, 2004). In this way, the SBF model can explain the most important behavioral findings, while also making explicit assumptions about the underlying neural mechanisms and, roughly, in what brain regions these functions are carried out (Van Rijn et al., 2014). In the SBF model, neural populations in the cortex oscillate at their own stable frequency. Salient events reset the phases of these oscillators, acting as a starting signal for timing. Since the oscillators have their own base frequency, the oscillators will slowly desynchronize after onset. In this way, multiple oscillators will form unique patterns from which the time that has passed can be inferred. Specifically, the SBF models proposes that these patterns are read out by medium spiny neurons in the striatum. This particular implementation has been inspired by neuroscientific studies showing the plausibility of the 'coincidence detection' function of the striatal medium spiny neurons (e.g., Coull, Cheng, & Meck, 2011; Matell, Meck, & Nicolelis, 2003).

Although the SET and SBF model can account for many behavioral findings, they face two problems in explaining timing in the real world. In everyday tasks, most forms of interval timing happen continuously and implicitly (Taatgen et al., 2007). Whereas complex real-world tasks require keeping track of different concurrent tasks that have their own temporal regularities, SET and SBF can only keep track of a single interval. In addition, these models require an explicit starting signal, while most timing behavior happens implicitly and without any preconceived plan to start timing.

As a potential alternative, therefore, Gu et al. (2015) introduced a way to integrate the SBF approach with oscillatory models of working memory (e.g., Burke et al., 2013; Jensen & Lisman, 1998), by proposing that the same neural oscillations might code for both working memory and interval timing. Working memory has been suggested to rely on gamma oscillations entrained within theta oscillations (Lisman, 2010; Lisman & Idiart, 1995). In this model, several items can be stored in memory through the reactivation of multiple gamma cycles within slower theta cycles. The nested oscillations that update the semantic information of working memory can also underlie the time perception of multiple items (Gu, Van Rijn, et al., 2015). In line with the SBF model, items in working memory have an associated oscillatory state that can be detected by medium spiny neurons. In contrast to the models outlined above, this working memory model does not require a starting signal. Instead, the consolidation of an item in working memory enables us to track how long ago an event was encountered. We will test this hypothesis in Chapter 2.

Intrinsic models

State-dependent network model. In contrast to internal clock models, state-dependent network or population-clock models propose that time can be inferred from naturally occurring neural dynamics that are not specifically dedicated to time (Buonomano & Karmarkar, 2002; Buonomano & Laje, 2011; Hardy & Buonomano, 2016; Karmarkar & Buonomano, 2007). When neural patterns are reproducible and unique at each time point, it is possible to read out how much time has passed from the state of the network. In this way, the time since the onset of a stimulus can be decoded from the state of the neural trajectory following the stimulus (Paton & Buonomano, 2018). Although most evidence for state-dependent network models as of yet comes from computational simulations (e.g., Karmarkar & Buonomano, 2007) and in vitro studies (e.g., Goel & Buonomano, 2014; Johnson, Goel, & Buonomano, 2010), recent studies suggest that subjective time can be decoded from the state of cortical dynamics in humans (e.g., Bueno et al., 2017).

Perceptual classification model. Similar to the population-clock models described above, Roseboom et al. (2019) proposed that time perception can be based on the neural dynamics of perceptual processing. Specifically, their model consists of an image classification network in which visual content is represented in several hierarchical layers. By adaptively tracking changes in each of the layers, the model creates a representation of how much change there is in the visual input. The model is trained to give an estimate of how much time has passed based on the amount of change. The image classification network shows similarities to the human visual processing system, which has been shown to process information in a comparably hierarchical way (e.g., Kriegeskorte, 2015). Human time perception might therefore be based on the processing dynamics in these perceptual brain networks. In this way, aspects of the perceptual classification model are similar to state-dependent network models, making the additional claim that it is not simply about network dynamics, but specifically about changes in perceptual processing networks. Overall, the model is able to naturally capture well-known effects of visual complexity and rate of change on perceived duration, that can only be modelled indirectly by dedicated internal clock theories.

Time in memory

Time perception and memory are closely intertwined. The subjective sense of time is calibrated by previous experiences in memory (for reviews see Matthews & Meck, 2016; Van Rijn, 2016). Specifically, previous experiences with stimulus features or durations influence perception in two ways: first, they systematically compress or prolong temporal *estimates*, and second, they adapt the timing of *preparation* for perception and action. As we will see, these mechanisms might make up for noise in the perceptual system and allow us to flexibly tune in to the temporal dynamics of the environment.

Memory calibrates time estimates

Stimuli in memory structurally contract or dilate subsequent subjective duration estimates. We can make a distinction in whether this happens because features other than duration in memory match with the to-be-timed stimulus (through *non-temporal adaptation* or through *non-temporal features in working memory*), because non-temporal dimensions inform the duration estimate (through a *general magnitude representation*), or because participants have been exposed to certain durations for a while (*duration adaptation* and the *temporal context effect*).

Non-temporal adaptation. When we are repeatedly exposed to a stimulus, the processing response to the stimulus tends to get weaker. Previous exposure to durations, but also to non-temporal features of a stimulus have been shown to affect its subjective duration (Matthews & Meck, 2016). For example, Johnston, Arnold, and Nishida (2006) presented sine gratings on the left or the right side of a fixation point. After an adaptation period of 15 s, participants had to compare the duration of a grating on the adapted and the unadapted side. The results showed that subjective duration of the stimulus on the adapted side was compressed. Similar results have been obtained for location and moving direction (Curran & Benton, 2012), luminance contrast (Bruno & Johnston, 2010), orientation (Zhou, Yang, Mao, & Han, 2014) and vibrotactile stimuli (Watanabe, Amemiya, Nishida, & Johnston, 2010). Whereas these results are based on low-level sensory adaptation, the 'oddball' paradigm shows that a similar principle holds when a new stimulus is presented after repeated exposure to a standard stimulus: The duration of this surprising stimulus, or oddball, is overestimated (Pariyadath & Eagleman, 2007; Tse, Intriligator, Rivest, & Cavanagh, 2004; Ulrich, Nitschke, & Rammsayer, 2006). These effects can be interpreted in the light of *predictive coding*: the brain actively predicts sensory input and prediction errors are sent back up the network (Friston, 2005). Recent experiences create expectations about the upcoming stimulus, after which repetitions are coded efficiently and mismatches create a prediction error response. Subjective duration might be highly dependent on the magnitude of this neural response to a stimulus (Matthews et al., 2015).

Non-temporal features in working memory. When a certain feature is actively maintained in working memory, time estimates of stimuli with that feature are modulated. Specifically, when a stimulus matches features in working memory, it is judged to last longer. For example, Pan and Luo (2012) presented participants with a square followed by two colored circles, with the instruction to indicate which circle lasted longer. Importantly, participants had to hold the square in memory during the temporal judgement task, because it was needed for a comparison question later in the trial. Pan and Luo showed that the estimated duration of the circle increased when its color matched the square in working memory. However, in a condition in which the color of the square did not need to be actively maintained, the duration of the matching circle was judged to be shorter, similar to the adaptation effects described above. Together, these results show that repeated exposure to a stimulus decreases its subjective duration, but the opposite effect occurs when the stimulus is task-relevant and actively maintained in working memory (Matthews & Meck, 2016).

General magnitude representation. Although time perception is often studied in isolation, strong interactions with other dimensions, such as space and number (e.g., Bonato, Zorzi, & Umiltà, 2012; Schlichting, De Jong, & Van Rijn, 2018), suggest that our subjective sense of time depends on, and is informed by other magnitudes. Indeed, it might not be coincidental that time is often expressed in spatial terms in everyday language (e.g., "it took a *long* time before he answered the phone"). It has therefore been suggested that time, space and quantity are part of a generalized magnitude system (Walsh, 2003). In A Theory Of Magnitude (ATOM), Walsh (2003) links these dimensions to a common metric for action that might be mainly located in the parietal cortex. Although many of the interactions predicted by ATOM have been demonstrated (Walsh, 2015), other evidence suggests specialized sensory systems with interactions occurring at later decisional stages (Anobile et al., 2018). In Chapter 7, we will test whether participants can flexibly report time estimates in different dimensions with equal accuracy.

Duration adaptation. Besides adaptation to non-temporal stimulus features, experience with a particular *duration* also changes subsequent time estimates. The duration adaptation effect shows that after repeated exposure to a short duration, a relatively long duration is estimated to be even longer, and after exposure to a long duration, a relatively short duration is underestimated (Heron, Roach, Hanson, McGraw, & Whitaker, 2012; Walker, Irion, & Gordon, 1981). This effect has been suggested to be caused by duration-selective *channels*, which respond selectively to a narrow range of preferred durations (Heron et al., 2012). Since the adaptation effect is modality specific (Walker et al., 1981), the channels would operate in a way that is sensory-specific and at an early stage of perceptual processing (Heron et al., 2012). The adaptation to a duration has been proposed to be useful in increasing the sensitivity to relevant temporal features of the environment (Shima, Murai, Hashimoto, & Yotsumoto, 2016).

Temporal context effect. A seemingly opposite phenomenon to the duration adaptation effect occurs when we are exposed to a *range* of intervals, instead of one repeated duration. In this case, a central tendency effect can be observed, also referred to as Vierordt's law: short intervals in the range are overestimated and long intervals are underestimated. In a particularly elegant demonstration of this effect, Jazayeri and Shadlen (2010) showed that the same interval was either under- or overestimated depending on whether it was presented in the context of a relatively short or long range of intervals. These results can be explained using a Bayesian observer model: the current noisy percept (the likelihood) is weighted with a representation of the distribution of previous intervals (the prior) to arrive at a final estimate (the posterior). Notably, the representation of the prior is not fixed: estimates are especially biased towards more recent experiences, such as the previous trial in an experiment (Dyjas, Bausenhart, & Ulrich, 2012; Taatgen & Van Rijn, 2011; Wiener, Thompson, & Coslett, 2014). These findings show that the memories that inform time estimations are flexibly adapted to the current situation. Although this process leads to a bias towards previous durations in memory, it might be an optimal strategy to compensate for the noise and uncertainty of percepts in everyday life (I will elaborate on this point in the General Discussion chapter of this thesis). In line with this reasoning, a larger central tendency has been demonstrated for more uncertain intervals (Jazayeri & Shadlen, 2010) and for participants with less temporal expertise (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Hallez, Damsma, Rhodes, Van Rijn, & Droit-Volet, 2019). Although the Bayesian computational models above implicitly assume that the effect of previous experiences only happens *after* perception, temporal context might already actively affect perception. Recently, for example, it was shown that the firing rate of neurons in the dorsomedial frontal cortex of monkeys adapt to the temporal context during perception, and that curved neural dynamics might underlie Bayesian biases in time estimates (Sohn, Narain, Meirhaeghe, & Jazayeri, 2019). In Chapter 5, we will investigate the temporal locus of the context effect by looking at neural signatures during perception.

Memory calibrates preparation

Events in the environment unfold dynamically, and the timing of a series of events is often predictable. This temporal structure allows for proactive preparation. Indeed, the view of the brain as a predictive organ has recently gained prominence (Friston, 2005; Nobre & Van Ede, 2018). Abundant behavioral evidence shows that temporal expectations can be used to optimize the timing of action and attention (Nobre & Van Ede, 2018). These temporal expectations can be quickly adapted to current needs based on experience with the task at hand. That is, humans are able to pick up and memorize temporal regularities in the environment over time and actively predict upcoming stimuli. Here, I will discuss three common types of temporal structures: associations, foreperiods and rhythms.

Associations. When stimuli follow each other with a predictable time interval in between, *temporal associations* can be formed. An example of this is the temporal cueing task. In this temporal version of Posner's spatial orientation task (Posner, 1980), symbolic cues predict the interval after which a target is most likely presented. A valid cue speeds up reaction times and increases the accuracy of responses to the target, especially for short intervals (Correa, 2012; Griffin, Miniussi, & Nobre, 2001). The performance benefit is smaller for long intervals, because expectations are updated once the short interval has passed (Nobre & Van Ede, 2018; Nobre, 2001). Importantly, associations between a specific stimulus and the timing of events can be learned and memorized over time, and can thereby improve target detection at learned intervals (Cravo, Rohenkohl, Santos, & Nobre, 2017; Olson & Chun, 2001). For example, Cravo et al. (2017) presented images of scenes that were predictive of the time interval after which a target appeared (either short or long). After an initial learning phase, they showed that reaction times and sensitivity were enhanced when the target occurred after the learned, compared to an unlearned, interval. In addition, the CNV, the slow EEG deflection mentioned above, was more negative when a short interval was expected. We will demonstrate a similar effect in an interval reproduction task in Chapter 5.

Foreperiods. Even when there is no explicit cue predicting the timing of an upcoming target, the onset of the target could be inferred from previous experiences. The effects of temporal preparation have been extensively studied by manipulating the foreperiod, the interval between a warning stimulus and target stimulus. Humans are able to form temporal expectations based on the specific foreperiod distribution, which influences their response time to the target (Los, Kruijne, & Meeter, 2014). In addition, detection responses become faster when the temporal variability between events decreases (Niemi & Näätänen, 1981). Besides improved motor responses, perceptual discrimination is more sensitive when the onset of a stimulus can be predicted (e.g., Lasley & Cohn, 1981; Rolke & Hofmann, 2007; Westheimer & Ley, 1996). These studies show that attention can be optimally directed in time based on temporal expectations. The temporal preparation effects have often been interpreted using the *hazard rate*: the probability that a stimulus will occur at a particular point in time given that it has not yet occurred (Luce, 1986; Nobre, Correa, & Coull, 2007), although this view may lack a cognitive basis (Los, 2013). Similar to the temporal context effect outlined above, temporal preparation depends on the foreperiod in the previous trial and previously learned distributions, showing that expectations are flexibly learned and adapted (Los et al., 2014; Mattiesing, Kruijne, Meeter, & Los, 2017).

Rhythms. Rhythms form a special case of temporal structure, and they are a fundamental basis of speech and music, but also movements such as walking and dancing. It has been shown that simple isochronous rhythms can facilitate perception in, for example, pitch judgment (Jones, Moynihan, MacKenzie, & Puente, 2002), near-threshold auditory gap detection (Henry & Obleser, 2012), and visual target detection (Kösem & van Wassenhove, 2012; Mathewson, Fabiani, Gratton, Beck, & Lleras, 2010). These improvements are often dependent on the phase of the rhythms, so that stimuli presented in phase with the isochronous stimulus are processed more efficiently: Attention waxes and wanes with the rhythm. This rhythmic entrainment of attention has been formalized in the Dynamic Attending Theory (DAT) (Jones, 1976; Large & Jones, 1999). DAT not only proposes that neural mechanisms of attention synchronize to external rhythms, but that this produces active predictions of the timing of upcoming events. Attentional entrainment could be implemented by low-frequency neural oscillations in the cortex that selectively enhance or suppress input (Henry & Herrmann, 2014; Schroeder & Lakatos, 2009). Although most behavioral and modelling work has focused on isochronous rhythms that require only a single oscillator, it has to be noted that natural rhythms are often more complex (Henry & Herrmann, 2014). As we will show in Chapter 3, the perception of music might rely on a hierarchical representation of temporal structures at multiple time scales: a faster rhythm at the beat level and a slower oscillator at the measure level.

Thesis outline

The studies outlined above suggest that our timing is remarkably adaptive: Duration estimation and anticipation are calibrated by learned temporal structures in order to synchronize behavior with the environment. However, several key questions remain unknown. First, it is as of yet unclear how time is represented in memory. Although it has been suggested that interval timing could rely on mechanisms that code for working memory, this hypothesis has so far remained largely untested. In addition, it remains an open question whether duration is represented as a separate dimension, or whether it is flexibly transformed into other dimensions, such as space. The second set of questions concerns the way learned temporal structures are used to calibrate attention and duration estimates. It is still unknown to what extent attention is automatically guided by temporal structure in the environment: is this the case even when we are focused on another task and when the structure is not useful for the task at hand? And, do our experiences with temporal context actively shape our perception of time? These are the questions that will be explored in the next chapters of this thesis.

In Chapter 2 we investigated a key prediction of the time perception model of Gu et al. (2015) outlined above: does the moment of memory consolidation act as the starting gun of interval timing? To this end, participants performed an attentional blink (AB) task in which target letters were embedded in a rapid stream of numbers. Participants were instructed to not only report which letters they had seen, but also *when* a letter was presented. In the AB task, the second target is often not reported when it follows quickly (~200–500 ms) after the first target. When the second target *is* reported, however, its memory consolidation has been shown to be delayed (Chennu, Craston, Wyble, & Bowman, 2009; Martens, Munneke, Smid, & Johnson, 2006; Sessa, Luria, Verleger, & Dell'Acqua, 2007; Vogel & Luck, 2002). In these studies, the P3 peak in the EEG signal was used as a measure of working memory consolidation (Donchin, 1981; Kok, 2001; Vogel, Luck, & Shapiro, 1998). Based on the model, we formulated two predictions: 1) we expected that the temporal estimates of the second target would be relatively late when it appeared shortly after the first target, and 2) we expected that the latency of the P3 peak would be predictive of the temporal estimates of the target. The results, however, showed that temporal estimates were not later when the second target followed quickly after the first and we found no evidence for a relationship between P3 latency and temporal estimates. These findings suggest that that there is no direct link between consolidation and the onset of timing of sub-second intervals.

Chapter 3 focusses on temporal expectations in musical rhythms. As outlined above, attention can be entrained to simple isochronous rhythms. However, theoretical models of beat perception suggest that humans are able to create a hierarchical representation of the rhythms they hear, or *meter*. These representations drive expectations about what will happen next, such that some beats are expected more than others. However, it is unclear to what extent these models indeed accurately describe the way humans perceive rhythms, especially when attention is focused on another task. In addition, it is unclear to what extent expertise is necessary to perceive meter. In our study, participants performed a visual target detection task while they were presented with a repeating standard rock drum rhythm. Now and then, one of the sounds of the rhythm was omitted. We measured pupil dilation in response to these omissions as a measure of surprise. We found that more salient omissions elicited a higher pupillary response than omissions at lower metrical levels. This result shows that temporal expectations are driven by metrical representations, even while attending to another task. The response was not affected by musical expertise. Overall, these results suggest rhythms induce hierarchical expectations over time, regardless of attention and expertise.

In Chapter 4, we tested whether there is an attentional bias towards temporal regularities. As discussed before, temporal regularities in the environment can be used to optimize perception and action. It has therefore been suggested that stimuli that contain a form of regularity are prioritized by the attentional system.

For example, Zhao, Al-Aidroos, and Turk-Browne (2013) showed that attention was spontaneously biased to stimuli that appeared in a regular order compared to a random order. In the study presented in Chapter 4, we tested whether this bias generalizes from order to metrical regular stimuli. We presented participants with several stimulus streams, of which one contained a temporal regularity. To test whether these particular stimuli attracted attention, the streams were interleaved with search tasks. If attention was biased towards the regularities, we expected that the response to target in the search task would be faster if it had the same features (i.e., location or color) as the regular stream. However, across six experiments, we found no evidence for such a bias. Thus, in contrast to order, attention might not be spontaneously biased towards metrical temporal regularities. We argue that, in contrast to order regularities, entrainment to metrical regularities might come at the cost of decreased sustained attention, and could therefore be suboptimal when there is no benefit for the task at hand.

In Chapter 5, we investigated the effect of temporal context on interval perception. As described above, time estimates are biased towards previous intervals in memory (i.e., the context), so that relatively short intervals are overestimated and long intervals are underestimated. Computational models often attribute this bias to the weighting of the interval with a representation of the prior after the current duration has been perceived. Alternatively, however, context might act directly on perception. To investigate this, participants performed an interval reproduction task while we measured EEG. In different blocks, the presented intervals were either relatively short or long, with one interval overlapping. As expected, the participants showed a bias towards the subjective mean of the range, as well as towards the most recent interval. The context affected EEG signatures associated with time perception during the perception phase. Specifically, longer recent intervals decreased the CNV and P2, and increased the power of beta oscillations. Multivariate pattern analysis showed that context can be decoded from transient neural activity right after the start of the perception phase. Together, these results suggest that previous intervals in memory act directly on perception. Previous experiences create temporal expectations that can flexibly scale neural activity.

In Chapter 6, we investigated whether the effect of context generalizes from simple laboratory timing experiments to more real-world stimuli. Participants were presented with videos of an animate figure performing every-day actions like drinking and mixing. They were asked to reproduce the duration of the action. So, in contrast to the usual laboratory experiments consisting of simple stimuli, the on- and offset were not clearly defined, but had to be determined by the participant. We found that the reproductions showed a clear pull towards the overall mean and the previous subjective duration, showing that they were influenced by the context. In addition, we found that the standard deviation increased linearly with the reproduced duration, confirming the so-called scalar property. Overall, these results provide a first step into taking timing studies into more realistic settings, and suggest that established effects of time perception might accurately describe the way people estimate the duration of actions in everyday life.

In Chapter 7, we tested the effect of different time estimation methods on accuracy and precision. One of the most common ways of probing subjective time in experiments is by letting the participant reproduce a previously perceived interval by pressing a key. Alternatively, however, the estimate can be expressed spatially (e.g., on a timeline) or verbally (e.g., providing a number). As mentioned above, time, space and magnitude might be represented in a common magnitude system, predicting that there should be little cost in expressing time in spatial or verbal terms. In Chapter 7, we compared the results of these methods in two interval estimation experiments. We found that verbal estimates were more accurate and precise than line estimates and motor reproductions, but they were biased towards familiar whole second units. The comparison of motor and spatial estimates was less consistent: in Experiment 1, motor reproductions were more precise, but not more accurate than timeline estimates while in Experiment 2, motor reproductions were more accurate, but not more precise. Together, these results suggest that time estimates can be quite flexibly transformed into space. In addition, they show that each estimation method comes with its own advantages, and that the choice of estimation method depends on choices in the experimental design.

Finally, in Chapter 8, I will summarize the empirical findings outlined in this thesis and discuss their implications for theories of time perception. Overall, I will show that humans exhibit a great flexibility in the way they estimate durations and predict upcoming salient events, and that these subjective time estimates are based on contextual representations in memory. I will argue that it is unlikely that there is one central dedicated clock in the brain that distributes timing information to other areas. Instead, timing might be based on flexible dynamics in different neural populations which do not exclusively represent duration.

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neural markers of memory consolidation do not predict temporal estimates of encoded items

Abstract

In contrast to the paradigms used in most laboratory experiments on interval timing, everyday tasks often involve tracking multiple, concurrent intervals without an explicit starting signal. As these characteristics are problematic for most existing clock-based models of interval timing, here we explore an alternative notion that suggests that time perception and working memory encoding might be closely connected. In this integrative model, the consolidation of a new item in working memory initiates cortical oscillations that also signal the onset of a time interval. The objective of this study was to test whether memory consolidation indeed acts as the starting signal of interval timing. Participants performed an attentional blink task in which they not only reported the targets, but also the estimated target onsets, allowing us to calculate estimated lag. In the attentional blink task, the second target (T2) in a rapid serial visual presentation is often not reported when it follows quickly after the first target (T1). However, if this fast T2 is reported, memory consolidation of T2 is presumably delayed. Consequently, if memory consolidation determines interval onset, we would expect a later estimated onset when consolidation is delayed. Furthermore, as the P3 ERP component is assumed to reflect memory consolidation, we expect that the estimated onsets and subjective lag are functions of the P3 latencies. The behavioral data show that the presumed delay in memory consolidation did not lead to later estimated onsets. In addition, the EEG results suggest that there was no relationship between P3 latency and subjective lag or estimated onset. Overall, our results suggest that there is no direct link between the encoding of items in working memory and sub-second interval timing of these items in the attentional blink task.

Introduction

Timing is an indispensable part of our system of cognitive functions. The temporal precision with which sequences of actions are undertaken is crucial in reaching our goals in complex tasks. Often, however, the tasks do not require time perception explicitly. One situation that illustrates the automaticity with which we use timing is contactless payments with bank- or credit cards or electronic devices. We quickly learn how long we need to hold our card or devices next to the scanner for a successful transaction. Our experience with this method of payment teaches us how long this interval is supposed to last and, importantly, makes us able to set off alarm bells when the transaction is taking too long, indicating that something is wrong with either our payment or the device.

Humans can distinguish remarkably well between time intervals of different lengths. Several theories have emerged that model how we keep track of time in the seconds to minutes range. One of the most influential cognitive models of interval timing is the Scalar Timing Theory (SST; Gibbon, 1977; Gibbon et al., 1984). STT proposes that timing behavior in humans and animals is controlled by three processes: the clock, memory, and decision process. The clock process consists of a pacemaker that outputs pulses at a regular rate and an accumulator that assembles these pulses over time. In between, there is a gate, or switch, component that allows the pulses to reach the accumulator when a salient starting signal is provided. The accumulated amount of pulses can be stored in memory and decisions about durations can be made by comparing the output of the accumulator with other interval durations stored in memory. Although the STT model does not make any assumptions about its neurobiological implementation, it has proven difficult to map its processes to specific brain mechanisms (Van Rijn et al., 2014).

Whereas STT focuses on a description of interval timing at a functional level, the striatal beat-frequency (SBF) model offers a model of the internal clock that is inspired by neurobiological mechanisms (Matell & Meck, 2004). In this way, an extended version of the SBF model (Van Rijn et al., 2014) can explain the most important behavioral findings, while also making explicit assumptions about the neural mechanisms that implement the timing behavior and, roughly, in what brain regions these functions are carried out. In the SBF model, groups of neurons in the cortex act as oscillators that have their own stable oscillating frequency. Through the influence of dopaminergic input, salient events can act as the starting signal by resetting the phases of these oscillators. Because the oscillators have their own frequency, the oscillators will drift out of phase after onset and this will result in predictable patterns of desynchronization corresponding to the time that has passed. The SBF model proposes that these patterns are then detected by medium spiny neurons in the striatum (Buhusi & Meck, 2005). In this way, for example, a specific group of striatal neurons always becomes active 2 seconds after the phase reset, while another group activates generally after 3 seconds.

Independent of the actual implementation, however, these models of interval timing face two problems in explaining timing in the real world, in which most forms of interval timing happen continuously and implicitly (Taatgen et al., 2007). First, they can only time a single interval and predict that timing multiple events is difficult (Van Rijn & Taatgen, 2008), whereas complex real-world tasks require keeping track of several simultaneous intervals. That is, humans are often faced with keeping track of different concurrent tasks that have their own implicit temporal regularities. Second, these internal clock models require an explicit starting signal. The onset and offset of an interval need to be consciously perceived in order to observe the passage of time, requiring attention to be directed to the events that mark the interval. For example, during the contactless payment described earlier, the customer is not anticipating a timing task when initiating the payment, as typically the payment will proceed before attention was drawn to the lack of confirmation. Nevertheless, as humans can detect that the transition takes too long, elapsed time must be actively monitored as it progresses and be compared to interval lengths stored in memory to notice that at some point one knows for sure the payment has not succeeded. We therefore have to keep track of how much time has elapsed since the introduction of the card until the point we hear a beep indicating the confirmation, while at the same time, for example, registering the temporal patterns in the social talk that is exchanged with the cashier.

Thus, whereas real-world timing often involves continuous, automatic tracking of multiple intervals, most traditional models of time perception propose a dedicated single clock that requires an explicit starting signal. As a potential solution to this problem, Gu et al. (2015) proposed that interval timing and working memory might be based on the same underlying oscillatory dynamics. It has been suggested that working memory consists of gamma oscillations entrained within theta oscillations (Lisman, 2010; Lisman & Idiart, 1995). In this oscillatory model of working memory, multiple items can be stored in memory through the reactivation of multiple gamma cycles within the slower theta cycles. Gu et al. (2015) proposed that, through multiplexing, this system of updating the semantic information of working memory can also code for time. In this way, each item in working memory has an associated oscillatory state that can be detected by medium spiny neurons, as proposed by the SBF. In contrast to STT-like models, including SBF, this integrative model does not require an explicit starting signal. Instead, the consolidation of a memory trace in and of itself makes it possible to estimate the time that has passed since an event was encountered. In addition, the nested oscillations in the working memory model allow temporal information of multiple items to stay active concurrently.

The integrative theory of time perception predicts that there is a tight link between the consolidation and maintenance of items in working memory and time perception. Indeed, there is cumulative evidence that working memory representations and working memory load influence subjective time perception (see Gu et al., 2015, and Matthews & Meck, 2016, for extensive reviews of the relation between memory and timing). For example, visual stimuli that match the features of active working memory representations are judged to be longer (Pan & Luo, 2012). One specific prediction of the integrative theory of time perception, however, has as of yet remained unexplored: temporal estimations should be based on the moment when an item is encoded in working memory. Here, we will test this hypothesis using the attentional blink (AB) paradigm, in which the temporal aspects of memory consolidation are well recorded and traceable through electrophysiological markers.

Participants in an AB study are shown a rapid serial visual presentation (RSVP), a fast stream of stimuli in the same location on a screen. Within this stream of stimuli, one or two targets are embedded. The task of the participant is to remember these targets and report them after each trial. The well-documented AB phenomenon arises when the second target (T2) is not correctly reported when it is presented in a period of ~200 to 500 milliseconds after the first target (T1) (Raymond, Shapiro, & Arnell, 1992; Vogel & Luck, 2002). This effect has been ascribed to a two-stage process, in which after an initial detection and identification stage, targets have to be consolidated in a memory system with limited, serial encoding capacity in order to create a stable representation that is available for report (e.g., Akyürek, Kappelmann, Volkert, & Van Rijn, 2017; Chun & Potter, 1995; Jolicœur & Dell'Acqua, 1998). Therefore, while T1 is consolidated, a subsequent target (T2) cannot be processed in working memory, thereby causing an AB.

In order to study the processing of targets in the AB task, the P3 component of the averaged event related potential (ERP) has been used as a measure of the latency of memory consolidation (Kranczioch, Debener, & Engel, 2003; Vogel & Luck, 2002). The P3 is sometimes referred to as the P300, because its onset generally occurs ~300 ms after the presentation of a salient target, although the range depends on factors such as modality and task conditions (Polich, 2007). It has been shown that targets presented within the window of the AB elicited a P3 when they were reported, but not when the targets were blinked (Vogel et al., 1998). In contrast, other ERPs related to early visual processing are still present when the second target is blinked. Therefore, the P3 component has been associated with memory consolidation (Akyürek, Leszczyński, & Schubö, 2010; Donchin, 1981; Kok, 2001; Vogel et al., 1998).

Interestingly, second targets that *are* correctly identified despite being presented within the AB window do elicit a P3, but this P3 exhibits an increased latency and variability. For example, Vogel and Luck (2002) reported the P3 of T2 during the AB window to be ~100 ms later than the P3 of a T2 that was presented outside the AB window, suggesting that this reflects delayed memory consolidation (see also Martens et al., 2006; Sessa et al., 2007). In addition, using single-trial ERP analyses, Chennu et al. (2009) reported that the P3 associated with T2 presented in the AB window were not only delayed, but also showed more temporal variation compared to trials with a longer T2 lag. Thus, these studies show that the timing of working memory consolidation is delayed and more variable when the second target follows quickly after the first.

In the current study, we will utilize these phenomena associated with T2 encoding to test whether memory consolidation determines the onset of temporal estimation. Specifically, we will investigate if the perceived time interval between T1 and T2 in an AB task will indeed be longer if the P3 component for T2 is delayed. Two AB experiments were conducted to explore this question. Crucially, in both experiments, participants not only report target identity, but also the perceived temporal positions of the targets. In Experiment 1, we will test the relation between encoding and time perception behaviorally, by comparing the perceived duration between targets in trials in which T2 is presented within the AB window with trials in which T2 is presented outside this window. We expect that the temporal estimations of the second targets that are presented in the AB window will be delayed compared to the estimations for targets outside of this window. As a result, we also expect that the estimated lag between T1 and T2 will be larger within the AB window. By measuring EEG in Experiment 2, we will compare the latency of the P3, as an electrophysiological index of memory consolidation, with temporal estimations. We hypothesize that an increased P3 latency associated with a target will result in a later temporal estimation for that target.

Experiment 1

Methods

Subjects. Forty-five participants were recruited for the first experiment (25 female, mean age: 20.7, *SD* = 2.1). One participant was excluded from the analysis due to a technical malfunction. All participants were recruited from the University of Groningen Psychology Participant Pool and received partial course credits for participating. The study was approved by the Psychology Ethical Committee of the University of Groningen (15163-NE), and participants gave informed consent before testing.

Stimuli and apparatus. Each trial consisted of an RSVP followed by a response screen, in which participants indicated the identity and temporal location of the targets in the RSVP. The stimuli and response screen were presented on a 19-inch CRT monitor with a resolution of 800x600 px and a refresh rate of 100 Hz, using Psychophysics toolbox running on Matlab 2015b under Windows 7. The alphanumeric characters in the RSVP were presented in Courier font in white on a black background with an average size of 0.8° visual angle. Subjects estimated the temporal position of the first target by clicking on a line presented on the left half of the screen and of the second target on a line on the right half of the screen. Both lines were presented simultaneously in white and spanned 320 pixels each (Figure 2.1). The horizontal position of the subjects' mouse clicks on the lines were transformed into relative temporal position within the stream of characters. Responses to the identity of the targets were recorded with a computer keyboard.

Procedure. Participants were instructed that they would see trials consisting of one or two letters within a fast stream of numbers and that their task was to report which letters they had seen and when they had seen them. Each trial consisted of an RSVP preceded by a 1000 ms fixation cross, and followed by a response screen (Figure 2.1). The RSVP consisted of 21 characters, presented 100 ms each. T1 and T2 were drawn from capital letters from the alphabet (A, B, C, D, E, F, H, J, K, P, R, T, U, V), the distractors were drawn from the digits 1 to 9.

A total of 300 trials was presented, divided into 6 equal size blocks. In addition, 10 practice trials were presented at the start of the experiment. In 3% of the trials no target was presented, in 16% of the trials only one target was presented and in

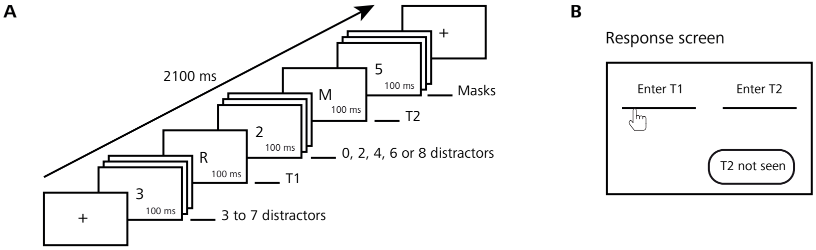

Figure 2.1. Overview of a trial in Experiment 1. A trial consisted of an RSVP with 0, 1 or 2 target letters in a stream of distractor digits (Figure A). A fixation cross was presented before and after the trial. At the end of the trial, participants saw a response screen in which they reported the estimated onset of the two targets on a line representing the trial duration (Figure B). In addition, they reported the target identity.

81% of the trials two targets were presented. T1 was always presented as the 4th, 5th, 6th, 7th or 8th character in the stream. T2 was presented lagging 1, 3, 5, 7 or 9 positions behind T1. Each combination of T1 position and T2 lag was presented equally often.

After the RSVP, a response screen was shown (Figure 2.1B). First, participants indicated the temporal positions of the targets relative to the entire stream. They did so by clicking on a line which length represented the duration of the RSVP. Second, responses were made pertaining to the identity of T1 and T2. Subjects were instructed to click the "Second target not seen" button if they had not seen T2. The experiment script is available at: https://osf.io/54xuj/.

Analysis. To analyze T2 accuracy and the temporal estimations, we fitted linear mixed models (LMMs) using the *lme4* package in R (Bates, Mächler, Bolker, & Walker, 2015). We performed model comparisons using likelihood ratio tests to evaluate whether a fixed factor improved the model fit. In these tests, subject was always included as a random intercept term. Only fixed factors that improved the model fit were included in the final model. Next, we gradually increased the random effect structure of this model by adding random slopes for the significant fixed factors and comparing the more complex model with the simpler model using a likelihood ratio test. In the case of multiple potential random slopes, we first added the random slope that improved the model fit most, at every step. To this end, we determined which random slope led to the model with the lowest AIC. A random slope term was only included if it improved the model significantly and the statistics of the fixed factors of the best model are reported here.

To quantify the evidence in favor of the null hypothesis compared to the alternative hypothesis we calculated Bayes factors. For the binomial models fitting the accuracy data, we approximated the Bayes factor using the BIC values of H_0 and H_1, as described in Wagenmakers (2007). For the temporal estimation models, Bayes factors were calculated using the *lmBF* function from the *BayesFactor* package in R (Morey, Rouder, & Jamil, 2014). We will denote the evidence for the null hypothesis (H_0) over the alternative hypothesis (H_1) as BF_{01}.

Results

Attentional blink. The mean accuracy for T1 and for T2 given correct report of T1 is shown in Figure 2.2A. A binomial linear mixed model was estimated with accuracy of T2 as the dependent variable, lag as a categorical fixed factor and subject as a random factor. The inclusion of lag improved the model significantly ($\chi^2 = 522.40$, $p < .001$, $BF_{01} < 0.01$). A post-hoc Tukey's HSD test showed that T2 accuracy was lower at lag 3 than at all other lags (*p*s < .001), indicating that an attentional blink occurred (see Table S1 for full Tukey's HSD test results). Also, T2

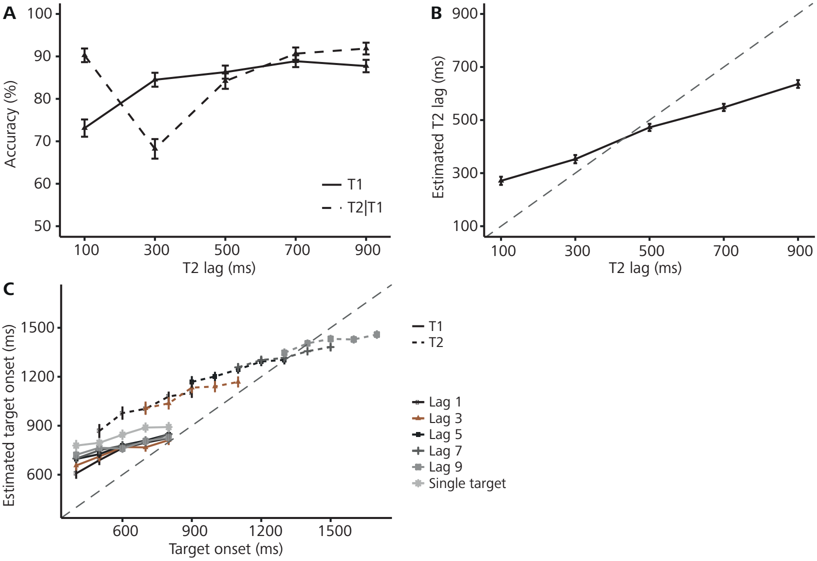

Figure 2.2. Behavioral results of Experiment 1. Figure A shows the average accuracy of T1 and T2|T1 per presented T2 lag, demonstrating that there is an attentional blink at lag 3 and lag-1 sparing. Figure B shows the average estimated lag as a function of the presented lag. The dashed line represents veridical estimation. Figure C presents the average estimated target onset as a function of target onset, relative to trial onset. Error bars represent the within-subject CIs.

performance at lag 1 was significantly better than at lag 3 ($p < .001$), indicating lag-1 sparing (Potter, Banks, Muckenhoupt, & Chun, 1998).

Temporal estimations. We calculated the estimated T2 lag as the difference between the estimated T1 position and the estimated T2 position. The average estimated T2 lag for each presented T2 lag is displayed in Figure 2.2B. A linear mixed model was fitted with estimated lag as the dependent variable and the centered presented lag as a continuous fixed factor. Subject was included as a random intercept term and lag as a random slope term. The model revealed an unstandardized coefficient of presented lag of $\beta = 0.45$ ($t = 13.80$, $p < .001$, $BF_{01} < 0.01$), showing that lag estimation increased linearly with presented lag. As can be seen in Figure 2.2B, responses to relatively short intervals tended to be overestimated and responses to relatively long intervals tended to be underestimated. To test if there was a significant pull towards the (subjective) mean, a linear mixed model was estimated with estimation bias (the difference between the presented lag and the estimated lag) as the dependent variable, presented lag as a continuous fixed factor, subject as a random intercept term and lag as a random slope term. Whereas a coefficient of 0 would indicate perfect estimation, the model yielded a coefficient of $\beta = -0.55$ ($t = -16.88$, $p < .001$, $BF_{01} < 0.01$). Post-hoc, we tested the possibility that the response format could lead to compressed lag estimations when T1 occurred later in the stream. To this end, we added T1 position to the model predicting estimated lag, but found that this did not improve the model fit ($\chi^2 < 0.01$, $p = .973$, $BF_{01} = 40.99$). This finding indicates that lag estimations did not depend on when the targets appeared in the stream.

Thus, estimated lag increased linearly with presented lag, but the estimations showed a significant pull towards the (subjective) mean. To test if lag estimations increased when T2 was presented within the window of the AB, we added the dichotomous factor “within AB window” to the model predicting estimated lag. The results showed that lag estimates for lag 3 were not longer than lag estimates outside the AB window. Instead, a trend in the opposite direction was observed ($\beta = -0.167$, $t = -1.94$, $p = .052$, $BF_{01} = 6.61$).

In addition, we hypothesized that when T2 was presented within the window of the AB (i.e., lag 3), the delay in memory consolidation would lead to later temporal estimations of T2. Figure 2.2C shows the temporal estimates of T2 for each T2 position and lag. If temporal estimates would be delayed in lag 3, we expected a relatively high intercept for the line corresponding to lag 3 compared to the other lags in this figure. To test whether T2 estimates were indeed delayed at lag 3, an LMM was estimated with temporal estimation of T2 as the dependent variable, actual temporal position of T2 as a continuous fixed factor, subject as a random factor and the random slope of temporal position of T2. Adding lag to the model as a categorical fixed factor yielded a significant improvement ($\chi^2 = 61.47$, $p < .001$, $BF_{01} < 0.01$). However, the model showed that T2 estimates at lag 3 were *earlier* than at lag 5 ($\beta = -0.75$, $t = -7.15$, $p < .001$), lag 7 ($\beta = -0.80$, $t = -6.30$, $p < .001$), and lag 9 ($\beta = -0.96$, $t = -6.14$, $p < .001$).

Figure 2.2C also shows the temporal estimates for T1 for each T1 position and lag. An LMM was estimated with temporal estimation of T1 as the dependent variable, actual temporal position as a continuous fixed factor and lag as a categorical fixed factor, subject as a random intercept and lag as a random slope term. Again, a pull towards the mean was demonstrated by the unstandardized estimate of the fixed factor ($\beta = 0.37$, $t = 22.02$, $p < .001$, $BF_{01} < 0.01$). Including lag in the model increased its descriptive value ($\chi^2 = 133.50$, $p < .001$, $BF_{01} < 0.01$), showing that the temporal estimation of T1 was also affected by if and when T2 was presented. A post-hoc Tukey's HSD comparison of the T2 lag conditions revealed that T1 estimations in single target trials were later than in two target trials (ps < .001) (see Table S2 for an overview of the test results). To further investigate the effect of T2 on T1 estimations, we post-hoc estimated an LMM predicting T1 estimation in single target and lag 3 trials (see also Figure S1). We found that T1 estimations were earlier when a second target was reported compared to when only one target was reported ($\beta = -0.86$, $t = -5.70$, $p < .001$, $BF_{01} < 0.01$), regardless of whether this T2 was reported correctly or not ($\chi^2 = 0.06$, $p = .799$, $BF_{01} = 2.97$) or whether it was a single target trial or a lag 3 trial ($\chi^2 = 2.43$, $p = .119$, $BF_{01} = 6.45$). These findings indicate that merely reporting two targets led to earlier temporal T1 estimates. All analysis scripts and data are available at: https://osf.io/54xuj/.

Discussion

In Experiment 1, we aimed to test whether time estimations of T2 are delayed if memory consolidation is delayed. We found a lower accuracy for T2 at lag 3 compared to longer lags, indicating that an AB was present. In line with previous studies, we therefore assume that a delay was induced in the latency of memory consolidation of T2 in the lag 3 condition, compared to lags outside the AB window (Chennu et al., 2009; Vogel & Luck, 2002).

We demonstrated that temporal estimations of T2 lag increased with presented T2 lag, but also showed a linear pattern of underestimations of the longer lags and overestimation of the shorter lags. This pull towards the mean effect is typically observed in experiments in which intervals have to be reproduced in a specific temporal context (Grondin, 2001; Jazayeri & Shadlen, 2010). In contrast to our hypothesis, temporal estimations of lag and T2 in the lag 3 trials were not later than temporal estimations in the other lag conditions: T2 was estimated to have occurred relatively early when it was presented within the AB window compared to later windows. Thus, whereas memory consolidation might have been delayed in lag 3 trials, this did not lead to a delay in temporal estimation.

In summary, the results do not support the hypothesized role of memory consolidation as the index of timing. Importantly, however, the current behavioral experiment can only give us indirect evidence about the link between memory consolidation and temporal estimation. Although we assume that memory consolidation of T2 is delayed in lag 3 trials, this assumption cannot be verified on the basis of purely behavioral data. In addition, the current experimental setup does not allow for taking inter-trial variation in memory consolidation - which could explain inter-trial variation in temporal estimates - into account. In Experiment 2, we will address these issues by measuring EEG during the AB task.

Experiment 2

An EEG study was conducted to further investigate if the latency of memory consolidation influences time perception. It has been suggested that the P3 component of the ERP is a neural correlate of memory consolidation (Donchin, 1981; Vogel et al., 1998; Kok, 2001). In Experiment 2, we will therefore use P3 latency as an index of delay in memory consolidation.

We investigated the relationship between P3 latency and temporal estimations in two ways. First, we compared the P3 latencies of relatively "early" and "late" estimations by creating a median split based on the temporal estimations of correctly identified T2s in the lag 3 condition. Second, using single-trial ERP analysis, we assessed whether there is a relation between inter-trial variation in P3 latency and temporal estimations. We expected that 1) the P3 for T2 will exhibit an increased delay and variability in lag 3 trials compared to trials in which the lag is longer, and 2) inter-trial variation latency in the P3 can account for variation in the temporal estimations. Specifically, we expected that in trials where a T2-elicited P3 was relatively early, the subjective estimation of T2 was also relatively early.

Methods

Subjects. Thirty subjects participated in Experiment 2 (21 female, mean age: 22.2, *SD* = 2.4). Nine participants were recruited from the University of Groningen Psychology Participant Pool and received partial course credits for participating, 21 participants were recruited via social media and were rewarded 15 euro. The study was approved by the Psychology Ethical Committee of the University of Groningen

(15163-NE), and participants gave written informed consent before testing.

Stimuli and apparatus. The same setup of stimuli presentation was used as in Experiment 1.

Procedure. A procedure similar to Experiment 1 was employed. However, following Chennu et al. (2009), the rapid serial stream of stimuli consisted of 35 characters, presented 100 ms each. In total, 312 trials were presented, divided into 6 equal size blocks. T1 was preceded by 4 to 16 characters in the stream. T2 was presented in 75% of the trials, lagging 1, 3 or 8 positions behind T1. Each combination of T1 position and T2 lag was presented equally often. Additionally, participants received feedback on the accuracy of target identity and their temporal estimations in the 10 practice trials preceding the experiment. The experiment script is available at: https://osf.io/54xuj/.

EEG recording. EEG was recorded using a WaveGuard EEG cap electrode cap (eemagine Medical Imaging Solutions GmbH, Berlin, Germany) and a TMSi amplifier (Oldenzaal, The Netherlands). Impedance was reduced to less than 15 KΩ. Electrical signals were measured at 1000 Hz from 23 electrodes placed at the following locations in the international 10/20 system: Fp1, Fp2, Fz, F3, F4, F7, F8, FCz, FC1, FC2, Cz, C3, C4, T7, T8, Pz, P3, P4, P7, P8, Oz, O1, O2. Horizontal eye movement was measured with two electrodes places by the participants' canthi, vertical movement was measured with two electrodes above and below the right eye.

EEG pre-processing. Raw EEG data was preprocessed and analyzed with EEGLAB 13.5.4b, ERPLAB 5.0.0.0, custom Matlab scripts and R. A bandpass filter was applied to the raw data with a 25 Hz high cut-off and 0.1 Hz low cut-off frequency. The EEG data was re-referenced to the average of the left and right mastoids. Independent component analysis was performed on each recording. After inspection of scalp topography, components associated with ocular movement were removed and remaining components were back-projected (Hoffman & Falkenstein, 2008). Epochs were created for each presented T1 starting 500 ms before the target was presented and ending 2500 ms after the target appeared. Baseline correction was applied using the 200 ms period before the target as the baseline period. Automatic artifact rejection was applied to epochs containing samples that exceeded the threshold of 150 μV. Following, for example, Chennu et al. (2009), Sessa et al. (2007) and Martens et al. (2006), all analyses were based on the EEG signal at the Pz electrode.

P3 latency estimation.

Average. A grand average ERP was calculated for trials in which T1 and T2 were reported correctly. To test whether the delay in memory consolidation was different between lags, we estimated P3 latencies per lag for each participant. First, because the P3 is a relatively low-frequency component, we applied a 3.5 Hz low-pass filter to the EEG signal (Jaśkowski & Verleger, 2000). Next, P3 latency was estimated as the local maximum within a particular window in the average ERP of each lag condition for each participant. For the P3 associated with T1, this window was 200-600 ms after T1 onset. Visual inspection of the grand average ERPs per subject showed that the P3s associated with T2 occurred slightly later than for T1. To capture these peaks, for T2 at lag 3 and 8, the time windows were 650-1050 ms and 1150-1550 ms after T1 onset, respectively.

Median split. To contrast P3 latencies of targets that were estimated relatively early and targets estimated relatively late, we split the latency estimations of the participants in two groups based on the median estimation. Specifically, the median split was based on temporal estimation bias and was performed for each participant separately on trials where T1 and T2 were correctly identified. First, to correct for the pull towards the mean effect (i.e., the consistent overestimation of the early targets and underestimation of late targets), the temporal estimation bias was corrected for temporal position. Second, we estimated a linear mixed model with temporal estimation of T2 as the dependent variable, actual temporal position of T2 as a fixed factor and subject as a random factor. The amount of deviation of each T2 estimation from the estimated model then gives a corrected value of estimation latency. Third, the median split was performed on the resulting residuals for each participant.

For each participant, lag and target, two average ERPs were calculated, corresponding to trials where the target was estimated to have occurred earlier or later than the median estimation. For peak detection, we used the same time windows and method as in the analysis of the grand averages, described in the previous section.

Single-trial. In order to investigate the relationship between memory consolidation and temporal estimations on a single-trial level, we estimated the P3 latency in every trial in which T1 and T2 were correctly identified for every participant. First, we applied a 3.5 Hz low-pass filter to the EEG signal (Jaśkowski & Verleger, 2000). Second, for each trial, a linear detrend function was applied. Third, to estimate the latency of the P3, we cross-correlated a peak template with the EEG signal. Following Jaśkowski and Verleger (2000), the template consisted of a positive half-cycle sinusoid of 300 ms. Peak latency was determined as the time point at which the correlation was highest within a particular time window. The same windows as in the average peak estimation were employed (see section 3.1.6.1). To filter out trials in which no peak could be distinguished, only those trials in which the correlation between the template and the signal exceeded 0.65 were included in the analysis. In addition, only trials in which the difference between T1 and T2 peak latencies was greater than 100 ms were considered. In this way, 19% of the trials were excluded, resulting in a total of 1313 single target trials, 1665 lag 8 trials, and 962 lag 3 trials.

All analysis scripts and data are available at: https://osf.io/54xuj/.

Results

Behavioral Results.

Attentional blink. The mean accuracy for T1 and for T2 given correct report of T1 is shown in Figure 2.3A. A binomial linear mixed model was estimated with accuracy of T2 as the dependent variable, lag as a categorical fixed factor, subject as a random intercept term and lag as a random slope term. The inclusion of lag yielded a significantly better model (χ^2 = 786.80, p < .001, BF_{01} < 0.01). A post-hoc Tukey's HSD test showed that T2 accuracy was lower at lag 3 than at lag 8, indicating that an attentional blink occurred (see Table S3 for full Tukey's HSD test results). Also, T2 performance at lag 1 was significantly better than at lag 3 (p < .001), indicating lag-1 sparing.

Temporal estimations. Average lag estimations for each presented T2 lag and mean estimation corresponding to each target position are displayed in Figure 2.3B and 2.3C, respectively. A similar analysis of temporal estimations was conducted as in Experiment 1. A linear mixed model was fitted with estimated interval length (subjective lag) as the dependent variable and the centered presented (objective) lag as a continuous fixed factor. Subject was added as a random intercept term and presented lag as a random slope term. The model revealed an unstandardized coefficient of β = 0.56 (t = 15.08, p < .001, BF_{01} < 0.01), showing that the lag estimations increased linearly with the presented lag. Adding the dichotomous factor "within AB window" did not improve the model, suggesting that temporal estimates were not delayed for lag 3 compared to lag 1 and lag 8 (χ^2 = 0.38, p = .535, BF_{01} = 35.54). Similar to Experiment 1, a linear mixed model was estimated with bias in lag estimation as the dependent variable, presented lag as a continuous fixed factor and subject as a random intercept factor and lag as a random slope term. This model showed that there was a significant pull towards the mean (β = -0.44, t = -11.63, p < .001).

To test whether T2 estimates were delayed at lag 3, an LMM was estimated with temporal estimation of T2 as the dependent variable, temporal position of T2 as a continuous fixed factor, lag as a categorical fixed factor, subject as a random factor and the random slopes of temporal position of T2 and lag. Including lag improved the model fit (χ^2 = 24.61, p < .001, BF_{01} = 0.04). The model showed that T2 estimates at lag 3 relatively early compared to lag 1 (β = -0.48, t = -3.56,

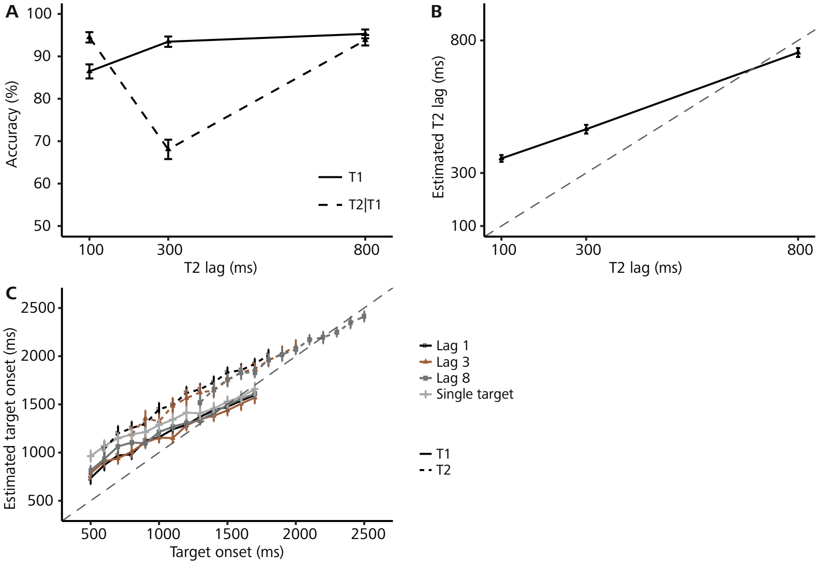

Figure 2.3. Behavioral results of Experiment 2. Figure A shows the average accuracy of T1 and T2|T1 per presented T2 lag, demonstrating that there is an attentional blink at lag 3 and lag-1 sparing. Figure B shows the average estimated lag as a function of the presented lag. The dashed line represents veridical estimation. Figure C presents the average estimated target onset as a function of target onset, relative to trial onset. Error bars represent the within-subject CIs.

$p < .001$), but there was no significant difference between lag 3 and lag 8 ($\beta = 0.29$, $t = 1.94$, $p = .052$).

Replication experiment. We have replicated the behavioral results of Experiment 2 in an additional experiment. Please find the results of this experiment in Supplementary Material section 1.2. Experiment 3 at https://osf.io/54xuj/.

EEG results.

Average P3 analysis. Figure 2.4A shows the grand average ERPs for lag 3 no-blink and blink trials, and lag 8 and single target trials in which both targets were correctly identified. For lag 3 no-blink and lag 8 trials, two large positive peaks can be observed, corresponding to the two presented targets. As expected, the second P3 was absent in lag 3 blink trials, indicating that T2 is not consolidated in working memory.

To evaluate if the P3 was delayed for T2 in lag 3 compared to T1 in lag 3 and T2 in lag 8, we estimated an LMM with P3 latency as the dependent variable, lag (lag 3 and lag 8) and target (T1 and T2) as categorical fixed factors and subject as a random factor. In the model, the contribution of each subject was weighted by the number of trials on which the subject average in each condition was based, using the *lmer* function in the *lme4* package in R.

The LMM showed that there was no difference in T2 P3 latency between lag 3 (M = 545.73 ms, SD = 113.56) and lag 8 (M = 544.53 ms, SD = 85.84) ($\beta = 8.03$, $t = 0.46$, $p = .646$, $BF_{01} = 3.56$), suggesting that the P3 for T2 was not delayed when this target was presented within compared to outside the AB window. However, within lag 3 trials, we found that the P3 was delayed for T2 compared to T1 ($\beta = -69.50$, $t = -3.71$, $p < .001$, $BF_{01} < 0.01$). Thus, these results suggest that the P3 for T2 within the AB window was delayed compared to the P3 for T1, but not compared to the P3 for T2 outside the AB window. Post-hoc, we compared T1 latency for no-blink and blink lag 3 trials by adding a fixed factor to the model coding for whether T2 was correctly reported, but we found no difference ($\beta = -21.50$, $t = -1.02$, $p = .311$, $BF_{01} = 3.90$).

Median-split P3 analysis. Fig. 4B and Fig. 4C show the average ERPs for estimates that were earlier and later than the median for lag 3 T1 and T2, respectively. Five linear mixed models were estimated to test whether P3 latencies of the early and late estimations were different for T1 and T2 in the lag 3 and lag

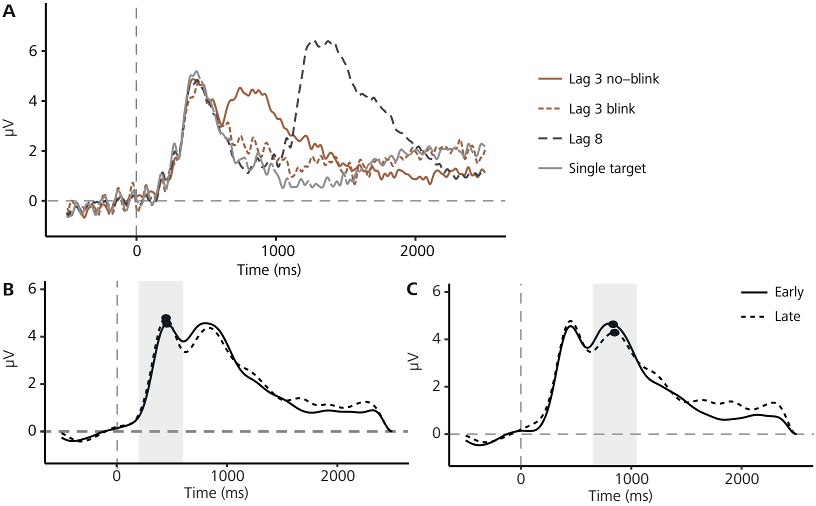

Figure 2.4. ERP results of Experiment 2. Figure A shows the grand average ERPs of lag 3, lag 8 and single-target trials in which both T1 and T2 were correctly identified. Figure B and C show the median-split ERPs for early and late estimations of T1 and T2, respectively, in lag 3 trials. The data in Figure B and C has been filtered with a 3.5 Hz low-pass filter. The grey areas show the windows employed for local peak detection. The black dots represent the average local peak for early and late estimations.

8 conditions and T1 in the single-target condition. In each model, P3 latency was the dependent factor, latency category (early or late) was the fixed factor and subject was entered as a random factor. Again, the contribution of each average data point was weighted by the number of trials on which the average was based.

The model for T2 at lag 3 showed that there was no difference in P3 latency between early (M = 835.43) and late (M = 849.20) estimations (β = 10.69, t = 0.44, p = .667, BF_{01} = 3.30). In line with this, we did not find differences in the P3 latencies associated with early and late estimations for T1 for lag 3, lag 8 and single-target trials (ps > 0.596, BFs_{01} > 2.85) and for T2 for lag 8 (β = -9.01, t = -0.76, p = .451, BF_{01} = 2.24). Thus, overall, these results suggest that the estimated target onsets did not depend on the latency of the P3. See Table S4 for an overview of the mixed model and Bayes factor results.

Single-trial P3 analysis. In our single-trial analysis we first tested whether there were latency differences of P3 associated with T1 and T2 in the different lags. To this end, we estimated an LMM with P3 latency as the dependent variable, lag and target as categorical fixed factors, subject as a random intercept factor and lag and target as random slope terms. The model showed that the P3 associated with T2 occurred later for lag 3 (M = 570.53) than for lag 8 (M = 541.76) (β = 31.44, t = 6.41, p < .001). In addition, the P3 was estimated earlier for T1 (M = 411.38 and M = 427.96 for lag 3 and lag 8, respectively) than for T2 in lag 3 (β = -162.19, t = -23.72, p < .001) and lag 8 trials (β = -115.82, t = -18.92, p < .001). Although the standard deviation of T2 P3 latency was only slightly larger for lag 3 (SD = 109.50) than for lag 8 (SD = 107.21), the standard deviation for T2 P3 in lag 3 was notably larger than for T1 (SD = 94.78). Thus, in contrast to average P3 analysis, the single-trial analysis suggests that the T2 P3 was delayed for lag 3 trials compared to lag 8 trials.

Figure 2.5A shows the color map for lag 3, which represents the single-trial ERP amplitude ordered by T2 P3 latency. Correspondingly, Figure 2.5B shows single-trial temporal estimations (relative to the median for each subject) in the same trial order as Figure 2.5A. The regression line in Figure 2.5B suggests that there was no clear correlation between T2 P3 latency and the time estimates. To investigate the influence of single-trial P3 latency on time estimations, eight linear mixed models were computed, predicting estimated T1 position in single target, lag 3 and lag 8 trials and estimated T2 position and lag in lag 3 and lag 8 trials. In all models, estimated T1 position was entered as the dependent variable, T1 position and P3 latency were continuous fixed factors and subject was a random factor. For all models, except the lag 3 model with P3 lag as a fixed factor, the random slope of T1 position was included because it improved the model significantly.

In line with Figure 2.5, we found no effect of P3 latency on the estimation

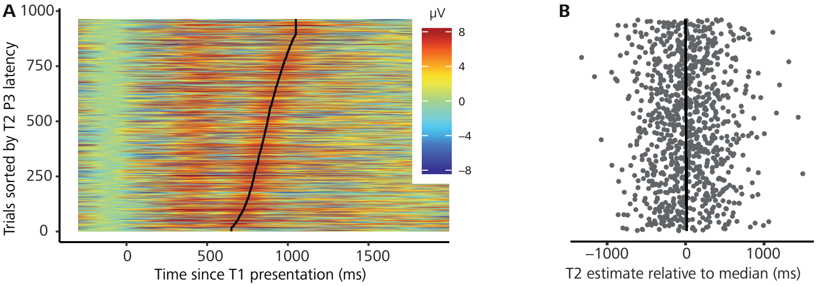

Figure 2.5. Single-trial P3 results of Experiment 2. Figure A shows the color map for lag 3 trials in which both T1 and T2 were identified correctly. The ERP amplitude of the trials are displayed sorted by T2 P3 latency. The black line represents the estimated single-trial P3 latency. Figure B shows the estimated temporal estimations of the target relative to the subject median for each trial. The trials are displayed in the same order as in Figure A.

of T2 ($\beta = 0.03$, $t = 0.28$, $p = .777$) and lag ($\beta = -0.03$, $t = -0.49$, $p = .625$) in lag 3 trials (see Table S5 for an overview of the mixed model results). The corresponding Bayes factors of 7.35 and 8.96, respectively, suggest that there was moderate evidence (Jeffreys, 1961) for the null hypothesis, i.e. the absence of an effect of P3 latency on temporal estimates. Over all lags and targets, we did not find a significant positive effect of P3 latency on temporal estimation (Table S5). We did find a small *negative* effect of P3 latency on T1 and lag estimations in lag 8 trials. However, the corresponding Bayes factors ($BF_{01} = 14.76$ and $BF_{01} = 1.26$, respectively) show that there was more evidence for the absence of an effect of P3 latency than for the alternative hypothesis. Thus, overall, the single-trial analysis does not deliver evidence in support of a relationship between P3 latency and temporal estimation.

Discussion

The goal of Experiment 2 was to relate electrophysiological signatures of memory consolidation to temporal estimations. We expected temporal estimations of identified T2s that were presented within the AB window to have increased latency and variance. If memory consolidation acts as an index of timing onset, we expected that the observed variance in temporal estimations could be explained by the variance of P3 latency.

We found similar behavioral results as in Experiment 1, despite the different combination of temporal positions and lags. In line with Experiment 1, temporal estimations for T2 in lag 3 trials, in which there is a presumed delay in memory consolidation, were not delayed compared to temporal estimations outside the AB window. Whereas the average ERP analysis revealed only a small, non-significant latency difference between the P3 evoked by T2 inside and outside the AB window, the single-trial analysis showed a ~30 ms delay in the lag 3 condition compared to the lag 8 condition. The latter finding is in line with previous studies (Chennu et al., 2009; Martens et al., 2006; Sessa et al., 2007; Vogel & Luck, 2002).

We expected that the latency of memory consolidation, as reflected by the P3, would determine the subjective onset timing of the participants. However, the analysis of the median-split ERPs revealed that there were no differences in P3 latency between early and late estimations. Similarly, we found no positive relation between P3 latency and temporal estimations on a single-trial level.

General discussion

This study was aimed at finding evidence of the involvement of memory consolidation in the starting of the internal clock in interval timing. We made use of the AB task, as it has been shown that memory consolidation is delayed and more variable when a target is presented within the AB window (Martens et al., 2006; Sessa et al., 2007; Vogel & Luck, 2002). If memory consolidation serves as the onset of interval timing, we expected that temporal estimations would be delayed when memory consolidation is delayed. In addition, we expected that inter-trial variation in temporal estimations could be explained by variation in memory consolidation.

In Experiment 1, we showed that participants could estimate the timing of the two targets in a predictable way, in which the temporal estimates increased with the presented onset. However, in line with typical temporal reproduction tasks, short lags were overestimated and long lags were underestimated (Grondin, 2001; Jazayeri & Shadlen, 2010; Van Rijn, 2016). Although a classic AB was observed, temporal estimations of identified T2s were not affected by the hypothesized delay of memory consolidation. Instead of temporal estimations of T2 being later when memory consolidation was delayed, we found that temporal estimations were slightly earlier. In Experiment 2, we found no latency differences between P3s for early and late temporal estimates and no relation between inter-trial variation in temporal estimates and single-trial P3s.

Thus, overall, we found no evidence for a relationship between memory consolidation as indexed by a P3 in an attentional blink task, and the associated temporal estimations. Whereas models of interval timing, such as the Scalar Timing model (Gibbon, 1977; Gibbon et al., 1984; Wearden, 1991) and the SBF model (Matell & Meck, 2004), propose a clock mechanism that an explicit starting signal starts a timing mechanism, Gu et al. (2015) proposed that, through multiplexing, the system of updating the semantic information of working memory can also code for time. In the latter case, working memory consolidation could serve as the "starting gun" that resets the phase of the oscillation coding for a specific item. However, the current study suggests that memory consolidation, as reflected by the P3, might not fulfill this role. It seems that, although memory consolidation is crucial for the conscious perception of an event, time information is coded for by another mechanism that is independent of the processes underlying the P3. However, a recent study suggests that the P3 might play a different role in timing, reflecting norepinephrine release in the overestimation of unexpected stimuli (Ernst et al., 2017).

It is important to note that the current study relies on three assumptions. First, working memory consolidation of T2 is delayed for no-blink trials in which T2 quickly follows T1, and second, the P3 component reflects working memory consolidation in the AB task. We believe that these assumptions are well supported by an extensive body of behavioral and EEG studies (for a review, see Martens & Wyble, 2010). In addition, most theoretical models of the AB assume that the second target is perceived, but fails in a limited-capacity memory system, and the latter process would therefore be delayed when T2 is reported in no-blink trials. Third, we assume the memory consolidation process has a dichotomous outcome: it is either successful or not. Consolidation was considered successful when an item was correctly recalled. However, we make no assumptions regarding the strength of memory consolidation, as was proposed in, for example, Wixted and Mickes (2010). It could be argued that stronger memory consolidation affects interval timing differently than weaker memory consolidation. For example, items that subjects judge to remember may have been consolidated into memory more strongly than the items of which subjects only have a vague idea. In our task, however, the weakly remembered items will often not be recalled correctly, since guessing correctly has only a 1/26 probability (or 1/14 if the participant was aware of the particular letter set used in our experiments).

A potential alternative to our working memory consolidation hypothesis is that timing onset might be established earlier than conscious stimulus detection. In line with this notion, Amano, Qi, Terada, and Nishida (2016) showed that the threshold of the MEG response related to the point of subjective simultaneity was earlier than the threshold for reaction time. They argued that although stimulus onset is determined prior to stimulus detection, the established time marker is only available when the stimulus is consciously perceived. Indeed, future studies might investigate the possibility that earlier perceptual processes, and associated earlier perceptual EEG components (e.g. N1 and P2), determine perceived timing.

Although the results suggest that temporal estimates in the sub-second range do not depend on the latency of working memory consolidation, potential shortcomings of the current study have to be considered. First, the variation in P3 latencies found in the AB task might be too small to reliably account for the variation in temporal estimations. Second, the assessment of temporal estimations by clicking on a timeline might not be precise enough to reveal small nuances in perceived timing. Even though the time estimation results show that, on average, the estimates increase linearly with the presented timing, the inter-trial response variation might lead to a decreased accuracy in mapping perceived timing to estimations. In addition, the observed pull towards the mean effect decreases meaningful inter-trial variation related to the presented lag. The response format could also compress the estimates for T2 when T1 appears later in the stream. However, in our models predicting estimated T2 position, any linear effects of position have been accounted for by the inclusion of actual temporal position of T2 as a fixed factor. In addition, our post-hoc test in Experiment 1 showed that lag estimations did not depend on when the targets appeared in the stream. The estimations of T1 and T2 do seem to interact in one particular way, however: we found earlier T1 estimates for trials in which two targets were reported compared to trials in which only a single target was reported.

In summary, the current study suggests that the timing of interval onset is not determined by memory consolidation as operationalized in this study: We found no relationship between neural markers of memory consolidation latency and reported target onset estimations.

Supplementary material

All supplementary materials can be found at https://osf.io/54xuj/.

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3

pupillary response indexes the metrical hierarchy of unattended rhythmic violations

Abstract

The perception of music is a complex interaction between what we hear and our interpretation. This is reflected in beat perception, in which a listener infers a regular pulse from a musical rhythm. Although beat perception is a fundamental human ability, it is still unknown whether attention to the music is necessary to establish the perception of stronger and weaker beats, or meter. In addition, to what extent beat perception is dependent on musical expertise is still a matter of debate. Here, we address these questions by measuring the pupillary response to omissions at different metrical positions in drum rhythms, while participants attended to another task. We found that the omission of the salient first beat elicited a larger pupil dilation than the omission of the less-salient second beat. This result shows that participants not only detected the beat without explicit attention to the music, but also perceived a metrical hierarchy of stronger and weaker beats. This suggests that hierarchical beat perception is an automatic process that requires no or minimal attentional resources. In addition, we found no evidence for the hypothesis that hierarchical beat perception is affected by musical expertise, suggesting that elementary beat perception might be independent from musical expertise. Finally, our results show that pupil dilation reflects surprise without explicit attention, demonstrating that the pupil is an accessible index to signatures of unattentive processing.

Introduction

Expectations in music

Fulfilments and violations of expectations are key in our appreciation of music (Huron, 2006). The perception of music is therefore a complex interaction between what we hear and our anticipatory interpretation (Vuust, Gebauer, & Witek, 2014). This is reflected in *beat perception*, in which a listener infers a regular pulse from a musical excerpt that does not necessarily contain this pulse explicitly (Honing, 2012). In addition, people are able to perceive a hierarchy of stronger and weaker beats, known as *meter*. This cognitive ability has an important social function by allowing people to synchronize movements and play music together, a capacity that children can utilize from about four years of age (Endedijk et al., 2015). The perceived beat drives our expectations about the timing and salience of the rhythm (Large & Kolen, 1994).

Although beat perception is a fundamental and widespread human capability, two major issues still need to be resolved. First, it is still unknown how much attention is needed to detect the beat (Bouwer & Honing, 2012). On the one hand, it has been argued that beat perception is pre-attentive (Bouwer, Van Zuijen, & Honing, 2014; Geiser, Sandmann, Jäncke, & Meyer, 2010; Ladinig, Honing, Háden, & Winkler, 2009; Winkler, Haden, Ladinig, Sziller, & Honing, 2009), while other studies have suggested that attention is necessary to establish a representation of the beat (Chapin et al., 2010; Geiser, Ziegler, Jancke, & Meyer, 2009). Second, to what extent beat perception is open for learning and dependent on expertise is still a matter of debate (Hannon & Trehub, 2005; Honing, 2013). Whereas Geiser et al. (2010) found that musicians were more sensitive to the metrical position of accents than non-musicians, Bouwer et al. (2014) found no difference in ERP response to beat omissions between musicians and non-musicians.

To investigate beat perception and metrical expectancy, recent studies have measured the mismatch negativity (MMN) as a response to expectancy violations (Bouwer et al., 2014; Honing, Bouwer, & Háden, 2014; Ladinig et al., 2009; Winkler et al., 2009). The MMN is a negative event-related potential (ERP) component that is elicited by unexpected stimuli in a sequence (e.g., Näätänen, Gaillard, & Mäntysalo, 1978, who manipulated loudness and pitch, or Kononowicz & Van Rijn, 2014, who demonstrated MMN-like responses in a task with temporal violations). The magnitude and latency of these early EEG potentials reflect the magnitude of the violation (Kononowicz & Van Rijn, 2014; Näätänen, Paavilainen, Rinne, & Alho, 2007; Schröger & Winkler, 1995), and thus allows for indexing subjective metrical salience. In addition, the MMN is elicited irrespective of attention, which makes it particularly suitable for studying *unattended* beat perception.

In order to test whether people perceive the beat without attention, several studies have investigated the MMN as a response to sound omissions in drum rhythms while the listeners were instructed to focus their attention elsewhere (Bouwer et al., 2014; Ladinig et al., 2009; Winkler et al., 2009). Based on theoretical models of hierarchical beat perception (Lerdahl & Jackendoff, 1983; Longuet-Higgins & Lee, 1984), one would predict that salient omissions are more surprising than less salient omissions. Thus, in a standard Western rock drum rhythm (Figure 3.1), in which the first beat of a measure is more salient than later beats, we can expect that the omission of the first beat violates expectations more than the omission of the second beat. In that case, the former omission is expected to elicit a larger MMN than the latter omission. However, empirical work has failed to find univocal evidence for this hypothesis.

To test whether hierarchical beat perception is innate or learned, Winkler et al. (2009) presented sleeping newborns with rock drum rhythms with occasional omissions at different metrical positions. They found that the omission of a bass drum at the first beat (the most salient metrical position) elicited a larger MMN than hi-hat omissions at the lowest level of metrical salience. Although Winkler et al. (2009) concluded that the newborns perceived the beat, the MMN difference might alternatively be due to the nature of the omitted sound instead of the metrical position (Bouwer et al., 2014). Controlling for this alternative explanation, Ladinig et al. (2009) presented adult participants with rock drum rhythms in which the bass drum sound was either omitted at the first or at the second beat while they performed a concurrent task. Whereas Ladinig et al. (2009) found a slightly earlier MMN for the first beat compared to second beat, they did not find a difference in amplitude. In a similar, more recent experiment, Bouwer et al. (2014) also reported a lack of significant differences in MMN amplitude elicited by the omission of the first and second beat, and also failed to observe any differences in the latency of the MMN as a function of the hierarchical level of the omitted sound. Thus, while these MMN studies show that participants detect violations of the beat without attention, it remains largely unknown whether people perceive a hierarchy of stronger and weaker beats when attention is focused on another task.

Although the study of Winkler et al. (2009) suggests that simple beat detection is already present at birth, the extent to which hierarchical beat perception is open for learning is still a matter of debate (Honing et al., 2014; Nozaradan, 2014). One way to tackle this question is by investigating whether musical training leads to a more pronounced representation of beat and meter. So far, this question has been approached by behavioral, fMRI and ERP experiments, which have resulted in partly ambiguous results. While some studies show that musical training enhances beat processing (Chen, Penhune, & Zatorre, 2008; Vuust et al., 2005), others found no differences between musicians and non-musicians (Bouwer et al., 2014).

Thus, while MMN studies suggest that people perceive the omission of beats without attention, it is still unclear 1) whether they perceive a hierarchy of stronger and weaker beats, and 2) to what extent musical expertise influences beat perception. As the MMN amplitude might not reflect differences in beat salience (Bouwer et al., 2014; Ladinig et al., 2009), we will employ a new approach to investigate these questions: pupil dilation. Several findings suggest that pupil dilation has the potential to be an accessible measure of musical expectation. First, a phasic pupillary response has been found in response to deviant, surprising stimuli (Friedman, Hakerem, Sutton, & Fleiss, 1973; Preuschoff, 't Hart, & Einhäuser, 2011; Steinhauer & Zubin, 1982). Second, pupil dilation has been suggested to reflect preconscious processing (Laeng, Sirois, & Gredebäck, 2012). Third, Wierda, Van Rijn, Taatgen, and Martens (2012) have shown that the relatively slow pupillary response accurately indexes processing at a high temporal resolution.

Pupil dilation reflects surprise

Decades of research have shown that pupil dilation reflects several fundamental cognitive processes. For example, it has been shown that phasic pupil size indicates mental effort (e.g., Ahern & Beatty, 1979; Granholm, Asarnow, Sarkin, & Dykes, 1996; Kahneman, 1973), emotional arousal (e.g., Hamel, 1974; Hess & Polt, 1960), memory strength and encoding (e.g., Van Rijn, Dalenberg, Borst, & Sprenger, 2012; Wolff, Scholz, Akyürek, & Van Rijn, 2014), language processing (e.g., Vogelzang, Hendriks, & Van Rijn, 2016), and dynamical attention (Verney, Granholm, & Marshall, 2004; Wierda et al., 2012). Although the pupillary response is relatively slow, recent studies have shown that the pupil reflects events with a high temporal resolution (Wierda et al., 2012; see also Willems, Damsma, Wierda, Taatgen, & Martens, 2015; Wolff et al., 2014; Zylberberg, Oliva, & Sigman, 2012). In this way, measuring pupil dilation offers an accessible, non-invasive and relatively inexpensive method to reveal online cognitive processing.

In addition to the cognitive processes listed above, there is increasing evidence that pupil dilation reflects surprise. As a first indication of this relationship, Friedman et al. (1973) found that pupil dilation was negatively correlated with stimulus probability. In line with this finding, Steinhauer and Zubin (1982) found a larger pupil dilation as a response to a rare target stimulus compared to the frequent distractor stimulus in an auditory oddball task. More recently, Preuschoff et al. (2011) found a larger dilation for surprising outcomes in a gambling task. In the experiment of Preuschoff et al. (2011), participants were presented with two sequential playing cards. Before this, they placed an uninformed bet on whether the first or the second card would be higher. The results showed that pupil dilation was higher when the second card resulted in a reward that was unexpected given the first card (e.g., when a 2 was shown after a 3), compared to when the expected reward indeed occurred.

Pupil dilation has been suggested to reflect brain activity in the locus coeruleus (LC; for reviews see Laeng et al., 2012; Sara, 2009). The LC is a nucleus in the brainstem that forms the hub of the noradrenergic (NA) system (Aston-Jones & Cohen, 2005). It has been argued that the LC is an important modulator in the attentional system, by regulating the neural responsivity of brain areas involved in selective attention, such as the frontal and parietal cortex (Coull, Büchel, Friston, & Frith, 1999; Sara, 2009). The LC-NA system is thought to facilitate "attentional and cognitive shifts and behavioral adaptation to changes in environmental imperatives" (Sara, 2009, p. 220), or context-updating in response to unexpected stimuli (Nieuwenhuis, 2011). In line with this proposed role of the LC-NA system and the finding that pupil dilation reflects surprise, Dayan and Yu (2006) showed that the phasic activation of NA neurons in rats and monkeys depends on the prior probability of a target: Infrequent targets elicited a larger phasic NA signal than frequent targets. In accordance with this result, Alexinsky, Aston-Jones, Rajkowski, and Revay (1990) found that an increased target frequency led to a decrease in phasic LC activity.

Pupil dilation and ERP components

Interestingly, the evidence that pupil dilation signals surprise suggests that it might be an accessible measure of expectation. As such, it might reflect expectancy violations in a similar fashion as ERP components such as the MMN and the P3. Whereas the MMN has been found to be relatively automatic (Näätänen, Paavilainen, Titinen, Jiang, & Alho, 1993; Otten, Alain, & Picton, 2000), the P3 reflects the evaluation of the stimulus in a given context, which requires active attentional allocation (Polich, 2007). The amplitude of the P3 depends on the amount of attentional resources allocated to the stimuli, so that the P3 is smaller when a secondary task is performed (Isreal, Chesney, Wickens, & Donchin, 1980) or when the stimuli do not require active processing (Polich, 2007). As a theoretical account, the P3 has been proposed to reflect context-updating: the revision of one's mental representation of the current environment based on the stimuli (Donchin, 1981). In line with this theory, the P3 has been suggested to reflect phasic activity of the LC-NA system (Nieuwenhuis, Aston-Jones, & Cohen, 2005). In this way, the P3 and phasic pupil dilation might be manifestations of the same underlying neural, as well as cognitive, process.

Recently, Kamp and Donchin (2015) investigated whether pupil dilation and the P3 indeed reflect the same cognitive function in a categorization task. Participants categorized words or pictures in either a frequent (e.g., living) or infrequent category (e.g., non-living), with the frequent words describing both living and non-living entities, and the infrequent pictures only depicting living entities. Kamp and Donchin (2015) found no correlation between the amplitude of the pupil dilation and the P3. In addition, whereas the P3 was higher for pictures than for words, pupil dilation only reflected category frequency. That is, while the P3 was also sensitive to perceptual deviance, the pupil only reflected categorical deviance. Kamp and Donchin therefore argued that response conflict - the need to inhibit a prepotent response tendency and give an alternative, appropriate response - might be crucial for eliciting a pupillary response.

With respect to whether attention is needed for a pupillary response, Laeng et al. (2012) suggested that pupil dilation might offer "a window to the preconscious" by reflecting cognitive processes outside of awareness and without an overt response. Evidence for this view comes from patients with *blindsight* who showed a pupillary response to visual stimuli presented in the blind visual field, that therefore were not consciously seen (Tamietto et al., 2009; Weiskrantz, Cowey, & Barbur, 1999). Similarly, Laeng et al. (2007) found that amnesic patients showed a larger pupil dilation for novel compared to old stimuli, even when the patients had no explicit memory of these stimuli. Also in healthy participants, a small number of studies have found a pupil dilation response to stimuli that are not consciously perceived. For example, Bijleveld, Custers, and Aarts (2009) found that pupil dilation reflected the value of subliminal reward cues. Overall, these findings suggest that pupil dilation may reflect cognitive processes even in the absence of attention.

In summary, both direct and neuroscientific evidence suggests that pupil dilation reflects the violation of expectations. However, it is still unclear whether attention or overt response is crucial for this pupil reaction. Whereas Kamp and Donchin (2015) argued that response conflict is an essential requirement for a pupillary response, others have suggested that the pupil might reflect processes below the threshold of consciousness (Laeng et al., 2012). In the latter case, we might expect that the pupillary response, like the MMN, reflects the violation of expectancy rather automatically. However, the pupillary response to unattended, surprising stimuli has not yet been investigated. Therefore, a secondary aim of the present experiment is to elucidate whether pupil dilation indeed reflects the violation of expectancy in the absence of attention.

Current study

In the current study, we will assess whether participants perceive beat and the hierarchical aspects of meter while they focus attention on another task by measuring pupil dilation. In addition, we will investigate whether higher musical expertise entails more pronounced beat perception. Participants are asked to perform a visual target detection task while a continuous stream of Western rock drum patterns is presented. The participants are instructed that the drum rhythms are irrelevant to the task at hand and are instructed to ignore the audio. The drum patterns in the stream contain omissions at different levels of metrical hierarchy, and thus of theoretical salience, as shown in Figure 3.1.

We expect that, first, if participants perceive the beat, salient omissions will elicit a pupillary response. Second, if participants perceive meter, we expect that salient omissions will elicit a higher pupillary response than less-salient omissions. Third, if beat perception is enhanced by musical training, we expect that the level of musical expertise as assessed by a validated questionnaire will be a predictor of the pupillary response to the omissions. If, on the other hand, unattended beat perception is a general human ability that is independent of expertise, we expect to find no effect of musical expertise.

Methods

Participants

Twenty participants enrolled in the Bachelor program Psychology at the University of Groningen (10 female, mean age 20.9, range 19–26) participated in the experiment in exchange for course credits. Participants were naive to the

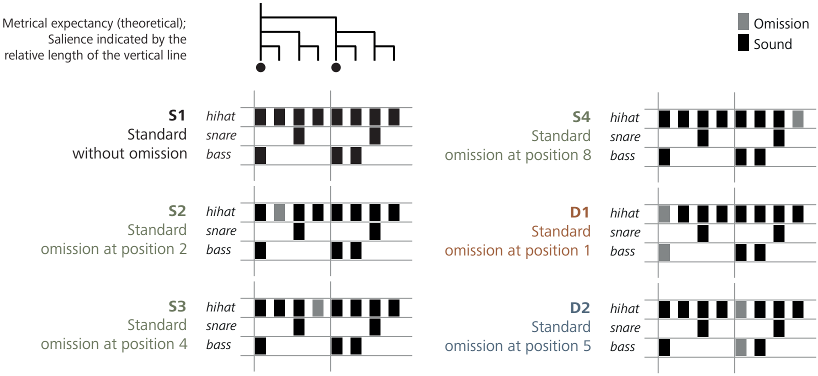


Figure 3.1. Graphic depiction of the six different drum patterns, consisting of hi-hat, snare and bass sounds, used in the current study. Metrical salience is denoted by the hierarchical tree-structure at the top, in which the dots represent the first and second beat. Base pattern S1 was a typical rock drum rhythm without any omission. In the three other standard patterns (S2, S3, and S4), a hi-hat sound was omitted at the lowest level of salience. Deviant pattern D1 contained the theoretically most salient omission: the bass sound on position 1. In deviant pattern D2, the bass sound on the second most salient position was omitted. (Figure partially adapted from Bouwer et al., 2014.)

purpose of the study. The Psychology Ethical Committee of the University of Groningen approved the experimental protocol (13223-NE) and all participants gave written informed consent prior to the experiment.

Materials

Stimuli were generated and presented using Matlab 2010 software running under Windows XP. Visual stimuli were presented on a 22-inch computer screen with a 100 Hz refresh rate. The '+' and '–' in the target detection task were presented in black, 22-point Arial on a light grey background. Drum rhythms were presented on a Superlux HD-662 F studio headphone at ~65 dB.

Similar to Ladinig et al. (2009), six different drum patterns were constructed that conform to typical drum patterns found in Western tonal music (Figure 3.1). Four patterns where standard patterns (S1–S4) and two were deviant patterns (D1 and D2). Whereas standard patterns contained either no omissions (S1) or an omission at the lowest level of salience (S2–S4), deviant patterns contained a salient omission on the beat.

The base pattern, S1, was a typical rock drum rhythm composed of bass, snare and hi-hat sounds. The bass and hi-hat sound consisted of samples from a Linn LM-1 drum computer, whereas the snare was sampled from a Sequential Circuits

DrumTraks drum computer. The S1 pattern consisted of eight consecutive sounds at equidistance intervals (150 ms onset-to-onset) and a total duration of 1200 ms. To collect data that can be used to rule out the alternative explanation that the measured responses to deviating patterns are a result of simple pattern matching (Ladinig et al., 2009), three additional standard patterns (S2–S4) were created that contained an omission of a hi-hat sound at the lowest level of metrical salience. In the deviant patterns D1 and D2, the bass and hi-hat sounds were omitted at the most salient position (position 1) or the second most salient position (position 5), respectively. All sound samples are available at https://osf.io/ezgup/.

Design and procedure

Participants performed a visual target detection task, during which drum rhythms were presented. In the target detection task, a '+' was presented at the middle of the screen. The task of the participant was to press the spacebar as fast as possible whenever the fixation cross was replaced with a '−'. The inter-target onset asynchrony (TOA) of the '−' was determined by a constrained non-aging distribution: Every 10 ms the '−' had a 1/1200 chance of appearing, with a maximum TOA of 20 s. In order to motivate participants to perform well, participants could keep track of their performance using a simple scoring scheme. Responses faster than 400 ms were rewarded with a score increase of 10 points. Participants were told that they would receive a candy bar when they had more than 1000 points at the end of the experiment. They were informed that drum rhythms would be presented during the experiment, which could be ignored.

At the start of the experiment, participants performed a practice block consisting of the target detection task combined with a continuous stream of 50 drum patterns presented without any pauses. Next, participants were presented with 20 blocks, each consisting of 100 drum patterns presented continuously. Eighteen blocks were Deviant blocks, in which standard and deviant patterns were presented. Two blocks served as Control blocks, which consisted of the repeated presentation of a deviant pattern. These blocks served to test whether the pupillary response towards deviants indeed reflects expectation and not a response to the omission itself. The order of the blocks was random.

A Deviant block consisted of 80 standard patterns (20 repetitions × 4 patterns) and 20 deviants (10 repetitions × 2 patterns). The order of the patterns within a Deviant block was pseudorandom with the constraint that there were at least three standard patterns between consecutive deviants. In addition, D1 could not follow S4, because that would lead to the presentation of two consecutive omissions. Each Deviant block started with at least two standard patterns. In the Control blocks, participants were presented with a stream of repeated D1, or repeated D2 patterns.

After the experiment, the musical expertise of the participants was assessed by completing the self-report inventory from the Goldsmiths Musical Sophistication Index (Gold-MSI; Müllensiefen, Gingras, Musil, & Stewart, 2014). The Gold-MSI combines the scores on multiple subscales (e.g., musical training, active musical engagement) into a General Musical Sophistication factor.

Pupil dilation

Pupil dilation was recorded using the EyeLink 1000 eyetracker (www.sr-research.com) at a sampling rate of 1000 Hz. Before recording, the eye tracker was calibrated to track the left eye. To minimize head movements, participants were asked to rest their chin on a chin-rest and their forehead against a forehead-bar (SR Research Head Support) that was fixed to the table resulting at a viewing distance of ~50 cm.

Pre-processing. The pupil data were down-sampled to 50 Hz. In every block, blinks and missing data were recovered using spline interpolation, but only when not more than 500 ms of sequential data was contaminated. Epochs were extracted from the continuous data by taking the data in a time window of 600 ms before and 3600 ms after the onset of every pattern. Epochs containing non-interpolated missing data or blinks, and patterns containing more than 200 ms of interpolated data were removed from analysis. Epochs were time-locked to omission onset and baseline corrected by the average pupil size during the 100 ms before the onset of the omission. The first and last two patterns of each block were not analyzed.

To investigate the effect of omissions, the pupil dilation in deviant patterns (D1, D2) and standard patterns (S2, S3, S4) was compared to the dilation in base pattern S1. In order to control for the different location of the omissions within the drum pattern, for each comparison pattern separately, S1 was time-locked and baseline corrected to the onset of the omission in that particular pattern. Thus, for comparison, the onset of S1 was matched to the omission onset of each pattern. To further eliminate differences in acoustic context between deviants and base pattern S1, the dilation in deviant patterns was compared to a subset of S1 patterns with a similar context. As deviants could not be followed by another deviant by design, the same constraint was applied to the selection of S1 patterns for the analysis of the deviant patterns. Thus, deviant patterns were compared to the subset of S1 patterns that did not precede a deviant. Similarly, as S4 patterns could not be followed by a D1 pattern by design, only the subset of S1 patterns that were not followed by D1 were used for the S4 analysis.

For another set of analyses, difference waves were calculated at trial-level by subtracting the participant-average S1 pupil dilation, time-locked and baseline corrected to the relevant omission onset, from the dilation of the different patterns. For these difference waves, we calculated the area under the curve (AUC) in the time window from 400 to 1600 ms after omission onset. Considering that the pupillary response peaks ~1 s after a relevant event (e.g., Hoeks & Levelt, 1993) the dilation was expected to be most apparent in this time window.

Statistical analysis. First, we tested whether the dilation of D1, D2, S2, S3 and S4 differed from base pattern S1 by comparing the dilation elicited by these patterns to the aligned S1 dilation. For this analysis, data in a time window from 0 to 2000 ms after omission onset were taken into account. For each comparison against S1, a nonparametric permutation test was performed (Maris & Oostenveld, 2007) in which the condition for each data point and participant was randomly labelled 10000 times. Conditions were compared with a standard *t*-test. To control for multiple comparisons, a critical *t*-value (t_{crit}) was calculated with a single threshold test (Nichols & Holmes, 2002). The null hypothesis, stating that there is no difference between two conditions, was rejected if the *t*-value exceeded the critical *t*-value.

To test the effect of omission position and musical sophistication on pupil dilation, the AUC of the difference waves was analyzed with Linear Mixed Models (LMM) using the *lme4* package (version 1.1-7) in R version 3.1.2 (Bates, Maechler, & Bolke, 2012). Before analysis, the fixed factors Baseline and Trial were centered and scaled to a range of −1 to 1 and the factor Pattern was recoded using effect coding.

Separate LMMs were performed for deviant patterns in the Deviant condition, for deviant patterns in the Control condition, and for standard patterns. A direct comparison of the pupillary response between all deviants and standards would not be informative, as not only their omission position differed, but also the omitted sound and the presentation frequency. That is, in deviant patterns a bass drum and hi-hat were omitted whereas only a hi-hat was omitted in the S2–S4 standard patterns. The LMMs were performed with Pattern, Musical Sophistication, and their two-way interaction term as fixed factors. In addition, the main effect of Trial and the absolute Baseline were entered in the models. In each model, Participant was entered as a random factor.

In addition to the LMMs, we performed Bayesian analyses. These analyses allow for quantifying the statistical evidence in favor of the null hypothesis. For non-significant fixed factors in the LMMs, we compared the Bayes factors of a model without the particular fixed factor with the original model using the *lmBF* function from the *BayesFactor* package in R (Morey et al., 2014). We will denote the evidence for H_0 over H_1 as BF_{01}.

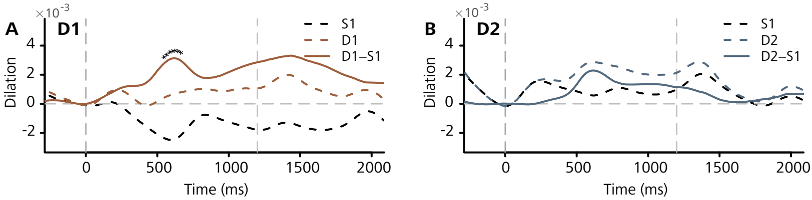
All materials and analysis scripts are available at https://osf.io/ezgup/.

Results

Pupil dilation results

Figure 3.2 and Figure 3.3 show the mean normalized pupil dilation and the difference waves for the deviant and standard patterns, respectively. The permutation test showed that the dilation for D1 was higher than for S1 in the time window of 540–660 ms after omission onset (t_{crit} = 3.18, *p*s < .027; Figure 3.2A). In contrast, no differences were found between D2 and S1 (t_{crit} = 3.18, *p*s > .906; Figure 3.2B). Thus, whereas the most salient deviant (D1) elicited an increased pupil dilation, the less salient deviant (D2) did not. Similarly, standard patterns S2, S3 and S4 did not differ from S1 (t_{crit} = 3.09, 3.08 and 3.00 respectively, *p*s > .210; Figure 3.3), indicating that the omission of a hi-hat sound at the lowest level of salience did not elicit a pupillary response. In addition, no differences were found between both D1 and D2 in the Control blocks and S1 (t_{crit} = 2.99 and 2.95 respectively, *p*s > .924; Figure 3.2C and D), showing that the deviating pupillary response to D1 and (if an effect

Deviant Condition



Control Condition

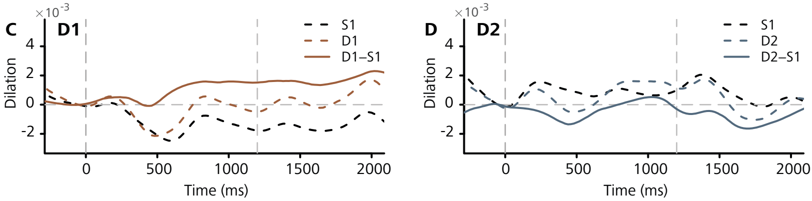


Figure 3.2. Average dilation and difference waves for deviant patterns D1 and D2 in the Deviant condition (A and B respectively) and the Control condition (C and D). Time point 0 corresponds to the omission onset. The dashed grey line presents the time-locked base pattern S1, the colored dashed lines present the dilation of the patterns and the solid lines present the difference waves of the patterns with S1. Significant differences between the pattern and S1 are denoted by asterisks. For these figures, the signals were smoothed with a 5-point running average filter.

would have been found) to D2 are driven by a context that provides a baseline compared to which D1 and D2 deviate.

The AUC of the difference waves of all patterns in the Deviant and Control condition can be found in Table 3.1. The model for the AUC of the deviants showed a significant negative effect of Trial ($\beta = -3.99$, $t = -3.65$, $p < .001$) and Baseline ($\beta = -134.82$, $t = -27.52$, $p < .001$), indicating that the pupillary response decreased over the scope of the experiment, and that higher pupillary baselines were associated with lower pupillary responses. The AUC for D1 was higher than for D2 in the Deviant condition ($\beta = -1.29$, $t = -2.14$, $p = .032$), showing that D1 elicited a larger pupillary response than the less-salient deviant D2. Post-hoc *t*-tests indicated that the AUC associated with the difference between D2 and S1 did not significantly differ from 0. When presented with a block consisting of only D1 or D2 patterns (the Control blocks), no difference between D1 and D2 was observed ($\beta = 1.09$, $t = 1.46$, $BF_{01} > 100$).

As a post-hoc analysis, suggested during review, we aimed to test whether the difference in AUC between D1 and D2 decreased over the course of a block. To this end, we added a factor corresponding to the trial number within a block and the interaction between this factor and Pattern to the LMM. The model showed that although the dilation decreased over the course of a block

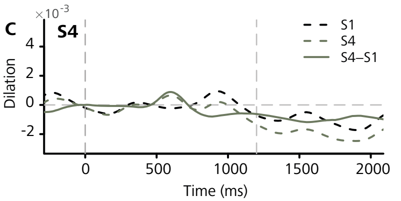


Figure 3.3. Average dilation and difference waves for standard pattern S2, S3, and S4 (A, B, and C respectively). Time point 0 corresponds to the onset of the hi-hat omission. The dashed grey line presents the time-locked base pattern S1, the colored dashed lines present the dilation of the patterns and the solid lines present the difference waves of the patterns with S1. For these figures, the signals were smoothed with a 5-point running average filter.

($\beta = -7.60$, $t = -6.92$, $p < .001$), the difference between D1 and D2 did not change ($\beta = 0.20$, $t = 0.20$, $BF_{01} = 21$).

Overall, Musical Sophistication was not a significant predictor of the AUC of the deviants ($\beta = 0.18$, $t = 0.42$), nor a predictor of the difference in AUC between D1 and D2 ($\beta = -0.08$, $t = -1.63$). Bayes factor analysis showed that a model excluding the main effect of Musical Sophistication and its interaction with Pattern was preferred over the model including these factors with $BF_{01} = 19$, providing strong evidence (Jeffreys, 1961) for the view that Musical Sophistication does not predict the pupillary response. Thus, participants with a greater musical expertise did not show a larger pupil dilation in response to deviants than participants with a smaller expertise. Furthermore, musical expertise had no influence on the difference in pupillary response to omissions of different salience.

For the standard patterns, we found that Pattern had no effect on the AUC ($\beta = 2.48$, $t = 0.61$). Bayes factor analysis showed that the restricted model excluding Pattern was preferred over the full model with $BF_{01} > 100$, providing decisive evidence (Jeffreys, 1961) that the position of the hi-hat omission did not influence the pupillary response. Furthermore, Musical Sophistication was not a significant predictor of the AUC of the standard patterns ($\beta = 0.24$, $t = 0.55$). In addition, the effect of Musical Sophistication did not differ between patterns (ps > .121). The model without Musical Sophistication was preferred over the model including Musical Sophistication with $BF_{01} > 100$, providing, again, decisive evidence against including Musical Sophistication as a predictor for the pupillary response.

Pattern	AUC	SE
Deviant Condition		
D1	3.14	1.31
D2	1.45	1.68
S2	1.16	1.47
S3	-0.37	1.21
S4	-0.53	1.43
Control Condition		
D1	1.57	1.52
D2	-0.45	1.31

Table 3.1. Average AUC of the difference waves per pattern and condition.

Behavioral results

The mean response time in the target detection task was 429.65 ms with a standard deviation, calculated over the mean response times per participant, of 72.30. Participants earned points when a response was faster than 400 ms. On average, participants were faster than 400 ms in 51.64% of the trials, showing that the task was considerably difficult to perform. We found no evidence that the auditory stimuli affected the performance on the target detection task. That is, responses to targets that appeared within 1 s after D1 or D2 omissions were not faster or slower than responses to targets outside this range ($t(37.9) = -0.28, p = .785$ and $t(34.4) = 0.63, p = .536$ respectively).

The mean Musical Sophistication score was 75.95 with a standard deviation of 12.40 and a range of 58.00–111.00. In a large scale online study (n = 147,633) aimed at the general public, the Musical Sophistication score was 81.58 (*SD* = 20.62) (Müllensiefen et al., 2014).

Discussion

In this study, we have investigated whether participants perceived beat and the hierarchical aspects of meter found in Western tonal music while paying attention to an alternative task by measuring pupil dilation. On the one hand, it has been argued that hierarchical beat perception is pre-attentive (Bouwer et al., 2014; Ladinig et al., 2009; Winkler et al., 2009), which would predict that salient omissions in rhythms elicit a larger pupillary response than less salient omissions. On the other hand, however, several studies have suggested that attention is necessary to perceive the beat (Chapin et al., 2010; Geiser et al., 2009), predicting no effect of metrical position on pupil dilation. Furthermore, in order to test whether beat perception is open to learning and exposure, we have investigated whether higher musical sophistication entails more pronounced beat perception. As a secondary objective, we have tested whether pupil dilation can index surprise as operationalized by the omission of expected stimuli in the absence of attention.

We found that salient omissions in the rhythm elicited an increased pupil dilation compared to standard rhythms without omission. However, this was only the case in the most salient deviant (D1) and not in the less-salient deviant (D2) or standard patterns in which a hi-hat sound at the lowest level of salience was omitted. In line with these results, we found that D1 elicited a larger pupil dilation than D2. With respect to musical expertise, we did not find an effect of musical sophistication on the pupillary response to omissions at the different metrical positions, nor did musical sophistication have an effect on the difference in dilation between D1 and D2.

Unattended beat perception

In line with Ladinig et al. (2009) and Bouwer et al. (2014), our study shows that violations of the beat can be perceived without paying explicit attention to the rhythmic patterns. Furthermore, the absence of an increased pupillary response in the control condition provides evidence against the alternative explanation that the pupillary response to D1 could be caused by an omission of a beat at that particular position in and of itself. Instead, the combination of these results suggests that the pupillary response to omissions depend on the context in which the pattern is presented. Thus, our results show that participants extracted a regular and hierarchical structure from the rhythm while attending to another task.

These conclusions are driven by the observed difference in pupil dilation between D1 and D2, which consisted of the omission of an identical bass drum and hi-hat sound at a different metrical position. This finding suggests that a meter representation was induced. That is, participants did not only perceive a regular beat, but also perceived a hierarchy of stronger and weaker beats. This in line with the theoretical model of beat perception proposed by Longuet-Higgins and Lee (1984), which predicts that the first beat of a measure is more salient than the second beat (Figure 3.1). Thus, our findings provide further evidence that hierarchical meter is not merely a theoretical concept, but actually drives our expectations when we listen to music (Ladinig et al., 2009), even while attending something else.

At first sight, the different pupillary response to D1 and D2 could be seen as being in contrast to the results of Bouwer et al. (2014) and Ladinig et al. (2009), who did not find a difference in MMN amplitude in response to D1 and D2. Although this latter finding might mean that no metrical hierarchy was induced, other explanations have to be considered. First, the MMN response to D1 and D2 might have been near ceiling level (Bouwer et al., 2014). Second, the drum rhythms did not contain explicit cues that indicate a hierarchy between the first beat and the second beat, other than the onset of the audio stream. It thus might be possible that participants perceived the second beat (position 5) as the first beat (position 1), and vice versa. These two alternatives potentially explain the discrepancy between our findings and both Ladinig et al. (2009) and Bouwer et al. (2014). First, as we measured pupil dilation instead of the MMN, we presumably did not encounter the ceiling effects present in ERPs. Second, we presented shorter blocks of continuous drum patterns than Ladinig et al. (2009) and Bouwer et al. (2014), which might make it more probable that participants used stream onset for the representation of meter during the whole block. If that is the case, we might expect that the difference in pupillary response to the different levels of salience decreases over the course of the continuous stream. However, we found no evidence that the difference in dilation between D1 and D2 decreased in an experimental block.

If participants indeed perceive meter in accordance with Longuet-Higgins and Lee (1984), we can expect that omissions on-the-beat are more salient than omissions off-the-beat. As a drawback of the current experimental paradigm, irrespective of whether EEG or pupillary measures are assessed, we cannot validly compare psychophysiological response to omissions in deviant patterns with the response in standard patterns: Not only their metrical position differs, but also both the sound that is omitted and the presentation frequency are different (Bouwer & Honing, 2012). Future studies could take this limitation into account, for example by presenting a bass drum omission off the beat (see also Bouwer et al., 2014).

Investigating the effect of musical expertise on beat perception, we found no evidence that higher musically sophistication leads to a more pronounced beat representation. This result suggests that beat perception is independent of musical expertise. This is in line with Bouwer et al. (2014), who found no difference in the MMN response to omissions between musicians and non-musicians. In contrast, Geiser et al. (2010) found that musicians were more sensitive to the metrical position of perceptual accents than non-musicians. However, the stimuli of Geiser et al. (2010) consisted of snare drum rhythms, whereas the stimuli in the current study consist of acoustically richer drum rhythms. The additional intensity and timbre information might make it easier to perceive the beat (Bouwer et al., 2014). In addition, it might be that musical expertise needs to be better specified. For example, Cicchini et al. (2012) demonstrated that percussionists show superior interval timing compared to non-percussionist musicians, indicating that the type of instrument played by the participant might play a role in rhythm perception. Finally, an effect of musical expertise might only be observed when participants are sampled from a broader range of expertise than the range present in a typical Psychology student population.

In summary, our results show that participants detected the beat while they attended to another task. In addition, we found that participants perceived a metrical hierarchy, in which the first beat is more salient than the second. Finally, we found that this unattended beat perception was independent of musical expertise.

Pupil reflects unattended surprise

To our knowledge, we are the first to show that pupil dilation is elicited by *unattended* surprising events. This finding suggests that the pupil dilation response is elicited by surprising stimuli relatively automatically. In addition, the different pupillary response to D1 and D2 shows that pupil dilation is modulated by the level of salience of an event.

The current finding that the pupil reflects the processing of stimuli that are not attended and not relevant to the task at hand provides further evidence for the role of the pupil as “a window to the preconscious” (Laeng et al., 2012). This is in contrast to Kamp and Donchin (2015), who suggested that detection of response conflict is crucial for eliciting a phasic pupillary response. Importantly, however, our finding that the pupil reflects the processing of unattended and irrelevant stimuli does not rule out that the pupil dilation magnitude is modulated by task-relevance as well as the need for a motor response. As one indication for the enhancing role of motor response on pupil dilation, Privitera, Renninger, Carney, Klein, and Aguilar (2010) found a larger pupil dilation when a button press was required when a visual target was detected, compared to the same detection task without a motor response. However, future studies are needed to further reveal the effect of both attention and response on pupil dilation.

Considering the hypothesis that the pupil is an indicator of activity in the locus coeruleus (LC), our findings are in line with studies showing that unexpected stimuli elicit larger phasic noradrenergic activity than frequent stimuli (Alexinsky et al., 1990; Dayan & Yu, 2006). In this way, the current study delivers further support for the proposed role of the LC-NA system as a signaler of the need for adapting the mental model of the environment (Nieuwenhuis, 2011). In addition, however, the current findings suggest that the LC-NA system also plays a role in signaling unattended expectancy violations.

Our results suggest that pupil dilation might reflect surprise in a similar way as the MMN: it is sensitive to different levels of salience without attention. However, two differences with previous MMN studies have to be considered. First, in contrast to Ladinig et al. (2009) and Bouwer et al. (2014), we found a difference in response to different levels of salient beat omissions (D1 and D2). This finding suggests that pupil dilation might be more sensitive to different levels of expectancy violation than the MMN. An alternative explanation is that, as mentioned above, the shorter lengths of the presented audio stream in the current experiment might have made it easier to distinguish between the first and the second beat.

Second, whereas Ladinig et al. (2009) and Bouwer et al. (2014) found a MMN in response to both D1 and D2, we only found an increased pupillary response for D1. This finding suggests that, in contrast to the MMN, only highly salient violations elicit a pupillary response in the absence of attention. However, the lack of a pupillary response to D2 might also be due to a slightly different experimental setup: Whereas Ladinig et al. (2009) and Bouwer et al. (2014) used a deviant probability of 5% and 3.3% respectively, we employed a deviant probability of 10%. The higher deviant probability might decrease the salience of the deviant. As a second alternative explanation, the absence of a significant pupil dilation to D2 might be due to interfering pupillary responses to the visual detection task. That is, the dilated pupil as a response to a visual target might have decreased the overall responsiveness of the pupil to the auditory stimuli, preventing the weaker response to D2 from reaching significance. In support of this hypothesis, we found that a larger absolute pupil size at the onset of an omission (i.e., the baseline) resulted in a smaller pupillary response.

In summary, we found that pupil dilation reflects surprise in the absence of attention. This is in line with the hypothesis that the pupillary response can be driven by subconscious processing (Laeng et al., 2012). In comparison with earlier MMN studies, we found that the pupil might be more sensitive to different levels of salience as we found that the pupil only responded to the most salient expectancy violation and not to weaker violations.

Conclusions

In this study, we observed that participants were able to perceive beat and hierarchical meter while paying attention to another task. This indicates that beat perception is an automatic process that requires minimal attentional resources. In addition, we found that hierarchical beat perception is independent of musical expertise, providing further evidence that beat perception is a general, widespread cognitive ability. Finally, our results show that pupil dilation reflects surprising events in the absence of attention, indicating that pupil size is an accessible index of subconscious processing.

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4

no evidence for an attentional bias towards implicit temporal regularities

Abstract

Action and perception are optimized by exploiting temporal regularities, and it has been suggested that the attentional system prioritizes information that contains some form of structure. Indeed, Zhao et al. (2013) found that attention was biased towards the location and low-level visual features of shapes that appeared with a regular order but were irrelevant for the main search task. Here we investigate whether this bias also holds for irrelevant metrical temporal regularities. In six experiments, participants were asked to perform search tasks. In Experiment 1a-1d, sequences of squares, each presented at one of four locations, appeared in between the search trials. Crucially, in one location, the square appeared with a regular rhythm, whereas the timing in the other locations was random. In Experiment 2a and 2b, a sequence of centrally presented colored circles was shown in between the search trials, of which one specific color appeared regularly. We expected that, if attention is automatically biased towards these temporal regularities, reaction times would be faster if the target matches the location (Exp. 1a-1d) or color (Exp. 2a, 2b) of the regular stimulus. However, no reaction time benefit was observed for these targets, suggesting that there was no attentional bias towards the regularity. In addition, we found no evidence for attentional entrainment to the rhythmic stimulus. These results suggest that people do not use implicit rhythmic temporal regularities to guide their attention in the same way as they use order regularities.

Introduction

When interacting with the environment, humans extract and exploit regularities in order to make inferences or anticipate future events. This kind of statistical learning can be used to optimize perception, motor timing and the allocation of attentional resources. Indeed, sensitivity to statistical regularities has been found to occur over a wide range of stimuli and different modalities, such as in regular spatial arrangements (Biederman, Mezzanotte, & Rabinowitz, 1982; Chun & Jiang, 1998; Fiser & Aslin, 2001), implicit artificial grammar (Reber, 1967; Saffran, Aslin, & Newport, 1996), and the order of presented shapes (Turk-Browne, Scholl, Chun, & Johnson, 2009). Interestingly, statistical learning often occurs without explicit knowledge or instructions about the regularities, indicating that it is an automatic and implicit process (e.g., Turk-Browne, Jungé, & Scholl, 2005).

In line with these examples, humans pick up temporal regularities in their environment rather automatically (Damsma & Van Rijn, 2017; Large & Palmer, 2002; Povel, 1981). Temporal regularities can be exploited to predict the timing of upcoming events and, thereby, allow one to prepare an efficient response (Nobre & Van Ede, 2018). For example, reaction times decrease when a target stimulus appears predictably after a specific foreperiod (Niemi & Näätänen, 1981). In addition, attention can be directed by temporal structures in a similar way as by predictable spatial arrangements, leading to temporal contextual cuing (Olson & Chun, 2001). That is, Olson and Chun found that predictable sequences of event durations preceding a target lead to faster reaction times.

In a similar way, humans are sensitive to rhythmic events in their environment. When a stimulus occurs with an isochronous rhythm, attention can be synchronized to the stimulus through entrainment (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Large & Jones, 1999). In this way, neural entrainment to rhythmic stimuli has been shown to facilitate perception, such as in pitch judgment (Jones et al., 2002), near-threshold auditory gap detection (Henry & Obleser, 2012), visual target detection (Kösem & van Wassenhove, 2012; Mathewson et al., 2010), and leads to faster reaction times in an oddball task in macaque monkeys (Lakatos et al., 2008).

Together, these studies show that temporal regularities can guide attention to optimize task performance. Considering the facilitating effects of perceived regularity, it has been proposed that the attentional system might prioritize structured information over more random sources (Yu & Zhao, 2015; Zhao et al., 2013). Indeed, Zhao et al. (2013) found that this was the case for order regularities. They showed that attention was biased towards the location and low-level visual features of shapes that appeared with a regular order, even when these regularities were not relevant for the task at hand. In Zhao et al.'s paradigm, participants performed search tasks in which they had to indicate the orientation of a T-shaped target presented among three L-shaped distractors. Crucially, the search tasks were interleaved by sequences of symbols. In three experiments, symbols with a certain feature (e.g., red) were presented in a fixed order, whereas symbols with a different feature (e.g., green) appeared in a random order. While the order regularity did not predict the location or timing of the target in the search task, Zhao et al. found faster reaction times when the features of the targets matched the regular symbols, indicating a bias towards these order regularities. They concluded that the implicit regularity in the task biased attention towards features associated with the regularity in a way that is not stimulus-identity driven, but also not driven by intentional goals.

While these results suggest that the attentional system is spontaneously tuned to order regularities, it is as of yet unknown whether this is also true for metrical temporal regularities, that is, for stimuli that occur isochronously. The goal of the current study is to investigate this question, by testing whether there is an attentional bias towards temporal regularities that are implicit (i.e., the participants are not informed about the existence of any regularities) and irrelevant for the task at hand. In six experiments based on the paradigm of Zhao et al. (2013), we tested whether attention was biased towards the location and color of the temporally regular-appearing stimuli. Participants were asked to perform search tasks in which a target appeared in one of four locations. In Experiment 1a, which was modeled after Experiment 1 of Zhao et al. (2013), sequences of squares were presented in between the search displays in the same four locations. Crucially, in one location, the square appeared with a regular rhythm. The temporal structure was uninformative about the visual search task in Experiment 1a. In contrast, in Experiment 1b, the structure of the regular stream could be used to predict target location in the search task. To test whether the speed and complexity of the regularity influence a potential attentional bias, both factors were manipulated in Experiment 1c and 1d.

Whereas location was the defining structural feature in Experiment 1, in

Experiment 2, which was modeled after Zhao et al.'s (2013) Experiment 2, we investigated whether attention was spontaneously biased towards color features associated with temporal structure. A sequence of colored circles was presented in between the search trials, of which one specific colored circle appeared at regular intervals. Similar to Experiment 1c, we tested the influence of presentation speed in Experiment 2b. We expected that, if attention is automatically biased towards the temporal regularities, reaction times would be faster if the target matches the location (Experiment 1) and color (Experiment 2) of the regular stimulus.

Experiment 1: Spatial bias

Experiment 1a

Methods.

Participants. Forty-eight participants enrolled in the Bachelor program Psychology at the University of Groningen (24 female, mean age 21.0, range 18-29) participated in the experiment in exchange for course credits. The Psychology Ethical Committee of the University of Groningen approved the experimental protocol (16030-S-NE). All participants gave written informed consent prior to the experiment. The participants were naive to the purpose of the study, but received a debriefing after the experiment.

Stimuli.

Square stream. The square stream consisted of black squares presented over four locations centered 5.1° from the central fixation cross: top-left, top-right, bottom-left and bottom-right of the central fixation cross (Figure 4.1A). In one of the locations, the square was presented with a regular inter-onset time interval (the structured location), while the squares in the other three locations were presented with a random time interval (the random locations). All shapes had a size of 3.3° and were presented on a white background.

Visual search task. The visual search displays consisted of one T-shaped target and three L-shaped distractors (Figure 4.1B). All shapes had a size of 3.3°. The four shapes were presented in the same four locations as the square stream. The target T-shape could point left (i.e., rotated 90°) or right (i.e., rotated 270°). The direction of the target was counterbalanced. The distractors consisted of an L-shape or an inverted L-shape, rotated 0° or 270°. The pointing direction of the distractors and target was counterbalanced in each visual search display, so that always two shapes pointed to the left and two shapes pointed to the right. The location of the shapes was randomized for each trial.

Apparatus. Stimuli were presented on a 1280 × 1024 Iiyama ProLite G2773HS screen with a refresh rate of 100 Hz. The experiment was built using Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007) in Matlab 2015.

Procedure. At the start of the experiment, participants were instructed that they would complete search tasks by finding the target T-shape among three distractor L-shapes and indicating whether it pointed to the left or the right as accurate and fast as possible. In addition, the participants were given the instruction that, between the search trials, they had to focus on the screen while task-irrelevant squares are presented.

In the structured location, the square was presented rhythmically with an ISI of 1.5 s. In the other three, random locations the same total number of squares was presented over the course of the experiment. However, the timing of the presentation of these squares was randomized, with the constraint that their onset could only be 0, 0.3, 0.6, 0.9, or 1.2 s relative to the onset of the square in the structured location. In total, a square was presented 1120 times in each of the four locations. The structured and the random squares were always presented for 0.05 s.

Interrupting the square stream, 120 search trials were displayed over the course of the experiment. Each search trial consisted of a 0.75 s presentation of the visual search display, followed by a 0.75 s presentation of a central fixation cross. During the search trial, the participant could indicate whether the T-shape pointed to the left or right by pressing the Z or the M-key, respectively. If the participant did not give a response during the presentation of the search trial, the central fixation

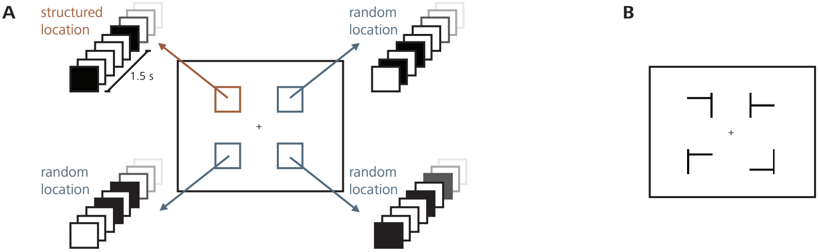


Figure 4.1. A) Overview of the stimuli in Experiment 1a. Black squares appeared briefly at four locations on the screen. In one of the locations (counterbalanced over participants, but the top left in this example), the square appeared with a regular rhythm with an ISI of 1.5 s (i.e. the structured stream). In the other three locations, the interval between the squares was random, but always 0, 0.3, 0.6, 0.9, or 1.2 s relative to the onset of the square in the structured location. B) The presentation of squares was occasionally interleaved by a visual search display, in which the task was to find the target T-shape among distractor L-shapes, and indicate its orientation.

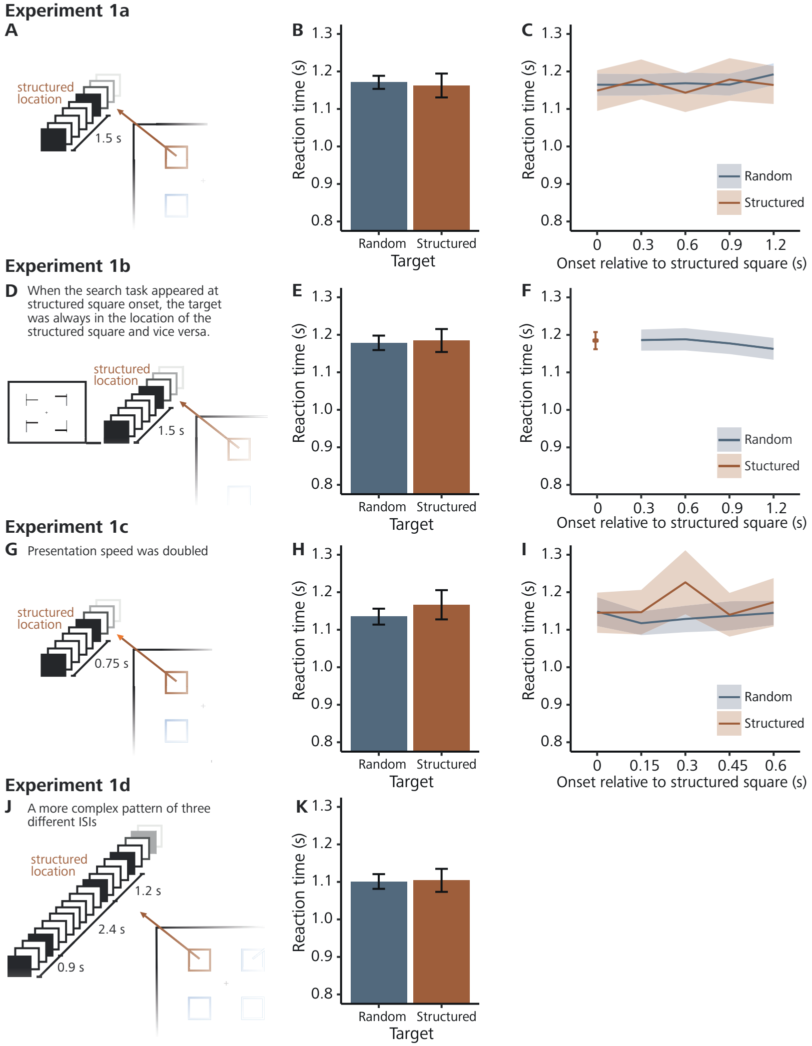
cross was presented until a response was given. The onset of the search trials was random, with the constraint that an equal number of trials was presented at five different onset intervals relative to the square in the structured stream: 0 (i.e., the search trial appeared at the expected onset of the structured square), 0.3, 0.6, 0.9, or 1.2 s. Thus, over the course of the experiment, 24 search trials were presented at each of these potential onset intervals.

The experiment was divided into four equal size blocks. In between the blocks, participants were instructed that they could take a break before continuing. After the experiment, participants filled in a short questionnaire in which they indicated whether they had noticed a pattern in the search trials or in the flashing black squares. For both questions, they were asked to describe the pattern if they indicated that they had noticed a pattern. After this, participants were informed about the regular nature of the square in one of the four locations and asked to identify the structured location. The experiment script is available at: https://osf.io/pnc4q/.

Results.

Target location. Figure 4.2B shows the average reaction time for the structured location compared to the random location. To test whether participants were faster in the structured location than in the random location, we created Linear Mixed Models (LMMs) using the *lme4* package (version 1.1-10; Bates et al., 2015) in R version 3.2.2 (R Development Core Team, 2008). In addition to the LMMs, in order to quantify the evidence in favor of the null hypothesis, we calculated Bayes factors using the *lmBF* function from the *BayesFactor* package in R (Morey et al., 2014). We will denote the evidence for the null hypothesis (H_0) over the alternative hypothesis (H_1) as BF_{01}. Only correct responses were included in the analysis. In addition, reaction times higher than 4 s were excluded from analysis. Reaction time was entered as the dependent variable and Subject was entered as a random factor. A variable coding whether the target was in the structured location was entered as a fixed factor. To control for a potential advantage of the actual location of the target, target location (top left, top right, bottom left, or bottom right) was also included as a fixed factor. In addition, the random slope of target location improved the model, and was therefore included. All analysis scripts and data are available at: https://osf.io/pnc4q/.

We found no difference in reaction time when the target appeared in the structured location compared to the random locations (β = -0.02, t = -0.52, p = .601, BF_{01} = 21.09). Including target location improved the model significantly ($\chi^2(3)$ = 43.76, p < .001, BF_{01} < 0.01). However, after inclusion of random slopes for target location, a post-hoc Tukey's HSD test showed that no difference in reaction time between the locations reached significance (ps > .068), suggesting no or only minor global effects of target location on reaction time.



Target onset. Figure 4.2C shows the reaction time for targets at the structured and the random location at the different onset times relative to the presentation of the rhythmic square. To test whether responses were faster at the moment of structured location onset, we compared an LMM including onset time as a fixed factor with a model excluding this factor. We found that the inclusion of onset time did not improve the fit of the model ($\chi^2(4) = 2.63$, $p = .622$, $BF_{01} > 100$).

◂ **Figure 4.2.** A) Temporal regularity at the structured location in Experiment 1a. A black square was presented isochronously with an ISI of 1.5 s, whereas the same black square was presented with random timing at the random locations. B) Average reaction times for targets in the structured or random locations in Experiment 1a. C) Average reaction times for targets in the structured or random locations as a function of target onset, relative to the onset of the structured square (e.g., 0 indicates that the search task appeared at the moment that the square would otherwise appear at the structured location). D) Change of the procedure in Experiment 1b, compared to Experiment 1a. E) Average reaction times for targets in the structured or random locations in Experiment 1b. F) Reaction times for the different onsets relative to the structured square in Experiment 1b. Given the more informative nature of the task, the target at the structured location always appeared at t=0, i.e. the moment that the structured square would have appeared. G) Change of the procedure in Experiment 1c, compared to Experiment 1a. H) Average reaction times for targets in the structured or random locations in Experiment 1c. I) Average reaction times for targets in the structured or random locations as a function of target onset in Experiment 1c. J) Change of the procedure in Experiment 1d, compared to Experiment 1a. K) Average reaction times for targets in the structured or random locations in Experiment 1d. In all figures, error bars represent within-subject confidence intervals (Morey, 2008).

Accuracy. Average accuracy for the orientation of the targets in the visual search task was 85.95% (*SD* = 9.69).

Questionnaire. Ten participants reported that they had noticed a pattern in the appearance of the squares, but none of the participants reported the rhythmic appearance of the square in one of the locations. When asked to identify the structured location after the experiment, 20.83% of the participants identified the correct location (chance level: 25%).

Experiment 1b

In Experiment 1a, we investigated whether attention was biased towards a location in which a stimulus appeared with temporal regularity. The results of the search task showed that there was no reliable difference in reaction time between this structured location and locations containing no regular timing. These findings suggest that attention was not spontaneously biased towards the implicit regularity. As we intended to test the spontaneous attentional bias towards temporal regularity, the structure in Experiment 1a was not informative about the onset of the search task, nor of the location and orientation of the target. That is, participants could not use the structure to decrease their response times or predict where the target would appear. This leaves open the question whether participants would be biased towards the implicit regularity when it can be used to optimize performance in the search task. To this end, in Experiment 1b, we manipulated the predictability of the search task, so that trials in which the target appeared at the structured location exclusively appeared at the expected onset of the structured square. Thus, in this case, the location of the target could be predicted by the onset of the search task, increasing the utility of attending to the temporal regularity.

Methods. Forty-four participants enrolled in the Bachelor program Psychology at the University of Groningen (23 female, mean age 20.5, range 17-26) participated in the experiment in exchange for course credits. Stimuli, apparatus and procedure were similar to Experiment 1a. In contrast to Experiment 1a, however, the timing of the onset of the visual search task was predictive of the location of the target: When the search task appeared at structured square onset, the target was always in the location of the structured square and vice versa (Figure 4.2D). Thus, the 25% of the trials in which the target was at the structured location was presented at structured square onset, and the other 75% of the trials was presented 0.3, 0.6, 0.9, or 1.2 s after the onset of the structured square.

Results.

Target location. Figure 4.2E shows the average reaction time for targets at the structured and random location. The same LMM as in Experiment 1a was performed. We found no difference in reaction time for targets in the structured or the random location ($\beta = 0.02$, $t = 0.65$, $p = .518$, $\mathrm{BF}_{01} = 22.51$). Again, including Target location improved the model ($\chi^2(3) = 46.86$, $p < .001$, $\mathrm{BF}_{01} < 0.01$). A post-hoc Tukey's HSD test showed faster reaction times for the two top locations compared to the bottom left location (*p*s < .046). No other contrasts reached significance (*p*s > .201).

Accuracy. Average accuracy in the search tasks was 84.24% (*SD* = 10.64).

Questionnaire. Seven participants reported that they had noticed a pattern in the presentation of the squares, but none of the participants reported that the square appeared rhythmically in one of the locations. In the forced-choice questionnaire, 20.45% of the participants identified the correct structured location (chance level: 25%).

Experiment 1c

In Experiment 1a and 1b, the isochronous stimulus was presented with an ISI of 1.5 s. One reason for the absence of an attentional bias towards this stimulus in these experiments might be that the presentation rate was too slow to (implicitly or explicitly) notice the regularity: the integration of the statistical regularity of stimuli might become more difficult when they are presented with a long ISI. For example, attentional entrainment studies have employed presentation rates faster than the current 0.66 Hz (e.g., Henry & Obleser, 2012; Jones et al., 2002; Mathewson et al., 2010). To test this hypothesis in the current experiment, we increased the presentation rate of squares at the structured and the random location. To balance the increase of speed with the ability to present the random stimuli at timeslots between the regular stimulus, we doubled the speed compared to Experiment 1a and 1b.

Methods. Twenty-seven participants (21 female, mean age 23.8, range 19-31) participated in the experiment in exchange for a 7-euro payment. Stimuli, apparatus and procedure were similar to Experiment 1a. In the current experiment, however, the presentation speed of the square at the structured location was twice as fast as in Experiment 1a: the ISI was 0.75 s instead of 1.5 s (Figure 4.2G). To keep the duration of the experiment, and the average duration between two consecutive search trials, the same as in Experiment 1a, the number of presented squares at the structured and random location was doubled (i.e., a total of 2240 presentations at each location).

Results.

Target location. Figure 4.2H shows the average reaction time for the search task with the target appearing in the structured and the random location. The same LMM as in Experiment 1a and 1b showed that the reaction time did not differ between the structured location and the random locations ($\beta = 0.02$, $t = 0.64$, $p = .526$, $BF_{01} = 3.99$). Again, including target location improved the model ($\chi^2(3) = 32.36$, $p < .001$, $BF_{01} < 0.01$). However, no post-hoc contrasts between the locations reached significance (ps > .147).

Target onset. Figure 4.2I shows the reaction time as a function of timing of the search task relative to the onset of the structured square. We found that including onset time in the LMM did not improve the model fit ($\chi^2(4) = 2.35$, $p = .672$, $BF_{01} > 100$).

Accuracy. Average accuracy in the search tasks was 80.94% (*SD* = 14.62).

Questionnaire. Ten participants reported that they had noticed a pattern in the presentation of the squares, but none of the participants reported noticing the rhythmic appearance of the square in one location. In the forced-choice question, 18.52% of the participants identified the correct location (chance level: 25%).

Experiment 1d

The regularity in Experiment 1a, 1b and 1c consisted of a simple isochronous stimulus. This regularity could be considered as simpler than the order regularities of Zhao et al. (2013). In interacting with their environment, humans might optimize learning by attending to medium levels of complexity, instead of stimuli that are either too predictable or too complex (the “Goldilocks effect”: Kidd, Piantadosi, & Aslin, 2012, 2014). In the current experiment, we therefore increased the temporal complexity of the rhythmic stimulus for closer correspondence with Zhao et al.’s work.

Methods. Thirty-five participants (29 female, mean age 19.57, range 18-23) participated in the experiment in exchange for a 7-euro payment. Stimuli, apparatus and procedure were similar to Experiment 1a. However, instead of an isochronous rhythm, the presentation of the square at the structured location followed a more complex repeating pattern. The following series of ISIs was repeated: 0.9 s, 2.4 s, 1.2 s (Figure 4.2J).

Results.

Target location. Figure 4.2K shows the average reaction time for search trials in which the target was in the structured or random location. The same LMM as in the previous experiments showed that there was no evidence for a difference in reaction times between these locations (β = -0.01, t = -0.21, p = .838, BF_{01} = 22.36). Target location did not improve the model ($\chi^2(3)$ = 6.29, p = .099, BF_{01}= 85.69).

Accuracy. The average accuracy in the search tasks was 78.92% (SD = 18.80).

Questionnaire. Eight participants reported noticing a pattern in the structured squares, however, no participants reported seeing a repeated rhythmic pattern in one particular location. When asked to identify the structured location, 17.14% of the participants were correct (chance level: 25%).

Discussion Experiment 1

In Experiment 1, we tested whether attention is spontaneously biased towards temporal regularities. In four studies, we presented a stimulus with a temporal regularity in one location on the screen. We hypothesized that if attention was biased towards this location, reaction times to targets presented in this location would be faster. However, we found no evidence for a difference in reaction times between the structured and the random location.

Three critical features of Experiment 1a might have prevented an attentional bias, which we subsequently manipulated in follow-up experiments. First, whereas attention was not spontaneously biased towards regularity, it might be biased when the temporal structure is useful for the task at hand. In Experiment 1b, we tested whether adding temporal predictability to the search task would increase a potential attentional bias towards the regular stream. However, the results again showed no decreased response time in the structured location, indicating that attention was not biased towards the structured stream. Thus, even when the temporal structure could be used to optimize task performance, no attentional bias was observed.

Second, previous experiments showing entrainment of attention to isochronous stimuli, have often used slightly faster presentation rates than the ISI of 1.5 s used in Experiment 1a and 1b (e.g., Henry & Obleser, 2012; Jones et al., 2002; Mathewson et al., 2010).. In Experiment 1c we therefore doubled the presentation rate, to test whether this might induce an attentional bias. Yet, in line with Experiment 1a and 1b, we found no difference in reaction time between the structured and random location, nor did we find entrainment effects (i.e., the reaction time did not depend on the onset of the search task) and, as in Experiments 1a and 1b, participants were unable to report the nature of the regularity.

Third, given the proposed inverted U-shape relation between stimulus complexity and attention (Kidd et al., 2012, 2014), the regularity in Experiment 1a might have been too simple to bias attention. In Experiment 1d, we therefore replaced the simple isochronous stimulus with a more complex pattern consisting of three consecutive ISIs. In line with the previous experiments, however, we found no evidence for spontaneous increased attention towards this pattern. Overall, these four experiments consistently showed that attention was not spontaneously biased towards temporal regularities and that participants were unable to explicitly report the nature of the temporal structure. In addition to the notion of regularity complexity, the use of simpler stimuli (squares) compared to the complex shapes in Zhao et al. (2013) could induce more peripheral processing, requiring less attention towards one particular spatial stream. Although also in Zhao et al. (2013) "participants were instructed to fixate while attending to the four locations" (p. 669), this potential difference in spatial attention may reduce a spatial bias. In Experiment 2, however, we will present colored stimuli in the center of the screen, so that these differences in spatial processing do not play a role.

While Zhao et al. (2013) found a spatial bias towards a stream containing regularly ordered stimuli, they also showed that this bias could be generalized to features other than location. For example, they showed that when a colored structured stream was interleaved with a random stream in a different color, there was a bias towards the structured color. Zhao et al. (2013) found that, in general, responses were faster when the target was colored compared to when a distractor was colored. Crucially, however, this difference was larger for the color associated with the structured compared to the random stream.

While we found no evidence for an attentional bias towards the location of the regular stimulus in Experiment 1, it is possible that a bias exists towards other features associated with temporal regularity. Therefore, in Experiment 2, we tested whether attention is biased towards the color of a temporally structured compared to a random stream. A stream of circles was presented in the center of the screen. The circles appeared in two colors: orange and blue. One of these colors appeared always after a regular inter-onset interval, while the other color appeared equally often, but with a random timing. Occasional visual search tasks appeared, in which one of the four items was colored. We expected faster reaction times when the target stands out by color compared to when a distractor is colored. However, if attention is biased towards the features of the regular stream, we expected that this difference in reaction times is larger for the structured color compared to the random color.

Experiment 2: Color bias

Experiment 2a

Methods.

Participants. Forty-five participants enrolled in the Bachelor program Psychology at the University of Groningen (37 female, mean age 20, range 17-26) participated in the experiment in exchange for course credits. The Psychology Ethical Committee of the University of Groningen approved the experimental protocol (16030-S-NE). All participants gave written informed consent prior to the experiment. The participants were naive to the purpose of the study, but received a debriefing after the experiment. Two participants were excluded from analysis, because they did not adhere to task instructions.

Stimuli.

Circle stream. The circle stream consisted of a sequential presentation of an orange and blue circle at the center of the screen (Figure 4.3A). The size of the circles was 3.3° and the orange color was luminance-matched to the blue color (rgb values: 0, 127, 255) using a luminance meter. One of the colored circles was presented with a regular inter-onset time interval (the structured color), while the other colored circle was presented with a random time interval (the random color). The structured color (i.e., either orange or blue) was counterbalanced over participants. In between the presentations of the structured and random colored circles, a light grey circle was presented as a fixation stimulus (rgb values: 230, 230, 230). All stimuli were presented on a white background.

Visual search task. Visual search displays were identical to Experiment 1a and 1b. However, whereas three shapes in the visual search displays were presented in black, one of the shapes was colored orange or blue: the singleton (Figure 4.3B). In 50% of the trials, the singleton was the same color as the structured circle, and in the other 50% of the trials, the singleton was the color of the random circle. For both singleton colors, the singleton was the target in 25%, and the distractor in 75% of the trials. Thus, the singleton was not informative about the target location or orientation.

Apparatus. Apparatus was similar to Experiment 1a and 1b.

Procedure. At the start of the experiment, participants were instructed that they would complete search tasks, by finding the target T-shape among three distractor L-shapes and indicating whether it pointed to the left or the right as accurate and fast as possible. They were instructed that the color of the singleton did not predict the target location. In addition, the participants were given the instruction that, between the search trials, they had to focus on the task-irrelevant circles at the center of the screen.

The structured circle was presented rhythmically with an ISI of 1.5 s. The timing of the presentation of the random circle was random, but always 0.3, 0.6, 0.9, or 1.2 s after the onset of the structured circle. The structured and the random circle were always presented for 0.15 s. In total, both circles were presented 1120 times. In between the presentations of the structured and random circle, the grey circle was presented.

Interleaving the circle stream, 160 search trials were displayed over the course of the experiment. Each search trial consisted of a 0.75 s presentation of the visual search display, followed by a 0.75 s presentation of a central fixation cross. During the search trial, the participant could indicate whether the T-shape pointed to the left or right by pressing the Z or the M-key, respectively. If the participant did not give a response during the presentation of the search trial, the central fixation cross was presented until a response was given. The onset of the search trials was random, with the constraint that an equal number of trials was presented at five different onset intervals relative to the structured circle: structured circle onset, 0.3, 0.6, 0.9, or 1.2 s after structured circle onset. Thus, over the course of the experiment, 32 search trials were presented at each of these potential onset intervals.

The experiment was divided into four equal size blocks. In between the blocks,

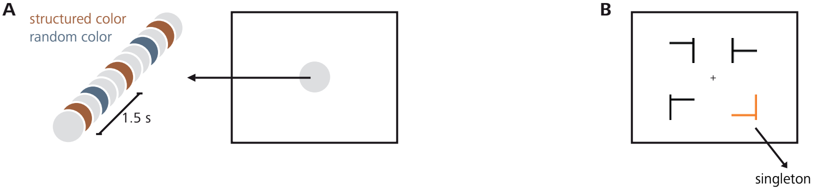


Figure 4.3. A) Overview of the stimuli in Experiment 2a. A sequence of circles was presented at the center of the screen. One colored circle appeared with a fixed rhythm (counterbalanced over participants, but the orange circle in this example), whereas the other colored circle appeared equally often, but with random timing (here, the blue circle). B) Occasional search displays appeared, in which one of the shapes was colored either blue or orange: the singleton. We refer to the singleton as structured if it matched the structured color, and random if it matched the random color. The singleton could be the target T-shape or one of the distractor L-shapes.

participants were instructed that they could take a break before continuing. After the experiment, participants filled in a short questionnaire in which they indicated whether they had noticed a pattern in the search trials or in the colored circles. If they had noticed a pattern, they were asked describe it.

Results.

Target color. Figure 4.4B shows the average reaction time for whether the singleton was the structured or random color and whether the singleton was the target or one of the distractors. An LMM was performed with reaction time as the dependent variable and subject as a random factor. Singleton color (structured or random) and singleton type (distractor or target) were entered as fixed factors. To control for a potential advantage of the actual location of the target, target location (top left, top right, bottom left, or bottom right) was also included as a fixed factor. The random slope term for target location improved the model fit and was included in the final model. Only correct responses were included in the analysis. In addition, reaction times higher than 4 s were excluded from analysis.

When the colored singleton was the target, participants respond faster than when the singleton was a distractor (β = -0.10, t = -6.83, p < .001, BF_{01} < 0.01). However, there was no difference between the reaction times between the structured and random color (β = -0.01, t = -1.36, p = .174, BF_{01} = 24.56). We expected that attention would be spontaneously biased towards the color of the structured circle, which would hypothetically lead to a faster reaction time for the structured color target and a slower reaction time for the structured color distractor (i.e. an interaction effect of singleton color and singleton type). However, this predicted interaction was not observed (β = 0.02, t = 0.85, p = .398, BF_{01} = 13.85).

Target location. Again, including target location improved the model significantly ($\chi^2(3)$ = 42.88, p < .001, BF_{01} < 0.01). A post-hoc Tukey's HSD test showed that reaction times to targets appearing at the top right position were faster than at the bottom right position (p = .046). No other contrasts reached significance (ps > .060).

Target onset. Figure 4.4C shows the average reaction time in the different singleton conditions for the five possible onsets relative to the structured color circle. Including target onset, relative to the structured circle, did not improve the fit of the model ($\chi^2(4)$ = 2.04, p = .728, BF_{01} > 100).

Accuracy. Average accuracy in the visual target detection task was 87.76% (SD = 8.62).

Questionnaire. Nine participants reported that they had noticed a pattern, but none correctly reported the rhythmic nature of the structured circle.

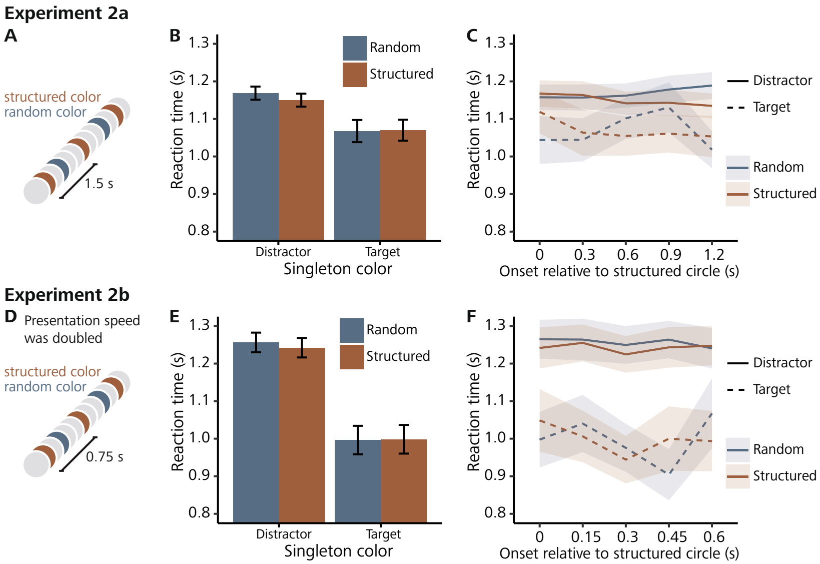


Figure 4.4. A) Overview of the stimuli presented at the center of the screen in Experiment 2a. B) Average reaction times for the search task in Experiment 2a, in which the colored singleton could be either the target or a distractor. In addition, the singleton could be presented in the structured or the random color. C) Average reaction times as a function of the onset relative to the presentation of the circle with the structured color in Experiment 2a. A) Stimuli presented at the center of the screen in Experiment 2b. The presentation speed was twice as fast as in Experiment 2a. E) Average reaction times in Experiment 2b for the singleton targets and distractors, presented in the random or structured color. F) Average reaction times as a function of the onset relative to the presentation of the circle with the structured color in Experiment 2b. In all figures, error bars represent within-subject confidence intervals.

Experiment 2b

In a similar manipulation as in Experiment 1c, we doubled the presentation rate of the stimuli in Experiment 2b. This resulted in an ISI of 0.75 s between two consecutive structured color stimuli.

Methods. Twenty participants enrolled in the Bachelor program Psychology at the University of Groningen (11 female, mean age 23.2, range 18-30) participated in the experiment in exchange for course credits. The procedure was similar to Experiment 2a, however, in a manipulation similar to Experiment 1c, we doubled the presentation speed (i.e., an ISI of 0.75 s for the rhythmic color) and the number of presented circles. Thus, the total duration of the experiment, as well as the average interval between consecutive search trials, was identical to Experiment 2a.

Results.

Target color. Figure 4.4E shows the average reaction times for the different singleton conditions. The same LMM as in Experiment 2a was performed. The model showed faster reaction times for singleton targets compared to singleton distractors (β = -0.25, t = -11.96, p < .001, BF_{01} < 0.01). There was no difference in reaction time between the structured and the random color (β = -0.01, t = -0.94, p = .346, BF_{01} = 18.24). In line with Experiment 2a, the effect of singleton type was not stronger for the structured compared to the random color (β = 0.01, t = 0.42, p = .676, BF_{01} = 12.08).

Target location. Including target location did not improve the model significantly ($\chi^2(3)$ = 2.71, p = .438, BF_{01} > 100), indicating that the reaction time did not differ between the four locations in which the target could appear.

Target onset. Figure 4.4F shows the reaction time for the different search trial onsets relative to the structured circle. Model comparison showed that the response time did not depend on the onset of the search task relative to the structured circle ($\chi^2(4)$ = 3.56, p = .470, BF_{01} > 100).

Accuracy. Average accuracy in the search tasks was 87.43% (*SD* = 14.09).

Questionnaire. Six participants reported a to have noticed a pattern in the colored circles, but none identified the rhythmic nature of one particular color correctly.

Discussion Experiment 2

In Experiment 2a, we have tested whether attention was spontaneously biased towards the color features associated with an isochronous stimulus. As expected, we found that reaction times were faster when the colored singleton was the target than when it was a distractor. However, this difference was similar for the structured color and the random color. In addition, overall reaction times were similar for the structured compared to the random color. Decreasing the ISI of the isochronous, regular stimulus (in Experiment 2b) did not affect this pattern of results. In line with Experiment 1, these findings do not provide evidence that participants were biased towards the features associated with temporal structure.

General discussion

We aimed to test whether attention is biased towards implicit metrical temporal regularities. In that case, we expected faster reaction times when targets in the search tasks matched the features of the regular stimulus. However, we found no difference in reaction time between the structured and random location (Experiment 1) or color (Experiment 2), failing to support the hypothesis that the present temporal regularity is prioritized over the random streams. We instead found some evidence that reaction times were faster for targets presented at the top of the search screen compared to the bottom. In addition, response time did not depend on the onset of the search task relative to the structured stream, suggesting that attention was not entrained to the isochronous stimulus.

Overall, our results show that attention was not biased towards the temporal regularities in the task. Thus, whereas previous studies have shown that temporal structure can be used to optimize attention and perception when the regularities reliably predict upcoming stimuli (Correa, Lupiáñez, & Tudela, 2005; Martens & Johnson, 2005; Niemi & Näätänen, 1981; Olson & Chun, 2001; Willems et al., 2015), the current results suggest that this might not be the case when such regularities are uninformative about the task at hand. A potential explanation is that, in the latter case, prioritizing attention to temporal regularities might actually be detrimental for task performance. Indeed, Schroeder and Lakatos (2009) proposed that the brain can operate in either a 'rhythmic' or a 'continuous' mode, depending on the nature of the task. The rhythmic mode is activated when the task contains a task-relevant rhythm, resulting in low-frequency entrainment of the sensory cortex and, thereby, enhanced perceptual sensitivity to stimuli that are in phase with the rhythm. However, if the task contains no relevant rhythm, the brain can operate in continuous mode. By suppressing low-frequency oscillations and enhancing gamma-band oscillations, a more continuous state of vigilance is achieved to deal with the temporal unpredictability of the upcoming stimuli. In this way, the cost of lower sensitivity in the low-excitability phase of the neural entrainment can be prevented.

A similar argument can be made to explain the apparent discrepancy between our results and Zhao et al. (2013), who found that attention was spontaneously biased towards features of a stream with a regular order. They proposed that attention and statistical learning could act in a closed-loop way: the fulfillment of predictions based on previous learning might increase attention, which in turn enhances learning. Crucially, however, we have shown here that this bias does not generalize to metrical temporal regularities. Although the statistical learning of order regularities might bias attention towards associated features, it does not necessarily interfere with the processing of the unpredictable search task. An attentional bias towards a rhythmic visual stimulus, in contrast, may come at the cost of diminished continuous sensitivity. In Experiment 1b, we tested whether there was a bias towards regularities when they were partly informative about the onset of the search task. In this experiment, trials in which the target appeared at the structured location always appeared at the expected onset of the structured square. While we found that there was still no attentional bias in this case, the manipulation only added predictability for part of the trials (i.e., trials that appeared at one particular phase), and attentional entrainment might therefore not have contributed significantly in optimizing task performance.

Although neural oscillations may reduce continuous sensitivity, previous studies have shown that attention can be guided by the phase of rhythmic stimuli, even when they are not necessarily related to the task at hand. For example, rhythmic stimuli have been shown to facilitate auditory and visual detection at specific phases in the rhythm (Bolger, Coull, & Schön, 2014; Henry & Obleser, 2012; Jones et al., 2002; Kösem & van Wassenhove, 2012; Mathewson et al., 2010). Our findings suggest that these temporal phase biases do not generalize to non-temporal features of the regular stimuli, such as, in this case, location and color. However, we also did not find an effect of phase on reaction time. One potential explanation for this absence, as well as the general absence of an attentional bias, might be that the temporal regularities in our experiments were too implicit and could therefore not be learned. Indeed, in contrast to the entrainment studies, the present rhythmic stimulus was embedded in other stimulus streams, without explicit instruction to pay attention to the rhythmic stream. Our questionnaire data showed that participants did not explicitly learn the regularities, but the results do not provide conclusive evidence about the precise nature of the learning. As implicit learning may be a prerequisite for an attentional bias, future studies could assess implicit learning after the experiment with, for example, a two-alternative forced choice task, in which participants have to pick the most familiar stimulus from a regular stimulus (as presented in the experiment) and a foil stimulus (Zhao et al., 2013).

A related point of consideration is the frequency at which the regular stimulus is presented. Whereas we used an ISI of 1.5 s (0.67 Hz, similar to the 0.5 Hz entrainment used by Bolger et al., 2014) in Experiment 1a, 1b, 1d, and 2a, previous studies showing an entrainment effect have often used slightly higher frequencies (e.g., 3 Hz in Henry & Obleser, 2012; 1.67 Hz in Jones et al., 2002; 12 Hz in Mathewson et al., 2010). It is possible that the relatively low frequency impeded the detection of, or the entrainment to, the structured stimulus. Therefore, we also tested an ISI of 0.75 s (1.33 Hz, matching the range used by Kösem &

van Wassenhove, 2012, who showed improvements in the 0.6-1.4 Hz range) in Experiment 1c and Experiment 2b. The results, however, were similar to those of the slower paradigms, indicating that increasing the presentation rate did not enhance a potential attentional bias.

At first sight, the regularities presented in our experiments might seem less complex than the order regularities in Zhao et al. (2013). Zhao et al.'s stimuli consisted of three sets of three shapes that always appeared in the same order, contrasted by a randomly sequenced set of nine shapes. In contrast, our temporal regularities consisted of a simple isochronous stimulus. The complexity of a stimulus has been suggested to influence the attention and learning strategy of an observer, given the observer's current mental representations (Berlyne, 1960; Dember & Earl, 1957). An optimal learning strategy in our dynamic world might involve seeking to minimize the prediction error and to maximize mutual information between the observers' mental representations and the environment, leading to a preference for conditions that are neither too predictable nor too complex (Clark, 2018; Little & Sommer, 2013). At this 'sweet spot' of optimal learning, cognitive resources are not wasted on stimuli that do not allow us to improve our understanding, and our predictions, of the world (Kidd & Hayden, 2015). Indeed, infants have been shown to pay most attention to visual event sequences of medium-level complexity, a phenomenon that has been dubbed the "Goldilocks effect" (Kidd et al., 2012, 2014).

Given the Goldilocks effect, the regularity in the current study could be too simple. This might have influenced a potential attentional bias in three ways. First, if we increase the complexity of the isochronous regularity, we would potentially find a spontaneous attentional bias. We tested this notion in Experiment 1d, in which the simple isochronous stimulus at the regular location was replaced by a square that was presented in a rhythmic, yet more complex pattern with three different, sequential ISIs. However, in line with Experiment 1a, the results showed no difference in reaction time between the structured and the random location. In addition, the questionnaire results showed that, also with this more complex stimulus, participants did not notice the regularity. Second, if the regularities were indeed simple, participants might have become aware of them and this might have led to explicit attentional strategies. However, none of the participants in the six experiments reported the rhythmic nature of one of the stimuli in post-experiment questionnaires, indicating that participants were unaware of the temporal regularities. This is in line with Zhao et al. (2013), who found indications of explicit awareness of the order regularities for only 3 out of 47 participants in Experiment 1 and 2. In addition, their response time effects were still reliable after the exclusion of participants who had noticed any regularity. Third, the high predictability of the simple isochronous stimulus might have led to a decrease in attentional bias over time. Indeed, prolonged presentations of regularities might lead to habituation and, thereby, a decrease in attention to repeated stimuli (Turk-Browne, Scholl, & Chun, 2008). In this case, we might expect that the regularity initially attracts attention, but over time, habituation decreases attention to the predictable stimulus. Therefore, as a post-hoc analysis, we tested the effect of habituation by adding experimental block (i.e., the experiments were divided in four blocks) to the mixed models. Whereas the models showed that the overall reaction time decreased over blocks (χ^2s > 75.83, *p*s < .001, BFs_{01} < 0.01), we found that the difference in reaction time between the structured and random location did not decrease in Experiment 1a-1d (χ^2s < 3.39, *p*s > .066, BFs_{01} > 3.93). In Experiment 2a and 2b, we found that the interaction between singleton type and color did not change over blocks (χ^2s < 5.96, *p*s > .114, BFs_{01} > 100). Thus, we found no evidence for an initial attentional bias that decreased over the course of the experiment. Overall, these results suggest that the current regularities were not too simple with regard to the Goldilocks rule.

On the other hand, certain sequence and stimulus features may have hampered participants' ability to pick up on the regularities. First, the similarity of the presented squares (in Experiment 1) and colored circles (in Experiment 2) might cause an automatic overwriting of items currently held in working memory (Alvarez & Thompson, 2009). Second, in Experiment 1, the presented squares at four locations on the screen were marked by abrupt visual onset. As it has been shown that object onsets capture attention (Yantis & Jonides, 1984) and may lead to automatically storing an object in working memory (Schmidt, Vogel, Woodman, & Luck, 2002), the onsets of the squares at the random location might have prevented an attentional bias towards the structured location. In this case, we would expect faster reaction times when, in one particular location, a target appears right after the presentation of a square. However, we did not find such a decreased response time when analyzing the effect of target onset relative to the structured square (in Experiments 1a and 1c). Future studies might investigate whether the detection of temporal regularities is improved by using sufficiently different stimuli, presented without a sharp onset.

In the current study, we have focused on rhythmic visual stimuli. However, compared to, for example, order or spatial regularities, a potential bias towards structured temporal information might be more apparent in the auditory than the visual modality. Although there is abundant evidence for sensitivity to visual temporal regularities, rhythmic processing of auditory information has been shown to be more precise than, and dominant over, visual information (e.g., Chen, Repp, & Patel, 2002; Kolers & Brewster, 1985; Recanzone, 2003; Repp & Penel, 2002). Future studies could test whether these modality differences influence a potential attentional bias towards metrical temporal structure.

In summary, in six experiments we found strong evidence that attention was not spontaneously biased towards implicit temporal regularities when they were not relevant for the task at hand. Whereas people might optimize task performance by exploiting regularities, the processing of irrelevant features of temporally regular events does not seem to be prioritized.

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5

temporal context actively shapes eeg signatures of time perception

Abstract

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

Introduction

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

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

In humans, evidence is now emerging that electroencephalography (EEG) signatures in timing tasks are modulated by recently perceived durations. Wiener and Thompson (2015) found that the contingent negative variation (CNV) in a bisection task reflected the duration presented in the previous trial. Specifically, the CNV amplitude was more negative when the prior duration was longer, while, behaviorally, the bisection point also increased with longer previous durations. Wiener and Thomson therefore suggested that the CNV reflects shifts in the standard interval in memory based on previous experience. The CNV is a slow negative deflection in the fronto-central EEG signal that is often found in perceptual and motor timing tasks (for a review, see Kononowicz & Penney, 2016). While the CNV has been proposed to reflect the neural counterpart of accumulation in pacemaker-accumulator models (Macar & Besson, 1985; Macar & Vidal, 2004; Macar, Vidal, & Casini, 1999; Macar & Vitton, 1982; Pfeuty, Ragot, & Pouthas, 2005), more recent findings have challenged this hypothesis (Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011) by showing habituation effects (Kononowicz & Van Rijn, 2011), plateauing (Ng, Tobin, & Penney, 2011) and temporal sensitivity after CNV resolution (Kononowicz & Van Rijn, 2014). Specifically, Kononowicz and Van Rijn (2014) showed that the N1P2 component after interval offset reflected the distance to the standard interval in a comparison task, and was a better predictor of behavioral performance than the CNV.

In addition to the CNV, the power of beta oscillations around the average interval offset has been shown to increase with longer previous durations in a bisection task, potentially reflecting updating of the subjective standard interval to which the intervals are compared (Wiener, Parikh, Krakow, & Coslett, 2018). Beta oscillations have recently been shown to be involved in different timing processes (Arnal, Doelling, & Poeppel, 2015; Bartolo & Merchant, 2015; Kononowicz & Van Rijn, 2015; Kulashekhar, Pekkola, Palva, & Palva, 2016), potentially as an index of motor inhibition during time interval productions (Kononowicz & Van Rijn, 2015).

Crucially, the temporal context studies outlined above required an active comparison to the standard interval, in which EEG signatures have been shown to reflect an adjustment of the decision threshold (Ng et al., 2011). So, any context-based changes in these signatures might reflect updating of the comparison process. It is therefore still an open question whether purely perceptual processes are affected by the prior. In addition, Wiener and Thompson (2015) and Wiener et al. (2018) only tested the effect of the previous trial (i.e., sequential context effects), whereas the effect of global temporal context built up over the course of an experimental block on EEG signatures is still unknown. We tested these questions in an interval reproduction task, which allowed us to distill EEG effects during the perception phase in which no decision or motor response was required. Participants reproduced two different interval ranges (the *short* and the *long context*). The ranges shared one interval (the *overlapping interval*), providing a condition in which the physical stimulus was the same, but the temporal context was different. To test the effect of temporal context on purely perceptual processes, we focused on three EEG signatures during the perception phase that have previously been associated with time perception: the CNV, the offset P2 and beta oscillations. If the CNV would represent the state of an absolute accumulator, we would expect a more negative CNV in the long compared to the short context: after all, the overlapping interval is subjectively estimated as being longer in the long context. If, however, the CNV represents a process of anticipating interval offset, the reverse effect is expected: a more rapid negative deflection in the short compared to the long context. The offset P2, on the other hand, might reflect both the actual duration (e.g., Pereira et al., 2014; Röder, Rösler, & Neville, 2000) and contextual expectations, either as a linear shift or as a function of the distance from the previous trial (e.g., Kononowicz & Van Rijn, 2014). Additionally, we took a data-driven approach to test whether temporal context could be decoded from transient neural dynamics during the perception phase using multivariate pattern analysis (MVPA). Finally, we expected higher beta power during the overlapping interval for the long compared to the short context (e.g., Praamstra, Kourtis, Hoi, & Oostenveld, 2006; Wiener et al., 2018).

Methods

Participants

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

Stimuli and apparatus

Stimuli were presented using the Psychophysics Toolbox 3.0.12 (Brainard, 1997; Kleiner et al., 2007) in Matlab 2014b. Intervals were presented as continuous 440 Hz sine wave tones. These auditory stimuli were presented on Sennheiser

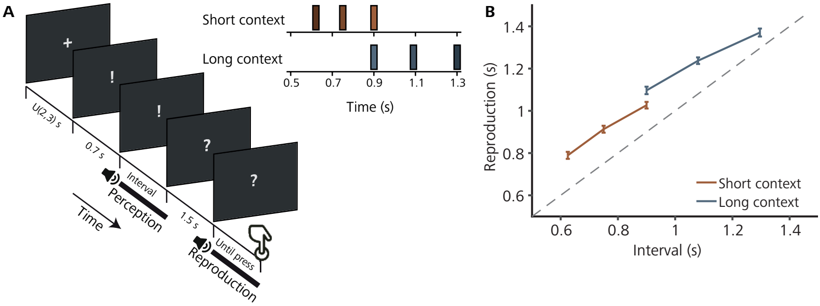

Figure 5.1. Task and behavioral results. A) Behavioral procedure of the experiment. Participants performed an interval reproduction task in which they heard a tone for a certain duration (perception phase). After an ISI of 1.5 s, they were asked to reproduce this duration by pressing a button to indicate the offset of the reproduction phase. In separate blocks, the perception phase consisted of three short or three relatively long durations (the short and the long context, respectively). One interval was presented in both contexts (the overlapping interval of 0.9 s). B) Average behavioral reproduction results. Error bars represent the standard error of the mean.

HD 280 Pro stereo headphones at a comfortable sound level. Visual stimuli were presented in the center of the screen in Helvetica size 25 in white on a dark grey background using a 27-inch Iiyama ProLite G27773HS monitor with a 1920x1080 resolution at 100 Hz. The back trigger buttons of a gamepad (SideWinder Plug & Play Game Pad, Microsoft Corporation) were used to record responses.

Procedure

Participants performed an auditory interval reproduction task (Figure 5.1A). Every trial started with a central fixation cross with a uniform random duration between 2 and 3 s. Then, an exclamation mark was presented for 0.7 s. While the exclamation mark stayed on the screen, the auditory interval was presented (the *perception phase*). To signal the next phase, a question mark was presented for 1.5 s. Next, the continuous tone was presented again, which participants had to terminate by pressing a button (the *reproduction phase*). Participants were instructed to match the duration of this second tone to the duration of the first tone as accurately as possible.

The task involved two different interval ranges, the short context (0.625 s, 0.75 s and 0.9 s) and the long context (0.9 s, 1.08 s and 1.296 s) (Figure 5.1A). Crucially, there was an *overlapping interval* that was presented in both contexts (0.9 s). The experiment consisted of four blocks, two of which used intervals of the short context, and two of which used intervals of the long context. Block order was counterbalanced across participants, with the constraint that the context would alternate every block. Within a block, each duration of the short or the long context was presented 30 times, amounting to a total of 90 trials per block and 360 trials over the whole experiment. The presentation order was random, with the constraint that every possible subsequent pair of intervals was presented equally often (i.e., first-order counterbalancing). The hand needed for reproduction was switched after two blocks. Prior to each block, participants were instructed which hand (i.e., which gamepad button) they would use to terminate the duration and which set of intervals would be presented (termed set A and set B for the short and long context, respectively; see also Maaß, Schlichting, et al., 2019), while they were not informed about the nature of these sets (i.e., that the sets were associated with interval range). Participants could take self-timed breaks between blocks. Prior to the experiment, participants performed two practice trials with durations outside the range of both context conditions (0.4 s and 2 s).

EEG acquisition

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

EEG pre-processing

EEG pre-processing was performed using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). EEG data was re-referenced to the averaged mastoids and filtered using a Butterworth IIR band-pass filter with a high-pass frequency of 0.01 Hz and a low-pass frequency of 80 Hz. Subsequently, trial epochs were created from -1 s until 6 s relative to the onset of the perception phase. Artifacts were corrected using independent component analysis (ICA). Epochs that exceeded an amplitude range of 120 μV were removed from the dataset. On average, 10.72% (*SD* = 6.10) of the 360 trials were discarded.

Data Analysis

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

ERP analysis.

CNV. All EEG analysis focused on the perception phase. The CNV analysis was performed on a fronto-central electrode cluster (FCz, FC1, FC2, and Cz) (cf., Kononowicz & Van Rijn, 2014). A 10 Hz Butterworth low-pass filter was applied and the ERP was baselined to the average signal in the 0.1 s window before interval onset. To test the effect of global context during the perception phase, we compared the ERP of the overlapping interval in the short and the long context using a cluster-based permutation test (Maris & Oostenveld, 2007) in the window 0-1.2 s from interval onset. The permutation test assessed whether the difference was different from zero by computing 100.000 permutations using the *t*-statistic, controlling for multiple comparisons with a cluster significance threshold of $p < .05$. To assess the influence of the previous trial (N-1) on CNV, we calculated the average amplitude in the time window that showed CNV differences in the previously mentioned permutation test (0.3-1.01 s), per participant, context and N-1 for the overlapping interval. Next, we tested an LMM predicting this amplitude, including N-1 and Context as fixed factors, and Subject as a random intercept term.

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

Multivariate pattern analysis. To investigate transient neural dynamics in more detail, we tested whether it is possible to decode global and local context through MVPA of the EEG signal. Following Wolff, Kandemir, Stokes, and Akyürek (2019), we used a sliding window approach in which the EEG fluctuations were pooled over electrodes and time. A window of 50 data points (98 ms) was moved across the signal in steps of 8 ms, separately for each channel. Within the window, the signal was down-sampled to 10 samples (by taking the average over 5 samples) and baseline-corrected by subtracting the mean within the window from all 10 individual samples.

To decode whether an overlapping-interval trial was presented in the short or the long context, the 10 samples per electrode in each time window served as input for 5-fold cross-validation. In each fold, we calculated the Mahalanobis distance (De Maesschalck, Jouan-Rimbaud, & Massart, 2000; Wolff et al., 2019; Wolff, Jochim, Akyürek, & Stokes, 2017) between the test trials and the averaged signal of the short and long context, using the covariance matrix estimated from the training trials with a shrinkage estimator (Ledoit & Wolf, 2004). To make the distance estimates more reliable, the 5-fold cross-validation was repeated 50 times and results were averaged. The eventual decoding distances were smoothed with a Gaussian smoothing kernel (*SD* = 16 ms). To test whether the distance between conditions was significantly different from zero, a cluster-based permutation test was performed.

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

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

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

Per participant, for every time-frequency point, we fitted a linear regression model including N-1 (a continuous variable ranging from the shortest to the longest interval in seconds) and Context (short and long context coded as 0 and 1, respectively) as predictors (following an approach similar to Wiener et al., 2018). For every time-frequency point, this resulted in two slope values, expressing the relative influence of the global context and the previous interval. Next, a one-sample *t*-test against zero was performed for the two slope values at each time-frequency point, which was corrected for multiple comparisons using cluster-based permutation (Maris & Oostenveld, 2007). The statistical testing was performed on the frequency range of 8-30 Hz to include alpha power (8–14 Hz; Kononowicz & Van Rijn, 2015) and beta power (15–30 Hz; e.g., Haegens et al., 2011; Jenkinson & Brown, 2011; Kononowicz & Van Rijn, 2015) during the time window of 0-1.2 s after interval onset.

Results

Behavioral results

Figure 5.1B shows the average reproductions for the different intervals. The results of the LMM showed that the reproductions increased with duration ($\beta = 0.77$, $t = 24.47$, $p < .001$). We found a significant effect of global context, showing that reproductions were longer in the long compared to the short context ($\beta = 0.046$, $t = 7.16$, $p < .001$). In addition, the increase with duration (i.e., the slope) was lower for the long compared to the short context ($\beta = -0.18$, $t = -7.15$, $p < .001$). Besides the global context effect, reproductions were influenced by the previous trial (N-1) ($\beta = 0.07$, $t = 3.55$, $p = .001$, not depicted).

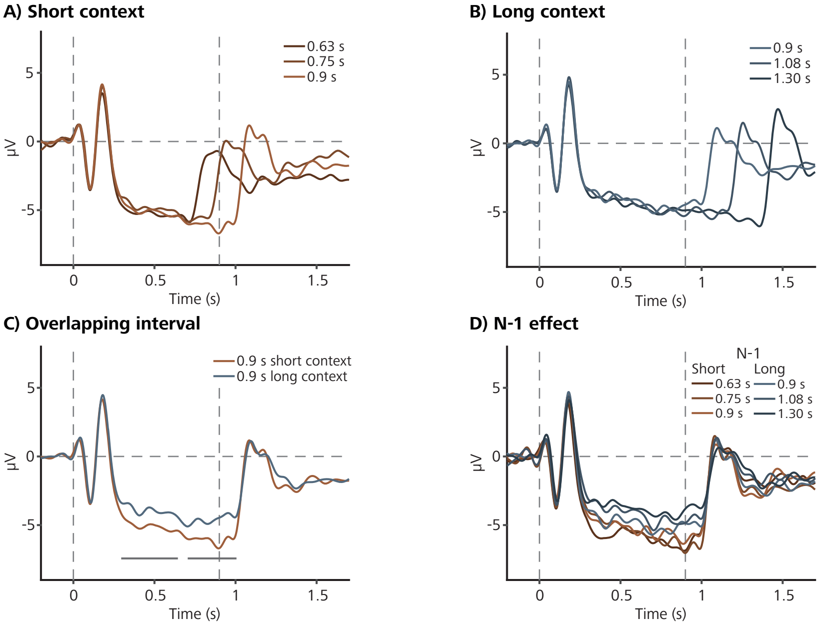

Figure 5.2. Average ERPs at the fronto-central cluster (FCz, FC1, FC2, and Cz) relative to the onset of the perception phase for the different durations in the short (A) and long (B) context. C) Average ERP of the overlapping interval (0.9 s) in the short and the long context. Grey horizontal bars indicate significant differences according to the cluster-based permutation test. D) Average ERP of the overlapping interval, split up according to the interval in the previous trial (N-1). Red and blue lines show whether the overlapping interval appeared in the short or the long context, respectively. In all panels, vertical grey dashed lines indicate interval onset and offset of the overlapping interval (0.9 s).

ERPs

CNV. Figure 5.2A and B show the average fronto-central ERP during the perception phase for the different intervals in the short and the long context, respectively. In addition, Figure 5.2C shows a direct comparison between the short and the long context of this ERP for the overlapping interval (0.9 s). The cluster-based permutation test showed that the CNV was more negative in the short than in the long context in the time windows 0.30-0.65 s (p = .004) and 0.71-1.01 s (p = .003). Thus, while the actual interval was the same, CNV amplitude during perception differed depending on the temporal context.

Figure 5.2D shows the average ERP for the overlapping interval, split for the different previous durations. The LMM results showed that CNV amplitude

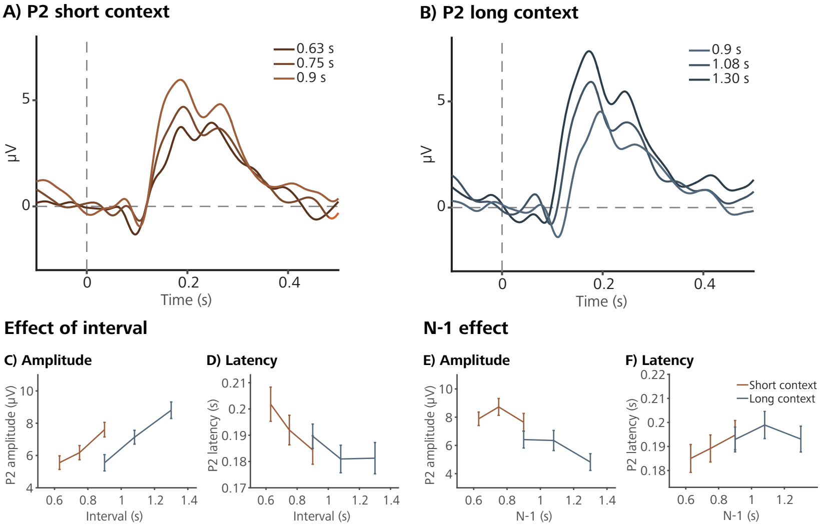

Figure 5.3. Amplitude and latency of the P2 at the FCz electrode after the offset of the perception phase. A, B) Grand average ERPs baselined at the offset in the short and the long context, respectively. C) Average peak amplitude, calculated as the maximum in the window 0.15-0.24 s after interval offset for every participant and interval. D) Average latency of P2 peak. E, F) Average P2 amplitude and latency for the overlapping interval as a function of the previous interval (N-1). In all figures, error bars represent the standard error of the mean.

became less negative with longer previous trials (β = 2.50, t = 2.49, p = .014). There was no additional significant effect of context (β = 0.49, t = 1.11, p = .267), suggesting that the global context effect on CNV might be largely driven by the previous trial.

Offset P2.

Amplitude. Figure 5.3A and B show the offset P2 for the different intervals in the short and the long context. Figure 5.3C shows the average peak amplitude as a function of interval and context. The LMM showed that the P2 increased with duration (β = 8.22, t = 10.71, p < .001), but that the intercept was significantly lower for the long compared to the short context (β = -1.21, t = -2.86, p = .004). Figure 5.3E shows the effect of the previous interval (N-1) on P2 amplitude for the overlapping interval. In line with the global context effect, the model showed that the P2 decreased with longer previous intervals (β = -2.28, t = -2.97, p = .003). Together, these results show that P2 amplitude reflects the actual duration, as well as the global and local context in which the duration appeared.

Latency. Whereas in Figure 5.3D P2 latency might decrease with the duration

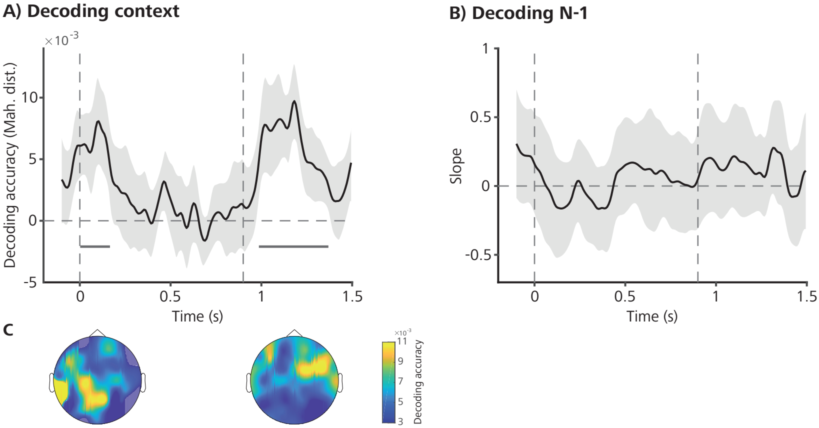

Figure 5.4. Decoding accuracy relative to the onset of the perception phase. A) Decoding accuracy of context for the overlapping interval as represented by the Mahalanobis distance. Grey horizontal bars indicate a significant difference from zero according to the cluster-based permutation test. Error shading represent 95% CI of the mean. B) Decoding accuracy of N-1 in the overlapping interval, represented by the slope value of the regression of Mahalanobis distance with N-1 and Context as predictors. C) Topographies of channel-wise context decoding accuracy for the overlapping interval, during the first significant cluster in panel A (left) and the second cluster (right). Colors represent the decoding accuracy in Mahalanobis distance.

of the current interval, the model showed that the only significant predictor of latency is the absolute difference between the previous and the current interval (β = -0.05, t = -11.64, p < .001). As can be seen in Figure 5.3F for the overlapping interval, the latency decreased when the current interval differed more from the previous. The other fixed factors did not reach significance (ps > .483). In summary, whereas P2 amplitude reflects the current duration and the general temporal context, P2 latency codes for the prediction error between the previous and the current interval.

Multivariate pattern analysis

Figure 5.4A shows the decoding accuracy for the overlapping interval. The permutation test showed a positive cluster immediately after interval onset (0-0.17 s; p = .009) and after interval offset (0.99-1.37 s; p < .001). Figure 5.4C shows the topographies of the channel-wise decoding results during these two clusters, which reflects high parietal and left-lateralized decoding accuracy and high fronto-central and right-lateralized decoding accuracy, respectively. Figure 5.4B shows the

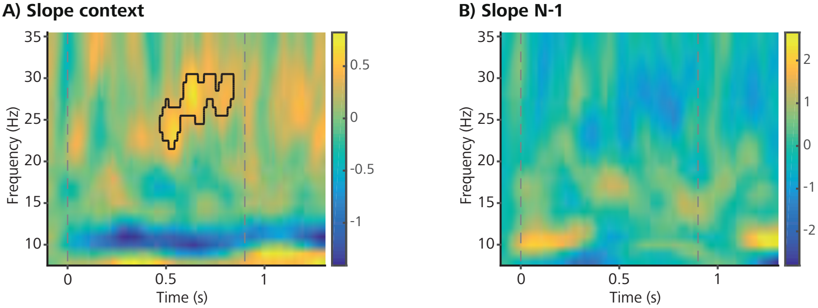

Figure 5.5. Slope values of regression on frequency power at FCz relative to the onset of the perception phase. A) Slope values of the factor Context (short vs long) in the regression analysis at every time-frequency point. The outlined area marks a significant cluster according to the cluster-based permutation test performed in the time window 0-1.2 s and the frequency window 8-30 Hz. B) Slope values of the factor N-1 in the regression analysis predicting power. There was no evidence for significant clusters. In both panels, vertical dashed grey lines indicate the onset and offset of the perception phase.

slope value of N-1 in the regression analysis predicting Mahalanobis distance. The permutation test showed that there was no evidence for significant clusters for the slope of N-1 or Context in the regression analysis (p = .999), showing that MVPA could not distinguish between N-1 conditions based on the transient EEG signal.

Time-frequency analysis

To assess oscillatory power during the perception phase, we calculated a linear regression of frequency power at FCz with global (short vs long) and local context (N-1) as predictors for every time-frequency point during the overlapping interval. Figure 5.5A shows the slope values representing the effect of global context on the power of the different frequencies over time. We found a positive cluster in the window 0.48-0.84 s after interval onset in the 22-30 Hz frequency range (p = .040), indicating increased beta power in the long context compared to the short context (see the outlined area in Figure 5.5A). Figure 5.5B shows the slope values for N-1, for which the permutation test indicated no evidence for a cluster of slopes different from zero. In summary, these results suggest that fronto-central beta power was higher in the long compared to the short context, while there was no evidence for a similar influence of the previous trial.

Discussion

As the temporal locus of Bayesian computations in human time estimation is still unknown, we investigated whether temporal context actively influences neural signatures during the perception of time intervals. Behaviorally, we found that reproductions were biased towards the global temporal context as well as the duration in the previous trial. The EEG results showed that the CNV, the P2 and beta power, which all have been associated with time perception, were modulated by previously perceived intervals and that context could be decoded from transient brain dynamics at an early stage during perception.

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

Our findings argue against the idea that the CNV represents the state of an absolute accumulator (Casini & Vidal, 2011; Macar et al., 1999), since no differences based on prior experience would be expected during the perception of an interval. Instead, we found that the CNV during the perception of the overlapping interval was more negative for the short compared to the long context, and for shorter previous durations. This is consistent with anticipation and preparation accounts of the CNV (e.g., Boehm, Van Maanen, Forstmann, & Van Rijn, 2014; Elbert, 1993; Leuthold, Sommer, & Ulrich, 2004; Mento, 2013; Ng et al., 2011): when the interval offset is expected quickly after the offset, the CNV amplitude increases more rapidly. This adaptation is in line with studies showing a faster CNV development for relatively short foreperiods (Miniussi, Wilding, Coull, & Nobre, 1999; Müller-Gethmann, Ulrich, & Rinkenauer, 2003; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000; Van der Lubbe, Los, Jaśkowski, & Verleger, 2004), shorter standard durations in an interval comparison task (Pfeuty et al., 2005) and after adaptation to a shorter interval (Li, Chen, Xiao, Liu, & Huang, 2017). The contextual adjustment of the speed with which the CNV develops suggests that neural populations in the supplementary motor area (SMA), which is typically associated with the CNV (e.g., Coull, Vidal, & Burle, 2016), can perform flexible temporal scaling based on the temporal context (Remington, Egger, Narain, Wang, & Jazayeri, 2018; Remington, Narain, Hosseini, & Jazayeri, 2018; Sohn et al., 2019), even in the absence of explicit motor preparation. The prior might calibrate the speed of neural dynamics through different initial states at the onset of the perception phase (Remington, Egger, et al., 2018; Sohn et al., 2019), as our multivariate pattern analysis showed that global context can be decoded from EEG dynamics immediately after the onset of the perception phase. Although the precise onset of significant decoding should be interpreted with caution, since the moving window approach and low-pass filtering could smear out the accuracy over time (Grootswagers, Wardle, & Carlson, 2017), these results suggest that temporal context affects the instantaneous neural response to to-be-timed stimuli.

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

Global context additionally influenced beta power, such that beta power was higher in the long compared to the short context. Higher beta power has been observed when a predictable interval between subsequent stimuli was longer (Praamstra et al., 2006) and beta power at interval onset has been shown to predict the produced duration in a given trial: productions were longer when beta power was higher (Kononowicz & Van Rijn, 2015). Although beta power has been proposed to reflect motor inhibition (Alegre et al., 2004; Hwang, Ghuman, Manoach, Jones, & Luna, 2014; Kononowicz & Van Rijn, 2015; Kühn et al., 2004), and most studies on the link between beta power and timing have a strong motor component, our results suggest that synchronized beta oscillations also play a role during interval perception after which no immediate motor response is required. This finding complements recent studies showing that the accuracy and precision of time estimates depend on beta (Wiener et al., 2018) and alpha-beta coupling (Kononowicz, Sander, Rijn, & Wassenhove, 2019). Additionally, the current global context effect on beta is in line with Wiener et al.'s finding that longer previous durations increased beta power in the current trial. It has to be noted, however, that we found no evidence for similar sequential effects on beta.

Besides the auditory stimuli which participants had to time, the current paradigm also consisted of visual stimuli that indicated the phase of the trial (i.e., perception or reproduction). The general overestimation we found in the behavioral results might potentially be explained by the integration of these visual stimuli in temporal estimation (Shi & Burr, 2016). Future studies might look further into potential modality differences in contextual calibration and their neural underpinnings (Rhodes, Seth, & Roseboom, 2018; Roach et al., 2017). Furthermore, we found no significant decoding corresponding to the windows of CNV differences. This can be explained by the specific decoding method we employed, which focused on transient dynamics, filtering out the stable CNV activity by baselining within a moving window. In addition, decoding might be especially sensitive to stimulus onset and offset, with accuracy peaking shortly afterwards and slowly dropping as the neural synchronization declines (e.g., Wolff et al., 2019; Wolff et al., 2017).

Comparison to Wiener and Thompson (2015), who found a larger CNV amplitude for *longer* prior durations, suggests that contextual ERP effects might be dependent on the specific experimental paradigm. In contrast to our reproduction experiment, their bisection task requires an active decision during perception, and the CNV has been shown to reflect this decision process by deflecting or plateauing after the standard interval in memory has been reached (Macar & Vidal, 2004; Ng et al., 2011; Pfeuty, Ragot, & Pouthas, 2003). The difference in task requirement could also explain the different nature of our offset P2 effect compared to Kononowicz and Van Rijn (2014). Future studies might directly compare these neural differences in paradigms involving decision, motor or only perceptual timing requirements. Indeed, as we focused on the perception phase in the current study, how the neural differences during perception translate to Bayesian effects in behavior (e.g., the central tendency effect) remains to be explored further. Potentially, the neural state at the end of the perception phase might set the speed of cortical dynamics during reproduction (Sohn et al., 2019).

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

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6

temporal context influences the perceived duration of everyday actions

Abstract

Timing is key to accurate performance, for example when learning a new complex sequence by mimicry. However, most timing research utilizes artificial tasks and simple stimuli with clearly marked onset and offset cues. Here we address the question whether existing interval timing findings generalize to real-world timing tasks. In this study, animated video clips of a person performing different everyday actions were presented and participants had to reproduce the main action's duration. Although reproduced durations are more variable then observed in laboratory studies, the data adheres to two interval timing laws: Relative timing sensitivity is constant across durations (scalar property), and the subjective duration of a previous action influenced the current action's perceived duration (temporal context effect). Taken together, this demonstrates that laboratory findings generalize, and paves the way for studying interval timing as a component of complex, everyday cognitive performance.

Introduction

Timing and the perception of time are fundamental aspects of our daily life. Anything we perceive and experience is expressed over time, and adaptive cognitive performance requires accurate timing, ranging from determining the time between glances in the rear-view mirror while driving, to a well-timed pause in a speech to increase rhetorical effectiveness. The timing of short intervals, referred to as interval timing, has been extensively studied. However, these studies typically entail processing an interval marked by simple and static stimuli with highly salient and clearly defined on- and offsets. This leaves no ambiguity about the exact start- and endpoint, whereas events in the real world often lack sharp and salient on- and offsets, as, for example, it is not clearly defined at what sound level a silence commences. In addition, unlike the focused setting of experimental studies, interval timing in the real world is usually embedded in a context consisting of many different durations associated with different subtasks perceived from the first- or third-person perspective. As a consequence, results from laboratory studies might have low external validity as it is unclear to what extent the general "laws" derived from extensive laboratory findings generalize to more complex environments (Darlow, Dylman, Gheorghiu, & Matthews, 2013; Matthews & Meck, 2014; Van Rijn, 2014). Here, we report on a study that addresses the question of whether the two prominent law-like properties, the scalar property and context effects, generalize to the timing of more realistic timing tasks.

The *scalar property* (e.g., Allman, Teki, Griffiths, & Meck, 2014; Wearden & Lejeune, 2008; for an extensive review, see Grondin, 2014) is a form of Weber's law, stating that the standard deviation of repeated estimations of a duration is proportional to the average estimated duration. Consequently, timing sensitivity follows Weber's law in that relative sensitivity is preserved for varying interval durations.

The second phenomenon is the effect of context on interval timing. Context effects can be found on a global level (Vierordt's law) and a more local level (trial-by-trial effects). Vierordt's law describes the central tendency effect: when confronted with varying interval durations, participants tend to overestimate short durations and underestimate long durations (Lejeune & Wearden, 2009). By manipulating temporal context, Jazayeri and Shadlen (2010) showed that participants under- or over-reproduced the duration of the same interval depending on temporal context, and explained their findings using a Bayesian model which takes into account the underlying distribution of samples. Local context effects are more concerned with the recent history of encounters with intervals of varying durations (i.e., sequential dependencies). Dyjas, Bausenhart and Ulrich (2012) explained sequential effects and fluctuations in behavioral performance with a mathematical model which, on each trial, combines previously and currently available information about stimulus durations to form one representation. Both global and local contexts effects have been extensively studied not only in laboratory-based timing tasks (see Van Rijn, 2016, for a review), but also in non-timing tasks (e.g., distance, length or angle estimations as reviewed in Petzschner, Glasauer, & Stephan, 2015), showing that these effects are highly robust and apply to many psychophysical tasks.

As stated above, these psychophysical laws have been established in artificial experimental settings. As a first step towards the use of ecologically valid stimuli a new line of research has emerged in which more dynamic stimuli are used (e.g., moving or rotating geometrical shapes; Matthews, 2011; Sasaki, Yamamoto, & Miura, 2013). Interestingly, this work demonstrated that using dynamic stimuli affects the subjective perception of time, as moving stimuli seem to last longer than static ones, and apparent duration increases with increasing stimulus speed, a phenomenon known as subjective dilation (Eagleman, 2008). These results thus indicate that findings observed in the traditional literature might be specific to simple, static stimuli, and not generalize to more realistic stimuli. This suggestion is supported by results of a "real-world" experimental paradigm in which the effect of speed of driving on time perception was estimated (Van Rijn, 2014). Video snippets from a recording of a driving simulator session served as stimuli (driver's perspective), and were played at either original, faster or slower speed. The data exhibited the same subjective dilation effects previously found (Eagleman, 2008): perceived duration increased with increasing driving speed. Interestingly, this study did not just demonstrate that previous findings on subjective dilation generalize to real-world-like settings, but also demonstrated that laboratory findings in which typically perspective is not manipulated generalizes to timing from a first-person perspective.

In fact, perspective seems to be a highly understudied factor — although perspective is an important aspect of being in the real world. Everything we perceive, and thus also time, is perceived from first-person perspective. With simple stimuli the effect of perspective cannot be tested because there is no change in perspective possible. Therefore, the effect of perspective on time perception is as of yet unknown. However, it has been shown that perceived or imagined distance affects time perception, in that events that happen further away from the observer seem to last longer (e.g., Gorea & Hau, 2013; Zäch & Brugger, 2008). One could imagine that first-person events happen spatially closer to the observer than third-person events — in line with the findings discussed above, perspective could alter time perception (in-)directly.

Yet another difference between timing static or moving shapes in laboratory studies and timing in real-life settings is that ecological timing is often part of human-object- or human-human-interactions. Studies focusing on differences in time perception between animate and inanimate figures have shown that animacy affects time perception (Carrozzo & Lacquaniti, 2013; Carrozzo, Moscatelli, & Lacquaniti, 2010; Orgs, Bestmann, Schuur, & Haggard, 2011). This work led to the proposition that different mechanisms underlie the timing of biological motion (animate stimuli) and visual motion (inanimate stimuli), providing additional arguments against generalizing results from traditional laboratory studies to real-life timing contexts (Lacquaniti et al., 2014). Further, these studies sketch interval timing as a multifaceted process, in which perspective and the nature of the action that needs to be timed could have significant impact on perceived duration. For example, Garsoffky, Huff and Schwan (2017) showed that depending on semantic temporal gaps in videos showing series of everyday actions performed by human actors the duration of a specific action was under- or overestimated. Videos in the long temporal gap condition consisted of clips of temporally distant actions and the target action was systematically underestimated, while in the short temporal gap condition videos consisted of clips of actions that are temporally closer together in the stream of events and caused the target duration to be overestimated in duration.

In the current study, we aimed to investigate interval perception in naturalistic contexts, while retaining optimal experimental control. Specifically, we asked whether common effects found in traditional laboratory studies, the scalar property and context effects, can be generalized to timing in real-world settings. Furthermore, we aimed to explore possible effects of perspective on time perception. To this end, participants were asked to reproduce the duration of an action demonstrated in a video. Each video showed an animated person performing six different everyday actions filmed from first- or third-person perspective (for an example, see Figure 6.1). After watching the video participants were asked to reproduce the duration of the action (e.g., "drinking") by pressing a key. Importantly, participants were not explicitly instructed when to start or end timing.

Materials and Methods

Participants

Twenty-three students enrolled in the Psychology programme of the University of Groningen (mean age: 19.3 years, range: 18-22 years, 17 female) participated in the experiment and received partial course credit. Sample size was based on past research (e.g., 12 participants in Carrozzo & Lacquaniti, 2013; 38 participants in Van Rijn, 2014). All participants had normal or corrected-to-normal vision. Informed consent as approved by the Psychology Ethical Committee of the University of Groningen (15008-NE) was obtained before testing.

Stimuli

Videos of an animated human reference model (see below for details) performing six different actions recorded from third- and first-person perspectives and performed over shorter or longer durations served as stimuli. The actions were *drink* (figure drinks from a cup), *mix* (figure uses a whisk to mix something in a bowl), *pour* (figure pours a liquid into a cup), *put on* (figure picks up a bowl and puts it on another object), *take down* (figure picks up a bowl placed on another object and puts it down on the table), and *pick & place* (figure picks up a whisk and puts it down at a different location on the table). All action-related objects were located on a table before, and put back on the table after, the actions were performed. Importantly, video length was not correlated with the speed of the action (e.g., drinking fast), but video length determined how long an action, performed at normal speed, was executed.

Animated videos were based on video recordings of a human actress performing each of the six actions over different time spans (Figure 6.1, top row). Movements were recorded by a marker-based motion capture system (VICON, http://www.vicon.com, sampling rate of 100 Hz, marker position accuracy < 1 mm). Human movement recordings were encoded using the Master Motor Map (MMM) toolkit (Terlemez et al., 2014), which is underlying a generic framework for unified representation and transfer of whole-body human motions to different embodiments (e.g., humanoid robots or animated characters). Finally, the scene and the animated human reference model were generated with MMM-based animated characters and 3D object models (e.g., a red cup) as described in Wächter and Asfour (2015) and illustrated in Figure 6.1. The entire motion data set, including MMM representations and object models, is publicly available as a part of the

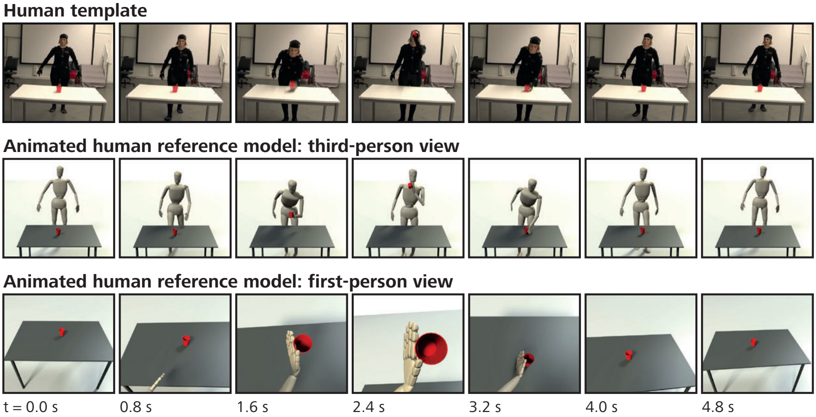

Figure 6.1. Exemplary depiction of the action drink in the short video condition. Animated videos were obtained from videos of an actress doing the same everyday actions with real objects and wearing a motion capture suit (top). The two bottom panels show the animated human reference model as seen from third- (middle) and first-person perspective (bottom) based on the human template video.

KIT whole-body human motion database (available at https://motion-database.humanoids.kit.edu/) (Mandery, Terlemez, Do, Vahrenkamp, & Asfour, 2015).

We chose to use an animated human reference model instead of human actors to control for confounding factors like variations in background noise or emotions conveyed by facial expressions (e.g., Fayolle & Droit-Volet, 2014). With 6 actions, 2 perspectives, and 2 length condition, a total of 24 animated videos were created to be used as stimuli.

Procedure

Participants were seated, at normal operating distance, in front of an *Iiyama* Vision Master Pro 513, 22-inch screen with a resolution of 1024 x 768px and a refresh rate setting of 100 Hz. Participants were provided with instructions informing them that they would be asked to reproduce the duration of an action observed in the video presented on that trial. Each experimental trial started with the presentation of a short text describing the action that would be presented (e.g., “mixing”). After 3 s, one of the 24 videos was presented centrally with a resolution of 960 x 540 pixels. After the end of the video the screen went blank for 1 s, followed by a grey circle presented in the center of the screen. This circle indicated that participant could reproduce the duration of the action by pressing down the spacebar. As a visual aid, the grey circled turned white while the spacebar was pressed down (i.e., during the interval reproduction). One additional trial sampled randomly from the 24 available videos served as a practice trial at the beginning of the experiment. Data from this trial were not analyzed. Importantly, no explicit instructions (or visual or auditory aids) were provided to indicate when an interval was supposed to start or end; the start- and endpoints of a specific action had to be determined by the participants themselves. However, it was explicitly stated in the instructions that the start- and endpoint of the action would not necessarily coincide with the start and end of the video. Videos were presented in random order. Each video was presented four times, resulting in a total of 96 trials. The experiment was programmed in OpenSesame version 3.0.3 (Mathôt, Schreij, & Theeuwes, 2012). The experimental script is available online at https://osf.io/y9zex.

Objective durations

To compare the reproduced durations to objective durations, we computed objective durations using the Semantic Event Chain (SEC) extraction algorithm that is used in AI and robotics to decompose actions or action sequences into atomic (sub-)actions (Aksoy, Aein, Tamosiunaite, & Worgotter, 2015; Wächter & Asfour, 2015). During SEC extraction, videos are examined and segmented according to spatiotemporal hand-object relations and actions can be categorized (e.g. *approach, grasp, withdraw*) based on semantic object-object and object-hand contact relations. Based on this segmentation process, we defined the duration of the main action as lasting from the first contact with the involved object until letting go of that object, resulting in the following durations (ordered from shortest to longest): 0.83 s (take down short version), 0.96 s (put on short), 1.07 s (pick & place short), 1.82 s (pick & place long), 1.88 s (put on long), 2.32 s (drink short), 3.02 s (take down long), 3.24 s (mix short), 3.68 s (pour short), 6.63 s (mix long), 8.06 s (pour long), 8.92 s (drink long). We validated this algorithm in an additional experiment (see Supplemental Material available at https://osf.io/y9zex).

Data analysis

The data analyses focused on three main questions: (1) Do the local and global context influence the perceived duration; (2) Is there an effect of perspective on perceived duration; (3) Is the scalar property observed in these data, operationalized by two different measures discussed below. For these analyses, we created Linear Mixed Models (LMMs) using the *lme4* package (version 1.1-10; Bates et al., 2015) in R version 3.2.2 (R Development Core Team, 2008). To test whether including a fixed factor improved the LMM, we performed model comparisons using likelihood ratio tests. Participant and action were always entered as random intercepts. After model comparison, we sequentially added random slopes for participant and the fixed factors, and action and the fixed factors (excluding objective duration), to the model to test whether this affected the results. In all LMM analyses, we found that the random slopes did not change the effects of the fixed factors qualitatively. Therefore, we will report the results of the simpler random intercept models here. For both significant and non-significant fixed factors in the LMMs, we used Bayesian analyses to quantify the evidence in favor of the alternative hypothesis. To this end, we compared the model including the fixed factor with the model without the factor using the *lmBF* function from the *BayesFactor* package in R (Morey et al., 2014). The evidence for H_1 over H_0 will be denoted as BF_{10}. All analysis scripts and data are available at https://osf.io/y9zex.

First, we tested the data for context effects. To test whether there was a global pull towards the (subjective) mean, an LMM was estimated with bias (the difference between the reproduction and the objective duration) as dependent variable and objective lag as fixed factor. Whereas perfect reproduction would yield a bias that is consistently 0 over durations, a pull towards the mean would result in a negative effect of duration on bias. To investigate local context effects, we tested the effect of the previous (N-1, N-2,...) *subjective* duration (i.e., the previous produced duration) and the previous *objective* duration (i.e., the objective duration of the action, as provided by the action segmentation algorithm) on the current trial (i.e., the current produced duration). Reproduced action duration was entered as dependent variable. Objective duration of the current trial, perspective, and previous subjective or objective trial duration were entered as predictors. Following Taatgen and Van Rijn (2011), we iteratively compared more complex models (e.g., a model including N-3, N-2, N-1) with simpler models (e.g., a model including N-2 and N-1). The same model comparison approach was used to test for effects of perspective.

To test the data for the scalar property, following Wearden and Lejeune (2008), the coefficient of determination (r^2) was determined by correlating the standard deviation of the reproduced action duration (S), averaged over all participants, with the mean reproduced duration (M) of each action in the long and short condition separately (i.e., for the 12 unique action-duration combinations, data from the different perspectives was pooled together). Additionally, the coefficient of variation ($CV = S \div M$) was calculated for each video and participant separately. An LMM was constructed to assess the influence of duration on CV, testing whether CVs differed across action durations.

Results

Figure 6.2 and Figure 6.3A depict the mean reproduced action durations for each action in the short and long version (i.e., for each objective duration). Visual inspection of the results in Figure 6.2 suggests that shorter durations were overestimated, whereas longer durations were underestimated. This can be seen in Figure 6.2 as the reproduced durations (green/orange dots) for the shorter durations (at the top of the figure) were reproduced as longer than the objective durations (grey dots), whereas the inverse is observed for the long action duration (at the bottom of the figure). Indeed, the LMM showed that the reproduction bias decreased with duration ($\beta = -0.51$, $t = -31.06$, $p < .001$, $\mathrm{BF}_{10} > 100$), indicating a significant pull towards the (subjective) mean.

If this pull towards the mean is driven by a continuously updating memory representation that reflects recent experiences, the durations perceived before the current trial must influence the current trial's estimate. Model comparisons showed that including subjective N-1 improved the model predicting reproduced action duration significantly ($\chi^2(1) = 66.19$, $p < .001$, $\mathrm{BF}_{10} > 100$). Thus, the subjective duration estimation in the previous trial influenced the duration estimation of the current trial ($\beta = 0.13$, $t = 8.23$, $p < .001$), with previous estimates being positively correlated with the current estimate. Adding N-2 to the model did not improve the goodness of fit ($\chi^2(1) = 2.08$, $p = .149$, $\mathrm{BF}_{10} = 0.11$). For theoretical reasons, and following Taatgen and Van Rijn (2011), we did not test for an influence of N-3 without including N-2. These results support the hypothesis that reproduced action durations deviate systematically from the objective durations, with a pull towards the mean.

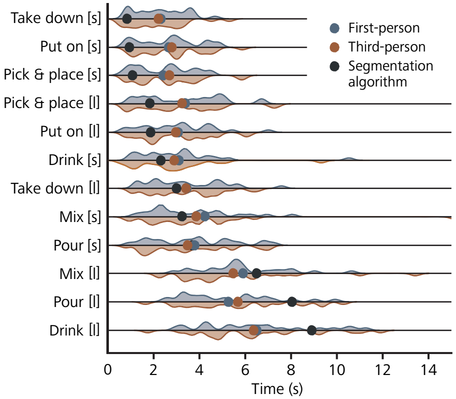

Figure 6.2. Estimated action durations. Colored dots indicate mean reproduced durations for each action (short indicated with [s], long with [l]), averaged over all participants. Violin plots illustrate the density distributions of participants' reproduced action durations. Grey dots depict the objective duration as defined by the action segmentation algorithm. Generally, shorter durations were overestimated and longer durations underestimated, demonstrating typical context effects.

Alternatively, however, the effect of the previous trial on the current reproduction could potentially be explained by attentional fluctuations or performance drift over the course of the experiment. It could, for example, reflect a change in the willingness of the participant to hold down the response key. To disentangle the influence of the subjective N-1 and these overall performance fluctuations, we calculated the relative bias (i.e., the difference between the reproduced and objective duration divided by the objective duration) for each trial. If the N-1 effect depends on performance fluctuations, we would expect that the bias in the current trial depends on the bias in the previous trial (e.g., if the estimation in the previous trial was too short, it will also be too short in the current trial). If, however, the N-1 effect depends on the actual subjective duration in the previous trial, we would expect that the current bias reflects the magnitude of this subjective duration (e.g., a negative bias if the previous subjective duration was shorter than the current duration). We created a mixed model with bias as the dependent variable, and objective duration, previous subjective duration and previous bias as fixed factors. Model comparison showed that both previous subjective duration ($\chi^2(1) = 44.39$, $p < .001$, $BF_{10} > 100$) and previous bias ($\chi^2(1) = 9.28$, $p = .002$, $BF_{10} = 5.59$) improved the model significantly. Both previous subjective duration and previous bias contributed positively to the current bias ($\beta = 0.06$ and $\beta = 0.05$,

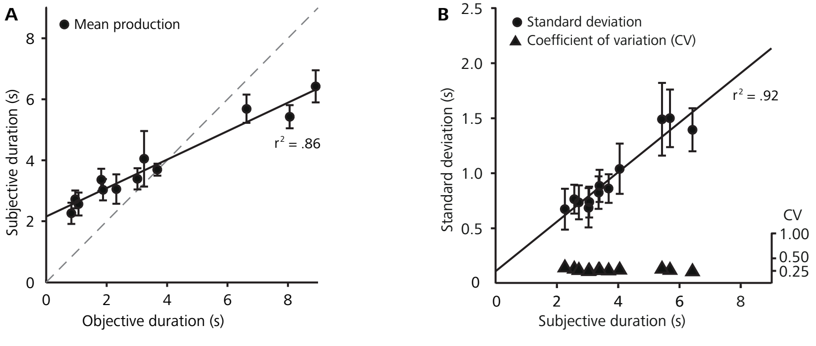

Figure 6.3. Estimated action durations (a) and variance associated with estimated durations (b) for the short and long version of the 6 different actions. Panel A depicts mean reproduced durations (error bars indicate the 95% CI, corrected for between-subject variability), averaged over all participants and first-/third-person perspective trials, plotted against the objective duration. Reproduced durations differ from the objective durations (diagonal dashed line): shorter durations were overestimated, whereas longer durations were underestimated, demonstrating context effects. Panel B depicts the standard deviation over subjective duration for all 12 actions. Conforming to the scalar property, regression of mean standard deviation (error bars indicate the 95% CI, corrected for between-subject variability) against mean reproduced duration (circles) revealed a linear relationship (solid line) with r2 = .92. Calculated coefficients of variation (triangles) did not differ significantly from each other.

respectively). Thus, whereas performance drift seems to play a role, it does not account for the effect of the previous reproduction on the current reproduction.

We also tested for the effect of the *objective* N-1. In contrast to the subjective N-1 duration, we found that adding the objective N-1 duration did not improve the model ($\chi^2(1) = 2.77$, $p = .096$, $BF_{10} = 0.11$). Thus, it is not the objectively observed duration of the previous trial that influences the current trial's estimate, but how this previous duration is observed.

As might be expected based on the similar locations of the orange and green dots in Figure 6.2, including perspective as a predictor of reproduced duration did not improve the model's fit ($\chi^2(1) = 1.90$, $p > .250$, $BF_{01} < 0.01$). Supported by a decisive Bayes Factor, it can be concluded that manipulating whether participants saw an action in first- or third-person perspective did not influence perceived durations in the current experimental setup. Consequently, data was pooled over perspective for subsequent analyses.

To assess whether the scalar property held in the current data, we addressed the correlation between the standard deviations and the mean reproduced durations and tested whether subjective duration predicted coefficients of variation. The results of both analyses suggest that the scalar property holds, as the standard deviations (S) and mean reproduced durations (M) were highly correlated with $r^2 = .92$, $p < .001$ (Figure 6.3B) and the CV values of the different action durations did not differ from each other, as revealed by an LMM performed on the CV values of all participants ($\beta = 0.00$, $t = -0.95$, $p > .250$, $BF_{10} = 0.23$).

Discussion

Do the general laws of interval timing, derived from scores of experiments using static and highly artificial stimuli, generalize to more real-world like settings? Although some studies using dynamic stimuli suggest that interval timing can be affected when more realistic stimuli are used, this study demonstrates that two basic time perception laws hold, even when naturalistic stimuli are used. These results pave the way for integrating interval timing theories in computational or quantitative theories of complex cognitive behavior studied in real-world settings. For example, when operating complex machinery, many intervals need to be tracked simultaneously as different aspects of complex machines may need attention at different intervals, or when speaking in front of a group of individuals, specific intervals might be associated with different aspects of interaction. This research demonstrates that in these cases, the global context effect will cause overestimation of the shortest duration and underestimation of the longest, local context effects predict sequential dependencies on a trial-by-trial basis, and the scalar property suggests that the error in shorter duration will be smaller than the error in longer durations. Taking these effects into account can explain additional variance when studying complex tasks, providing researchers with a more direct picture of the non-temporal aspects of the task under study.

Before turning to the effect of context and the scalar property, one aspect of the empirical data needs to be discussed as it deviates from the results obtained with more standard stimuli. As can be seen in Figure 6.3B, the average coefficient of variation is around .25, and the regression line fitted through the average standard deviations and subjective durations has a slope of .23. These values are notably larger than reported in a review of coefficients of variations by Gibbon, Malapani, Dale and Gallistel (1997). In this review, durations between 2 and 8 seconds have an average coefficient of variation below .2, often closer to .1. This difference can also be observed by comparing the probability densities of interval reproductions of the current study (Figure 6.2) with a laboratory-based reproduction task using auditory stimuli with clear on- and offsets (Figure 2 in Kononowicz, Sander, & Van Rijn, 2015), as the artificial stimuli resulted in narrower distributions. A major difference is that in the current experiment on- and offsets of the duration were, on purpose, not clearly defined as distinct events, so one possible explanation of the higher variance could be that participants encountered difficulties in determining or remembering the exact on- and offset of an action. However, in the additional experiment (see Supplemental Material available at https://osf.io/y9zex) we found that participants in general have a very precise and consistent idea of when an action started and ended, and how long it lasted. To shed more light on this matter, a future experiment could experimentally manipulate whether distinctiveness of on- and offsets has an effect on how well the interval marked by those events can be reproduced.

Context effects

A consistent finding in studies on interval perception that use multiple, slightly different interval durations is the context effect. The duration of the previous trial (i.e., local context) and even the complete history of previously encountered interval durations within an experiment or experimental block (i.e., global context) affect the perception of the current interval (for a review, see Van Rijn, 2016). Data from the current study exhibited similar effects of temporal context. Figure 3A shows the typical pattern of global context effects: shorter durations are systematically overestimated while longer durations are underestimated.

The analysis of local context effects revealed that not the *objective* duration of the previously presented stimulus, but the *subjective* previous duration influences our current interval perception. Since the previous subjective duration was in fact the previous interval reproduction, it may be a better measure of how participants perceived and stored a given interval than the objectively measured duration of the previous interval. Furthermore, any given subjective N-1 trial comprises the subjective N-2 trial (the N-1 of the N-1 trial), which itself comprises the subjective N-3 trial, and so on. Thus, subjective N-1 reflects the complete history of encountered intervals - the temporal context (see also Dyjas, Bausenhart, & Ulrich, 2012). These results demonstrate that in naturalistic tasks, empirical estimates of previously perceived durations, instead of objective duration, is a more powerful predictor of subsequent behavior.

Scalar property

Data from the current study is in conformity with the scalar property of time perception. We found that variation in interval reproduction linearly increased with interval duration, and that the coefficient of variation did not differ across interval durations (see Figure 6.3). Thus, participants' timing sensitivity remained constant as the action durations varied from trial to trial. In principle, violations of, or large variations in, the coefficient of variation can hint at participants using counting strategies while performing interval timing tasks (Allman et al., 2014; Wearden & Lejeune, 2008). This was not the case in the current study. These results indicate that even though the onsets and offsets might be more difficult to perceive, timing sensitivity is stable and will play a similar role in ecologically valid settings as it does in laboratory studies.

Perspective

The present data showed no sign of an effect of first- versus third-person perspective. A possible explanation is that perceiving an action (or more generally: a scene) from first-person perspective is not sufficient to induce a feeling of authorship (Ebert & Wegner, 2010) or embodiment. That is, in our experiment, participants only passively viewed actions being performed - they did not perform actions themselves. Although the Bayes Factor provided decisive evidence against an effect of perspective in our setup, we prefer to refrain from making strong claims about general effects of perspective (see also the introduction) until methods that elicit stronger effects of perspective (i.e., paradigms utilizing virtual reality) have been tested.

Conclusion

Timing is extremely important in many tasks and settings, and this study demonstrates that deviations to veridical timing as observed in the laboratory also affect timing in the real world. We established that findings from artificial laboratory studies can be generalized to more real-world like settings and highlighted that, as in many domains, any percept is influenced by and embedded in context. Taken together, this study paves the way for studying interval timing as a component of complex, everyday cognitive performance.

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*shared first authorship

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estimating time: comparing the accuracy of estimation methods for interval timing

Abstract

In interval timing experiments, motor reproduction is the predominant method used when participants are asked to estimate an interval. However, it is unknown how its accuracy, precision and efficiency compare to alternative methods, such as indicating the duration by spatial estimation on a timeline. In two experiments, we compared different interval estimation methods. In the first experiment, participants were asked to reproduce an interval by means of motor reproduction, timeline estimation, or verbal estimation. We found that, on average, verbal estimates were more accurate and precise than line estimates and motor reproductions. However, we found a bias towards familiar whole second units when giving verbal estimates. Motor reproductions were more precise, but not more accurate than timeline estimates. In the second experiment, we used a more complex task: Participants were presented a stream of digits and one target letters and were subsequently asked to reproduce both the interval to target onset and the duration of the total stream by means of motor reproduction and timeline estimation. We found that motor reproductions were more accurate, but not more precise than timeline estimates. In both experiments, timeline estimates had the lowest reaction times. Overall, our results suggest that the transformation of time into space has only a relatively minor cost. In addition, they show that each estimation method comes with its own advantages, and that the choice of estimation method depends on choices in the experimental design: for example, when using durations with integer durations verbal estimates are superior, yet when testing long durations, motor reproductions are time intensive, making timeline estimates a more sensible choice.

Introduction

In the growing research field on interval perception the number of ways to measure subjective time are seemingly growing, too. As a researcher, one has to decide whether a task is retro- or prospective (e.g., Block, Grondin, & Zakay, 2018), in which modality intervals are presented (e.g., auditory or visually; Wearden, Todd, & Jones, 2006), how exactly intervals are presented (e.g., filled or empty; Grondin, 1993), the paradigm used (e.g., temporal reproduction, production, bisection, or comparison; for a review, see Grondin, 2010; Wearden, 2016), and how responses are being collected (e.g., verbal or motor responses; e.g., Block et al., 2018; Mioni, 2018). While subjective (distortions of) time perception may be captured no matter which choice was made regarding the listed options, often neglected from this choice are the potential differences in cognitive strategy or what representation of time underlies a given task.

One prominent idea is that time is represented in spatial terms (for a review, see Bender & Beller, 2014). Indeed, visuospatial representations of time are reflected in how we think and communicate about time, and also in how we process and act on time (Bonato et al., 2012; Núñez & Cooperrider, 2013). For example, time-related notions in language are often spatialized: the future lies ahead of us, we are looking back at earlier times, or the vacation was too short. The latter notion, how we process and act on time, is reflected in the commonly found Spatial-Temporal Association of Response Codes (STEARC) effect (Conson, Cinque, Barbarulo, & Trojano, 2008; Fabbri, Cancellieri, & Natale, 2012; Fabbri, Cellini, Martoni, Tonetti, & Natale, 2013; Ishihara, Keller, Rossetti, & Prinz, 2008; Vallesi, Binns, & Shallice, 2008; Vicario et al., 2008; Weger & Pratt, 2008). The STEARC effect describes a space-related representation of time and temporal magnitudes, such that *before/shorter* responses have a processing or response advantage when associated with the left side of space, and, vice versa, *after/longer* responses show the same advantages when associated with the right side of space. This spatialization of time can also be observed in children as young as five years (Coull, Johnson, & Droit-Volet, 2018). Mental timeline theories in particular suggest that time is represented as a spatial linear axis that allows absolute (i.e., how long a stimulus lasted) and relative timing (i.e., temporal order; Bonato et al., 2012; Magnani & Musetti, 2017). The orientation of the timeline is heavily influenced by culture and experience, such as, for example, reading direction (e.g., English speakers, who read from left to right, map events on a timeline directed rightward, while Arabic speakers, who read from left to right, showed the reverse pattern; Boroditsky, 2001; Fuhrman & Boroditsky, 2010) or commonly used spatial metaphors to talk about time (e.g., Mandarin speakers use horizontal and vertical terms to temporally order events, while English speakers commonly use only horizontal terms; Boroditsky, Fuhrman, & McCormick, 2011). A number of neurobiological and cognitive models even suggest that space and time share their neural representation (e.g., A Theory Of Magnitude (ATOM): Walsh, 2003, 2015; hippocampal time and space cells: Buzsáki & Llinás, 2017), emphasizing the intertwinedness of these two dimensions. ATOM, for example, is based on i) behavioral findings showing a tight link between spatial (size, length) and temporal magnitudes, in that spatial magnitude influences the perception of temporal magnitudes in a "more is more" fashion (i.e., more spatial magnitude is more temporal magnitude, Cai & Connell, 2016; Cai, Wang, Shen, & Speekenbrink, 2018; Casasanto & Boroditsky, 2008; Xuan, Zhang, He, & Chen, 2007); and ii) on neuroimaging studies revealing shared neural representations in the parietal cortex during the processing of spatial, numerical and temporal magnitudes (e.g., Bueti & Walsh, 2009; Dormal, Dormal, Joassin, & Pesenti, 2012; Hayashi et al., 2013; Riemer, Diersch, Bublatzky, & Wolbers, 2016). Adding to this theory, Coull and Droit-Volet (2018) highlight that explicit representations of time are not solely rooted in space but also in motor interactions with the world, which have a temporal and a spatial component. The authors offer a developmental approach of how we construct a representation of time by performing actions in space during childhood (see also Loeffler, Cañal-Bruland, Schroeger, Tolentino-Castro, & Raab, 2018).

Assuming that time is indeed represented spatially or in an ATOM-like common magnitude system, an additional method to estimate intervals is the use of a timeline or visual analogue scale. While visuospatial estimation formats are commonly used in intentional binding studies (e.g., Haggard, Clark, & Kalogeras, 2002), to our knowledge, only few interval timing studies have made use of them (e.g., Damsma, Van der Mijn, & Van Rijn, 2018; Roseboom et al., 2019). Apart from the more conceptual question of how exactly time may be represented in the brain, there are practical issues regarding the implications for different response modes at hand, too: So far it has not been tested whether an explicit translation from time to space affects precision and/or accuracy of temporal estimates compared to other commonly used estimation methods. In two separate experiments we aimed to test the advantages and disadvantages of using different estimates of time, namely reproductions in the time dimension, estimates in the spatial dimension, or estimates in a symbolic form.

In Experiment 1, participants estimated intervals by either pressing a button (motor reproduction), clicking on a timeline (timeline estimation), or giving a numerical estimate (verbal estimation). The to-be-estimated interval was a white square appearing and disappearing on a black screen. The results of Damsma, Van der Mijn and Van Rijn (2018) suggested that participants exhibit a response bias when using timeline estimations, seen in avoidance of clicking close to the end of the line or screen. To test whether this bias can be prevented participants performed one of two versions of this experiment: one in which the range of the timeline corresponded to the tested intervals, and one in which the timeline corresponded to intervals longer than the tested intervals. In other words, participants were either calibrated to the test durations or to slightly longer durations. When estimating an interval using a timeline or verbal estimates, participants can be more deliberate in their estimates (i.e., go back and forth in time) compared to motor reproductions, in which participants have only one chance to make an estimate. While intervals had a clear on- and offset and required no further processing steps in Experiment 1, we used a more complex temporal estimation task in Experiment 2. Participants saw a stream of digits and one target-letter and were subsequently asked to first estimate the onset of the target letter within the stream, and second to reproduce the duration of the complete stream by either motor reproductions or timeline estimations. Again, half of the participants were calibrated to the test durations, while the other half were calibrated to longer durations. In this more complex setup, participants did not only have to attend to and memorize one duration, but they had to attend to the content of the stream and memorize two durations. Timeline estimates may allow for relative timing (e.g., when did the target occur relative to the estimated offset), while motor reproductions require a strictly sequential order of interval reproductions. In both experiments we will compare accuracy (i.e., the estimations) and precision (i.e., the absolute error and the coefficient of variation (CV)) of temporal estimates. A common finding in temporal estimation tasks, especially in reproduction tasks, is that previously encountered intervals influence the perception of the current interval (also known as sequential context effects; for a review, see Van Rijn, 2016). We will compare the magnitude of these context effects for temporal estimation methods and calibration conditions. If there is a cost to a potential spatial transformation, we expect that the timeline estimates show lower accuracy and/or precision than motor reproductions and verbal estimates. In addition, we expect that calibration with longer intervals may increase the accuracy of the estimates, especially for longer intervals, in the timeline estimation condition.

Experiment 1

Methods

Participants. Sixty healthy adults (20 male, mean age 22.65) participated in exchange for course credits or a financial compensation of €8. All participants had normal or corrected-to-normal vision. Informed consent as approved by the Ethical Committee Psychology of the University of Groningen (identification number 17408-S-NE) was obtained before testing. Sample size was based on past research (e.g., Damsma et al., 2018; Schlichting et al., 2018), no statistical *a priori* power analysis was conducted.

Experimental Design and Procedure. Participants were asked to perform a temporal estimation task using three different estimation methods: motor reproduction, timeline and verbal estimation. Stimuli were displayed on a 1920 × 1080 LED-based monitor screen (Iiyama ProLite G2773HS) with a refresh rate of 100 Hz.

The to-be-reproduced interval (equally spaced between 1 and 4 s in steps of 0.5 s) was presented at the beginning of the trial. Appearance of a white square (50 by 50 pixels) at the center of the screen marked the onset, and the disappearance of the square the offset of the interval. After a fixation period of 1 s participants were asked to estimate the previously perceived interval in one of three ways: a) motor reproduction: the white square re-appeared, marking the onset of the reproduction, and participants were asked to press the spacebar to end the interval; b) timeline estimation: participants were asked to click on a timeline at the point where the interval ended (1 pixel on screen corresponded to 0.01 s), apart from a tick demarking the onset of the interval there were no further spatial/temporal indications (ticks) given; c) verbal estimation: participants were asked to enter a numerical estimate in seconds with one decimal place. After the estimation participants received immediate feedback on each trial (practice and experimental trials) in form of a timeline (1 pixel on screen corresponded to 0.01 s). The feedback format was the same for all conditions to make the tasks as equal as possible. Two grey bars on top of the timeline depicted the on- and offset of the veridical interval, and two white bars below the timeline depicted participants estimates (i.e., both onset bars were always aligned). See Figure 7.1 for a schematic depiction of the experimental design. The experiment was run in Matlab R2014b (The MathWorks) using the Psychophysics Toolbox version 3.0.12 (Brainard, 1997) in Windows 10.

The experiment was divided into three blocks (i.e., one block for each estimation method) of 42 experimental trials (i.e., four trials per duration) each. Order of blocks, and thus estimation methods, was counterbalanced between participants. Before the start of each block, participants received instructions about the estimation method to be used in the upcoming block, and they performed 12 practice trials in order to get accustomed to the timeline and the estimation method before the start of the experimental trials. The order of trials was the same in each block, but varied between participants.

Crucially, half of the participants performed a calibrated version of the estimation tasks. In the calibrated version the training-trials consisted also of longer intervals than those in the test trials (1.0, 2.5, 5.0, and 6.0 s), while in the uncalibrated version training trials were chosen from the range of intervals of test trials (1.0, 2.0, 3.0, and 4.0 s). Importantly, this changed the length of the timeline in the feedback screen and also in the timeline estimation condition: in the calibrated version the timeline was longer, so that during test trials participants did not have to click as close towards the end of the line to estimate the longest duration as they had to in the uncalibrated version. In both the calibrated and uncalibrated condition, the timeline was presented centrally on the screen. The experiment files can be found at https://osf.io/w38qg/.

Analysis. All estimates shorter than 0.2 s and longer than 10 s (0.34% of the

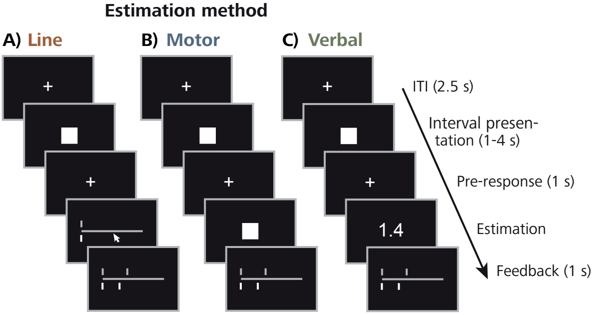

Figure 7.1. Trial procedure of Experiment 1. Participants performed a simple temporal estimation task, in which they had to estimate the duration of a square in three ways: A) pressing a key to indicate the estimated offset of the interval (motor reproduction), B) clicking on a timeline (line estimation), and C) typing a verbal estimate in seconds (e.g.: "1.4"; verbal estimation). Feedback was presented at the end of each trial.

data) and all trials in which no estimates were provided (0.34% of the data) were excluded from analysis. The estimates were analyzed using Linear Mixed Models (LMMs) from the *lme4* package (Bates et al., 2015) in R (R Core Development Team, 2013). To compare the *accuracy* of the different conditions, we tested a model predicting estimates. In addition, we compared the *precision* of the conditions by testing models predicting the absolute error and the CV. Finally, we tested a model predicting reaction time. In each model, *duration* (i.e., the veridical duration of the interval), *estimation method* (motor, timeline or verbal) and *calibration condition* (uncalibrated or calibrated) and their interactions were sequentially added as fixed factors. Only fixed factors that significantly improved the model according to a likelihood ratio test were included in the final model. To assure the interpretability of significant interaction terms, the relevant main effects were also included in the model. In addition, the fixed factor *duration* was centered at 2.5 and *calibration condition* was recoded using effect coding (-0.5 and 0.5 for uncalibrated and calibrated, respectively), to make main effects of *duration* and *estimation method* easier to interpret. *Participant* was always included as a random intercept term. After establishing the final model, we sequentially added random slope terms, starting with the random slope that decreased the AIC value most. We tested whether the inclusion of the random slope term was warranted using likelihood ratio tests. Given the final model, we compared the three estimation methods with post-hoc contrasts using the *glht* function in the *multcomp* package in R (Hothorn et al., 2017). Here, we will report the most important findings, but the complete analysis scripts and final model results can be found at: https://osf.io/w38qg/.

Results

Estimates. Figure 7.2A shows the average estimates for each duration and estimation and calibration condition. Model comparison showed that adding duration as a continuous fixed factor improved the basic model that included estimate as the dependent variable and subject as a random factor ($\chi^2(1) = 7647.90$, $p < .001$), indicating that, overall, estimates increased with the presented duration. In addition, estimation method and its interaction with duration improved the model fit ($\chi^2(2) = 63.33$, $p < .001$ and $\chi^2(2) = 33.89$, $p < .001$, respectively), showing that the intercept and slope of the estimates differed between estimation methods. In line with the average bias depicted in Figure 7.3, post-hoc contrasts showed that the intercept at the middle interval (2.5 s) was higher for verbal estimates than for line estimates and motor reproductions (ps < .005). In addition, the slopes of line estimates and motor reproductions were smaller than for verbal estimates (ps < .001), suggesting a larger central tendency effect for line estimate and motor reproductions. There was no evidence for intercept or slope differences between the line estimates and motor reproduction condition (*p*s > .666). Adding calibration condition as a fixed factor did not improve the model fit ($\chi^2(1) = 0.85$, $p = .361$). However, we found a significant three-way interaction between duration, estimation

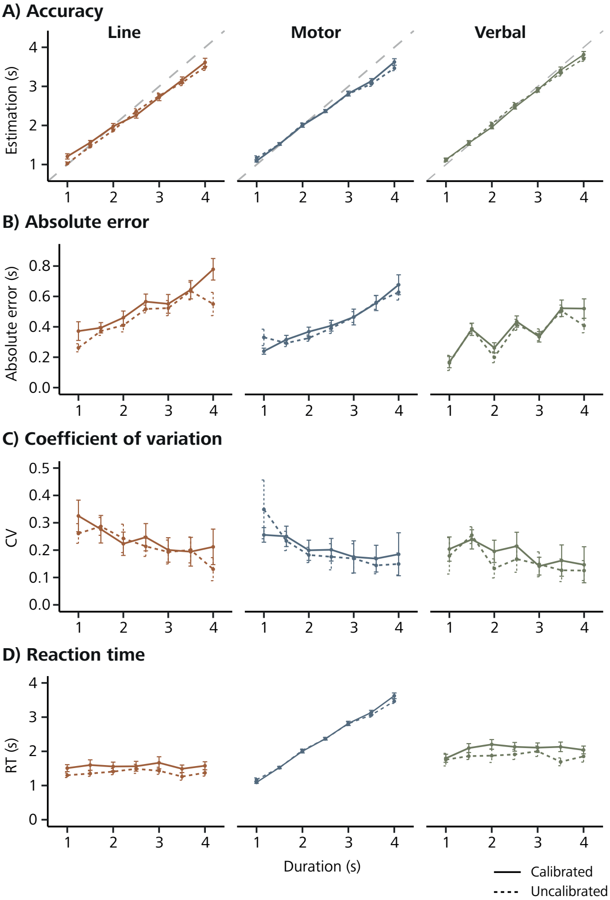

Figure 7.2. A) Average estimates for the timeline, motor and verbal conditions and calibration conditions. The grey dashed line represents veridical performance. B) Average absolute error of the timeline, motor and verbal estimations and calibration conditions. C) Average CV of the timeline, motor and verbal reproductions and calibration conditions. Average reaction times (RTs) of the timeline, motor and verbal reproductions and calibration conditions. While the RTs are stable over durations for the timeline and verbal estimates, the motor reproductions of course scale with the presented duration. In all figures, the error bars represent the standard error of the mean.

method and calibration condition ($\chi^2(2) = 6.13$, $p = .047$). Post-hoc contrasts showed that the slope difference between the calibration condition was higher for motor reproductions than for line estimates ($p = .031$).

Absolute error. Figure 7.2B shows the average absolute error for the different presented durations and experimental conditions. Presented duration improved the model fit ($\chi^2(1) = 467.25$, $p < .001$), indicating that overall the absolute error increased with duration. Adding estimation method as a fixed factor also improved the model ($\chi^2(2) = 128.70$, $p < .001$). Post-hoc contrasts showed that the error of verbal estimations was lower than for line estimations and motor reproduction (ps < .004) and lower for motor reproductions than for line estimations ($p < .001$). Model comparison showed that the interaction between presented duration and estimation method also improved the fit ($\chi^2(2) = 7.71$, $p = .021$). Post-hoc contrasts revealed a larger slope for motor reproductions compared to verbal estimations ($p = .033$). Adding calibration did not improve the model fit ($\chi^2(1) = 1.01$, $p = .314$).

Interestingly, Figure 7.2B shows that the error in the verbal estimations systematically diverged from a linear pattern: visual inspection suggests that it was lower for integer durations (1, 2, 3 and 4 s) than for the durations in between (1.5, 2.5, and 3.5 s). Post-hoc, we tested this notion by adding a dichotomous fixed factor indicating whether a duration was an integer to a model predicting the absolute error in the verbal estimation condition. Duration, calibration version and their interaction were also included as fixed factors. We found that this dichotomous fixed factor improved the model significantly ($\chi^2(1) = 71.93$, $p < .001$), indicating that the error was indeed lower for rounded integers. This was not the case for the line estimations ($\chi^2(1) = 3.46$, $p = .063$) and the motor reproductions ($\chi^2(1) = 0.83$, $p = .363$).

Coefficient of variation (CV). We calculated the CV per participant and presented duration as the standard deviation divided by the average estimate. Figure 7.2C shows the average CV for every presented duration for the different estimation and calibration conditions. Presented duration improved the model significantly ($\chi^2(1) = 128.28$, $p < .001$), showing that - overall - the CV was smaller for longer durations. We found no evidence that this negative slope differed between estimation conditions ($\chi^2(2) = 4.26$, $p = .119$). However, we found that the intercept (at 2.5 s) did differ between estimation conditions ($\chi^2(2) = 50.75$, $p < .001$): In line with the absolute error, the CV was larger for line estimates and motor reproductions compared to the verbal estimates (ps < .007) and larger for line estimates compared to motor reproductions ($p = .004$). We found no evidence for a difference between the calibration conditions ($\chi^2(1) = 1.27$, $p = .260$).

End of the line effects. We expected that the calibration conditions would mostly affect the participants' tendency to not respond close to the end of the line.

In this case, we would expect that calibration most strongly influences estimates of longer intervals, and that this effect would be most pronounced in line estimates. To test this hypothesis, we investigated the influence of calibration on the accuracy and precision of the longest interval (i.e., 4 s). An LMM predicting these estimates showed that they differed between estimation methods ($\chi^2(2) = 17.89$, $p < .001$). However, we found no evidence that calibration improved the overall estimates ($\chi^2(1) = 3.06$, $p = .080$), or that the calibration effect differed between estimation methods ($\chi^2(2) = 0.27$, $p = .874$). Looking at the precision, we also found that the absolute error at the longest interval differed between estimation methods ($\chi^2(2) = 26.24$, $p < .001$), and that the error was higher in the calibrated condition ($\chi^2(1) = 4.61$, $p = .032$). Although the visual inspection of Figure 7.2B suggests that the effect of calibration condition was larger for the timeline estimations compared to the other methods, we found no evidence that this effect differed between estimation methods ($\chi^2(2) = 4.29$, $p = .117$). The CV showed a similar pattern: it differed between estimation methods ($\chi^2(2) = 6.12$, $p = .047$) and was higher in the calibrated condition ($\chi^2(1) = 8.17$, $p = .004$), but there was no evidence for a difference in the effect of calibration between estimation methods ($\chi^2(2) = 4.26$, $p = .119$). Overall, these results indicate that calibrating participants with longer durations did not improve the accuracy of the line, motor or verbal estimates, but did decrease their precision.

Sequential context effects. To test whether there were differences in sequential context effects between the estimation methods, we tested the impact of previously presented durations. We started with the LMM predicting estimated duration including estimation condition, presented duration and their interaction as fixed factors. We gradually added previous presented durations (N-1, N-2, etc.) to the model as continuous fixed factors and tested whether they improved the model fit. We found that only the most recent previous trial (i.e., N-1) improved the model ($\chi^2(1) = 75.28$, $p < .001$), and that this factor differed between the estimation conditions ($\chi^2(2) = 7.07$, $p = .029$). Post-hoc contrasts showed that the effect of N-1 was larger for motor compared to verbal reproductions ($p = .017$). There were no other differences (*p*s > .239).

Reaction time. Figure 7.2D shows the average reaction time (RT) for every estimation method and calibration condition. The model showed that the overall reaction time, and the change of (RT) with duration, differed between estimation methods ($\chi^2(2) = 731.77$, $p < .001$ and $\chi^2(2) = 848.88$, $p < .001$, respectively). Post-hoc contrasts showed that the RT at the 2.5 s interval intercept was higher for the verbal compared to the line estimation ($p < .001$) and higher for the motor reproductions compared to the verbal and line estimation (*p*s < .001). Because the motor reproductions increased with the presented duration, whereas the other two methods are independent of the presented duration, the slope was larger for the motor reproduction method (*p*s < .001). There was no difference in slope between the verbal and line estimation ($p = .837$). Adding the interaction between estimation method and calibration condition improved the model significantly ($\chi^2(2) = 14.40$, $p < .001$), but there were no significant differences in the final model (*p*s > .328).

Discussion

In Experiment 1, we compared three estimation methods in a simple interval estimation task. The results showed that the verbal estimates were overall more veridical than the motor and line estimates. We found no evidence for a difference in the accuracy of the motor and line estimates. When we look at precision of estimation, we found that the CV decreased with the presented duration. This is a violation of Weber's law, or the scalar property of time perception, which states that the CV should be constant over different durations (although violations are frequent in the timing literature: see Grondin, 2014). Comparing the absolute error and the CV between estimation methods, we found that verbal estimates were most precise. Notably, however, this precision depended on the specific presented duration: it was higher for rounded integers than for durations with a fractional part. In addition, motor reproductions were generally more precise than line estimates. Overall, these results suggest that there is no cost in accuracy to the potential spatial transformation required for line estimates, but there might be a small cost in precision, that is, the variability of the estimates. Note, however, that any difference between motor reproductions and line estimates, especially, may arise due to differences in the amount of motor noise rather than because of their underlying representation and translation into another dimension.

We expected that calibrating participants with a larger interval range and a longer corresponding timeline at the start of the experiment would diminish the underestimation of longer durations. However, we found no evidence that this calibration increased the overall accuracy, or the accuracy of the longest duration. Instead, we found a small cost in the precision of the longest interval estimates. These results suggest that calibration did not improve the timeline estimates by diminishing a potential end of the line bias. Alternatively, the end of the line effects here (and in Damsma et al., 2018) could reflect a general pull towards the mean in which the estimate is biased towards previously presented durations. Indeed, sequential context effects were observed in all three conditions. Verbal estimates were less affected by the duration of the previous trial, which can be explained by their generally higher accuracy and precision. According to the Bayesian view of perception, it is optimal to rely more on prior experience in making an estimate when the current observation is less precise (Acerbi et al., 2012; Jazayeri & Shadlen, 2010).

When reproducing longer time intervals using a motor response, the duration of a trial scales with the interval to be reproduced. Line and verbal estimates, on the other hand, have the advantage of a stable response time of - in our experiment - around 1.5 and 2 s, respectively. Based on these results, we suggest that researchers can increase the number of trials in their experiment when testing longer intervals by using line or verbal estimates, and thereby increase statistical power.

Another potential advantage of timeline estimates over motor reproductions is that there is more time for a deliberate decision, compared to the 'one shot' approach of motor reproductions: in the latter case, participants are by definition unable to decrease their estimate at any point in time. This 'time asymmetry' might induce biases specific to motor reproduction, such as systematic under-reproduction (Riemer, Trojan, Kleinböhl, & Hölzl, 2012). In contrast, in the line estimation condition, participants can move the cursor freely to the left or right to decrease or increase their estimate. This could make timeline estimates more accurate in situations that are more complex than the reproduction of a single interval to which participants can fully direct their attention, such as when estimating an interval concurrently with other tasks (e.g., Brown, 1997, 2006; Zakay, 1993) or estimating multiple intervals (e.g., Brown & West, 1990; Van Rijn & Taatgen, 2008). To test this notion, Experiment 2 consisted of a stream of stimuli that contained one target. Participants had to estimate both the target onset and the duration of the stream.

Experiment 2

Methods

Participants. Thirty-nine healthy adults (9 male, mean age 20.64 years) participated in exchange for course credits. None of the participants in Experiment 1 took part in Experiment 2. Informed consent as approved by the Ethical Committee Psychology of the University of Groningen (identification number 17054-S-NE) was obtained before testing. Sample size was based on past research (e.g., Experiment 1; Damsma et al., 2018; Schlichting et al., 2018), no statistical *a priori* power analysis was conducted.

Experimental design. Participants were asked to perform a temporal estimation task using two different methods: motor reproductions and timeline estimations (Figure 7.3). Stimuli were displayed on a 1280 × 1024 CRT-based monitor screen (Iiyama Vision Master Pro 513) with a refresh rate of 100 Hz. The interval was presented as a stream of numeric characters (1 to 9 characters in total) and one alphabetic character, the target (A, B, C, C, E, F, H, J, K, P, R, T, U, or V). The alphanumeric characters were presented in Arial with a font size of 16 pt. Within the stream alphanumeric characters were chosen randomly, while no two consecutive characters were the same. Participants were asked to estimate both the interval from stream onset to target onset as well as the duration of the total stream. There were six different total stream durations (4.75, 5.25, 5.75, 6.25, 6.75, and 7.25 s) and 11 positions where the target could occur from stream onset (1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5, and 6 s). Target onset was chosen completely random, that is, for some participants not all target positions may have occurred. Each alphanumeric character was presented for 0.25 s with 0.25 s between two successive characters, so that each stream consisted of 10 to 15 alphanumeric characters in total. The estimation methods were similar to Experiment 1, with the only difference that two responses were required. In the motor reproduction task, a first spacebar press corresponded to the time point of target occurrence, and a second spacebar press corresponded to the end of the stream. Similarly, a first mouse click on the timeline

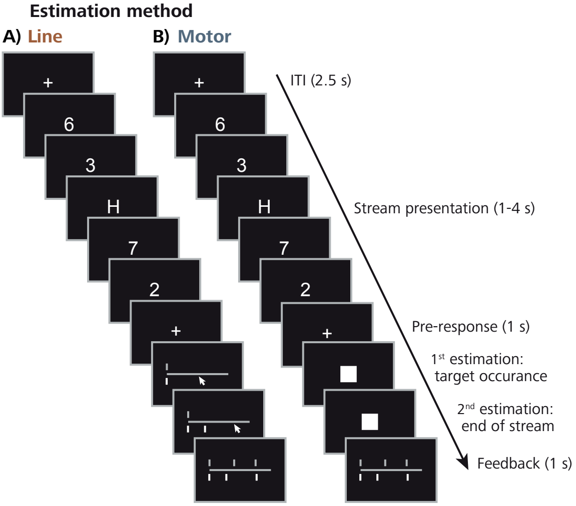

Figure 7.3. Trial procedure of Experiment 2. Participants were presented with a stream of numbers with one target letter. Their task was to estimate the interval from the beginning of the stream until the target onset, and also of the total duration of the stream by either A) pressing a key at the estimated moments (motor reproduction) or B) clicking on a timeline (line estimates). Feedback was presented at the end of each trial.

corresponded to target occurrence, and a second mouse click to the end of the stream in the timeline estimation task. Participants received immediate feedback similar to the feedback in Experiment 1, with two additional bars corresponding to the veridical and estimated target occurrence (or interval to target onset).

The experiment was divided into two blocks (i.e., one block for each estimation method) of 60 experimental trials (i.e., ten trials per duration) each. Order of blocks, and thus estimation methods, was counterbalanced between participants. Before the start of each block, participants received instructions about the estimation method to be used in the upcoming block, and they performed 12 practice trials in order to get accustomed to the timeline and the estimation method before the start of the experimental trials. The order of trials was the same in each block but varied between participants.

As in Experiment 1, half of the participants performed a calibrated version of the estimation tasks. In the calibrated version the training-trials consisted also of longer overall intervals than those in the test trials (3.25, 6.25, and 9.75 s), while in the uncalibrated version training trials were chosen up to the longest duration of test trials (2.25, 4.75, and 7.25 s). The experiment files can be found at https://osf.io/w38qg/.

Analysis. All estimates shorter than 0.2 s and longer than 11 s (1.95% of the data) were excluded from analysis. The longest durations of the target estimates (5, 5.5 and 6 s) were also excluded from analysis, because there were on average less than 4 trials per condition per participant, leading to unreliable calculations of the error and CV measures. The analysis procedure was similar to Experiment 1. Target and stream estimates were analyzed separately. The durations were centered at 2.75 s and 6 s for target and stream estimations, respectively. All categorical fixed factors were recoded using effect coding (-0.5 and 0.5), to facilitate the interpretation of main effects when interactions are included in the model. In the current experiment, there were two estimation methods (motor reproduction and timeline estimation) instead of three methods in Experiment 1. Therefore, instead of post-hoc contrast results, we will report the β-coefficient and t-value of factors in the final LMM, as they are a direct representation of the difference between the estimation methods. The analysis scripts and results can be found at https://osf.io/w38qg/.

Results

Estimates.

Interval to target onset. Figure 7.4A shows the average estimates of the interval between stream onset and target onset for the different conditions. We found that, overall, target estimates increased with the presented onset ($\chi^2(1) = 2105.36$,

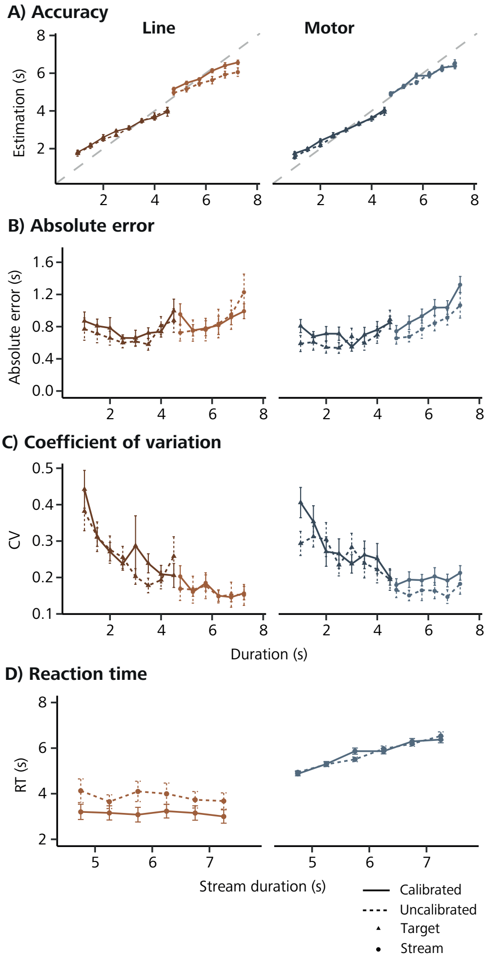

Figure 7.4. A) Average interval-to-target and total stream duration estimates for the timeline and motor conditions and calibration conditions. The grey dashed line represents veridical performance. B) Average absolute error of the target and stream estimates for the timeline and motor conditions and calibration conditions. C) Average CV of the target and stream estimates for the timeline and motor conditions and calibration conditions. The error bars represent the standard error of the mean. D) Average response time (RT) of the stream estimation for the timeline and motor conditions and calibration conditions. In all figures, the error bars represent the standard error of the mean.

$p < .001$; $\beta = 0.66$, $t = 19.54$). In addition, motor reproductions were shorter than line estimates ($\chi 2(1) = 26.31$, $p < .001$; $\beta = -0.14$, $t = -2.94$). No other fixed effects reached significance.

Total stream duration. The stream estimates also increased with the presented duration ($\chi^2(1) = 792.99$, $p < .001$; $\beta = 0.57$, $t = 16.87$), but here the slope was steeper for motor reproductions than for line estimates ($\chi^2(1) = 7.13$, $p = .008$; $\beta = 0.09$, $t = 2.55$). Model comparison showed a stronger effect of calibration for the line estimates compared to the motor reproduction methods ($\chi^2(1) = 24.85$, $p < .001$), although this effect did not reach significance after including random slopes in the final model (β = -0.35, t = -1.68, p = .101). In addition, the effect of calibration on the slope was larger for the line estimates compared to the motor reproductions ($\chi^2(1)$ = 4.44, p = .035; β = -0.17, t = -2.31). Overall, these results suggest that stream estimates were more veridical for the motor compared to the line condition, but that calibration with a longer time line decreased this difference.

Absolute error.

Interval to target onset. Figure 7.4B shows the average absolute error for the estimations of different durations for each condition. The LMM showed that the absolute error of target estimates increased with duration ($\chi^2(1)$ = 5.37, p = .020; β = 0.03, t = 2.57). Model comparison suggested that there was a difference between line estimates and motor reproductions ($\chi^2(1)$ = 4.60, p = .032), but this effect was not significant after including random slopes (β = -0.06, t = -1.12, p = .271). Overall, calibration condition did not affect the absolute error.

Total stream duration. In line with the absolute error of the target estimates, the error of the stream estimates increased with duration ($\chi^2(1)$ = 45.02, p < .001; β = 0.15, t = 9.60). In addition, model comparison showed an interaction effect of estimation method and calibration condition, but this effect did not remain significant in the final model ($\chi^2(1)$ = 5.69, p = .017; β = 0.17, t = 0.96). However, the slope difference between the calibration conditions was larger for the motor compared to the line estimates ($\chi^2(1)$ = 4.64, p = .031; β = 0.18, t = 3.00). The final model also revealed a steeper slope for the motor compared to the line condition (β = 0.07, t = 2.34).

Coefficient of variation (CV).

Interval to target onset. Figure 7.4C shows the CV for the different duration and conditions. We found that the CV decreased with duration ($\chi^2(1)$ = 75.60, p < .001; β = -0.04, t = -8.98). We found no differences between the estimation methods or the calibration conditions.

Total stream duration. In contrast to the target estimates, the CV of the stream estimates did not change with duration ($\chi^2(1)$ = 0.44, p = .509). However, the slope was more positive for motor compared to target reproductions ($\chi^2(1)$ = 4.85, p = .028; β = 0.02, t = 2.21).

Sequential context effects.

Interval to target onset. We started with the LMM established to predict the target estimates (including duration and estimation method as fixed factors). We then sequentially added previous target and stream durations. We found that target estimates were significantly influenced by target estimates in the previous trial (i.e., N-1; $\chi^2(1)$ = 23.16, p < .001; β = 0.05, t = 4.82). This effect did not differ between the motor and line estimates. There was no significant effect of N-2 ($\chi^2(1)$ = 2.65,

$p = .104$). We also tested whether the stream estimates in the current trial influenced the target estimates, but there was no evidence that this was the case ($\chi^2(1) = 0.89$, $p = .345$).

Total stream duration. The estimates of the stream durations were influenced by the stream duration in the previous trial ($\chi^2(1) = 38.24$, $p < .001$; $\beta = 0.14$, $t = 7.33$). This effect did not differ statistically between estimation methods ($\chi^2(1) = 2.89$, $p = .089$). The stream estimates were also influenced by target onset ($\chi^2(1) = 27.55$, $p < .001$; $\beta = 0.66$, $t = 5.14$) and target onset in the previous trial ($\chi^2(1) = 9.59$, $p = .002$; $\beta = -0.04$, $t = -3.18$). The latter effect was stronger for line estimates compared to motor reproductions ($\chi^2(1) = 8.23$, $p = .004$; $\beta = 0.06$, $t = 2.59$).

Reaction time. Figure 7.4D shows the average response times. We found that duration, estimation method and their interaction improved the model fit ($\chi^2(1) = 47.82$, $p < .001$, $\chi^2(1) = 1282.98$, $p < .001$ and $\chi^2(1) = 5.95$, $p = .015$, respectively). In line with Figure 7.4D, the final model showed that RTs were higher ($\beta = 0.91$, $t = 3.21$), and the increase of RTs with duration was larger ($\beta = 0.71$, $t = 11.63$), for motor reproductions compared to line estimates. There was no overall effect of calibration condition ($\chi^2(1) = 2.33$, $p = .013$). Although the interaction between estimation method and calibration condition improved the model ($\chi^2(1) = 43.98$, $p < .001$), this fixed effect was not significant in the eventual model including random slopes ($\beta = 0.76$, $t = 1.47$).

Discussion

In Experiment 2, participants were asked to reproduce the interval between the onset of an alphanumeric stream and a target letter in the stream as well as the end of the stream. The results suggest that the motor reproductions had a slightly more veridical slope than the line estimates, but only for the stream estimates. In line with Experiment 1, the CV decreased with duration, violating the scalar property. The overall precision of the responses of the motor reproductions and line estimates was similar, however, the variability increased more with the presented duration for motor reproductions. Whereas calibration had no effect on motor reproductions, it improved the average accuracy of the stream estimates in the line condition. As in Experiment 1, we found that reaction times were stable over the different test durations and lower overall in the line condition.

We again found that previously perceived target or stream durations influenced target and stream estimates in the current trial, and there was no difference between estimation methods. There was also an effect of target onset on stream estimates, in that the later the target appeared, the longer the stream was estimated. One explanation is that participants use a sort of relative timing: if the target occurred relatively late, the duration of the stream was probably longer (see also Van Rijn & Taatgen, 2008). In the line estimation condition, another explanation of this finding is that participants tend to keep their distance from the target estimates when making the second estimates on the stream duration, an effect that might be similar to the bias of avoiding the end of the scale. Thus, if the target occurred relatively late, the stream duration estimate will be shifted to having occurred later (see also Damsma, Van der Mijn, & Van Rijn, 2018, who show that estimates of the timing of targets in an attentional blink paradigm are not independent of each other). Interestingly, we found a difference between estimation methods in the effect of the previous target onset on stream estimates. This effect may have been more prevalent in the line estimation condition because of the strong visual representation in the line compared to the motor condition. Not only were participants able to see their target estimate in the line condition, but it was also potentially easier to incorporate the feedback of the previous trial because it was visualized in the exact same way as participants gave their estimates. Because of the increased task complexity in Experiment 2, the visual representation might have been taken more into account as compared to Experiment 1.

General discussion

In the current study, we compared the accuracy and precision of interval estimations using a visual analogue scale (or, a timeline) to non-spatial estimation methods (motor reproductions in Experiment 1 and 2 and verbal estimations in Experiment 1). If, regardless of estimation method, temporal estimates undergo the same or similar transformations, we expected to find no differences between the different estimation methods. If, on the other hand, a mental transformation from time to space is required, we would expect costs in accuracy and precision in the timeline estimates. In Experiment 1, we found similar accuracy for line estimates and motor reproductions, whereas the precision was higher for motor estimates. Verbal estimates seemed to lead to the most accurate and precise estimates. However, the pattern we found in absolute errors suggests that this estimation method comes with its own unique problems that we discuss further below. In the more complex paradigm of Experiment 2 we found that estimates were slightly more accurate for motor reproductions compared to timeline estimates, while the precision was similar.

Taken together, these results suggest that both motor reproduction and timeline estimation can be reliably used to measure subjective timing. This could indicate that space and time have a similar neural representation (e.g., Walsh, 2003, 2015) or that transformation into space has only a relatively minor cost, roughly equivalent to the effect of noise introduced by manual reproduction. Alternatively, it is possible that time is represented in a sufficiently abstract way to make transformation to any other representational form effortless and equally accurate. In either case, however, it is important to note that both motor reproductions and line estimates might come with their own respective sources of noise. For motor reproductions, this would be motor noise and also the previously discussed 'one-shot' approach in reproducing intervals. For timeline estimates, participants first have to learn how exactly time translates into space when using a specific timeline. This means that even if time would be represented spatially, a source of noise in line estimates could be that participants have to scale their spatial representation of time before giving an estimate. Because it is difficult to disentangle these sources of noise from noise in the representation of time, the differences in accuracy and precision between the estimation methods do not allow arguing in favor or against the idea of a spatial time or general magnitude representation.

In Experiment 1, we found that verbal estimates were more accurate and precise than timeline estimates and motor reproductions, implying that verbal estimates are superior to other estimation methods. However, participants were encouraged to express their subjective estimate in familiar terms (in this study: seconds). This familiarity might come at a cost: We found that the verbal estimates displayed an inconsistent pattern of precision, in which rounded integer intervals were estimated with higher precision than non-integer intervals. This pattern can be explained in three ways: 1) the emphasis on 'seconds' might lead participants to think about time in terms of these pre-learned units, 2) the method might have encouraged participants to count (although they were explicitly instructed not to count), and 3) the method of report might have encouraged some participants to round their estimate to the nearest integer, without using the fractional part. Regardless of the origin of the precision pattern, the results indicate that verbal estimates might encourage participants to think about time in a less 'linear' and a more 'categorical' way. Indeed, this is in line with the idea that verbal estimates are "contaminated by linguistic and semantic tags associated with traditional units of time perception" (Hancock & Block, 2012). These hypotheses imply that verbal estimates might be less accurate or precise when, for example, a range of sub-second intervals is reproduced. Future studies might test this idea by comparing estimation methods in different interval ranges.

The differences in the results of Experiment 1 and 2 might be due to the different paradigms. First, participants had to reproduce two intervals in Experiment 2 (i.e., target onset and stream offset), and only a single interval in Experiment 1. This makes the task more difficult, which results in a higher absolute error in Experiment 2 (see also Brown, Stubbs, & West, 1992; Brown & West, 1990). In addition, the estimates of the first and second interval might not be completely independent: the results show that there is an intercept difference, accompanied by a 'local' pull towards the mean, dependent on whether the first or the second interval is reproduced (see also Damsma, Van der Mijn, & Van Rijn, 2018). These dependencies might be stronger when they are visually represented on a timeline compared to motor reproductions. Second, longer intervals were presented in Experiment 2, which would also decrease the precision, in line with the scalar property.

One explanation for the lower accuracy in the timeline estimates in Experiment 2 is an increased response bias (i.e., reluctance to use the end of the scale), because the timeline offers a more explicit physical range compared to motor reproductions. If this is the case, we expected that estimates would be more accurate when the interval range is artificially increased in pre-experiment calibration trials. Indeed, the results of Experiment 2 showed that calibrating participants with a larger range increased the accuracy for longer intervals (i.e., the stream duration estimates), with similar precision. In Experiment 1, the calibration neither improved the overall accuracy, nor the accuracy of the longer intervals. Overall, these results suggest that the range of the timeline should be taken into account, as a range that is larger than the actual test durations might reduce the response bias for longer intervals. In the current study, the resolution of the timeline was identical in the calibrated and non-calibrated condition (1 pixel on screen corresponded to 0.01 s). Future studies could test whether this property of the timeline affects accuracy and precision of estimates, especially if the range of test durations is much larger than in the current study. Additionally, participants in our experiments received feedback about their accuracy on a line in every estimation condition, to keep the conditions as similar as possible. This way of presenting feedback could potentially bias participants towards a spatial representation of time. Future studies might test this notion by removing the feedback or varying the feedback modality.

Overall, the results show that each estimation method comes with its own unique advantages and drawbacks. Line estimations offer the advantage of a stable response time, which can allow the researcher to increase the number of trials in supra-second interval estimation experiments (i.e., using intervals longer than ~1.5 s). However, compared to motor reproductions, there might be a small cost in accuracy, potentially because of a required spatial transformation. This difference might be overcome by calibrating participants with a suitable interval range. Motor reproductions offer an intuitive estimation method, but the response times scale linearly with the presented intervals. In addition, it is difficult to disentangle the precision of the actual temporal estimate from motor inaccuracies (Droit-Volet, 2010; Hallez, Damsma, Rhodes, Van Rijn, & Droit-Volet, 2019). In Experiment 1, we showed that verbal estimates are more accurate and precise than line estimates and motor reproductions. However, the precision of verbal estimates depends on whether the interval is a whole integer, indicating a bias towards familiar whole second units. Although future research should further investigate the reliability of estimation methods in different timing experiments, the current study can point timing researchers to a more optimal estimation method given their specific paradigm.

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8

general discussion

The way we perceive time is critically dependent on memory. After all, when we want to estimate how much time has passed since we turned on the coffee machine, we need to have a representation of this event in memory, and our time estimate relies on internal processes and external events that have unfolded since we switched on the machine. In addition, our subjective sense of duration will be informed by all the previous times we have gone through the coffee-making process. These experiences in memory allow us to adapt to the dynamics of the environment through increased attention and readiness for action at the right anticipated moment.

The present thesis investigated the interaction between memory and interval perception by focusing on two open questions: How are time intervals represented in memory and how are these experiences in memory used to optimize attention and duration estimates? In the following section, I will summarize the results of the empirical work in this thesis and discuss the implications for theories of time perception. After that, I will argue that the memory biases we see might actually reflect adaptive processes in everyday life, and I will come back at a major point of distinction in the time perception field: Is there a dedicated internal clock? Finally, based on our findings and these discussions, I will present recommendations for future directions.

Adaptive timing: summary and implications

The representation of time

Gu, Van Rijn, and Meck (2015) proposed that the system of updating semantic information in working memory can also code for time. In Chapter 2, we investigated the prediction of this model that memory consolidation acts as the starting gun of interval timing. The results, however, suggested that there is no direct link between consolidation and the onset of timing of sub-second intervals in an attentional blink task: We showed that temporal estimates were not later when the second target followed quickly after the first, a case in which a delay in memory consolidation was expected, and we found no evidence for a relationship between P3 latency and temporal estimates.

Thus, we did not find the relationship between working memory consolidation and the perceived time of onset as predicted by the theory of Gu et al. (2015). From our results, it seems that, although memory consolidation is crucial for the conscious perception of an event, time information is coded for by another mechanism that is independent of the processes underlying the P3. Although the results are not directly in line with Gu et al.'s theory, the absence of an effect could also be attributed to the variation in P3 latencies and responses, which might not have been large enough to uncover a potential relationship. Future studies could study the relation between memory consolidation and subjective timing in other paradigms and might investigate earlier components that might prove to be predictive of onset timing.

While the subjective onset of an event did not seem to depend on the latency of memory consolidation, the results showed that participants instead used contextual cues to inform their estimates in three ways. First, estimates of second target onset were structurally later than estimates of the first target, even when they occurred at identical stream positions. This suggests that participants were either strategically applying a rule of thumb that second targets must generally occur later in the stream relative to first targets, or, alternatively, were biased towards two separate prior distributions for the two targets. Second, first target estimates were earlier in two-target trials compared to single-target trials, showing that the estimate of the first target depended on the presence of another target. Third, we found a central tendency effect in all onset estimates, suggesting that participants were biased towards the temporal statistics of previous trials. Overall, these internal and external contextual cues might prove to be a primary source for the extraction of onset time and duration in everyday situations: The representation of temporal information does not happen in isolation for every separate event, but observers tend to take sequential episodic information into account. Models of time perception should be able to account for these effects.

The timeline estimates in Chapter 2 might have decreased the accuracy or variability of responses, because of a potential transformation of time representations into space. However, the results in Chapter 7 suggest that time estimates can be quite flexibly transformed into other dimensions. We found that verbal estimates were more accurate and precise than line estimates and motor reproductions, but they were biased towards familiar whole second units. Motor reproductions were not consistently more accurate or precise than spatial estimates. These findings suggest that space and time have a similar neural representation in accord with ATOM (Walsh, 2003, 2015), or that the transformation into space has a relatively small cost, roughly equivalent to the effect of noise introduced by manual reproduction. We see the interchangeability of time and space in everyday language - for example, when we say "it took a long time before he answered the difficult question" – but our results suggest that this interchangeability generalizes to the way humans are able to report their temporal estimates. Whether a common representation of space and time is inherent in low-level accumulation or only occurs at later stages in the representational or decision process (Anobile et al., 2018) remains an open question. As I will discuss later in this chapter, in everyday episodic memory, time and space may be encoded by the same neural populations in a non-separable way (Buzsáki, 2019).

Salient regularity

Previous experience with durations and rhythms inform our predictions about what will happen next. In this way, our attention can be optimized over time: In the case of intervals, attention focused at the right moment can increase perceptual sensitivity (e.g., Lasley & Cohn, 1981; Rolke & Hofmann, 2007; Westheimer & Ley, 1996; Willems, Damsma, Wierda, Taatgen, & Martens, 2015), and in the case of rhythms, expectations can be entrained to, for example, external isochronous stimuli (e.g., Henry & Obleser, 2012; Jones et al., 2002). The results in Chapter 3 show that drum rhythms induce hierarchical expectations over time: We found that more salient omissions elicited a higher pupillary response than omissions at lower metrical levels. Additionally, we found that this representation of meter was induced rather automatically, in the absence of attention and expertise. These results are in line with rhythmic entrainment accounts of attention (e.g., Jones, 1976; Large & Jones, 1999). Importantly, however, our results suggest that the entrainment goes beyond a single oscillator: Participants formed a hierarchical sense of beat, so that some beats were more anticipated than others (Henry & Herrmann, 2014). This hierarchical entrainment could be implemented by nested low-frequency neural oscillations in the cortex that selectively enhance or suppress input (Henry & Herrmann, 2014; Schroeder & Lakatos, 2009). We show that this sense of hierarchical meter can be induced even when participants were performing another task.

Our pupil dilation results show that the pupillary response indexes the violation of expectations, complementing previous studies demonstrating pupil size to be a measure of surprise (Friedman et al., 1973; Liao, Yoneya, Kidani, Kashino, & Furukawa, 2016; Steinhauer & Zubin, 1982). In line with the predictive coding framework (Friston, 2005), predictions are made based on previous experience, and stimuli that are not in line with the predictions are flagged as salient events. Considering that pupil size is thought to reflect noradrenaline (NA) release in the locus coeruleus (LC) (Laeng et al., 2012; Nassar et al., 2012; Sara, 2009), the LC-NA might play a role in the automatic signaling of prediction error to other cortical and subcortical target regions when presented with novel, salient stimuli (Krebs, Park, Bombeke, & Boehler, 2018). In this way, the current study delivers further support for the proposed role of the LC-NA system as a signaler of the need for adapting the mental model of the environment (Nieuwenhuis, 2011).

Given the importance of rhythms and other temporal regularities in guiding expectations, and the automaticity with which this seems to happen demonstrated in Chapter 3, we reasoned that rhythmic stimuli in the environment might receive some special attention. While this is usually demonstrated through the entrainment of perceptual sensitivity, we wondered whether this special attention also manifests itself when there is no direct relevance for the task. In other words, do humans show increased attention to regularities, even when they do not help them in the task they need to perform? In Chapter 4, we found no evidence for such a bias towards temporal regularities. Specifically, across six experiments, we found no lower reaction time for targets in a search task that matched the features of regular, isochronous stimuli.

Whereas previous studies have shown that temporal structure can be used to optimize attention and perception when the regularities reliably predict upcoming stimuli (Correa et al., 2005; Martens & Johnson, 2005; Niemi & Näätänen, 1981; Olson & Chun, 2001; Willems et al., 2015), the current results suggest that this might not be the case when such regularities are uninformative about the task at hand. A potential explanation is that, in the latter case, prioritizing attention to temporal regularities might in some cases be detrimental for task performance. In line with this notion, Schroeder and Lakatos (2009) proposed that the brain can function in either a "rhythmic" or a "continuous" mode, depending on the task at hand. The rhythmic mode, involving low-frequency entrainment in the cortex, is useful when there is a task-relevant rhythm, enhancing perceptual sensitivity in phase with the rhythm. However, if the task contains no relevant rhythm, the brain can operate in a more continuous state of vigilance by suppressing low-frequency oscillations and enhancing gamma-band oscillations. In this continuous mode, the cost of lower sensitivity in the low-excitability phase of slow neural entrainment can be prevented.

Interestingly, the difference between Chapter 3, where participants form rhythmic expectations in the absence in the attention, and Chapter 4, where attention was not biased towards the temporal regularities in the task, suggests that the process of neural entrainment might be modality specific. When the rhythmic information is in a different modality than the visual detection task (in Chapter 3), there is no cost in entraining expectations to the auditory rhythm. However, when the regularity occurs in the same modality as the detection task (in Chapter 4), entrainment might come at the cost of decreased continuous vigilance. Future studies could test this by measuring EEG or pupil dilation responses to deviations in regular stimuli in different modalities, while participants perform a detection task in either the same or the other modality.

Context matters

Flexible cortical dynamics. When we try to estimate the duration or onset timing of events, we do not do this in isolation: We take cues and our memory of temporal structure in the environment into account. The results of Chapter 5 suggest that previous intervals in memory act directly on perception. Specifically, longer recent intervals decreased the CNV and P2, and increased the power of beta oscillations. Multivariate pattern analysis showed that context can be decoded from transient neural activity right after the start of the perception phase. Together, these results suggest that Bayesian computations in the brain might not be performed in a separate post-perceptual stage, but instead inherently shape the way in which we perceive the world.

We found that the speed with which the CNV component builds up during interval perception depends on the temporal context. In the context of a short interval range, the CNV was more negative compared to a long interval range. Strikingly, this adaptation even occurred on a trial-by-trial basis, demonstrating the flexibility of neural signatures associated with time perception. These results show that cortical dynamics are tuned to the current environment based on recent experience, forming expectations about the on- or offset of relevant stimuli. Together with other recent findings (Kononowicz & Van Rijn, 2011, 2014; Ng et al., 2011; Van Rijn et al., 2011), this interpretation goes against the idea that the CNV represents the state of an absolute accumulator (Casini & Vidal, 2011; Macar et al., 1999). After all, if this were the case, we would not expect any differences in the accumulation process in the short and long context. Following the CNV-as-accumulator view, the more negative CNV in the short context should have resulted in longer estimates than in the long context, while the behavioral results showed the opposite effect.

The finding that the CNV does not represent the state of an absolute accumulator does not rule out that an internal pacemaker-accumulator system exists, but it does make it less likely that the role of the SMA is to keep track of time in an absolute way, like a physical clock. Indeed, so far, it has been difficult to pinpoint the underlying neural areas or mechanisms of a dedicated internal clock (Van Rijn et al., 2014). The alternative that seems more likely given our results is that expectations are flexibly adapted based on experience (Nobre & Van Ede, 2018), and these expectations are reflected in context-specific modulations of neural signatures, such as the CNV, the P2 and beta power. When the offset of the stimulus is expected to occur early during interval timing, the CNV builds faster than for later expected offsets. The expectation effects we observed might be closely related to motor preparation in the SMA (Coull et al., 2016), which may in turn determine the trial-by-trial fluctuations in reproductions. In this way, motor timing could be accomplished by neural populations that flexibly scale their activity based on the current task requirements and previously learned temporal statistics (Remington, Egger, et al., 2018; Remington, Narain, et al., 2018; Sohn et al., 2019), without a separate central clock that orchestrates or times these dynamics.

Priors in the real world. While Chapter 5 shows that participants are biased toward priors acquired in blocks of simple tone durations, Chapter 6 provides a first step of taking timing studies into more realistic settings. Do ‘laws’ of time perception, such as the context effect and scalar property, still hold? In contrast to the usual laboratory experiments, using simple stimuli like in Chapter 5, the on- and offset of the actions in Chapter 6 were not clearly defined, but had to be determined by the participant. The results suggest that established effects of time perception might accurately describe the way people estimate the duration of actions, such as mixing or drinking, in everyday life. Reproductions showed a clear pull towards the overall mean and the previous subjective duration, indicating that they were influenced by the context. In addition, we found that the standard deviation increased linearly with the reproduced duration, confirming the so-called scalar property.

These findings show that a Bayesian prior, one’s *a priori* belief about the probability of a duration, might consist of a single probability distribution for several different events and stimuli, such as the actions in our experiment. This sparks the question: To what extent are different experiences represented as separate priors? Of course, in everyday life, we need to group experiences in a meaningful way in order to learn temporal statistics. Roach, McGraw, Whitaker, and Heron (2017) suggested that an important aspect in this regard is the action that is required for a specific input. In their experiments, participants did not automatically create separate priors for stimuli of different stimulus modalities or locations, except when a different motor response was required. However, Rhodes, Seth, and Roseboom (2018) showed that responses could be biased towards the range of stimuli depending on the modality or characteristics within the same modality, suggesting that multiple priors can be employed simultaneously when sensory characteristics are sufficiently different. Our results in Chapter 6 suggest that a single prior is used for different actions, potentially because the stimulus source and motor response was similar across the actions. Future studies could investigate how different priors are obtained in everyday situations through interaction with the environment.

Another interesting observation in Chapter 6 is that not the previously objective duration, but the subjective previous duration (as measured by the previous reproduction) influenced the current interval perception. This suggests that the prior in Bayesian inference is not built on the durations *as presented*, but the durations *as perceived* (see also Taatgen & Van Rijn, 2011). In line with Chapter 5, the *perception* of the presented interval might already be actively influenced by previous durations, which in turn is integrated in a prior upon which subsequent behavior is based (Dyjas, Bausenhart, & Ulrich, 2012). This mechanism also illustrates the great flexibility with which the prior is adapted. The prior is not static, but is updated with every new experience. This mechanism might be highly adaptive when we interact with a dynamic environment based on sensory information that is not always reliable, as we will see in the next section.

Distortion or optimality?

When we compare human timing behavior to a clock or stopwatch, we often observe that they structurally deviate from what we could call ‘objectively perfect time perception’. For example, in several chapters of this thesis, temporal estimates showed a clear regression towards the mean. These findings suggest that the central-tendency effect is highly robust and occurs when estimating target onsets (Chapter 2), reproducing time intervals (Chapter 5), and even in estimating the duration of everyday kitchen-related actions (Chapter 6), irrespective of whether the estimate is expressed spatially, verbally or using a button press (Chapter 7).

Deviations of subjective time from the duration measured with clocks, such as the central tendency effect, are often interpreted as a shortcoming, or ‘distortions’, ‘illusions’, and ‘biases’ (Eagleman, 2008; Matthews & Meck, 2016). However, why would a biological system be equipped with a flawed timing mechanism, given that accurate timing is essential for many everyday activities? Would it be possible that biases in time perception instead are in some way adaptive, or even optimal?

In perceiving and interacting with the environment, humans can use their memories of previous experiences to make predictions. They have an internal model of the world, in which the probability is represented of *when* something will occur, or *how long* an event typically lasts. This idea is often proposed in the light of the Bayesian framework, in which an observer combines an uncertain percept of the world (the likelihood) with *a priori* knowledge of the world (the prior) to arrive at an eventual estimate (the posterior). Given that our senses are inherently noisy, taking prior information about the likely state of the world into account might be the best way to come to accurate percepts and predictions to act on.

Several studies suggest that humans indeed perform near Bayes-optimal inference (Beierholm, Quartz, & Shams, 2009; Ernst, 2006; Ernst & Banks, 2002; Körding & Wolpert, 2004; Ma, Beck, Latham, & Pouget, 2006; Petzschner & Glasauer, 2011; Shi, Church, & Meck, 2013; Stocker & Simoncelli, 2006). Similarly, in time perception, humans are able to adapt their duration estimates to the temporal range (Jazayeri & Shadlen, 2010) and distributions (Acerbi et al., 2012) of presented intervals. There is also evidence that these mechanisms are specifically pronounced in uncertain circumstances. Longer intervals, which are perceived with more uncertainty according to Weber’s law (e.g., Chapter 6), show a larger central tendency effect (Cicchini et al., 2012; Jazayeri & Shadlen, 2010). Moreover, individuals with superior timing abilities, such as expert percussionists, show a smaller central tendency (Cicchini et al., 2012), while young children that have noisier temporal representations show more reliance on the prior (Hallez et al., 2019). In line with these examples, individuals respond earlier or later in a so-called Beat-the-Clock task depending on their endogenous timing uncertainty, showing optimal reaction times (Balci et al., 2011).

Together, these studies suggest that human perception might be well described by the Bayesian ideal observer model. They show that humans are able to pick up on the statistics of temporal distributions, and the resulting bias depends on the individual’s perceptual noise. Indeed, in this framework, subjective duration estimates might represent a ‘best guess’ about the true duration in an uncertain world (Matthews & Meck, 2016). Taking into account prior knowledge about the world could potentially also explain other ‘biases’, such as the overestimation of large stimuli compared to relatively small stimuli (e.g., Ono & Kawahara, 2007;

Rammsayer & Verner, 2014): In everyday life, larger objects are generally slower-moving and might therefore take longer to disappear from view.

Distortions in subjective duration might also be functional in a second way: They could index the significance of stimuli (Matthews & Meck, 2016). Indeed, the conditions that dilate subjective time seem to be those in which something behaviorally relevant is happening, as signaled by emotion, magnitude, salience and attention. A salient stimulus, such as a threatening face, not only expands duration, but also signals behavioral relevance and increases information processing. In this way, a long subjective duration may be a flag of importance: this is an event that needs attention and action.

Thus, while deviations of subjective timing from physical durations are often considered distortions, they might actually be optimal when we consider the noisy nature of the perceptual system, as well as the organism's need to distinguish salient from unimportant events. In this way, they may also prove to be vital mechanisms to implement in artificial agents interacting with the world.

Time at the center or at the side?

One of the key questions in modelling interval timing that has sparked debate in the past few decades is: Is there a central, dedicated timing mechanism or is time extracted from naturally occurring neural processes that are not dedicated to timing (Ivry & Schlerf, 2008; Wittmann, 2013)? As we have seen, it has been hard to pinpoint the correlates of a timekeeper in the brain. So far, no dedicated central brain area that distributes 'ticks' to other brain regions has been identified, and, as we have shown in Chapter 5, processes that were proposed to track the accumulation of time are more likely to reflect other functions, such as preparation. Although the inability to trace internal clock mechanisms to specific neural populations might be due to limitations of our current knowledge or brain imaging methods, the problem may be more fundamental. Neuroscientists have been looking for clock-like mechanisms in the brain, because they have the preconceived notion that this dimension is separate from, for example, space and one should therefore be able to find separate neural populations keeping track of duration. However, this basic assumption might be flawed (Buzsáki, 2019).

When we look at physics, the classical laws of Newton present space and time as independent dimensions. Einstein's relativity theory, however, showed that distance and duration cannot be measured independently. Time and space are tightly linked in a four-dimensional continuum, and one can only be considered in light of the other. Neuroscience, however, has so far treated the perception of time and space in the brain as two largely separate fields with their own literature, although it might be "no more than an historical accident that time, space, and number have been studied for a century as three separate subjects" (Walsh, 2015, p. 555).

In examining the neural code for time, human brain mechanisms and behaviors are compared to the representation of time and duration offered by time-measuring instruments, or *clocks*. In this way, neural activity that tracks sequences of events changes predictably along with units of the clock. It is important to note, however, that when neural activity reliably correlates with the passing of time of a clock, it does not necessarily mean that this neural activity computes duration (Buzsáki, 2019). A temporal sequence of representations and behaviors changes dynamically, but does not need to be a representation of time.

The search for a central, dedicated internal clock might be a case of trying to fit our preconceived idea that duration is a separate dimension that is tracked by a *timer* on the brain. In reality, Buzsáki (2019) proposes, neuronal networks that are suggested to track time always compute other dimensions too. For example, neurons in the parietal cortex of monkeys that have been related to the judgment of time also track velocity, distance, spatial attention and movement planning. When hippocampal neurons code for the velocity of a rat moving through a maze, duration can automatically be inferred from the state of these neurons. One dimension can be inferred from the other. Conclusions about the function of the neurons in these brain areas could therefore be largely dependent on the questions and assumptions of the experimenter. The cells in the hippocampus may not selectively code for space or time. Instead, the hippocampal-entorhinal system might act as a general sequence generator that create a nominal order of sequential events, and is able to reproduce these sequences as episodic memories when needed (Buzsáki & Tingley, 2018).

The interdependence of time and space generalizes to other dimensions. For example, "we never see 'pure' color or 'pure' motion" (Walsh, 2015, p. 555), but any attribute always appears in the context of other features. And although we might identify brain regions that are more specialized in one dimension relative to another, these interpretations might just as well be guided by our assumptions about the modularity of the brain (Walsh, 2015). Terms as "the number area" or "time cells" might in that sense not so much reflect the specialization of neural populations, but of the particular question that is asked in the experiment.

The notion that the time dimension is closely interlinked with other dimensions opens up the possibility that duration is extracted from internal and external dynamics. For example, we could base our subjective duration estimate on the number of salient visual events that we have encountered (Roseboom et al., 2019). Indeed, in general, the passage of time can be inferred from naturally occurring neural dynamics (Buonomano & Karmarkar, 2002; Buonomano & Laje, 2011; Hardy & Buonomano, 2016; Karmarkar & Buonomano, 2007). As long as neural patterns are reproducible and unique at each point in time, one can infer duration relative to the onset of a stimulus from the state of the neural network. Of course, there still needs to be some way of translating the state of the network to the flexible temporal, spatial and verbal representations that humans are able to produce (Chapter 7). Potentially these mappings are calibrated and learned during childhood through motor interactions with an environment in which space, time and size are often highly correlated (Walsh, 2003, 2015).

Although internal clock models, like the pacemaker-accumulator framework, might be useful for flexibly explaining and predicting simple timing behavior, we do not have compelling evidence for a central time-keeper in the brain that distributes duration information to other brain areas. This idea might be based on the false projection of our sense that time is a separate dimension that requires separate neural mechanisms. Instead, it seems that there are relatively independent mechanisms in multiple brain areas from which duration at different scales can be extracted (Paton & Buonomano, 2018).

Future directions

Time in interaction

Time perception has so far been largely treated as a separate field which is focused on the workings of an internal timekeeper, while interactions with other cognitive processes, such as memory and decision making, have received less attention (Van Rijn, 2016). The chapters in this thesis illustrate the great flexibility with which humans are able to perceive, report and use time. And, importantly, they show that previous experiences and clues about temporal statistics in memory shape the way we perceive duration and actively predict the onset of upcoming events.

Our findings highlight the need to integrate time perception with other dimensions and cognitive processes, such as memory. In doing so, it is important to keep in mind that time perception is in many ways informed by these other dimensions, and does not happen in isolation. Indeed, on the neural level, the processing of time might not be so easily separated from other dimensions, such as space or magnitude (Schlichting, De Jong, et al., 2018). By focusing on finding an 'internal clock', we might disregard other functions of brain areas that are active in timing tasks (Walsh, 2015) and lose track of the way people base their timing on other dimensions in everyday life (e.g., Buzsáki, 2019; Roseboom et al., 2019).

Flexible neural processes

As we showed in Chapter 5, neural signatures of time do not reflect an absolute timekeeping mechanism. Instead, they adapt to current temporal statistics, based on previous experience. This flexibility suggests that neural dynamics that code for duration can be scaled in time to enable motor responses that fit the task at hand (Remington, Egger, et al., 2018; Remington, Narain, et al., 2018; Sohn et al., 2019). So far, these kinds of dynamics have mostly been demonstrated using single cell measurements in monkeys. Our work suggests that these findings might generalize to cortical dynamics in humans, which adapt to context and, potentially, to temporal preparation based on cues. A future challenge lies in the translation between the neural dynamics and eventual motor behavior or decisions. Indeed, in general, "one of the most pressing problems in the timing field is the need to establish a causal relationship between the neural patterns of activity that seem to underlie many forms of timing and behavior" (Paton & Buonomano, 2018, p. 700). As mentioned above, neural change over time does not necessarily code for a representation of time that guides behavior. Promising approaches in this regard might be active manipulations such as transcranial alternating current stimulation (tACS) (Wiener et al., 2018) and transcranial magnetic stimulation (TMS), or *in-silico* network perturbations (Sohn et al., 2019).

Timing in the real world

In Chapter 6, we presented a first step in testing whether general laws of time perception established in the laboratory generalize to more ecologically-valid situations. Although most research on time perception has been focused on simple timing tasks, laboratory studies have several limitations (Van Rijn, 2018). First, simple prospective time perception studies are unable to account for the continuous nature of timing that we exhibit in everyday life. Whereas stimuli in studies in the lab have clear on- and offset, and it is clear to the participants that they have to estimate duration, realistic situations often require us to estimate how long ago an event has happened only at a later point in time. This also entails being able to track multiple events at the same time. Second, studying more realistic settings allows us to consider non-temporal dimensions that inform temporal behavior and neural signatures over time, as mentioned above.

To explain behavior in these more realistic settings, it is important for theories to make quantitative predictions (Van Rijn, 2018). In this sense, pacemaker-accumulator models are often too flexible and unconstrained. Model parameters, such as the speed of the pacemaker, can easily be manipulated to post-hoc explain why certain situations lead to under- or overestimations. A challenge in modelling more realistic settings lies in the need for constrained theories in which timing mechanisms are modeled in interaction with, or rely upon, other processes (e.g., Roseboom et al., 2019). It also requires experimenters to think of realistic situations in which timing plays an implicit, but important role, such as decision making (e.g., Boehm, Hawkins, Brown, Van Rijn, & Wagenmakers, 2016) or temporal preparation (e.g., Van Ede, Niklaus, & Nobre, 2017).

Conclusion

This thesis demonstrates the great flexibility with which humans are able to estimate and use time. Memory plays an important role in this adaptive process: Previous experience with temporal context biases interval perception and shapes its underlying neural dynamics. In addition, regularity creates expectations about the onset of salient events, although this dynamic attention may be inhibited when there is a cost to continuous vigilance. The flexible way in which durations are estimated is unlikely to arise from a central dedicated internal clock. Instead, neuroscientists could focus on intrinsic neural dynamics that adapt to regularities in the environment to optimize the anticipation of important events.

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adaptieve timing

Vergeleken met bijvoorbeeld zien of horen is het bestuderen van tijdwaarneming niet eenvoudig: er is geen orgaan voor tijd. In plaats daarvan lijkt het afhankelijk te zijn van een uitgebreid netwerk van hersengebieden. Daarbij komt nog dat tijdsduur niet in isolatie wordt beleefd: het is onderhevig aan externe invloeden zoals emoties, beweging, aandacht, en eerdere ervaringen in het geheugen. Zo kan het dat onze subjectieve ervaring van tijd vaak afwijkt van de fysieke tijd op ons horloge: vier minuten bij de bushalte kunnen voelen als een eeuwigheid, terwijl een uur voorbijvliegt als we genieten van een goede film.

Het geheugen speelt een belangrijke rol in tijdwaarneming. Om in te schatten hoe lang geleden iets is gebeurd, is een herinnering nodig van de gebeurtenis zelf en van ontwikkelingen die in de tussentijd hebben plaatsgevonden. Enkele recente theorieën stellen daarom zelfs dat de hersenprocessen van het geheugen ook de basis vormen voor tijdsperceptie (Buzsáki & Tingley, 2018; Gu, Van Rijn, et al., 2015). Daarnaast wordt onze tijdsinschatting geïnformeerd door regelmatigheden in eerdere ervaringen. Een voorbeeld hiervan is het *context effect*: wanneer proefpersonen een reeks tijdsintervallen inschatten, worden korte intervallen overschat en lange intervallen onderschat. De inschattingen worden als het ware naar eerdere ervaringen in het geheugen toegetrokken. Het detecteren van dit soort regelmaat in de omgeving stelt ons in staat ons aan te passen aan een dynamisch veranderende wereld. Op basis van het geheugen proberen we niet alleen te voorspellen *wat* er gaat gebeuren, maar ook *wanneer* iets zal plaatsvinden.

Hoewel deze recente theorieën en bevindingen misschien anders suggereren, staat ons begrip van de interactie tussen subjectieve tijd en het geheugen nog in de kinderschoenen. Specifiek zijn er twee onbeantwoorde vragen: hoe worden tijdsintervallen gerepresenteerd in het geheugen, en hoe worden deze ervaringen in het geheugen gebruikt om de timing van aandacht te leiden? In dit proefschrift worden deze vragen onderzocht met gedragsexperimenten en hersenmetingen.

De theorie van Gu et al. (2015) stelt dat tijdsduur kan worden afgeleid uit de mechanismen in het brein die ten grondslag liggen aan het werkgeheugen. In Hoofdstuk 2 onderzochten we een belangrijke voorspelling van dit model: wordt het startsignaal van tijdsperceptie bepaald door het moment dat iets in het werkgeheugen wordt opgenomen? Proefpersonen zagen een reeks cijfers en letters en moesten aangeven wanneer ze de letters hadden gezien. We vonden geen verband tussen deze tijdsinschattingen en de timing van werkgeheugenconsolidatie, gemeten met elektro-encefalografie (EEG). Er lijkt dus geen direct verband te bestaan tussen geheugenconsolidatie en de timing van tijdsintervallen.

We slaan informatie over regelmatigheden in de omgeving op in het geheugen zodat we dingen kunnen voorspellen. Dit speelt bijvoorbeeld een belangrijke rol in muziek. Componisten creëren door middel van harmonie en ritmes verwachtingen bij de luisteraar. Hoofdstuk 3 laat zien dat mensen hiërarchische verwachtingen van ritme opbouwen, waarin sommige *beats* belangrijker zijn dan anderen. We lieten op verschillende plekken in een ritme stiltes vallen, en lieten door middel van pupilverwijding zien dat mensen meer verrast werden door belangrijke dan minder belangrijke beats, zelfs wanneer ze ondertussen een andere taak uitvoerden en onafhankelijk van expertise. Het lijkt er daarom op dat het opbouwen van deze verwachtingen een automatisch proces is.

Gegeven dat temporele regelmaat belangrijk is in het leiden van onze verwachtingen, zou het mogelijk zijn dat ritmische stimuli in de omgeving de aandacht trekken. In Hoofdstuk 4 onderzochten we deze hypothese door proefpersonen visuele vormen te tonen die met een regelmatig ritme of willekeurige timing verschenen. We vonden geen aanwijzing dat het regelmatige ritme meer aandacht kreeg. Meer specifiek waren reactietijden niet sneller wanneer targets in een zoektaak dezelfde kleur of locatie hadden als de regelmatige stimulus. Dit kan erop duiden dat ritmes geen speciale aandacht krijgen wanneer dit ten koste gaat van constante alertheid die nodig is voor de taak.

De regelmatigheden in het geheugen beïnvloeden ook onze tijdsinschattingen, zoals in het bovengenoemde context effect. In theorieën van tijdsperceptie wordt vaak aangenomen dat het waargenomen interval wordt gewogen met een representatie van eerder aangeboden intervallen. In Hoofdstuk 5 laten we echter zien dat eerdere tijdsintervallen een directe invloed hebben op de waarneming zelf. Verschillende EEG-componenten die vaak met tijdsperceptie worden geassocieerd verschilden wanneer eerdere intervallen kort of lang waren. Een langzame component, de CNV, bouwde bijvoorbeeld sneller op na het aanbieden van een reeks kortere intervallen, wat duidt op actieve anticipatie. Deze resultaten laten zien dat hersenprocessen tijdens het waarnemen van tijd zich flexibel aanpassen aan de context.

In Hoofdstuk 6 laten we zien dat het context effect ook standhoudt in meer realistische situaties. Proefpersonen zagen video's van een geanimeerd figuur dat verschillende handelingen in de keuken uitvoerde, zoals drinken en mixen, en moesten de tijdsduur van deze handelingen reproduceren. Net als in Hoofdstuk 5 werden de reproducties beïnvloed door eerdere tijdsintervallen. Daarnaast waren de inschattingen van lange intervallen minder precies dan van kortere intervallen. Deze bevindingen suggereren dat 'wetten' van de tijdsperceptie die in het laboratorium worden gemeten ook terug te zien zijn in de echte wereld.

In alledaags taalgebruik wordt tijd vaak uitgedrukt in ruimtelijke termen, zoals "de bijeenkomst duurde erg lang" of "de toekomst ligt voor ons". In Hoofdstuk 7 laten we zien dat tijdsinschattingen inderdaad gemakkelijk kunnen worden getransformeerd naar andere dimensies. Proefpersonen werd gevraagd om een tijdsinterval in te schatten door een knop in te drukken, door op een tijdlijn te klikken of door een waarde in seconden te geven. We vonden dat de knopinschattingen niet consistent beter waren dan de andere twee methoden. Dit laat zien dat mensen tijd op een flexibele manier kunnen uitdrukken.

Al met al laten de resultaten in dit proefschrift zien dat mensen erg flexibel zijn in het waarnemen en gebruiken van tijd. Het geheugen speelt hierin een belangrijke rol: eerdere ervaringen beïnvloeden onze tijdsinschattingen en de onderliggende hersenprocessen. Op deze manier kan imperfecte tijdswaarneming worden gecorrigeerd op basis van eerdere ervaringen. Daarbij stelt de waargenomen regelmaat ons in staat om voorspellingen te maken over wanneer iets belangrijks zal gebeuren. Tijd kan daarom worden gezien als een inherent onderdeel van hersenprocessen die zich aanpassen aan de regelmaat in de omgeving.

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