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Contents

Intermediate results on human brain mechanisms over time

1 Introduction: Why we need to rethink existing models

Recent years have seen an explosion of papers focusing on the brain mechanisms involved in interval timing, the capacity to perceive time in the range from seconds to minutes. Interval timing is fundamental for a wide spectrum of behavior, including optimal decision making in a world filled with temporal regularities, and in which time is a limited resource. Importantly, interval timing is also essential in effective communication between multiple agents, as temporal cues provide information about the intended message (e.g., Arnold, Kam, & Tanenhaus, 2007). Interestingly, work on the neuroscience of interval timing has mainly focused on the brain signatures of timing tasks in relatively artificial laboratory settings in which the to be timed intervals are clearly demarcated by the onset and offset of highly salient stimuli. Because of this, these types of neuroscientific studies have typically focusses on tasks in which just a single interval is presented. In contrast, interval timing in more real-life like contexts is often defined by much vaguer boundaries, and at any point in time multiple intervals might be tracked in parallel. For example, during a conversation with a passenger while driving, a driver keeps track of the durations of the passenger's speech pauses (Kotz & Schwartze, 2010; Wilson & Wilson, 2005), of how long ago the overtaking car disappeared in the mirror's blind spot (Kujala & Salvucci, 2015), and whether to again check the navigational device for the next instruction (Kun et al., 2009). All these estimations are highly automatic and seemingly effortless. However, instead of focusing on these real-world temporal patterns that often have started at some point in the past (the disappearance of the overtaking car) and that continue until some point in the future (the reappearance of the car in the side window), the literature on interval timing typically uses fairly artificial experimental paradigms that either assess retrospective or prospective timing (Block & Zakay, 1997; Zakay & Block, 2004; Zakay, 1993), an distinction that was already made in the first studies on timing. Retrospective timing describes the estimation of the duration of an experience in hindsight, whereas prospective timing encompasses the timing of an interval that is purposively started in the present and will have a well-defined end sometime in the near future, allowing for actively attending to the passage of time (see Figure 1).

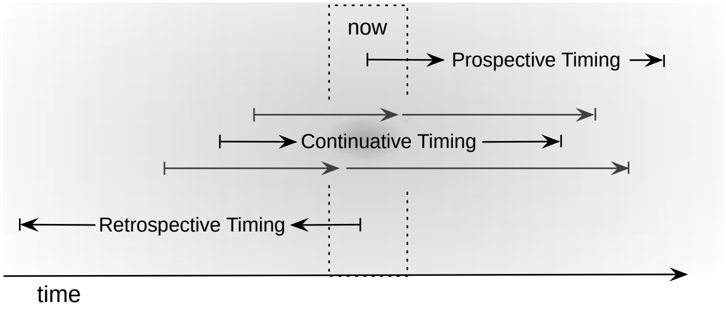


Figure 1. The prospective and retrospective timing dichotomy; and the timespan of the Continuative Timing Theory discussed here.

Although many slightly differing mechanisms are proposed in literature, prospective timing is typically explained, as hinted at above, by assuming that there is a well-defined "start signal" indicating the onset of the interval, after which the accrual of neural information tracks the passing of time. Note that various theories that have been used as springboard for neurophysiological studies fit into this broad category, including pacemaker-accumulator (Allman, Teki, Griffiths, & Meck, 2014; Gibbon, Church, & Meck, 1984; John H Wearden, 2003) and drift-diffusion accounts (Balci & Simen, 2014; Simen, Balci, de Souza, Cohen, & Holmes, 2011) of interval timing.

In contrast, retrospective estimations are assumed to rely on distinctive memory components (e.g., the amount of contextual change or the number of temporal segments that can be retrieved from memory), with more change reflecting longer retrospective durations (Grondin, 2010; MacDonald, Lepage, Eden, & Eichenbaum, 2011). The distinction between retrospective and prospective timing is thus based on both the experimental paradigms and on assumed underlying mechanisms. Interestingly, interval timing in everyday life cannot be easily dichotomized as either unexpectedly ending at or explicitly starting from the current moment. Rather, we often need to adapt our behavior based on the estimation of a duration that has, sometimes implicitly, started some time ago and is still continuing. Adhering to the retrospective versus prospective timing dichotomy renders it practically impossible to study how interval timing affects complex, everyday, real-life behavior.

In addition, prospective timing theories typically assume that time is estimated in one continuous take (e.g., Taatgen, van Rijn, & Anderson, 2007), and predicts that estimating multiple concurrent intervals is difficult (van Rijn & Taatgen, 2008). As humans constantly switch between different concurrent tasks (Nijboer, Borst, Van Rijn, & Taatgen, 2014) that all have their own temporal regularities and might influence timing processes (J. H. Wearden, O'Rourke, Matchwick, Min, & Maeers, 2010), theories that reduce timing to tracking a single interval that either ends or starts at the present have a low ecological validity. Although the field has recently become aware of the negative consequences of the reliance on artificial tasks and dichotomies (Matthews & Meck, 2014; Moon & Anderson, 2013; van Rijn, 2014), and some work has (implicitly) provided initial accounts of integrating retrospective and prospective timing (Howard, Shankar, Aue, & Criss, 2015; Staddon & Higa, 1999), no solution has yet been provided that can explain how multiple intervals are estimated concurrently.

In the recent studies and reviews that focused on the neuroanatomical and neurochemical basis of interval timing (Coull, Cheng, & Meck, 2011; Ivry & Spencer, 2004; Merchant, Harrington, & Meck, 2013; Wiener, Turkeltaub, & Coslett, 2010; Wittmann, 2013), "climbing neural activation" (CNA) played an important role. This idea assumes that the passing of time is tracked by an increase in activation in particular brain regions. Although this notion has an elegant analogue in the flow of sand in an hourglass, and climbing activation can indeed be found in many brain regions, the University of Groningen team together with some colleagues has recently demonstrated in a number of studies and theoretical evaluations that some of the key findings regarding this phenomenon need to be reinterpreted (Kononowicz, Sander, & van Rijn, 2015; Kononowicz & van Rijn, 2011, 2014; Ng, Tobin, & Penney, 2011; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011). More specifically, we have shown that CNA is associated with decision making in temporal tasks, and as such is driven by temporal information, but that it does not reflect timing itself (Boehm, Van Maanen, Forstmann, & Van Rijn, 2014). Interestingly, when more realistic tasks would have been used, it is unlikely that climbing neural activation would have played such an important role in the studies on the human brain mechanisms of time.

Realizing that the current experimental work might be based on a framework that is critically dependent on artificial tasks that have a low construct validity for predicting temporal performance in real-world settings, we have started with working on a new theoretical framework that can explain interval timing in real world settings based on a reinterpretation of existing knowledge about human brain mechanisms. For now, we have labeled this framework the Continuative Timing Theory (CTT), as it focusses on the continuation of time during the estimation of multiple intervals.

1.1 Brain Mechanisms for Timing

Below we will discuss the relevant human brain mechanisms/components of the proposed continuative timing theory one by one, focusing on how combining these components synergistically allow for keeping track of continuative time.

1.1.1 Feature detectors for time

The proposed CTT is partly based on the Striatal Beat Frequency Model (SBF) that allows for the perception of intervals of arbitrary duration (Matell & Meck, 2004). SBF assumes that at the onset of an interval the phases of a cluster of cortical neurons, each with their own intrinsic frequency, are aligned. Although the onset signal aligns the phases of the neurons, the varying intrinsic frequencies will cause a gradual divergence of the phases. At each point in time, the collective state of these diverging neurons forms a pattern that is unique for that specific duration. Medium spiny neurons in the striatum are connected with these oscillating neurons and act as feature detectors for specific time intervals as each is tuned to a specific oscillatory pattern. The right-part of Figure 2 depicts this process, with medium spiny neuron A sensitive to a coincidence pattern associated with a shorter duration than neuron B. CTT, following the SBF model, thus explains how a cortico-striatal circuit could support the perception of time by means of striatal "feature-detectors for time".

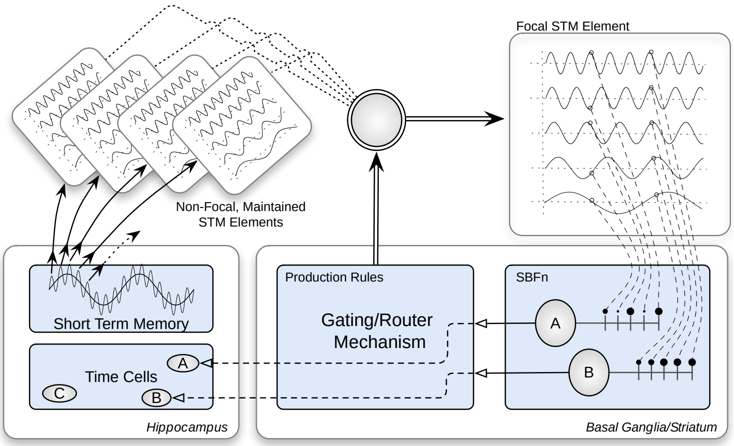


Figure 2. Schematic outline of the human brain mechanisms underlying the Continuative Timing Theory.

1.1.2 Memory traces as source of oscillations

Building on recent work at the University of Groningen and the work of colleagues (Broadway & Engle, 2011; Gu, van Rijn, & Meck, 2015; Lustig, Matell, & Meck, 2003), we propose that the cortical oscillations are related to the episodic memory trace that is currently in focus (Borst & Anderson, 2013; Oberauer, 2002; Unsworth & Engle, 2007). In the context of laboratory experiments, this focal memory trace will typically encode the onset of the current interval as no distracting information is present. Unlike earlier memory-based explanations of interval timing, CTT does not depend on the inspection of decaying activation traces, a concept that has proven difficult to align with the neurobiology of memory storage (Schooler & Hertwig, 2005). Instead, it is assumed that the oscillatory encoding of this focal short term memory (STM) element represents, by means of oscillatory multiplexing (Gu et al., 2015), both the semantic information of the element, and the time that has passed since it was encountered. This proposal also provides an elegant answer to the still open question of the nature of the start signal, as CTT predicts that the instantiation of a focal memory trace is sufficient for estimating the time that has passed since that item was encountered. Thus, CTT will be based on the notion that a memory trace of a salient event acts as the source of the cortical oscillations, and the trace's instatement reflects the onset of the interval. To ensure that this new theory is well embedded in the existing literature on the role of memory in interval timing, the UoG has worked on a review paper on the influence of memory processes on interval timing which is published as *Van Rijn (2016) How Memory Mechanisms Influence Interval Timing: A Review, Current Opinions in Behavioral Sciences* and which is added to this document as an appendix.

1.1.3 A nested-oscillations model of working memory

The approach sketched above still suffers from the one-continuous-take limitation, as SBF-based models require that there are no perturbations in the oscillations caused by, for example, a switch of the focal STM element. The models therefore fail to account for the concurrent timing of multiple intervals, a fundamental property of everyday temporal cognition, nor does it easily explain how attention during a timing task can be temporarily directed to a concurrent task. From the perspective of the SBF model, the main issue is to keep the oscillations active that were synchronized at the onset of the interval, even though the memory trace encoding the onset is not in the focal STM anymore. Interestingly, the nested-oscillations model of working memory by Lisman, Jensen and coauthors (e.g., Jensen & Lisman, 1998; Jensen, 2006; J E Lisman & Idiart, 1995; John E. Lisman & Jensen, 2013) provides exactly this prerequisite. According to this model, short-term memory elements are stored and kept active by means of nested theta-gamma oscillations: Each memory trace is stored in a different gamma (high-frequency) subcycle that is embedded in a theta (low-frequency) cycle. The nested oscillation model assumes that the oscillations representing the different elements in STM are kept active by theta-wave triggered reactivations, which means that the original oscillatory patterns are still available even if an element is currently not in focus. This process is assumed to be automatic, not requiring any attentional processes. Thus, as long as an element is stored in STM, the oscillatory patterns associated with that element are still active, and multiplexing would allow the SBF model to identify how long ago that element was created. This hypothesis is supported by work demonstrating the close link between aspects of working memory (C Fortin & Breton, 1995; C Fortin, Rousseau, Bourque, & Kirouac, 1993), and more specifically, with the observation that concurrent STM processing has the strongest negative impact on temporal accuracy (Brown, 1985; C Fortin et al., 1993). The top-left corner of Figure 2 depicts this process, showing the oscillatory patterns (on top) associated with the unique items (depicted as the high-frequency wave nested in a slower wave) in STM. In line with nested-oscillation theories of STM, CTT assumes that elements in STM provide the anchoring points to different concurrent intervals.

1.1.4 Gating to switch between intervals

In the SBF model, the medium spiny neurons could only process the input of one cluster of oscillatory neurons, but as the medium spiny neurons do not need to accrue incoming information over a longer period of time, providing the neurons with new oscillatory patterns is sufficient to track the time associated with the new input. To allow for exchanging the input to the medium spiny neurons, a gating mechanism is required that explains at a functional level how certain elements in STM can be made focal (Borst, Taatgen, Stocco, & van Rijn, 2010; Borst, Taatgen, & van Rijn, 2011, 2010), but also at a neurobiological level how the activation patterns associated with the focal event can be routed to the medium spiny neurons. The feasibility of routing input from different sets of spiking neurons to a coincidence detection unit has been demonstrated by a gating model proposed by (Zylberberg, Fernández Slezak, Roelfsema, Dehaene, & Sigman, 2010), who demonstrated how a motor response could be driven by gating one of two sets of input neurons through a router. One potential caveat is that the router's exchanging of the input could affect the temporal process itself. However, research (Claudette Fortin, Schweickert, Gaudreault, & Viau-Quesnel, 2010) has shown that although temporal accuracy is affected by the actual processing or modification of information stored in memory, it is not affected by switching tasks, an action that largely depends on the router. Thus, these behavioral results indicate that it is unlikely that the switching of context affects the subjective experience of time. CTT's integrated account, shown in Figure 3, of working memory encoding, gating, and the Striatal Beat Frequency model thus allows for continuative timing, as the onset of an interval is implicitly encoded in working memory and the cognitive system can assess the amount of time that has passed since that onset by bringing the element back into focus, even after other tasks have used focal memory in between. Integrating a gating system in CTT explains how STM elements can be sequentially brought into focal memory, after which the duration associated with the focal element can be determined, thus allowing for a serialized estimation of the duration of intervals that unfold concurrently.

1.1.5 Hippocampal Time Cells

One often ignored difference between the pacemaker-accumulator models and the models based on feature detectors for time, such as the SBF model, is that the former allows for a read-out of the accrued time at any moment. In contrast, in the SBF theory the firing of a medium spiny neuron indicates that a certain amount of time has passed since the reset of the oscillators, but it has not been specified how one arrives at an assessment of time in between the firing of two medium spiny neurons. If an temporal assesment is needed, and no medium spiny neuron is currently active, the only solution within the standard SBF framework is to wait until the next medium spiny neuron fires. For very short intervals, this does not necessarily pose a problem, as the temporal distance between the firing of subsequent medium spiny neurons is small. However, for slightly longer durations the waiting time can become too long (i.e., in our simulations the interval between two medium spiny neurons that encode for objective durations around 2000ms is about 400ms). This suggests that the passing of time, as reflected by the sequential firing of medium spiny neurons, might also be encoded elsewhere so that the information about the most current temporal estimate is always available. The necessity of this proposal is further strengthened if one considers the concurrent timing of intervals. That is, after a switch of the focal event no assessment of the elapsed time is available until a next medium spiny neuron has fired. If the concurrent tasks represent intervals of more than two seconds ago, temporal information would only become available after 200ms on average. As real-world timing requires us to be much more precise, the brain needs to keep track of the elapsed time for the different events by encoding each event's most recent experienced duration.

In this project we will explore how this keeping track of time in the context of specific events can be encoded by hippocampal "time cells", analogous to hippocampal "place cells". Recent reviews (Eichenbaum, 2014; Howard & Eichenbaum, 2013) have proposed that these time cells provide a fundamental mechanism for organizing the elements of experiences into coherent memories. Interestingly, although time cells could play an important role in interval timing, most researchers attribute a minor role to the hippocampus or ignore it altogether (for a discussion of exceptions, see (Meck, Church, & Matell, 2013)). As argued by Macdonald (e.g., MacDonald, Fortin, Sakata, & Meck, 2014), the relative lack of integration of these "time cells" in the literature on interval timing might be based on the literature's bias towards prospective timing, where time is estimated in one continuous take. In those situations, there is no direct need for a memory mechanism, as in those tasks one can wait until the designated medium spiny neuron fires. This is why Macdonald has argued for a renewed study into retrospective timing. In the context of the present project, the role of episodic time cells is even more critical, as the information stored using time cells allow the system to quickly recalibrate its temporal bearings when a new event is brought into focus. Thus, as depicted in Figure 2, hippocampal time cells will play an important role in the integrative CTT model as they provide continuative assessment of passed of time, even when an element is currently not in focal STM.

1.1.6 Testing the Proposed Continuative Timing theory

Although many empirical questions will surface during the integration of the above discussed components into one neurobiologically plausible model of continuative timing, there are a number of predictions than can be derived from the proposed integration. These predictions are related to the necessity of changing the focal element in STM during concurrent timing conditions, and the assumption that elements in STM keep oscillations active that can be used to assess the time that has passed since encountering that element.

However, another type of prediction that can be derived from this approach is that human observers should be able to time meaningful intervals without explicit start- and end-signals. That is, whenever a salient memory update is performed, a memory trace is created that can be used to assess how much time has passed between the creation of the trace, and the current time. As described in Deliverable 4.1, the University of Groningen and Karlsruhe Institute of Technology have collaborated on a series of experimental studies, in which human participants had to estimate the duration of continuous, everyday actions performed by a humanoid robot.

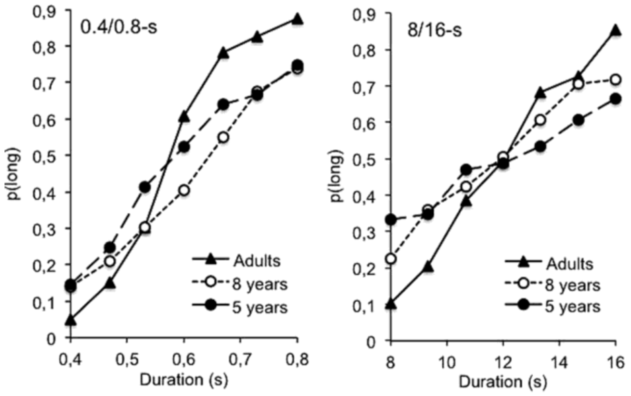
2 Factors Affecting Time Perception

Although interval timing is a skill that is often performed effortlessly, many factors have been identified that affect the accuracy and precision of this skill. Timestorm capitalizes on the expertise of partner Universite Blaise Pascal Clermont-Ferrand II (UBP) to explore subjective experience of time in relation to physical (clock) time in children and adults. The next paragraph summarize relevant work in the first year of the project. This is followed by a description of the influence of emotional moderators on timing. This section is then concluded by a short discussion of the perception of metrical hierarchy in musical beat perception.

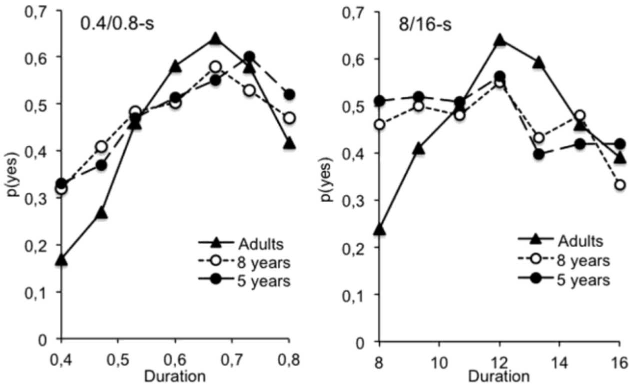
2.1 A comparison of time judgments in children and adults

It is now established that infants and young children are able to discrimination time. However, in different contexts, young children are unable to correctly judge time. The question is to identify the mechanisms explaining their poor capacities to judge time and the underlying mechanisms.

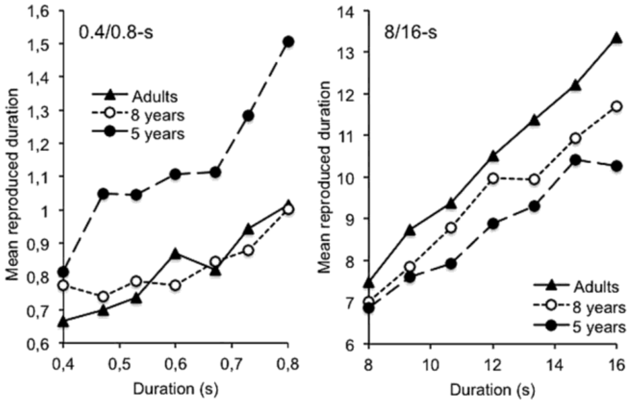
In the context of TIMESTORM, UBP has conducted developmental studies to provide insight into the time perception maturation mechanisms. The first experiment aimed to test children and adults' time judgment in different temporal tasks to examine the differences in terms of time judgment as a function of temporal tasks and cognitive abilities required for each task.



(A) Temporal bisection



(B) Temporal generalization



(C) Temporal reproduction

Figure 3. Time judgment in temporal bisection (A), temporal generalization (B) and temporal reproduction (C) in children aged 5 and 8 years and adults.

In particular, children aged 5 and 8 years, as well as adults, were given 3 temporal tasks: temporal bisection, temporal generalization and temporal reproduction. In addition, their cognitive abilities were assessed via different neuropsychological tests. The results showed differences in development of time abilities as a function of tasks, the temporal bisection task being easier for young children than the other temporal tasks, because less cognitive capacities (attention) are required to process time in temporal bisection. The development of abilities to judge time thus depends on context and cognitive abilities required. This work has been published in the paper *Droit-Volet, S., Wearden, J. & Zélanti, P. (2015). Cognitive abilities required in time judgment depending on the temporal task used: a comparison of children and adults. Quarterly Journal of Experimental Psychology,* that is included in the present document as appendix.

2.2 Emotional effects on time perception

Moreover, both UBP and UoG have investigated time-emotion interactions. More specifically, it is now well established that the emotional state of humans significantly affects their time-perception and the accuracy of time judgments. In a new study, UBP investigated how the declarative knowledge of emotion-related time distortions modulates the effect of emotional stimuli on time perception. This work has been published in *Droit-Volet, S., Lamotte, M. & Izaute, M. (2015). The conscious awareness of time distortions regulates the effect of emotion on the perception of time. Consciousness and Cognition*. A pre-print version of the paper is included in Appendix.

Our experiment showed that the conscious awareness of time distortions may change the effect of emotion on time perception. The conscious awareness of time distortions was manipulated by providing either: (1) correct information, (2) incorrect information, or (3) no-information to the participants. The results showed that the awareness of time distortions modulated the emotional effect on time judgment. However, knowledge itself was not sufficient to induce a time distortion.

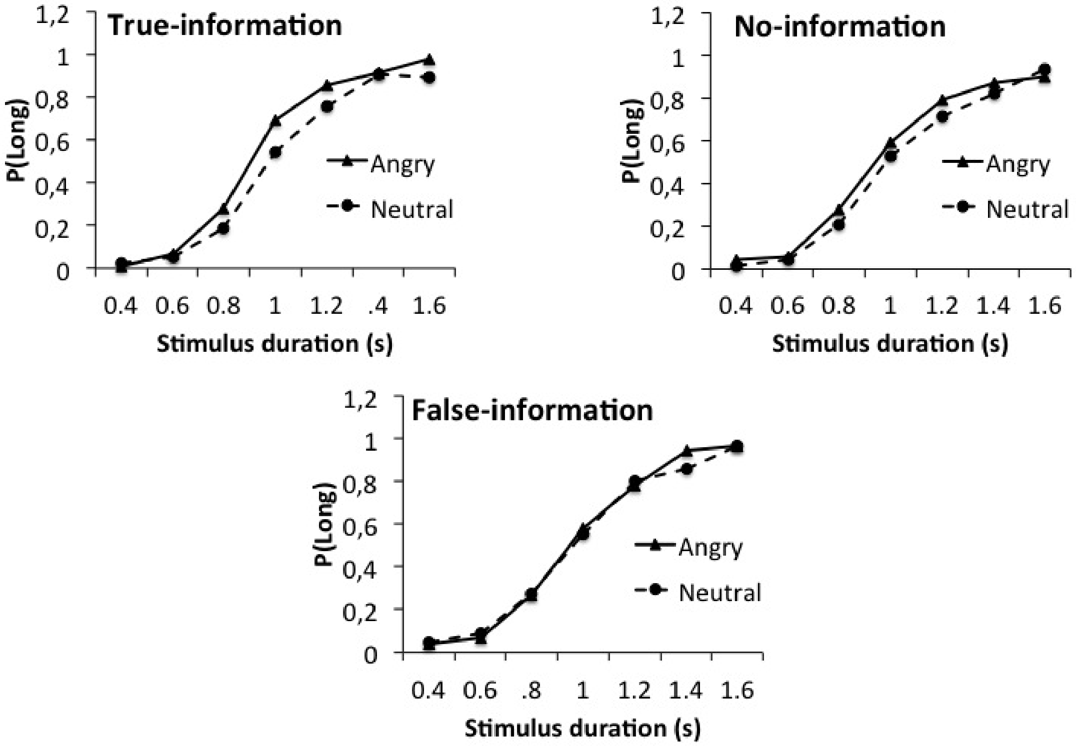


Figure 4. Time perception in different cases of time distortion awareness

In addition to this study, the UoG performed a series of replication studies looking at the role of auditory emotional stimuli on time perception. This work, inspired by the work of Schirmer and Penney at the National University of Singapore, replicated some of the effects, but at the same time demonstrated that the effects are less robust than sometimes claimed. This work has been published as *Halbersma & Van Rijn (2016) An Evaluation of the Effect of Auditory Emotional Stimuli on Interval Timing; Timing and Time Perception*, a preprint of this document is attached.

2.3 Perception of Temporal Structure in Music

In another line of work, the UoG has explored how temporal regularities, the "beat", is perceived while listening to music. One of the major topics in music cognition is beat perception: our ability to infer a temporal regular pulse from a rhythm. Although this is a fundamental human ability, it is still unknown whether explicit attention is necessary to induce beat perception or whether it is an unattentive, automatic process. In addition, the extent to which beat perception depends on expertise or musical training is still under debate. Because recent EEG experiments addressing these questions have led to inconsistent results, we have employed a novel approach: pupil dilation. We have used the pupillary response to omissions in typical rock drum rhythms as an index of metrical salience. In a submitted journal article, researchers from the UoG demonstrate that participants indeed perceived the beat while they performed another task. Importantly, they found that the omission of the salient first beat elicited a larger pupillary response than the omission of the less-salient second beat. This finding shows that participants not only detected the beat without explicit attention to the music, but also perceived a hierarchy of stronger and weaker beats. Overall, these results indicate that hierarchical beat perception is an automatic process that requires minimal attentional resources. Furthermore, no evidence was found that could indicate that beat perception was affected by musicality, suggesting that beat perception is a general ability that is independent of expertise.

In addition to these new theoretical insights in the way we perceive music, we believe that the method of pupil dilation as a signaler of unattended expectancy presented in this manuscript can open up a wide range of new methods to study interval timing in complex environments. The submitted manuscript, *Damsma and Van Rijn, Pupillary Response Indexes the Metrical Hierarchy of Unattended Rhythmic Violations*, is attached to this document.

3 Early modeling work on multi-modal time perception

Inspired by the ongoing experimental work with human subjects and the state of the art approaches on time perception modeling, partner FORTH in collaboration with UoG has devised an SBF-inspired model that is capable to estimate and memorize not only how-long an event has lasted but additionally when it occurred in the past. The combined consideration of these two temporal aspects is vital for an artificial agent to understand the sequence and evolution of real world events in a rich and meaningful way that adequately informs future human-robot interaction sessions.

More specifically, we adopt a neural network modeling approach to develop a composite distributed system that is capable to support the how-long and when aspects of temporal cognition. In short, the structure of the model is summarized in Figure 5.

We use four oscillatory signals at different frequencies as inputs to the model. Recurrent connectivity in the composite TimeSense module aims at gradually transforming oscillatory input to a time flow representation that is adequate for both interval timing and past time perception. In the current implementation we explore scenarios assuming the random occurrence of six events (the capacity of short-term memory) in a session of 1000 simulation steps.

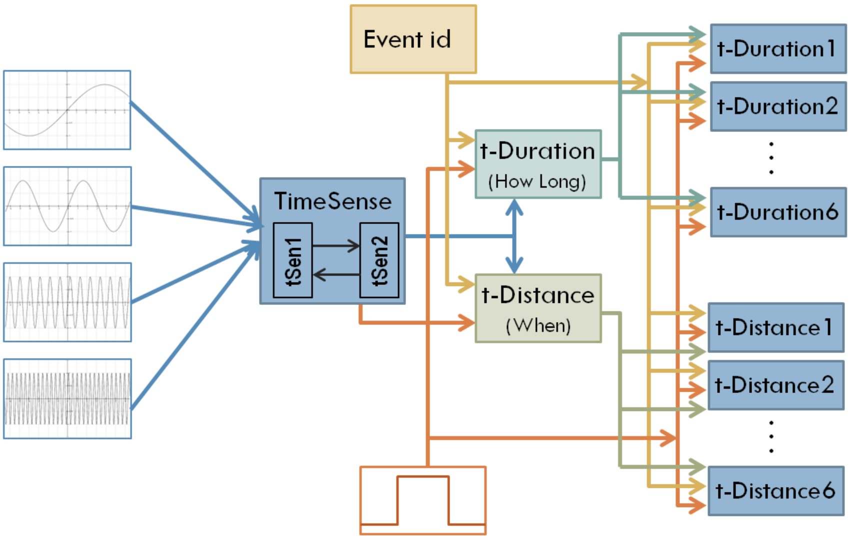


Figure 5. The structure of the enhanced SBF inspired model that aims to address both interval timing and past time perception.

Two central components aim to combine general purpose sense of time with even experiencing into two new representations appropriate for measuring duration (t-Duration module) and temporal distance (t-Distance module). we use dedicated modules t-Duration1, t-Duration2 ... t-Duration6 to memorize durations and modules t-Distance1, t-Distance2 ... t-Distance6 to memorize temporal distances for the six tone-events considered in the current experimental setup. These components represent short-term memory that temporally stores information about the experienced events. In the next step (not currently implemented in the model) information encoded in short-term memory will be either transferred into long-term memory or forgotten due to low importance. This procedure will free short-term memory space enabling the temporal storage of new events.

This work has been submitted for publication and it is currently in the stage of second revision. It is expected to be published online, in the next couple of months.

M. Maniadakis and P. Trahanias, When and How-long: A unified approach for time perception, submitted in the Frontiers Research Topic: Understanding the role of the time dimension in the brain information processing.

Abstract

The representation of the environment assumes the encoding of four basic dimensions in the brain, that is the 3D space and time. The vital role of time for cognition is a topic that recently attracted increasing research interest. Surprisingly, the scientific community investigating mind-time interactions has mainly focused on interval timing, paying less attention on the encoding and processing of distant moments. The present work highlights two basic capacities that are necessary for developing temporal cognition in artificial systems. In particular, the seamless integration of agents in the environment assumes they are able to consider when events have occurred and how-

long they have lasted. This information, although rather standard in humans, is largely missing from artificial cognitive systems. In this work we consider how a time perception model that is based on neural networks and the Streatal Beat Frequency (SBF) theory is extended in a way that besides the duration of events, facilitates the encoding of the time of occurrence in memory. The extended model is capable to support skills assumed in temporal cognition and answer time-related questions about the unfolded events.

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5 Appendix

In the following pages, we include the full version of the paper published by partners UBP and UoG as part of the ongoing TIMESTORM research.

How Memory Mechanisms Influence Interval Timing: A Review

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Interval timing tasks can only be performed efficiently when the output of a clock system can be stored over a longer period of time, and be retrieved and reused during later trials. Although the importance of temporal reference memory for accurate timing has been acknowledged since the earliest theoretical work on interval timing, formal accounts of the role of memory in interval timing are fairly recent. An short overview is given of the first formal models in which memory effects were accounted for, followed by a review of the current theoretical approaches, which can be categorized on the basis of whether they assume a dynamic or static memory system.

From humans and other mammals to insects, animals have sought ways to benefit from temporal regularities in their environments, ranging from millisecond timing for proper motor control to circadian and infradian timing for adjustment to day-night or other long-term biological cycles. In between these two extremes is the timing of intervals that are relevant for cognitively controlled behavior, spanning durations from a couple of hundred milliseconds to minutes, often referred to as interval timing. Already the first modern theories of interval timing [see 1 for a recent review] proposed that a triad of cognitive processes underlie all behavior driven by interval timing. In these theories, a clock-system generates a value that systematically changes over time, a temporal reference memory system stores previously experienced durations, and a decision system determines how the current read-out of the clock-system relates to values stored in memory, and whether to take actions based on this comparison. The most prominent theories that adhere to this scheme are pacemaker-accumulator theories, which assume that temporal information, operationalized as the pulses emitted by a pacemaker, is accrued in an accumulator, analogous to the working of an hourglass. Interestingly, although alternative theories propose different mechanisms underlying the clock part, all theories assume and require a memory and decision system.

Perhaps unsurprisingly, most of the work on interval timing has focused on the clock part, and the memory and decision systems have typically played an auxiliary role. Recently, however, a number of new theories have been proposed that provide a detailed model the decision stage in an interval timing process [e.g., 2], that propose mechanisms that could explain how interval timing and memory processes interact [3], or that acknowledge that temporal cognition can only be accounted for by an interaction of general cognitive skills and the triad assumed by clock theories [4,5]. However, most literature simply assumes that a memory system holds a fairly stable and accurate representation of relevant durations that does not directly interfere with temporal performance, and takes a similar stance towards the decision component.

The lack of focus on the memory system is surprising as one of the best known empirical phenomena related to interval timing, Vierordt's law, is clearly driven by the way information is stored in memory [6,7]. Vierordt's law is most easily observed in experiments in which durations of different lengths are presented. When asked to reproduce such durations, the reproduced durations demonstrate a regression towards the mean with long durations underestimated, and short durations overestimated. Recent accounts of this phenomenon are typically based on the assumption that memory traces representing previously presented durations interfere with later temporal processing [6,8–10]. This regression towards the mean is observed even when the different durations easily distinguishable, for example when they are represented by unique, easily identifiable stimuli [11,12].

Vierordt's law demonstrates that although the importance of memory for timing has been acknowledged since the earliest work on interval timing, the formal theoretic accounts of the role of memory in interval timing are fairly recent. All these accounts assume that a perceived duration is affected by earlier perceived durations, but differ in their assumptions related to the processes underlying this biasing. In the remainder of this document, I will discuss three approaches that have been proposed to account for specific memory effects observed in interval timing tasks.

Memory Mixing in Interval Timing

The first systematic exploration of how the internal representation of earlier durations influences future estimation was reported by Penney et al [13]. Penney et al presented participants with a bisection experiment in which participants are presented a short and a long standard duration that they are asked to memorize, and then a series of comparison durations of which participants have to indicate whether they are more similar to the long or the short duration. The elegant manipulation in this experiment is that the comparison durations were either presented in the auditory or in the visual domain. As durations presented by means of an auditory signal are overestimated compared to durations presented as visual signals, one would expect that auditory presented trials have a higher proportion of “similar-to-long” responses than visually presented trials, which was indeed found when both modalities were presented in different blocks. However, if previous trials influence subsequent trials, a duration presented in the auditory domain should be perceived as shorter (and vice-versa for durations presented in the visual domain) in a condition in which trials of both modalities were presented in intermixed fashion. This pattern of results was indeed observed, suggesting that the memories of the auditory and visual durations are indeed mixed into one larger pool that influence subsequent responses, giving rise to the term “memory mixing”. Interestingly, the visual trials were affected by the auditory information to a stronger extend than vice versa.

Although this work pioneered the more detailed study of the role of the memory system on interval timing performance, no formal theory was provided on how specific traces of earlier temporal experiences influence subsequent performance. For example, this model does not account for trial-by-trial effects, as one might assume a differential response if a visually presented duration follows a sequence of stimuli presented in the same modality, than if it follows a sequence of auditory-presented durations.

Another question that was not addressed in this memory-mixing paper is how the veridical durations of earlier trials influence performance on subsequent trials – if memory plays such an important role, one would expect trial-by-trial effects with a previous short trial having a differential effect on the current trial than a previous long trial.

Bayesian Memory Models of Interval Timing

A natural match to the notion that previous experiences influence later perceptual processes is the Bayesian approach in which the observed duration (called the likelihood) is weighted by the experience (the prior) to obtain a subjective percept (the posterior). The application of this approach has been popularized by a highly influential paper by Jazayeri and Shadlen [14] in which they present a Bayesian account of a phenomenon similar to the Vierordt effect. With their experiment, they demonstrated that when participants are asked to reproduce durations sampled from a small range of possible durations, a regression towards the mean can be observed that is larger for the longer durations than for the shorter durations.

The proposed Bayesian model accounts for this effect by assuming that already at the perceptual stage the input (i.e., the likelihood) differs as a function of the presented duration. That is, the explanation for the asymmetrical regression towards the mean hinges on the assumption that the purely bottom-up percept of a shorter duration is represented more accurately (i.e., a more narrow distribution) than that of a longer duration. The prior experiences exert their influence at the next stage, as the filter-like function of an uniformly distributed prior gives rise the observed asymmetry by truncating more of the long durations than of the short durations. Although the prior experiences play a critical role in this model, the model presented in the original work does not account for how the prior is learned or how it is amended over time. In other words, although the proposed model does take into account prior experience in an elegant, principled way, it needs to be extended to account for more dynamic memory effects, such as the influence of a trial immediately preceding the current trial. Moreover, the assumption of a uniformly distributed prior is an elegant simplification of the model, and well suited if the model focuses on explaining expert behavior (i.e., performance after extensive training), but is unlikely to account for data in more typical, less well-trained temporal tasks.

Acerbi, Wolpert and Vijayakumar [15] specifically focused on the prior, and assessed whether the prior would indeed reflect the properties of the environment. In their experiments, they presented either a higher proportion of short, or a higher proportion of long durations, or even sampled the presented durations from bimodal distributions. Although the priors that Acerbi et al reconstructed on the basis of the behavioral data did not perfectly mirror the empirical distributions, the results clearly indicated that the distribution of the prior roughly reflected the empirical distribution, and thus that the prior is indeed learned from prior experience. However, even this more elaborate model still assumes a static prior over the scope of the experiment, and thus does not incorporate any trial-by-trial effects. Although implementing a Kalman-filter, which could account for how the prior is updated on a trial-by-trial basis, is feasible [16], it has not been applied to the domain of interval timing as of yet [see for an alterantive approach, 17].

Nevertheless, the elegant and powerful mathematical properties of this type of model have allowed people to used the Bayesian approach as a tool to identify in what way subgroups in a population might differ based on individual differences, medical condition, or training [18,19].

Trial-by-Trial Effects in Interval Timing

The simplest approach to account for trial-by-trial effects in interval timing is to assume that only the most recent trial influences the processing of the current duration. According to such an account, only a single trace needs to be stored in memory, which can be updated on every trial. Although some initial data seemed to support this notion [20], later work led the authors to conclude that such a perturbation account is probably to simplistic, and that older traces are likely to still exert some influence [21].

A more refined model for trial-by-trial effects applied to the domain of interval timing is the Internal Reference Model [IRM, 8,22] proposed by Dyjas, Bausenhart and Ulrich. According to this model, sharing some similarities with a Kalman filter [16], the perceived duration for the current trial (I_n) is a weighted average of the current duration (D_n) and an internal reference based on all previous durations (I_{n-1}): $I_n = g * I_{n-1} + (1-g) * D_n$, with *g* reflecting the relative weight of the current experience in relation to the previous experiences. As the perceived duration on trial *n* will be used as the internal reference on trial *n+1,* IRM's history of presented durations follows a geometrically moving average. This central feature of IRM allows this model to capture how the internal reference builds up during an experiment, and also allows for explaining how a memory representation can be build in experiments in which the presented durations generated from a non-stationary processes [22].

This model provides elegant and solid accounts for a number of phenomena related to memory effects in interval timing, including the Vierordt law [8]. At the same time, it only provides a functional description of how the memory system might work and, because of that, the IRM lacks the flexibility to account for more complex experimental setups, for example including multiple, separate streams of stimuli or feedback. An example of such a study is reported by Taatgen and Van Rijn [12] as in their experiment participants had to alternate between reproducing two durations of 2 and 3.2 seconds, with each stream represented by visually unique stimuli. The behavioral data was best fit by a model that assumed that a trial was mostly influenced by earlier encounters from the same stream, but that the alternative stream also exerted some influenced. This type of behavioral pattern is difficult to align with the IRM and Bayesian approaches that assume a static prior.

To account for their data, Taatgen and Van Rijn applied their earlier developed integrative timing model [4] to this task. According to this model, all previous encounters of durations are stored in a central memory store. Each encounter has an associated value reflecting its activation, a value that decreases of time. When a retrieval is initiated from memory, for example when a perceived interval needs to be reproduced, a blending process weighs the encoded durations by their activation values, and calculates an average. This way, older or less frequently presented durations will have a smaller influence that more recent, of very frequent durations. The basic version of this model is very similar to the IRM. However, by encoding, for example, the feedback that was provided when a certain duration was presented, or with what visual stimuli a duration is encoded, the blending process can weigh the encoded information for the similarity with the current context, and this can account for the role of the temporal reference memory story in more elaborate interval timing tasks. The notion that previous durations are encoded in memory traces that become less accessible over time is obviously a very generic approach, which allows for the application in many different contexts. For example, Los, Kruijne and Meeter [23] have recently proposed that hazard-rate effects in foreperiod studies can be explained by assuming a trace-based memory system of previously experienced foreperiods, recent theories that assume an influence of the passing of time on the processes underlying decision making [for a review, see 24] need to assume that an internal representation of previous trial durations feed into decision processes, and Moon et al [25] have shown that this approach can be used to inform a fMRI study into the interference between temporal information and encoded length.

This latter study is related to another line of research that focuses on the internal representation of time. According to Walsh's A Theory Of Magnitude [26, 27], any magnitude-related information that is stored in the brain might influence future magnitude processing. Because of this intimate connection between different dimensions, it is essential that a proposed memory system is as flexible as possible, as it might be necessary to explain how space, number, time and any other dimension that can be expressed as a magnitude can influence performance on a future interval timing trial [28].

Conclusions

All discussed theories provide support for the claim that a mixture of bottom-up input (the clock-system) and top-down influences (the memory system) determines how an objective duration is subjectively perceived, and reproduced. The Bayesian approaches and the Internal Reference Model provide elegant, mathematical models of how the temporal reference memory system can provide top-down influences on interval timing. On the other hand, when interval timing is an element of more complex tasks, and especially when interval timing is studies in more real-world task environments [29,30], the limited flexibility of these models might prevent successful application, whereas a temporal reference memory system based on a more general memory model can still be applied [see for an example, 31]. As papers focusing on trial-by-trial effects become more common in the field of interval timing [e.g., 32,33,34], incorporating more detailed memory models will become unavoidable.

However, instead of focusing on a single type of model, it is important to realize that all these models share many features with the traditional and highly-successful triad-based interval timing models [16,35]. It is therefore likely that researchers who manage to combine the different types of models will drive future developments, and provide new theories to explain how perceived duration is affected by prior experience [36].

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Cognitive abilities required in time judgment depending on the temporal tasks used: A comparison of children and adults

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Cognitive abilities required in time judgment depending on the temporal tasks used: A comparison of children and adults

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The aim of this study was to examine age-related differences in time judgments during childhood as a function of the temporal task used. Children aged 5 and 8 years, as well as adults, were submitted to 3 temporal tasks (bisection, generalization and reproduction) with short (0.4/0.8 s) and long durations (8/16 s). Furthermore, their cognitive capacities in terms of working memory, attentional control, and processing speed were assessed by a wide battery of neuropsychological tests. The results showed that the age-related differences in time judgment were greater in the reproduction task than in the temporal discrimination tasks. This task was indeed more demanding in terms of working memory and information processing speed. In addition, the bisection task appeared to be easier for children than the generalization task, whereas these 2 tasks were similar for the adults, although the generalization task required more attention to be paid to the processing of durations. Our study thus demonstrates that it is important to understand the different cognitive processes involved in time judgment as a function of the temporal tasks used before venturing to draw conclusions about the development of time perception capabilities.

Keywords: Timing; Time; Temporal tasks; Children; Neuropsychology.

Studies on time perception have shown that humans, like other animals, can accurately discriminate durations, and that the variability (standard deviation) of their estimates (sensitivity to time) increases with the length of the intervals to be timed. This led researchers to consider that humans and animals share a primary time sense with its hallmark characteristic—the scalar property—and the same underlying cerebral mechanism called the internal clock. Developmental studies of time perception have observed this scalar property of time in children of different ages (Droit-Volet, 2002; Droit-Volet, Clément, & Wearden, 2001; Droit-Volet & Wearden, 2001). However, they also found an improvement in time sensitivity throughout childhood. The question is: what are

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the sources of this age-related difference in time sensitivity, given that the internal clock mechanism seems to be functional at an early age?

To examine the perception of time in human beings, many researchers have used tasks similar to those used in animals, namely temporal generalization (Church & Gibbon, 1982), or temporal bisection (Church & Deluty, 1977). These tasks have been adapted to human beings. For example, participants are presented with very few examples of reference durations (usually between three and five) whereas animals are given several sessions, involving hundreds of trials, to learn reference durations. Verbal instructions are also given to humans explaining that they must pay attention to stimulus durations to correctly judge time. However, adjustments of these temporal tasks have modified the nature of the time judgment, with an explicit time judgment being now required rather than an implicit one. Recent studies have shown that explicit time judgment requires high-level cognitive skills linked to executive functions (Block, Hancock, & Zakay, 2010; Brown, Collier, & Night, 2012; Ogden, Salominaite, Jones, Fisk, & Montgomery, 2011; Zélanti & Droit-Volet, 2011, 2012). It is thus likely that differences in time sensitivity across ages would be linked to the development of the cognitive control abilities required in explicit judgment of time (Droit-Volet, 2013).

There is indeed ample evidence that the different components of executive functions including working memory, attentional control (selective attention, inhibition) develop throughout childhood (e.g., Anderson & Reidy, 2012; Gathercole, 2002). This is explained by the slow maturation of the brain with a progressive increase in activation of prefrontal cortex and in the efficiency of its connections with striatal and parietal regions (e.g., Casey, Totenham, Liston, & Durston, 2005; Rubia, 2013; Sowell et al., 2003). Recently, in a series of studies on time judgment in children, Droit-Volet and Zélanti showed that the sensitivity to time improved along with the increase of working memory capacity as children aged (Droit-Volet & Zélanti, 2013a; Zélanti & Droit-Volet, 2011, 2012). However, these authors only tested sensitivity to time in children with the temporal bisection task without analyzing the degree of involvement of different cognitive functions as a function of the temporal tasks used. The extent to which the judgment of time depends on cognitive resources may indeed depend on the temporal tasks used. Time judgment could therefore be more difficult in certain tasks than in others for children with limited cognitive resources. The aim of the present study is thus to assess children's capacity in terms of working memory, attentional control and processing speed with a series of neuropsychological tests and to examine how the scores on these tests account for individual differences in time judgment as a function of the temporal tasks used.

In our study, children aged 5 and 8 years, as well as adults, were submitted to 3 temporal tasks currently used with children: the temporal bisection task (e.g., Droit-Volet & Wearden, 2001; McCormack, Brown, Maylor, Darby, & Green, 1999), the temporal generalization task (e.g., Droit-Volet, 2002; Droit-Volet et al., 2001; McCormack, Brown, Smith, & Brock, 2004), and the temporal reproduction task (e.g., Crowder & Hohle, 1970; Droit-Volet, 2010; Szelag, Kowalska, Rymarczyk, & Pöppel, 2002). In temporal bisection, participants are initially presented with two reference durations (one short, *s*, and one long, *l*), and must then judge whether comparison durations (equal to *s* or *l*, or of intermediate value) are more similar to *s* or *l*. In temporal generalization, they are presented with only one reference duration, *g*, and must judge whether comparison durations (equal to, shorter or longer than *g*) are equal or not to *g*. The temporal reproduction task differs from these two temporal discrimination tasks, because the reference duration, *r*, is given at the beginning of each trial. The participants must reproduce *r* by pressing a button when they judge that a second, comparison, stimulus has lasted for the same time as *r*.

To date, no study has directly compared children's time judgment on these 3 tasks by taking into account individual differences in cognitive resources. Temporal reproduction has, however, been compared with temporal production in young and elderly adults (Baudouin, Vanneste, Isingrini, & Pouthas, 2006b; Baudouin, Vanneste, Pouthas, & Isingrini, 2006a; Perbal, Droit-Volet, Isingrini, & Pouthas, 2002). The results showed that working memory capacities explained a larger proportion of individual variance in temporal performance in the reproduction task than in the production task (Baudouin, Vanneste, Isingrini et al., 2006b; Baudouin, Vanneste, Pouthas et al., 2006a; Perbal et al., 2002). The judgment of time thus requires greater working memory capacity in temporal reproduction than in temporal production. Recently, Ogden, Wearden, and Montgomery (2014) have also compared the young adults' performance on the temporal generalization and the temporal reproduction tasks. They found that working memory capacities were significantly correlated with time accuracy on both generalization and reproduction. Indeed, both these tasks required the monitoring and the maintenance of reference durations and comparison durations in working memory. However, the attentional control-related capacities also explained part of the individual differences in temporal accuracy for temporal reproduction. Ogden et al. (2014, p. 92) suggested that temporal reproduction requires participants to maintain the referent duration in working memory whilst concurrently maintaining the duration of their reproduction. Thus temporal reproduction is more demanding in terms of attention than the other temporal discrimination tasks.

Some developmental studies have identified the critical role of the development of attentional capacities in determining age differences in temporal reproduction performance (for a review see Droit-Volet, Delgado, & Rattat, 2006). According to attentional models of timing (Zakay, 1989; Zakay & Block, 1996, 1998), the less a person attends to time, the more they underestimate stimulus durations. Consistently with these predictions, developmental studies have found a greater shortening of judged time in young children aged 5 years than in older children or adults in a dual-task paradigm, when they processed temporal and non-temporal information in parallel (Arlin, 1986a, 1986b; Gautier & Droit-Volet, 2002a, 2002b; Zakay, 1992). In addition, Block, Zakay, and Hancock (1999) argued that children are impatient during the reproduction phase and terminate their response early, thus increasing the shortening effect. Consequently, the development of inhibition capacity is also assumed to play an important role in temporal reproduction in children. Its role nevertheless depends on durations used. In temporal reproduction, children underestimate long durations, but overestimate short ones (Droit-Volet, 2010). In her modelling of children's reproduction, Droit-Volet (2010) suggested that the implementation of the motor response involved in the reproduction took longer in 5-year-old children, and that this lengthens their reproduction of short durations (<1 s). Slow processing speed is also characteristic of cognition in young children (Kail, 1991, 2001), so this can also account for age-related differences in temporal reproduction, especially for short durations. In the present study, children and adults were given 3 temporal tasks with both short (<1 s) and long durations. We assumed that the reproduction task would demand more cognitive capacity (working memory, attentional control, processing speed) than do the temporal discrimination tasks (generalization and bisection), as these primarily require working memory capacities (Droit-Volet & Zélanti, 2013a, 2013b; Zélanti & Droit-Volet, 2011, 2012). Consequently, individual scores on neuropsychological tests assessing working memory but also attention and processing speed would explain a larger proportion of individual variance in temporal performance for the reproduction task than for the discrimination tasks (generalization and bisection), and this to a greater extent in young children.

The interest and originality of the present study also lies in its attempts to model individual subject data by using common parameters for the 3 temporal tasks tested, as this will enable a comparison of these tasks using the same statistical analyses and will allow us to evaluate the respective weight of these parameters as a function of the task (see Results for details). In the models of temporal bisection and temporal generalization that fitted well the results from both adults and children (see Church & Deluty, 1977; Droit-Volet, Tourret, & Wearden, 2004; Droit-Volet & Wearden, 2001;

McCormack et al., 1999; Penney, Gibbon, & Meck, 2000; Wearden, 1991, 1992; Wearden & Jones, 2013), there is always a memory variability parameter, *C*. In models derived from scalar timing theory, indeed the main source of variance in time judgment results from the variability (noise) in the representation of reference durations (Gibbon, 1977; Gibbon, Church, & Meck, 1984). The *C* parameter which measures this is a sort of coefficient of variation of the value of reference durations in memory: The higher its value, the fuzzier the representation of reference durations is. To account for children's temporal behaviour, McCormack et al. (1999) added a memory distortion parameter, *K*, to their model of temporal generalization. This idea was then successfully employed by Droit-Volet in modelling generalization (Droit-Volet et al., 2001) and bisection (Delgado & Droit-Volet, 2007). This distortion parameter is a simple multiplicative factor applied to reference durations. If *K* is 1.0, the reference duration value is remembered on average correctly. If *K* is $<$ or $>$ 1.0, it is remembered on average as shorter or longer, respectively, than it really was. For the temporal reproduction task, there is no model similar to those used for the bisection and the generalization task (see Droit-Volet, 2010), because the reference duration is not stored in long-term memory and reactivated during the judgment of comparison durations, but instead maintained in working memory on each trial. However, from a comparative perspective, we can apply the same parameters, *C* and *K*, to reference durations in reproduction. In this case, these parameters indicate that the representation of reference durations is more or less fuzzy from one trial to another, and distorted (shorter or longer than it really is). Our hypothesis was that reference durations are fuzzier and more distorted in the reproduction task than in the two discrimination tasks, especially in younger children, and that their poor representation of reference durations in temporal reproduction is associated with their low cognitive capacity in terms of working memory, attentional control and processing speed.

In sum, in the present study, we present the results of performance on 3 different temporal tasks (bisection, generalization, reproduction) in both children and adults, and we examine how working memory, attentional control and processing speed capacities assessed by a battery of neuropsychological tests might explain inter-individual differences in performance on each temporal task. Then, we give the results of *C* and *K* parameters resulting from our modelling of individual data and use statistical analyses examining the effect of age on these parameters as a function of the temporal task type. In addition, correlation and hierarchical regression analyses were conducted to determine which cognitive abilities, as assessed by neuropsychological tests, would best explain inter-individual differences in these parameters.

EXPERIMENTAL STUDY

Method

Participants

The sample was composed of 68 participants: 21 5-year-olds (8 girls and 13 boys; mean age = 5.71, *SD* = 0.45), 26 8-year-olds (12 girls and 14 boys; mean age = 8.31, *SD* = 0.45) and 21 adults (11 females and 10 males; mean age = 24.78, *SD* = 2.82). The children were recruited from nursery and primary schools at Saint-Germain-des-Fosses, and the adults were students in Clermont-Ferrand, in the Auvergne region of France. The adults and the parents of the children signed a consent form for participation in this experiment. At the end of the experiment, the children received cartoon cards and the adults 10 Euros to thank them for their participation.

Material

The children and the adults were tested individually in a quiet room in their school or in their university, where they were seated in front of a PC computer that controlled the experimental stimuli and recorded data via E-prime software. The responses were verbal responses for the bisection and the generalization task, and motor responses for the reproduction task. In the reproduction task, the participants pressed the space bar on the computer keyboard. In the other tasks, they gave their responses orally, and the experimenter pressed the corresponding key to record their response. For all tasks, the stimulus to be timed was a red circle (6 cm in diameter), which was presented in the centre of the computer screen. In addition, in the bisection and the generalization task, a 500-ms feedback stimulus in the form of a cartoon picture (which varied from trial to trial) was presented for a correct response and a picture of unhappy Calimero (a cartoon duck) was presented for an incorrect response.

Procedure

The participants performed 6 temporal tasks at a rate of one per day (a bisection, generalization, and reproduction task), each with 2 duration conditions: 0.4/0.8-s and 8/16-s. In the 0.4/0.8-s condition, the 7 stimulus durations used were 0.4, 0.47, 0.53, 0.6, 0.67, 0.73, and 0.8 s, and in the 8/16-s condition, 8.0, 9.33, 10.67, 12, 13.33, 14.67, and 16 s. The temporal task order was randomized across participants. Furthermore, the experimenter instructed the participants not to count and explained that counting time may bias the scientific data (for a test of the methods used to prevent counting, see Rattat & Droit-Volet, 2012). The results found in our study clearly differed from the accurate time judgments found when participants use counting to make time judgments (Clément & Droit-Volet, 2006; Rattat & Droit-Volet, 2012), suggesting that our instruction not to count was effective. Each day, the participants also completed a series of neuropsychological tests assessing their cognitive capacities.

Temporal bisection task. In the bisection task, the participants were initially presented with the short reference duration (*s*) (0.4 or 8-s) and the long reference duration (*l*) (0.8 or 16-s) five times each in alternation. They were then trained to respond “short” or “long” on a series of 4 training trials presented in random order (2 for *s* and 2 for *l*), with an inter-trial interval randomly chosen between 0.5 and 2 s. Each response was followed either by the “correct” or “wrong” feedback. This training phase was immediately followed by a testing phase using the same experimental conditions, except that the participants were presented with the 7 comparison durations described above. In addition, feedback was given for the 2 comparison durations which were the same as the 2 reference durations, but not for the 5 intermediate comparison durations. Each participant completed 9 series of 11-trial blocks (i.e., 99 trials): with 3 trials for each reference duration, and 1 trial for each of the 5 intermediate durations. The trial presentation order within each block was random. After 3 blocks, the participants were again twice presented with each reference duration.

Temporal generalization task. In the generalization task, the participants were initially presented 5 times with the same reference duration (*g*) (0.6 or 12 s). They were then trained to judge whether the presented durations were (yes) or were not (no) the same as the reference duration. There were 4 training trials: 2 for the reference duration and 2 for 2 other durations (0.3 and 19 s). The inter-trial interval was randomly chosen between 0.5 and 2 s. In this training phase, a “correct” or “wrong” feedback display was given when the response was correct and incorrect, respectively. Immediately after the training phase, the participants were given the testing phase. This was subject to the same experimental conditions as those used in training, with feedback being given after each response. In the testing phase, the participants were given 9 series of 9-trial blocks (81 trials): 3 trials for the comparison duration identical to the reference duration (0.6 or 12-s) and 1 trial for each of the 6 other comparison durations. The trial presentation order was randomized across each trial block. The reference duration was presented twice after every 3 blocks.

Temporal reproduction task. In the temporal reproduction task, the participants were instructed to reproduce as accurately as possible the reference duration of the stimulus they saw on the computer screen. On each trial, a first (reference) stimulus duration (*r*) was presented followed, after a 500-ms interval, by a second stimulus whose onset was indicated by a symbol. The participant had to press the space bar of the computer keyboard when he/she judged that the presentation duration of the second stimulus was the same as that of the first stimulus. The participants received 2 demonstrations and were trained on 4 trials with 2 durations (0.3 s and 19 s) presented in random order. In the testing phase, they were given 42 trials: 6 trials for each of the 7 probe durations. Both the stimulus presentation order and the inter-trial interval (between 0.5 and 2 s) were randomized.

Neuropsychological tests. In our study, we used a battery of neuropsychological tests to assess working memory, attention and information processing speed (see Miyake, Friedman, Emerson, Witzki, & Howerter, 2000). To assess working memory capacities, we used the backward version of the Corsi Block-Tapping test from the Wechsler Memory Scale (WMS-III; Wechsler, 1998) which has been shown to account well for individual differences in the estimation of the duration of visual stimuli (Ulbrich, Churan, Fink, & Wittmann, 2007; Zélanti & Droit-Volet, 2012). In this test, the experimenter taps a number of blocks on a board containing nine blocks and the participant has to recall this block-tapping sequence in reverse order. The length of the sequence gradually increases from two to eight blocks, with two trials per sequence length. The working memory score is equal to the total number of correct trials (1 point per correct trial). The attention-concentration index of the Children's Memory Scale (CMS; Cohen, 1997) was also measured. This is also an index of working memory, but is referred to as an attention-concentration index because it requires dynamic/continuous monitoring and updating of the content of working memory (Riccio, Garland, & Cohen, 2007). Previous studies have shown that participants' scores on this index were better predictors of temporal performance in bisection than the scores on a memory span test (e.g., Zélanti & Droit-Volet, 2011). Indeed, the attention-concentration index is based on two subtests. The first, called number, measures forward and backward digit span. The second, called sequence, assesses the ability to mentally manipulate a sequence of verbal material as quickly as possible, for example saying the days of the week backward or counting in fours. The total raw score is 114 points, and the higher the attention-concentration index is, the greater the participant's attention/concentration capacities are. To measure selective attention, we used the selective visual attention test from a developmental neuropsychological assessment scale (NEPSY; Korkman, Kirk, & Kemp, 1998), which assesses participants' ability to selectively focus their attention on a visual target (i.e. a cat or a specific face) located in an array of 96 different items. The score is the time in seconds needed to complete the task divided by the number of correct visual targets found. Consequently, high scores on this test correspond to poor selective attention capacities (see Table 1). To assess selective attention with an inhibitory dimension, we used a Stroop test adapted for use with children (Albaret & Migliore, 1999). In this task, the participant initially reads 50 colour words (e.g. blue, yellow, green, red) printed in black and white. He/she then names the colours of 50 squares and, finally, he/she must read a colour word printed in a colour different from that of the word. The score is the time taken to complete this last phase: The higher it is, the lower

Table 1. *Mean and error standard of scores on the neuropsychological tests for the 5-year-olds, the 8-year-olds, and the adults*

	5 years		*8 years*		*Adults*	
Neuropsychological scores	*M*	SE	*M*	SE	*M*	SE
Working Memory	4.40	*0.36*	6.23	*0.30*	8.38	*0.33*
Att. Concentration	34.80	*1.87*	58.23	*1.67*	88.62	*1.68*
Selective Attention	8.72	*0.50*	5.68	*0.25*	2.98	*0.13*
Att. Inhibition	46.10	*3.87*	48.22	*2.77*	18.63	*0.94*
Processing Speed	37.79	*3.34*	25.76	*1.29*	11.22	*0.67*

the attention inhibition capacities are (Table 1). Finally, we measured information processing speed, which is a major measure of cognitive efficiency (Grégoire, 2007), by using the well-known Trail Making Test part A (TMT-A, Reitan, 1992). In TMT-A, the participant is presented with 25 circles, each of which contains a number, which are distributed randomly on a sheet of paper. He/she has then to connect these circles in ascending numerical order, as quickly as possible. The score is the amount of time required to complete this task. The higher the score on the TMT-A, the slower the information processing speed is (Table 1). The mastery of numbers was previously verified in the children we tested.

Results

Temporal performance

Temporal Bisection. Figure 1 shows the proportion of "*long*" responses (p(long)) plotted against test stimulus durations for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition. To examine the participants' temporal performance in bisection,[1] two indices were calculated: the Bisection Point (BP) and the Weber Ratio (WR). The BP is the point of subjective equality, i.e., the stimulus duration where $p(\text{long}) = .50$. The WR is a sort of coefficient of variation. It is the Difference Limen ($[D(p(\text{long}) = .75 - D(p(\text{long}) = .25] / 2$) divided by the BP. The higher the WR, the flatter the psychometric function, and the more variable the temporal discrimination is. In other words, the higher the WR, the lower the sensitivity to time is. The BP and the WR were obtained by approximating each participant's bisection function using the statistical linear function from the SPSS program. This linear function produced the best fits for all participants. For each of these temporal indexes, an ANOVA was performed with duration range (0.4/0.8-s *vs.* 8/16-s) as within-subjects factor and age as between-subjects factor.

Bisection point. The ANOVA on the BP did not reveal either a significant main effect of age, $F(2, 65) = 0.15$, $p > .05$, or any significant age × duration interaction, $F(2, 65) = 0.21$, $p > .05$ (Figure 2). There was only a significant main effect of duration, $F(1, 65) = 1569$, $p < .05$, indicating that the BP was higher for the long than for the short durations.

Weber ratio. In contrast to the BP, there was a significant main effect of age for the WR, $F(2, 65) = 10.67$, $p < .05$, revealing a developmental improvement in sensitivity to time. The 5-year-olds ($M = .48$, $SE = .03$) exhibited a higher WR, indicating lower sensitivity to time, than the 8-year-olds ($M = .37$, $SE = .03$) and the adults ($M = .26$, $SE = .03$) (Scheffé test, all $p < .05$). The WR did not differ significantly between the 8-year-olds and the adults ($p = .06$). In addition, the main effect of duration, $F(1, 65) = 36.73$, $p < .05$, as well as the age × duration interaction, $F(2, 65) = 3.27$, $p < .05$, reached significance. The main effect of age was always significant whatever the duration condition (0.4/0.8-s: $F(2, 65) = 7.77$, 8/16-s: $F(2, 65) = 6.77$, all $p < .05$). However, as illustrated in Figure 2, the sensitivity to time was lower in the long ($M = .48$, $SE = .04$) than in the short duration condition ($M = .25$, $SE = .01$), even though the magnitude of the difference in time sensitivity between the two duration conditions decreased with increasing age. Indeed, the adults produced similar WRs in the 8/16-s and in the 0.4/0.8-s duration condition, $t(20) = 1.96$, $p > .05$, whereas the 5-years-olds and the 8-year-olds produced higher WRs in the long than in the short duration condition [$t(20) = 4.99$; $t(25) = 3.33$, respectively, $p < .05$). In fact, as far as the children are concerned, this significant effect of duration ranges on the WR revealed a violation of Weber's law (i.e., the scalar property of variance) that postulates that WR values should remain constant for different duration ranges. This violation of the scalar property of variance is clearly illustrated in Figure 3 which shows that

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[1] The initial ANOVA run on p(long) is not reported because it provided results close to those obtained for the Bisection Point and the Weber Ratio.

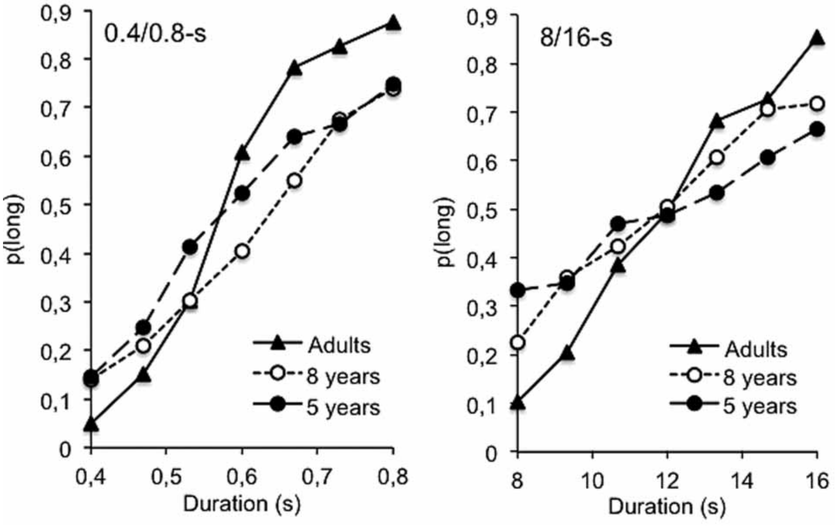

Figure 1. *Temporal Bisection. Proportion of long responses (p(long) plotted against stimulus durations for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

the children's psychometric functions derived from different duration ranges did not superimpose well when plotted on the same relative scale. This illustrates children's difficulties in processing long durations in bisection.

Temporal Generalization

The mean generalization gradients for each age group are presented in Figure 4, which plots the proportion of "yes" responses (judgments that the just-presented stimulus had the same duration as the standard) against the stimulus duration. Temporal discrimination seems poorer in the generalization task than in the bisection task, with temporal gradients being particularly flat in the two groups of children. However, to further examine generalization performance, we calculated two temporal indices: (1) the peak time of the generalization gradient, which is the stimulus duration which gives rise to the highest proportion of *yes* responses and (2) the width of the generalization gradient at half of its maximum height (full width at half maximum, FWHM). The FWHM divided by the peak time is also a sort of coefficient of variation. The higher its value, the larger the width of the generalization gradient, and the lower the sensitivity to time. The peak time and the FWHM were obtained by approximating each participant's generalization gradient using the Gaussian (*Amplitude*) function from the PeakFit program (PeakFit version 4.2 for Windows) that provided the best fit for the temporal gradients of most of the participants. For one 5-year-old child, it was impossible to obtain a peak time because his/her temporal gradient was totally flat. The maximum value of FWHM/peak time (1.0) was thus attributed to this participant (for this method, see e.g., Droit-Volet, 2008; Droit-Volet & Zélanti, 2013a) and her/his peak time was not included in the subsequent statistical analysis.

Peak time. An ANOVA[2] on the peak time with the same factorial design as that reported in bisection found a significant main effect of duration, $F(2, 64) = 3235$, $p < .05$, but neither a main effect of age, $F(2, 64) = 1.95$, $p > .05$, nor an age × duration interaction, $F(2, 64) = 1.84$, $p > .05$ (Figure 5). Consequently, there was no significant developmental difference in temporal accuracy.

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[2] The initial ANOVA run on p(yes) is not reported because it provided results close to those obtained based on peak time and the width of the generalization gradient.

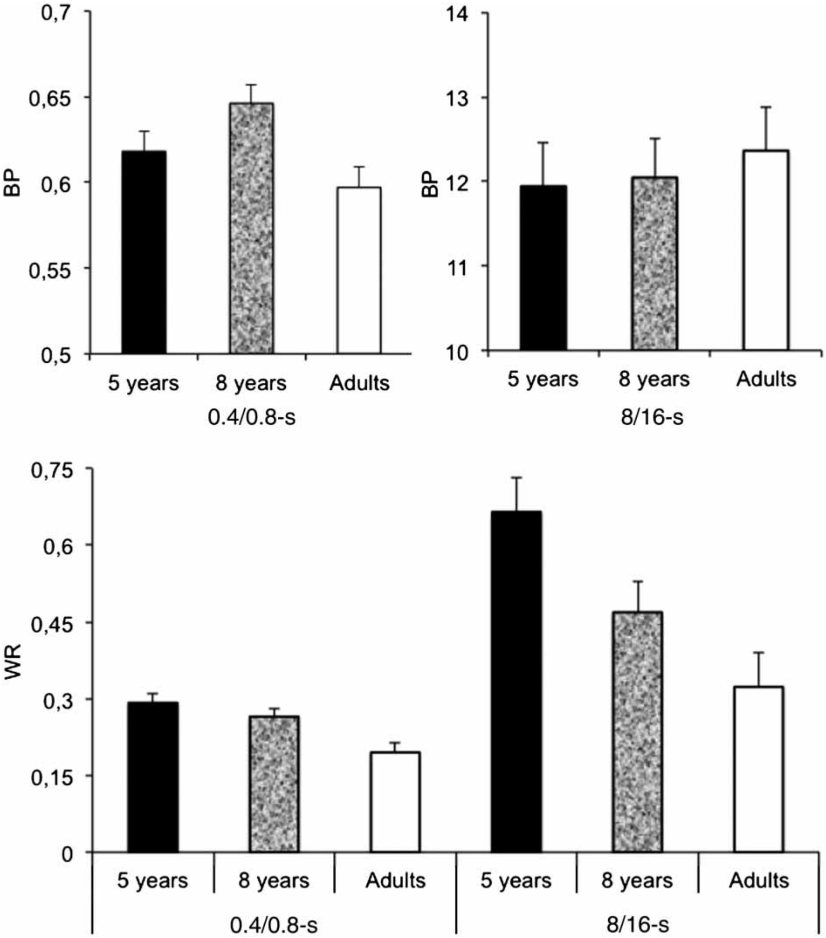

Figure 2. *Temporal Bisection. Mean (standard error) Bisection Point (BP) and Weber ratio (WR) for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

FWHM/peak time. As in the temporal bisection task, the index of time sensitivity (FWHM/peak time) in the generalization task changed with the age. However, in generalization, the age-related difference did not increase with the length of the durations judged. Indeed, the ANOVA showed a significant main effect of age, $F(2,\ 65) = 5.51$, $p < .05$, without a significant interaction between age and duration, $F(2,\ 65) = 1.43$, $p > .05$. As suggested by the particularly flat generalization gradients, sensitivity to time was particularly low in the 8-year-olds (.59) and was at a level close to that observed in the 5-year-olds (.54) (Scheffé test, $p > .05$), whereas it was higher in the 8-year-olds than in the 5-year-olds in the bisection task. However, the only significant difference revealed by the results was between the adults and the youngest children (.46 *vs.* .59, $p < .05$). The time sensitivity index (FWHM/peak time) in generalization thus suggested a slower age-related improvement in performance on the generalization task than on the bisection task. The ANOVA also showed a significant main effect of duration, $F(1,\ 65) = 7.68$ $p < .05$, demonstrating that variability in temporal discrimination was greater for the long than for the short durations (.58 *vs.* .48). This finding is consistent with the violation of Weber's law found in bisection.

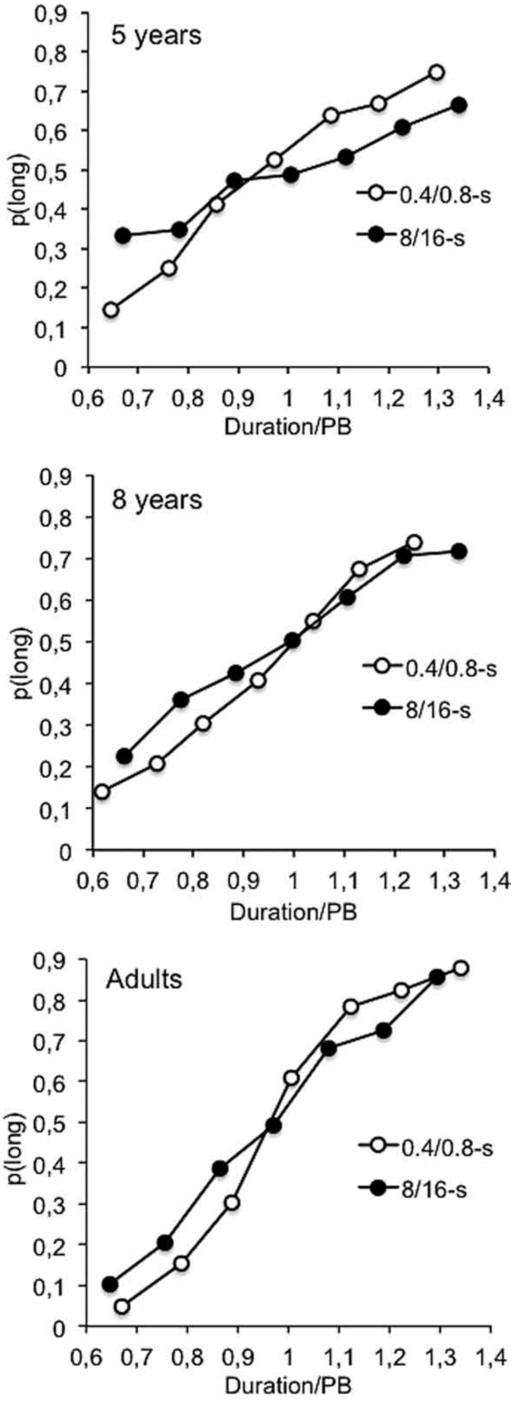

Figure 3. *Temporal Bisection. Psychometric functions for the short (0.4/0.8-s) and the long (8/16-s) duration condition plotted against the same relative scale for the 5-year-olds, the 8-year-olds and the adults.*

Temporal reproduction

Mean reproduced duration. In the temporal reproduction task, the mean reproduced durations increased on average in an orderly way as a function of stimulus duration both in the children and in the adults (Figure 6). However, there was a systematic bias in the reproduced durations in the younger children compared to the older participants, with the 5-year-olds producing longer durations in the 0.4/0.8-s condition and shorter durations in the 8/16-s condition. An ANOVA was conducted on the mean reproduced durations with stimulus duration and duration range as within-subjects factor and the age as between-subjects factor. The stimulus duration, $F(6, 390) = 76.74$, $p < .05$, the duration range, $F(1, 65) = 1756$, $p < .05$, and the interaction between these 2 factors, $F(6, 390) = 49.28$, $p < .05$, were all significant. More interestingly, the main effect of age was also significant, $F(2, 65) = 3.44$, $p < .05$, and age interacted significantly with duration range, $F(2, 65) = 7.33$, $p < .05$. The other interactions were not significant. In the 0.4/0.8-s condition, the 5-year-olds ($M = 1.13$, $SE = .08$) produced longer durations than did the 8-year-olds ($M = 0.82$, $SE = .03$) and the adults ($M = 0.82$, $SE = 0.06$) (Scheffé test, both $p < .05$), while the mean reproduced durations were similar between the 8-year-olds and the adults ($p > .05$). In contrast, in the 8/16-s condition, the 5-year-olds reproduced durations ($M = 8.75$, $SE = .04$) shorter than those of the adults ($M = 10.43$, $SE = 0.03$) ($p < .05$), with the length of durations reproduced by the 8-year-olds ($M = 9.45$, $SE = .04$) lying between those reproduced by the 5-year-olds and the adults. In sum, while temporal "accuracy" was similar across age groups in the temporal discrimination tasks, in temporal reproduction, temporal accuracy was lower in the youngest children because they produced greater overestimations and underestimations of the short and the long durations, respectively.

Variability of durations reproduced. The ANOVA on the coefficient of variation of temporal reproductions (SD/M) also showed a main effect of duration range, $F(1, 65) = 30.97$, $p < .05$, with

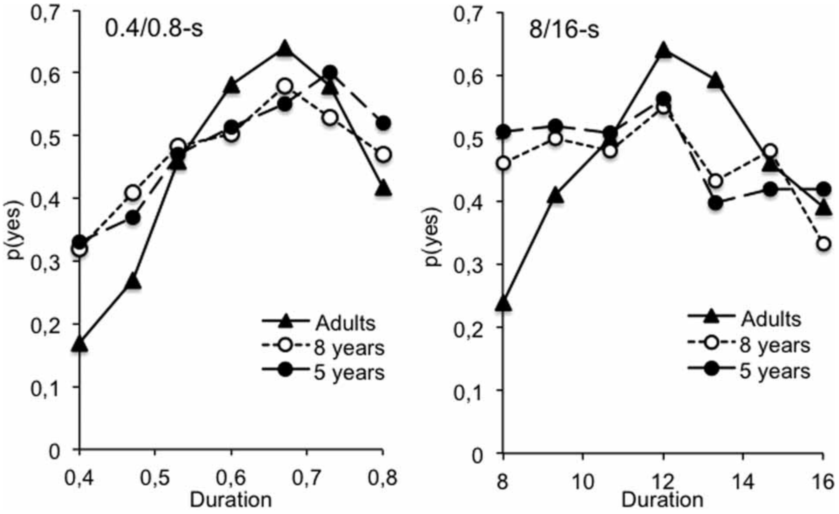

Figure 4. *Temporal Generalization. Proportion of yes responses (p(yes)) plotted against stimulus durations for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

no interaction involving this factor ($p > .05$). This therefore pointed to a violation of Weber's law in the temporal reproduction task as in the other temporal discrimination tasks. However, in contrast to these discrimination tasks, temporal variability assessed by coefficient of variation was greater in the reproduction task for the short than for the long durations (.46 *vs.* .34) and not the reverse (Figure 7). There was also a main effect of age, $F(2,\ 65) = 35.71$, $p < .05$, which revealed an increase between each age group in the sensitivity to time (5 years: $M = .52$, $SE = .02$; 8 years: $M = .38$, $SE = .02$; Adults: $M = .29$, $SE = .02$, Bonferroni tests for all comparisons, $p < .05$). The age × stimulus duration interaction was also significant, $F(12,\ 390) = 2.11$, $p < .05$. The statistical analyses nevertheless revealed that this significant interaction was linked to the effect of stimulus durations on SD/M that tended to be significant in the 5-year-olds, $F(6,\ 120) = 2.16$, $p = .08$. However, no difference in the coefficient of variation between the stimulus durations reached significance.

Correlation between the timing measures and neuropsychological scores

Table 1 presents the mean and the standard error of scores obtained by the children and the adults on the different neuropsychological tests.[3] For each neuropsychological test, the effect of age was significant: Working memory, $F(2,\ 64) = 34.70$; Attention concentration, $F(2,\ 64) = 222.07$; Selective attention, $F(2,\ 64) = 76.66$; Attention inhibition, $F(2,\ 57) = 42.36$; Processing speed, $F(2,\ 64) = 42.16$ (all $p < .05$), with all pairwise comparisons between age groups being significant (Scheffé, all $p < .05$).

Table 2 shows, for the 3 temporal tasks, the correlations between the timing measures for the short (0.4/0.8-s) and the long (8/16-s) duration condition and the *z*-scores on neuropsychological tests calculated for the 3 age groups. When there were significant correlations between the timing measures and scores on several neuropsychological tests, we entered these different scores into the equation and ran hierarchical regression analyses to identify which factor was the best predictor of

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[3] Among the twenty-one 5-year-olds, one child did not perform the different neuropsychological tests. The attention inhibition scores for 8 children were not included in Table 1 because they were unable to read the color name correctly.

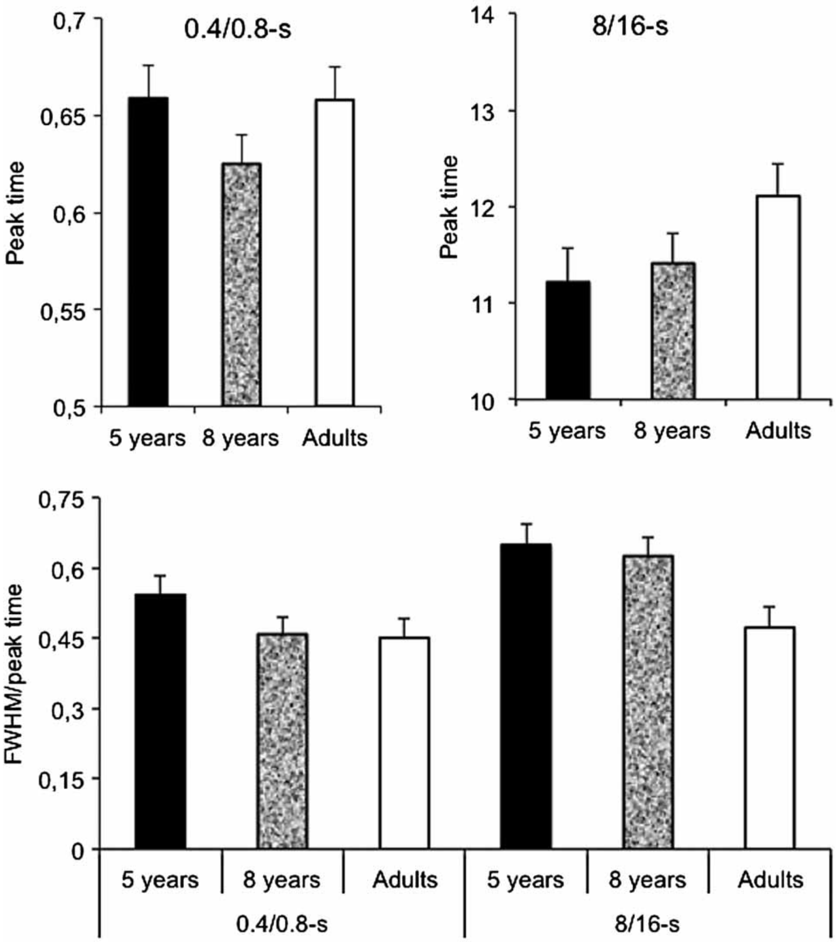

Figure 5. *Temporal Generalization. Peak time and FWHM/peak time for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

individual variance in these timing measures for each type of task.

Temporal Bisection

Bisection point. In line with the absence of an age effect on the BP, there was no correlation between the BP and the scores on the neuropsychological tests (Table 2), with the exception of the BP in the short duration condition, in which we observed a significant correlation between the BP and the scores on the attention inhibition test, $R = .30$, $p < .05$. This result suggests that when the attention inhibition capacities decreased, the BP for the short durations shifted toward the right (lower BP values), a finding which is consistent with a shortening effect.

Weber ratio. Table 2 shows that the WR for the short and the long duration were significantly correlated with 5 and 4, respectively, of the different neuropsychological scores. The various significant scores were therefore entered into the equation of the hierarchical regression analyses. This analysis revealed that the only reliable predictor of individual variances in time sensitivity was the scores on the attention-concentration test and that this

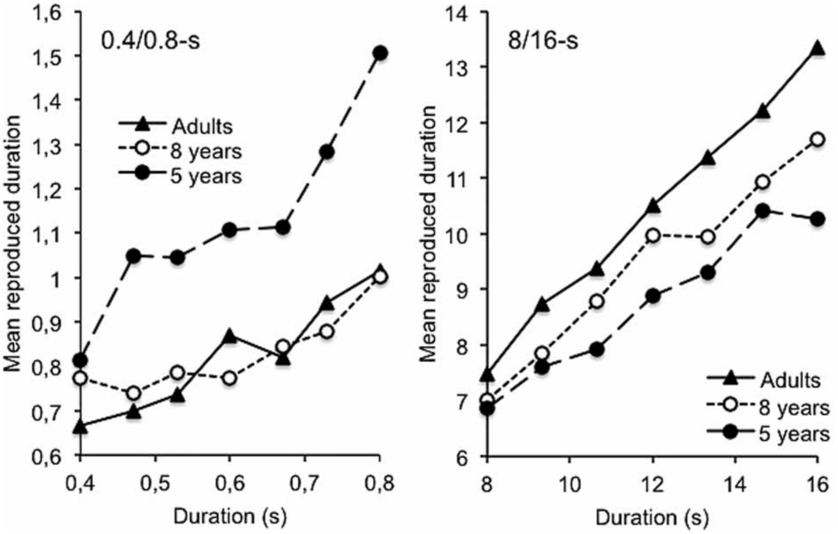

Figure 6. *Temporal reproduction. Mean reproduced duration for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

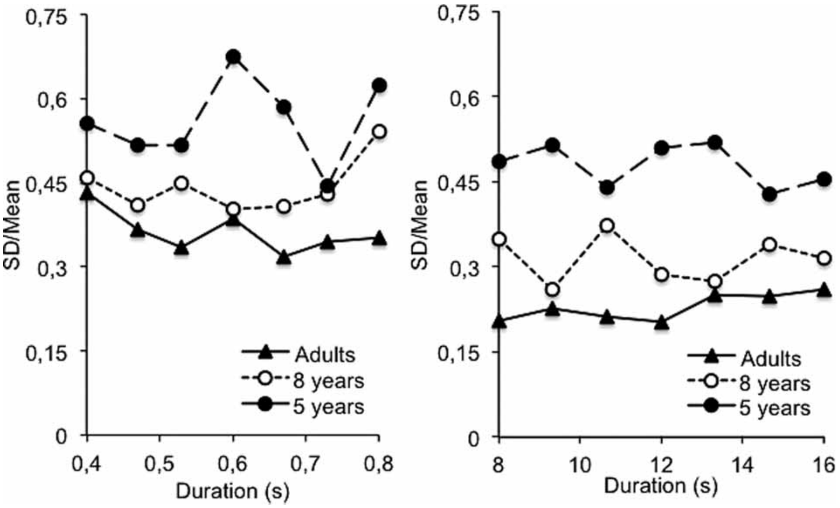

Figure 7. *Temporal reproduction. Coefficient of variation (SD/M) of reproduced duration for the 5-year-olds, the 8-year-olds and the adults in the short (0.4/0.8-s) and the long (8/16-s) duration condition.*

was true both for the short (ß = −.49, $R^2 = .24$, $p < .05$), and for the long duration condition (ß = −.56, $R^2 = .31$, $p < .05$). The higher the attention-concentration scores, the lower the WR and the higher the sensitivity to time was. This finding is entirely consistent with that obtained in previous bisection studies using neuropsychological tests in children that showed that the improvement in time sensitivity depends on working memory capacities assessed by this neuropsychological test (Zélanti & Droit-Volet, 2011).

Table 2. *Correlation between neuropsychological scores and timing measures on bisection, generalization, and reproduction for the 0.4/0.8 and the 8/16-s duration condition?*

	Bisection				*Generalization*				*Reproduction*			
	PB		*WR*		*Peak Time*		*FWHM/Peak*		*Mean*		*SD/Mean*	
Neuropsychological scores	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*
Working Memory	−.04	.03	$-.36^{**}$	$-.38^{**}$	.02	$.30^{*}$	−.14	−.18	$-.37^{**}$	$\underline{.33^{**}}$	$-.49^{**}$	$-.62^{**}$
Att. Concentration	−.16	.01	$-\underline{.48^{**}}$	$-\underline{.40^{**}}$	.09	$\underline{.31^{*}}$	−.18	$-.31^{*}$	$-.38^{**}$	$.31^{*}$	$-.50^{**}$	$-.63^{**}$
Selective Attention	.11	−.06	$.43^{**}$	.21	.07	−.20	.08	$\underline{.33^{**}}$	$.40^{**}$	−.22	$.47^{**}$	$.59^{**}$
Att. Inhibition	$.30^{*}$	−.09	$.40^{**}$	$.39^{**}$	$-.26^{*}$	−.11	$.27^{*}$	$.26^{*}$	.02	−.17	$.30^{*}$	$.36^{**}$
Processing Speed	.17	.19	$.46^{**}$	$.34^{**}$	−.05	−.12	.16	$.31^{*}$	$\underline{.45^{**}}$	−.23	$\underline{.50^{**}}$	$\underline{.64^{**}}$

Note: Underlined numbers = significant predictors resulting from the hierarchical regression analyses. Neuropsychological scores = z-scores. Duration condition: S (short) = 0.4/0.8 s; L (long) = 8/16 s.
$^{*}p < .05$; $^{**}p < .01$.

Temporal Generalization

Peak Time. In the generalization task, temporal accuracy was significantly correlated with attention inhibition scores for the short durations, $R = .26$, $p < .05$ (Table 2). When the attention inhibition capacities decreased, the peak time also decreased, a finding that is consistent with the shortening effect observed in bisection. However, concerning the long durations, the peak time value was correlated with both the working memory scores, $R = .30$, $p < .05$, and the attention-concentration scores, $R = .31$, $p < .05$. The hierarchical regression analyses with these two scores nevertheless revealed that the attention-concentration scores were better predictors of individual variance in the peak time value, irrespective of the order in which the factors were entered into the equation (ß = .30, $R^2 = .09$, $p < .05$), although the amount of variance explained remained low. In other words, the temporal gradient tended to peak at a shorter value when the individuals' attention-concentration capacities decreased.

FWHM/peak time. The attention components of cognitive functions were also related to differences in the width of the temporal generalization gradient (FWHM/peak time). There was a significant correlation between this index of temporal variability and the scores on the attention inhibition test in the short duration condition, $R = .27$, $p < .05$ (Table 2). For the long duration condition, the hierarchical regression analyses revealed that participants' scores on selective attention were the only reliable predictor of individual differences in the width of the generalization gradient (ß = .29, $R^2 = .08$, $p < .05$). The variability in time judgments in generalization therefore increased when the attentional components of executive functions decreased.

Temporal Reproduction

Mean reproduced duration. An initial inspection of the results in Table 2 shows that a great number of cognitive factors significantly interacted with the performance indices calculated for the temporal reproduction task compared to those calculated for the temporal discrimination tasks. The hierarchical regressions performed with the significant neuropsychological scores nevertheless indicated that the scores for information processing speed were the only reliable predictor of individual differences in the mean reproduced duration for the short durations (ß = .45, $R^2 = .20$, $p < .05$), whereas this role was played by the working memory scores in the case of the long durations, (ß = .33, $R^2 = .11$, $p < .05$). There was therefore a lengthening effect on estimates of short durations when the information processing speed slowed down. Furthermore, estimates of long durations also shortened with decreasing memory capacities.

Variability of durations reproduced. The hierarchical regressions also revealed that, taken together, the scores for information processing speed and working memory helped explain individual differences in the variability of reproduced durations (*SD*/Mean) for the long durations (ß = .69, $R^2 = .48$, $p < .05$), although processing speed appeared to be the best predictor of this performance index (ß = .64, $R^2 = .41$, all $p < .05$). For the short durations, processing speed was the only reliable predictor (ß = .50, $R^2 = .25$, $p < .05$). The increase in variability of time estimates was thus associated with a slowing down of information processing speed.

Modeling of Data

Model description. As mentioned in the introduction, we modelled each participant's data for the 3 temporal tasks by selecting two parameters of scalar timing-consistent models used to account for temporal performance on both the bisection and the generalization task (see Wearden & Jones, 2013). The first parameter, *C*, is a variability parameter applied to the reference durations: The higher its value, the fuzzier the representation of reference durations is. The second parameter, *K*, is a distortion parameter, which was applied to reference durations. If *K* is 1.0, the reference duration value is remembered correctly. If *K* is < or > 1.0, it is remembered as shorter or longer, respectively, than it really is.

Applied to the bisection task, the model calculated two absolute differences – $abs[D(s^*K,\ t)]$ and $abs[D(l^*K,\ t)]$ – between the stimulus duration to be judged, *t*, and *s* or l**. *s* or l** (*s* for the short reference duration, and *l* for the long reference duration) differed from trial to trial and were drawn from Gaussian distributions with means equal to *s* and *l*, and some coefficient of variation, *C* (for an illustration of this model, see Delgado & Droit-Volet, 2007). *K* was a multiplier of the short or long reference duration. This *K* value was drawn from a large list of *K* values. Finally, the model assumed that the participant responded "short" when $abs[D(s^*K,t)] < abs[D(l^*K,\ t)]$ and "long" when $D(s^*K,\ t) > D(l^*K,\ t)$.

The same *C* and *K* parameters were used in the generalization model, except that they were applied to one reference duration, *g*. In addition, in the generalization task, a decision parameter was required to fit the individual data correctly. Based on the decisional values found in other studies (e.g., Droit-Volet et al., 2001; McCormack et al., 1999), we decided to set this decisional parameter value to .20 for all the participants (for an illustration of the effect of this parameter in the model, see Droit-Volet et al., 2001). A lower value did not produce significant fits with our data. When $abs[(g^*K) - t)]/t < .20$, then the model assumed that the participant responds "yes".

In the reproduction task, after unsuccessfully testing a series of models related to the complexity of this task, we decided to simply consider that the participant uses the remembered reference duration, *r*, in working memory and responds when he/she judges that the reference duration is ended. The *C* and *K* parameters were thus applied to *r* values (the 7 reference durations) using the previously described procedure (r^*K).

For each task, the model, which was implemented in a computer programme written in Visual Basic 6.0 (Microsoft Corporation), was run for 1000 trials, and *C* and *K* were varied over a wide range to obtain the best-fitting simulation for data from each individual participant in terms of mean absolute deviation (MAD), the sum of the absolute deviations between the predictions of the simulation and the individual data, divided by 7, the number of stimulus durations to be judged (*t*). Table 3 gives the mean individual values of parameters obtained with our modelling, with the mean MAD. The MAD, equal or smaller than 0.10 for each task revealed that our model fitted the data reasonably well, although the fit was poorer for the generalization task than for the other tasks, especially in children.

Analyses of age and task effects on K (reference duration distortion) and C (reference duration variability) parameters

Distortion in temporal reference (K parameter). As illustrated Figure 8, the magnitude of the distortion of reference durations was larger in the temporal reproduction task in terms of shortening for the long durations and of lengthening for the short durations than in the discrimination tasks. An ANOVA

Table 3. *Mean and standard deviation of the K parameter and the C parameter resulting from modelling of individual data for the 5-year-olds, the 8-year-olds and the adults in the temporal bisection, generalization and reproduction tasks for the short and the long duration conditions*

			K		*C*		*MAD*	
Group	*Task*	*Duration condition*	*M*	*SD*	*M*	*SD*	*M*	*SD*
5-year-olds	Bisection	Short	0.95	0.02	0.50	0.04	0.06	0.01
		Long	0.86	0.05	0.70	0.05	0.07	0.01
	Generalization	Short	1.03	0.03	0.35	0.03	0.08	0.01
		Long	0.91	0.03	0.40	0.03	0.09	0.01
	Reproduction	Short	1.65	0.09	0.82	0.03	0.07	0.01
		Long	0.68	0.03	0.78	0.04	0.02	0.01
8-year-olds	Bisection	Short	0.98	0.02	0.49	0.03	0.06	0.01
		Long	0.87	0.05	0.63	0.05	0.07	0.01
	Generalization	Short	1.02	0.03	0.37	0.03	0.08	0.01
		Long	0.92	0.03	0.40	0.03	0.08	0.01
	Reproduction	Short	1.21	0.08	0.80	0.03	0.05	0.01
		Long	0.74	0.03	0.77	0.03	0.02	0.01
Adults	Bisection	Short	0.97	0.02	0.26	0.04	0.01	0.01
		Long	0.98	0.05	0.37	0.05	0.04	0.01
	Generalization	Short	1.05	0.03	0.30	0.03	0.04	0.01
		Long	0.99	0.03	0.32	0.03	0.06	0.01
	Reproduction	Short	1.25	0.09	0.82	0.03	0.04	0.01
		Long	0.83	0.03	0.73	0.04	0.01	0.01

Note: K parameter = reference duration distortion; C parameter = reference duration variability; MAD = mean absolute deviation, the sum of the absolute deviations between the data and the model fit divided by the number of data points. Duration condition: short = 0.4/0.8 s; long = 8/16 s.

was run on the *K* parameter, with task and duration as within-subjects factor and age as between-subjects factor. This ANOVA revealed a significant main effect of task, $F(2, 130) = 10.85$, $p = .0001$. However, there was also a significant 3-way interaction between task, duration and age, $F(4, 130) = 5.83$, $p = .0001$, which subsumed a significant main effect of duration, $F(1, 65) = 209.16$, $p = .0001$, and significant 2-way interactions between task and age, $F(4, 130) = 3.77$, $p = .02$, and task and duration, $F(2, 130) = 68.09$, $p = .0001$. Only the main effect of age did not reach significance, $F(2, 65) = 2.37$, $p = .10$, although age significantly interacted with duration, $F(2, 65) = 14.10$, $p = .0001$.

To examine this significant 3-way interaction, we conducted ANOVAs on the *K* parameter for each age group taken separately. For each age group, there was a significant task × duration interaction [5 years, $F(2, 40) = 31.39$; 8 years, $F(2, 50) = 18.11$; adults, $F(2, 65) = 16.29$, all $p < .001$]. To further analyze our results in terms of a shortening or lengthening of the reference duration for the two ranges of durations, we calculated the difference between *K* and 1 and ran a series of one-sample *t*-tests.

For the long durations, the analyses of this value ($K - 1$) revealed that the reference durations were systematically distorted in the reproduction task in line with a shortening effect [all one-sample *t*-tests[2]: 5 years, −0.31, $t(20) = -11.63$; 8 years, −0.26, $t(25) = -7.01$; adults, −0.17, $t(20) = -5.66$, $p < .05$]. In the generalization task, this shortening effect for the reference durations disappeared in the adults, $t(20) = -0.50$, $p > .05$, but was still observed in the 5-year-old, $t(20) = -2.82$, and 8-year-old children, $t(25) = -3.32$, both $p < .05$. Similarly, the adults remembered the reference durations correctly in the bisection task,

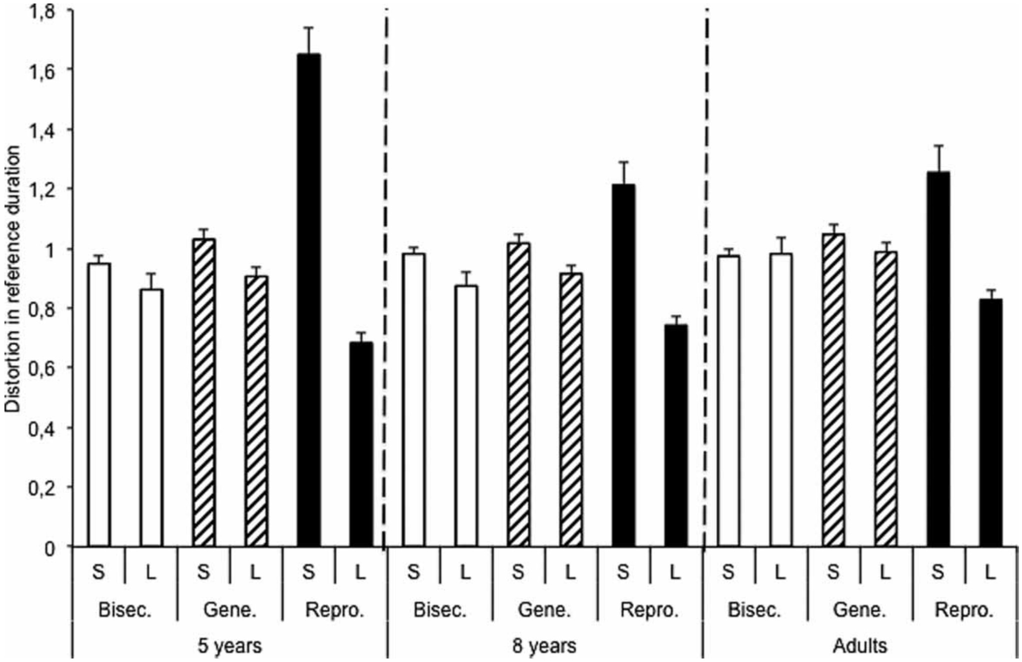

Figure 8. *Reference duration distortion parameter, K, resulting from our modelling of individual data for the 5-year-olds, the 8-year-olds and the adults in the temporal bisection, generalization and reproduction tasks, for the 0.4/0.8 (S) and the 8/16-s (L) duration conditions.*

$t(20) = -0.66$, $p > .05$, whereas the children remembered or tended to remember these durations as being shorter than they actually were at 8 and 5 years of age [$t(25) = -3.18$, $p < .05$; $t(20) = -1.87, p = .07$].

For the short durations, in the reproduction task, the $K - 1$ difference was significantly greater than zero in all age groups, indicating a lengthening rather than a shortening effect on the reference durations [all one-sample t-tests[2]: 5 years, 0.65, $t(20) = 6.22$; 8 years, 0.21, $t(25) = 3.70$; adults, 0.25, $t(20) = 2.71$, $p = .01$]. This lengthening effect was nevertheless greater in the 5-year-old children than in the 2 older age groups (Bonferroni tests, all $p < .05$) for which similar memory distortion values were observed ($p > .05$). Unlike in the reproduction task, for the short durations, no significant distortion of the reference duration was found in any age group in the generalization task, suggesting that both the children and the adults accurately remembered the short reference duration in generalization (all $p > .05$). Similarly, the $K - 1$ difference differed from zero in the bisection task only in the youngest children. In other words, the 8-year-old children and the adults remembered the reference durations correctly in the short condition, whereas the 5-year-olds remembered the reference durations as shorter than they actually were [-0.5, $t(20) = -2.09$, $p = .049$]. However, for the short durations, the magnitude of the temporal memory distortions did not significantly differ between age groups in the two discrimination tasks (all pairwise comparison using the Sheffé tests, $p > .05$), whereas it was greater in the 5-year-olds than in the 8-year-olds and the adults in the reproduction task ($p < .05$), with no difference being observed between these two older age groups.

Variability in temporal reference (C parameter). In the same way as for the results for the distortion parameter, those for the variability parameter, C, revealed important differences between the temporal reproduction task and the other discrimination tasks (Figure 9). The ANOVA run on the *C* parameter, using the factorial design described above, showed a significant main effect of task, $F(2, 130) = 197.80$, $p = .0001$, indicating that the variability in the representation of reference durations was higher in the reproduction task than in the generalization and the bisection task (Bonferroni tests, all $p < .05$). Although not expected, the *C* parameter value was also higher in the bisection task than in the generalization task ($p < .05$). However, there was a significant task × age interaction, $F(4, 130) = 7.72$, $p = .0001$, as well as a significant main effect of age, $F(2, 65) = 17.86$, $p = .0001$, which suggested that the variability in the memory representation of reference durations was lower in the adults than in the children (Scheffé tests, $p < .05$), with no difference being observed between the two groups of children ($p > .05$). No other interaction involving age was significant. For each age group taken separately, the task effect was significant [5 years, $F(2, 40) = 61.20$; 8 years, $F(2, 50) = 45.85$; adults, $F(2, 40) = 161.46$, all $p = .0001$]. This indicated that the proportion of noise in the representation of reference durations was greater in the reproduction task than in the two temporal discrimination tasks (bisection and generalization) in all age groups (Bonferroni tests, $p < .05$). However, the *C* parameter values were similar in the two discrimination tasks for the adults, ($p > .05$), whereas they were higher in the bisection than in the generalization task for the 5-year-olds and for the 8-year-olds ($p < .05$). In sum, the time judgment in the reproduction task resulted in part from the fact that the representation of reference durations was more variable than in the temporal discrimination tasks, although the variability in temporal memory appeared to be higher in the bisection than in the generalization task.

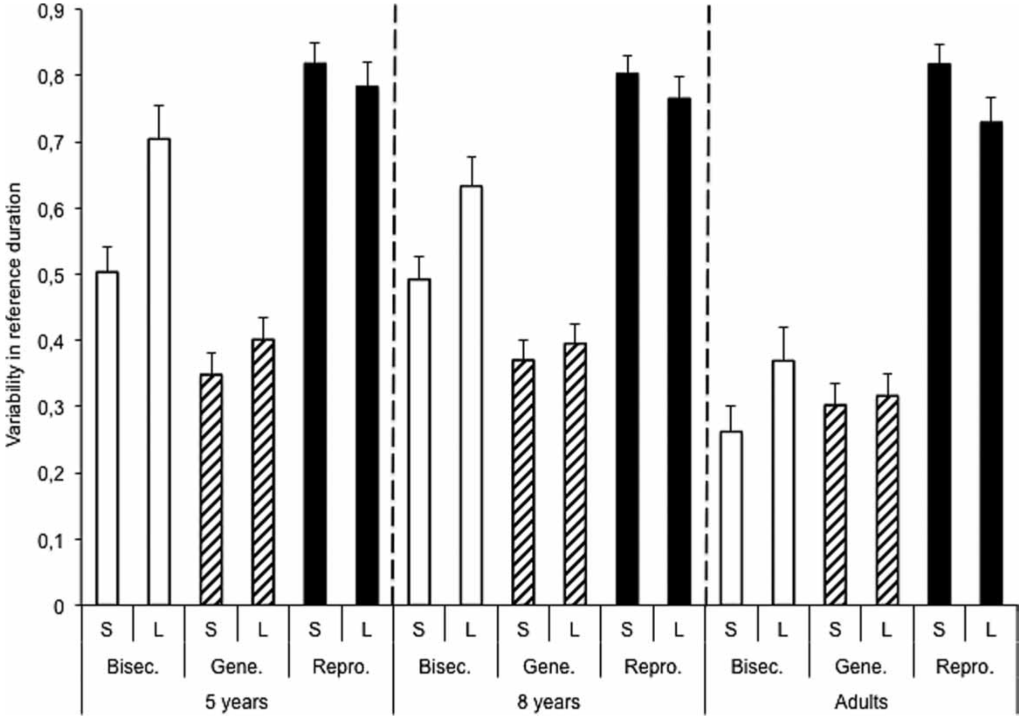

Figure 9. *Reference duration variability parameter, C, resulting from our modelling of individual data for the 5-year-olds, the 8-year-olds and the adults in the temporal bisection, generalization and reproduction tasks, for the 0.4/0.8 (S) and the 8/16-s (L) duration conditions.*

In addition, the overall ANOVA run on the C parameter showed a significant main effect of duration, $F(1, 65) = 8.72$, $p = .004$, and a significant interaction between duration and task, $F(4, 130) = 12.22$, $p = .0001$. This revealed that the memory variability parameter was similar for both the short and the long durations in the generalization task ($p > .05$), whereas it was higher for the long than for the short duration in the bisection task ($p < .05$). At the same time, the C parameter was higher for the short than for the long durations in the reproduction task ($p < .05$).

Moreover, the analyses of correlation between the C and the K parameters for each task taken separately revealed significant correlations between these two parameters, except for the reproduction of short durations (Bisection: Short, $R = -.42$, Long, $R = -.46$, both $p < .01$; Generalization: Short, $R = -.47$, Long, $R = -.42$, $p < .01$; Reproduction: Short, $R = -.13$, $p > .05$, long, $R = -.32$, $p < .01$). These results suggest that the shortening of reference durations was related to "noise" introduced into their representation, as discussed later.

Correlation between K and C parameters and neuropsychological scores

Table 4 shows correlations between the z-scores on the different neuropsychological tests and the memory parameter values resulting from the modelling of our data for bisection, generalization and reproduction. In line with the statistical analyses reported above, we ran hierarchical regression analyses by entering into the equation the significant neuropsychological scores in order to identify which factor was the best predictor of individual variances in these memory parameters.

Distortion in reference memory (K parameter). There was no significant correlation between cognitive abilities and the distortion of reference duration for the short durations in bisection and generalization, with the reference durations being remembered correctly. It was only for the long durations, when a shortening effect occurred for the reference durations, that the K values were significantly correlated with the attention inhibition scores in the bisection task, $R = .27$, $p < .05$, as well as with the working memory, $R = .31$, $p < .05$, and attention concentration scores, $R = .35$, $p < .05$, in the generalization task (Table 4). However, in the generalization task, the best predictor of individual variance in the memory distortion parameter was attention concentration (ß = .34, $R^2 = .12$, $p < .05$). Consequently, the distortion of reference durations decreased as attention inhibition capacities and attention-concentration capacities increased in the bisection and the generalization task, respectively.

Table 4. *Correlations between neuropsychological scores and both the reference duration distortion parameter, K, and the reference duration variability parameter, C, derived from modelling of data for the 0.4/0.8 and the 8/16-s duration conditions*

	Distortion parameter (K)						*Variability parameter (C)*					
	Bisection		*Generalization*		*Reproduction*		*Bisection*		*Generalization*		*Reproduction*	
Neuropsychological scores	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*
Working Memory	.13	.16	−.09	.31*	−.28*	.27*	−.37**	−.46**	−.11	−.11	.03	−.11
Att. Concentration	.13	.14	−.01	$\underline{.34^{**}}$	−.30*	$\underline{.27^{*}}$	−.50**	−.50**	−.14	−.21	−.13	−.08
Selective Attention	−.15	−.11	−.09	−.17	.34**	−.21	.47**	.31*	.25*	.09	.03	.16
Att. Inhibition	−.07	−.27*	−.20	−.25	−.03	−.20	$\underline{.58^{**}}$	$\underline{.53^{**}}$	.20	.28*	.10	.06
Processing Speed	−.16	.07	.02	−.07	$\underline{.37^{**}}$	−.22	.50**	.37**	.02	.05	.04	−.02

Note: Underlined numbers = significant predictors resulting from the hierarchical regression analyses. Neuropsychological scores = z-scores. Duration condition: S (short) = 0.4/0.8 s; L (long) = 8/16 s.
*Significant at .05. **Significant at .01.

As far as the reproduction task is concerned, the scores on several tests assessing different neuropsychological scores were significantly correlated with the memory distortion parameters for both the short and the long durations (Table 4). The hierarchical regression analyses nevertheless revealed that the only reliable predictor of distortions in temporal memory was the information processing speed score in the case of short durations (ß = .37, $R^2 = .14$, $p < .05$), and the attention-concentration score in that of long durations (ß = .27, $R^2 = .07$, $p < .05$), although the variance explained was low. In other words, when the participants had to reproduce short durations, the reproduced reference durations lengthened as information processing speed slowed down. In contrast, when they had to reproduce long durations, the representation of reference durations shortened with decreasing working memory capacities.

Variability in reference duration (C parameter). The correlational analyses (Table 4) and the hierarchical regression analyses with the significant neuropsychological scores entered into the equation revealed that the same factor accounted for inter-individual variance in the memory variability parameter for the bisection and the generalization task, namely the score on the attention inhibition test (Bisection-Short, ß = *.58*, $R^2 = .33$, Bisection-Long, ß = .53, $R^2 = .28$, Generalization-Long, $R = .28$, all $p < .05$), except in the case of the short duration in the generalization task where the only significant correlation found was with the selective attention score, $R = .25$, $p < .05$. However, for the bisection task, the selective attention and working memory scores increased the proportion of variance explained for the short durations ($\Delta =$ 0.5, ß = .63, $p < .05$), and the long durations ($\Delta = 0.7$, ß = .59, $p < .05$), respectively. For reproduction, as discussed below, none of the scores on the neuropsychological tests used in our study accounted for the individual differences in the memory variability parameter.

DISCUSSION

In the present study, children and adults were given 3 different temporal tasks: a temporal bisection, generalization, and reproduction task. The results showed a difference in temporal performance and developmental course between these 3 temporal tasks. Indeed, no age-related effect was observed on the accuracy of temporal judgments for the two temporal discrimination tasks, while the younger children's temporal judgments were less accurate in the reproduction task. In contrast, the variability of time judgment decreased with age in all temporal tasks. The speed of improvement in the sensitivity to time was nevertheless greater in the two discrimination tasks than in the reproduction task, and also greater in the bisection than in the generalization task. As reported in the introduction, temporal performance results from the combination of different cognitive processes related to executive functions (e.g., updating, inhibition) that are required to a greater or lesser extent as a function of the task in question. In our study, by analyzing the correlations between the indices of temporal performance and scores on a wide battery of neuropsychological tests and then modelling our data, we have been able to provide findings allowing us to gain a better understanding of the processes involved in the variations in time judgments as a function of temporal task.

Distortion in the representation of reference durations

As regards the "accuracy" of temporal judgment (BP, Peak Time, Mean Duration), our study revealed age differences in the reproduction task but not in the two discrimination tasks. Indeed, the bisection point and the peak time of the generalization gradient did not significantly vary between age groups in the bisection and the generalization task. The 5-year-old children were thus as accurate as the adults in their temporal judgments in the temporal discrimination tasks. In contrast, there was a general tendency for participants to overestimate short durations and underestimate long durations in the reproduction task, and the magnitude of this temporal over- or underestimation was larger in the younger children. Consequently, the children found it more difficult to make adult-like judgments in the reproduction task than in the other tasks. The modelling of our data suggests that the temporal distortions in reproduction were linked to a distortion of the reference durations (*K* parameter). In addition, the analyses of regressions revealed that this distortion of reference durations was related to young children's limited cognitive capacities, i.e. to their slower speed of information processing in the case of short durations, and to their lower working memory capacities in that of long durations. Consequently, our study with participants of different ages suggested that the representation of reference durations are more distorted (*K* parameter) in the temporal reproduction task than in the other discrimination tasks because the former task is more demanding in terms of cognitive resources, although the processes involved in the reproduction of short and long durations differ, as discussed below.

Independently of the age effect, our modelling of the data also suggested that the cognitive processes involved in the representation of short and long reference durations differed. Indeed, when the durations were short (< 1 s), no temporal distortion was found in the representation of reference durations (*K* parameter) in the temporal discrimination tasks, i.e. either the bisection or the generalization task and only a lengthening effect occurred in the reproduction task. In contrast, when the durations were long (>8 s), a shortening effect occurred in the representation of reference durations in all the temporal tasks, although this was more pronounced in the reproduction task than in the other discrimination tasks. In addition, the predictor of individual differences in the representation of reference durations (*K* parameters) changed as a function of duration, taking the form of the scores on the information processing speed test for the reproduction of short durations and those on the attention-concentration test for the judgment of long durations in all the temporal tasks, with the exception of the bisection task as we discuss later.

For the lengthening of short durations (<1 s) only observed in the temporal reproduction task, the significant role of information processing speed suggests that the young children took longer to implement their motor responses in reproduction, which necessarily affected the value of reproduced durations. In her model of temporal reproduction, Droit-Volet (2010) considered that motor dexterity plays a critical role in the reproduction of short durations of a few hundred miliseconds, when the time required to initiate a motor response is particularly long. Recently, we showed that the durations reproduced by children with poor motor dexterity due to lesions of the cerebellum were longer than those of healthy control children in response to short (<1 s), but not to long durations (<4 s) (Droit-Volet et al., 2013). It is therefore possible that the motor component of temporal reproduction was responsible for the fact that over-estimations of short durations were more frequent in the children than in the adults.

With reference to the shortening of long durations, which was observed in all the temporal tasks, our regression analyses emphasized the critical role of scores on the attention-concentration test for the temporal reproduction and the generalization task. Contrary to what was assumed, the cognitive components related to inhibition or selective attention did not appear to be reliable predictors of shortening effect observed in the reproduction task. Consequently, the children's difficulty in inhibiting their response is not the major cause of their underestimation of time in reproduction. Indeed the attention-concentration test assesses working memory capacities rather than attentional control capacities. It is, however, referred to as attention-concentration because it requires the continuous manipulation and updating of the content of working memory. Our data thus demonstrated that major causes of time distortions for long reference durations (>8 s) were related to individual capacities in the updating and monitoring of reference durations in working memory during time judgments (see also Ogden et al., 2011). The lack of resources in working memory would therefore result in a shortening of the representation of long reference durations. However, our analyses also revealed a significant correlation between the distortion (*K* parameter) and the variability (*C* parameter) of reference durations. It is therefore likely that a poor working memory capacity results in fuzzier representations of reference durations, that in turn produces a shortening effect. In the case of the reproduction of long durations, when the children have fuzzier (noisier) representation of reference durations, they necessary terminate their reproduction more quickly, because the duration of reproduced durations reaches the point of subjective equality more quickly (Riemer, Trojan, Kleinböhl, & Hölzl, 2012). As explained further later, our model thus suggests that the major parameter of age-related differences in time judgment is a mis-representation of reference durations.

For the bisection task, surprisingly enough, the shortening of long reference durations (8/16-s duration condition) was not significantly correlated with scores on the working memory tests, as was the case for the reproduction and the generalization task, but with those on attention inhibition. A similar correlation was also found in bisection between attention-inhibition and the variability of time judgment (i.e., *C* parameter). The attention inhibition test (Stroop test) assesses the deliberate suppression of automatic or prepotent responses (Miyake & Shah, 1999; Miyake et al., 2000). In bisection, we can suppose that the prepotent response is the verbal response "short". The "short" response is indeed activated in working memory before the "long" response. Individuals perceive a short duration before they realize that it is a long one. Using a partition task without reference durations, Droit-Volet and Rattat (2007) showed that children do indeed tend to respond "short" in a bisection task more often than adults do. The difficulties children experience in inhibiting the automatically activated "short" response could thus go some way to explaining the shortening effect observed in bisection. Finally, this suggests that the nature of the verbal response required in a temporal task (temporal categorization strategy) should also interfere with the representation of durations in memory. However, our bisection model does not take account of decision processes, unlike other models of temporal bisection (Wearden & Jones, 2013) that assume that there is a tendency to respond "long" more often in ambiguous cases, i.e. when $D(s^*, t)$ is close to $D(l^*, t)$. In fact, it is difficult to dissociate memory and decision processes in bisection because they both produce a shifting of the BP in the same direction (left-shifting). However, this shifting of the BP is greater for distortions of temporal memory than for biases in decision processes (see Delgado & Droit-Volet, 2007). It is nevertheless possible that the decision to respond "short" or "long" might be, in part, related to this capacity to inhibit the "short" response. In this case, taking account of decision processes in our model would have perhaps produced a better fit of our model to our individual participant data, but to the detriment of a good between-task comparison.

Variability of time judgment

Unlike the results on the accuracy of temporal judgment (BP, Peak Time, Mean Duration), which demonstrated that the age effect varied as a function of the temporal task and the duration used, those on the variability of time judgment (WR, FWHM/Peak Time, SD/Mean) revealed a general effect of age irrespective of temporal task and duration. Our study using a within-subject factorial design thus provides convincing evidence of an improvement in time sensitivity during childhood on all temporal tasks. However, our results also showed different patterns of age-related improvement in time sensitivity as a function of the type of temporal task used. In the reproduction task, there was a systematic improvement in time sensitivity between ages, i.e. from 5 to 8 years and from 8 years to adulthood. In the bisection task, a difference in time sensitivity was observed between 5 and 8 years, whereas the older children reached a level of performance similar to that of adults. In the generalization task, the age differences in sensitivity to time were somewhat less clear since the temporal gradients were particularly flat in the 5-year-olds and the 8-year-olds. In this case, it is likely that the lack of an age-related difference was due to the older children's poorer performance in the generalization task. Consequently, the results showed that the 8-year-olds exhibited similar levels of temporal sensitivity to those found in younger children. Overall, these findings indicate that age-related differences in time sensitivity are smaller in the two discrimination tasks than in the reproduction task, and are probably smaller in bisection than in generalization.

Our model confirmed that the variability of the representation of reference durations (C parameter) was higher in the reproduction task than in the two discrimination tasks. However, no score on the different neuropsychological tests explained individual differences in the C parameter values (Table 4), except for attention inhibition in the bisection and the generalization tasks. In contrast, scores on numerous neuropsychological tests were significantly correlated with the indices of variability of time judgment (i.e., WR, FWHM, SD) in the 3 temporal tasks. Consequently, we can argue that this reveals that the major source of individual differences in the variability of time judgment does not lie in the representation of reference durations, but rather in the encoding of time. In their model, McCormack et al. (1999) introduced a parameter representing the amount of "noise" added to the perceived duration and achieved a good fit with their data by revealing a higher proportion of noise in perceived time in children than in adults. By manipulating variability in the sample durations used as references in a bisection task, Delgado and Droit-Volet (2007) also demonstrated that the source of noise in temporal reference memory, as measured by the C parameter, derives from initial noise introduced during the encoding of time.

In our models, we have implicitly considered that the encoding of time is similar in the 3 temporal tasks. Consequently, contrary to our initial hypothesis, variations in the encoding of time would occur as a function of the temporal task used. Our regression analyses, conducted with the different indices of time sensitivity (WR, FWHM, SD) (Table 2), showed that the attention-concentration scores were the best predictors of individual differences in sensitivity to time (WR) in the temporal bisection task (also see Zélanti & Droit-Volet, 2011). In the generalization task (FWHM) the best predictor was selective attention, and in the reproduction task (SD) both working memory and information processing speed fulfilled this role. The relationships between information processing speed, working memory and attention are difficult to understand because none of these cognitive dimensions represents a uniform set of processes (Fougnie, 2008). This is the major problem that is often discussed in the literature on executive functions (Brown et al., 2012; Packwood, Hodgetts, & Trembaly, 2011). Nevertheless, models of the development of intelligence suggest that cognitive development results from a cascade of related processes in which age-related changes in the speed of information processing play a critical role (Camos & Barouillet, 2014; Case, 1985; Demetriou, Mouyi, & Spanoudis, 2008; Fry & Hale, 1996). According to Demetriou et al. (2008), the changes in information processing speed would be "followed in time" by changes in working memory and, later, by changes in selective attention.

Finally, our study suggests that the improvement in time sensitivity in the reproduction task required the development of greater cognitive abilities than were required for the bisection and generalization tasks. Individual differences in time sensitivity were indeed linked to the development of both information processing speed and working memory capacities in the reproduction task, while they were linked only to working memory or to selective attention in the case of the bisection and the generalization tasks, respectively. Since the encoding of current durations is theoretically similar for these two discrimination tasks, this suggests that the nature of the required judgment (e.g., identity or categorization judgment) influences the encoding of time. A judgment of identity between current durations and a reference duration would therefore be more cognitively demanding than a judgment categorizing current durations as either short or long. Indeed, some bisection studies have demonstrated that participants are able to categorize current durations as short or long without the initial presentation of two anchor reference durations (Jones & McAuley, 2005; Killeen, Fetterman, & Bizo, 1997; Wearden & Ferrara, 1995, 1996).

In conclusion, our study, conducted with both children and adults, provides evidence that the age-related differences in explicit time judgments depend on the cognitive demands imposed by the temporal task used. Our study thus demonstrated that age-related differences in time judgment are greater in a reproduction task than in a temporal discrimination task, because this task is more demanding in terms of working memory and information processing speed. At the same time, we found that the bisection task was easier for the children than the generalization task in terms of time judgment, whereas these tasks were similar for the adults. Temporal performance in the bisection task was associated with a greater variability in the representation of durations in reference memory than was the case in the generalization task. However, this latter task required more attention to be paid to the processing of current durations in order to judge the similarity between these durations and the reference duration. In conclusion, our study suggests that it is better to use a temporal bisection than a generalization task in children, whereas these tasks are equivalent for adults. Whatever the case, researchers should avoid using the complex task of temporal reproduction for all ages, and more particularly in participants with limited cognitive resources and motor dexterity for the short durations.

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The conscious awareness of time distortions regulates the effect of emotion on the perception of time

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This study examined how the awareness of emotion-related time distortions modifies the effect of emotion on time perception. Before performing a temporal bisection task with stimulus durations presented in the form of neutral or emotional facial expressions (angry, disgusted and ashamed faces), some of the participants read a scientific text providing either correct or incorrect information on the emotion–time relationship. Other participants did not receive any information. The results showed that the declarative knowledge allowed the participants to regulate (decrease) the intensity of emotional effects on the perception of time, but did not trigger temporal effects when the emotional stimuli did not automatically induce emotional reactions that distorted time.

1. Introduction

The last decade has seen a huge growth in research into the effect of emotions on the perception of time, and especially that of the emotional facial expressions currently used for measuring people's emotions (for a recent review, see Droit-Volet, Fayolle, Lamotte, & Gil, 2013). Most of the studies that have used facial expressions as emotional stimuli have employed the temporal bisection task (e.g., Doi & Shinohara, 2009; Droit-Volet, Brunot, & Niedenthal, 2004; Gil, Niedenthal, & Droit-Volet, 2007; Tipples, 2008, 2011). In this task, participants are trained to recognize a short and a long standard duration. They are then presented with comparison durations, including the two standards and intermediate stimulus durations. Their task is to judge whether these comparison durations are more similar to the short or the long anchor duration. However, in studies involving emotions, the standard durations are presented in the form of a neutral stimulus (pink oval), while the comparison durations are presented as emotional stimuli, namely faces expressing different emotions. The results systematically show that the bisection functions shift toward the left, with a lowering of the bisection point (BP) (i.e., point of subjective equality), for faces expressing high-arousal emotions (i.e., anger, fear) compared to neutral faces, with the result that participants respond long more often for emotional facial expressions than for neutral expressions, even though both are presented for the same duration. Consequently, the perception of negative high-arousal emotional stimuli has been demonstrated to produce distortions in time judgment consistent with a lengthening effect.

This lengthening effect has been explained in terms of the perception of negative high-arousal emotional stimuli, which increases the level of activation of the central nervous system and thus causes a speeding up of the internal clock system underlying the representation of time. According to the internal clock models, which are the models most frequently invoked

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in order to account for behavioral data (Gibbon, 1977; Gibbon, Church, & Meck, 1984; Treisman, 1963), the subjective measurement of durations depends on the number of pulses emitted by a pacemaker-like clock system and accumulated during the stimulus duration to be timed. When the clock runs faster, more pulses are accumulated and time is judged to last longer. The speeding-up of the internal clock system in threatening conditions would result from an automatic survival mechanism which prepares the organism to act as quickly as possible when confronted with a potential danger, e.g. to attack or flee when faced with an aggressive person (Droit-Volet & Meck, 2007). Indeed, there is ample evidence that threatening situations automatically trigger innate defense responses in both humans and animals (LeDoux, 1998, 2000). In threatening conditions, individuals are therefore ready to act quickly because their internal clock runs faster and they experience the passage of time as lasting longer than normal. However, human time judgments in an emotional context cannot be reduced to an automatic process of action readiness. As suggested by theories of the appraisal of emotion, the behavioral expression of emotions also depends on people's cognitive appraisal of their emotional state and of the events that have induced this emotional state (Lazarus, 1991; Scherer, 2001). Introspective awareness of an emotional reaction that is too intense for a given situation can, for example, lead individuals to reduce the behavioral expression of emotion (Sanders & Scherer, 2009).

The aim of the present study was to examine how the declarative knowledge of emotion-related time distortions modulates the effect of emotional stimuli on time perception. No study of the role of individual awareness of emotion-related time distortions has investigated the effect of emotion on the judgment of time. However, a recent study has examined how subjects' awareness of the fluctuation of the passage of time in their everyday lives affects their time judgments in a laboratory situation (Lamotte, Izaute, & Droit-Volet, 2012). In this study, the participants were required to estimate stimulus durations in a single temporal task and a dual-task in which they had to process both temporal and non-temporal information. The results replicated those found in numerous studies and showed that the stimulus durations were judged shorter in the dual-task than in the single temporal task (e.g., Coull, Vidal, Nazarian, & Macar, 2004; Fortin, Rousseau, Bourque, & Kirouac, 1993; Macar, Grondin, & Casini, 1994). However, the extent of this shortening effect was smaller in the participants who were more conscious of being subject to time distortions in their everyday lives. In this study, the degree of consciousness was assessed through subjects' responses to the statement "the more I focus attention on time, the slower time goes". The results thus revealed a significant correlation between agreement with this statement and temporal accuracy: The more the participants agreed with the statement, the smaller the distortion of their time judgments in the dual-task was. Based on metacognitive studies, the authors argued that the participants' individual knowledge of time distortion caused them to monitor the attentional resources they allocated to time processing. The participants thus developed a cognitive control strategy allowing them to compensate for their tendency to shorten time when they performed a secondary non-temporal task. In conclusion, people's individual consciousness of their temporal abilities also contributes to their time judgments.

In the emotion-related domain, no studies have investigated the effect of individual knowledge on the perception of time. Using an extensive series of questions, Lamotte, Chakroun, Droit-Volet, and Izaute (2014) assessed individuals' explicit knowledge and beliefs about factors that may affect how time is perceived. Factorial analyses allowed the authors to extract two discriminant factors: one related to attention and the other to emotion. However, as far as emotion was concerned, there was individual variability in the consciousness of time distortions in the presence of happiness and sadness, but not in response to the high-arousal emotions of anger or fear, even though these emotions have a considerable impact on time perception. As reported above, this may be due to the temporal effects produced by these basic emotions, which derive directly from automatic unconscious mechanisms. Consequently, to examine the effect of individual knowledge of emotion-related time distortions, we decided to compare angry faces and neutral faces, and to manipulate the knowledge provided to the participants before they performed the temporal bisection task. To do this, we provided some of the participants with a text which they had to read before performing the temporal task and which contained either correct or incorrect information about the effect of emotion on time perception. More specifically, the text stated that the perception of an angry face produces a lengthening of time (true information) or a shortening of time (false information) compared to that of a neutral face. Certain other participants did not receive any information. Our hypothesis was that declarative knowledge of emotion-related time distortion would modulate the basic effects of emotional stimuli on the perception of time in bisection.

2. Experiment 1

2.1. Method

2.1.1. Participants

Fifty-two women students ($M = 19.35$, $SD = 1.37$) from Blaise Pascal University (Clermont-Ferrand, France) took part in this study in return for course credits after signing a consent form to participate in the experiment.

2.1.2. Materials

The participants were tested individually in a quiet room in the laboratory of the Psychology department. They were seated in front of a PC computer that controlled the experiment and recorded the data via an E-prime program (1.2. Psychology Software Tools, Pittsburgh, PA). They gave their responses by pressing the *D* ("*Short*") and *K* ("*Long*") keys on the computer keyboard and the button-press assignment was counterbalanced across subjects. The stimuli to be timed were an oval with a mottled texture (white, gray, black) in the training phase and the faces of 3 different women in the testing

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phase, all presented at the center of the computer screen against a black background. These faces were taken from a validated set of facial expressions (Ekman & Friesen, 1976). Two emotional expressions were used: an intense expression of anger and a neutral expression.

2.1.3. Procedure

Participants were randomly assigned to one of the 3 groups as a function of the information received before performing the temporal bisection task: true information, no information, and false information. In the true information group, a text informed participants that, according to time research, angry faces cause a subjective lengthening of time in humans, with the result that the presentation time of angry faces tends to be overestimated compared to that of neutral faces. In the false information group, the text wrongly informed the participants that angry faces cause a subjective shortening of time, with the result that the presentation time of angry faces tends to be underestimated compared to that of neutral faces. In the no-information group, the participants did not read any text before the temporal bisection task.

In all the experimental groups, the participants were given a temporal bisection task consisting of a training and a testing phase. In the training phase, the short (400-ms) and the long (1600-ms) standard duration was presented five times each, in a random order, in the form of an oval and the participants were trained to press the corresponding button on the keyboard to respond "*Short*" or "*Long*". In the testing phase, they were presented with 7 comparison durations which took the form of facial expressions. Two of these were identical to the short and the long standard (400, 1600-ms) and five had intermediate values (600, 800, 1000, 1200 and 1400-ms). The participants had to judge whether these comparison durations were more similar to the short or to the long standard duration. Each participant was given 126 trials, i.e. 9 trials for each of the 2 emotional expressions (neutral *vs.* anger) for the 7 comparison durations. The 9 trials consisted of 3 trials for the 3 different women. The trials were randomly presented within each block of 42 trials (3 women × 2 emotions × 7 durations) and the inter-trial interval was between 1 and 2 s.

In addition, after the bisection task, the participants assessed the arousal level of the angry and neutral expressions of the 3 different female faces using the 9-point scale of the Self-Assessment Manikin (SAM) (Lang, Bradley, & Cuthbert, 2008). The presentation duration of the facial expressions was at the mid-point between the short and the long standard durations, i.e. 600 ms. In each group, the participants therefore rated 6 different emotional stimuli presented in a random order (3 faces × 2 emotions).

2.2. Results

Fig. 1 shows the proportion of "long" responses (p(long)) plotted against the comparison durations for the neutral and the angry facial expressions in the 3 information groups (true information, no-information and false information). An examination of Fig. 1 shows that the psychophysical functions were shifted toward the left, consistent with a lengthening effect, for the angry faces compared to the neutral faces, except in the false information group. This finding was confirmed by the statistical analyses run on the Bisection Point (BP). Statistical analyses were initially run on p(long) but are not reported because they provided results similar to those obtained for the BP. The BP is the point of subjective equality at which the stimulus duration is judged long as often as it is short ($p(\text{long}) = .50$). This temporal parameter was derived from the significant fit of the individual data with the pseudo-logistic function which provided good fits for the bisection data in the different conditions. A second parameter, the Weber Ratio (WR), was also calculated. This is the difference limen ($(D(p(\text{long}) = .75) - D(p(\text{long}) = .25))/2$, divided by the BP. It is an index of time sensitivity: The lower the WR, the steeper the psychophysical function and the higher the sensitivity to time.

However, the statistical analyses on the WR (Table 1) did not reveal any significant effect (all $p > .05$). In line with the results of numerous studies of emotions (for reviews, see Droit-Volet, 2013; Droit-Volet et al., 2013), this indicated that the perception of emotional facial expressions did not change the sensitivity to time. In contrast, the ANOVA run on the BP with faces as within-subjects factor and information as between-subject factor revealed a significant main effect of faces, $F(1,49) = 4.58$, $p = .04$, $\eta^2_P = .09$, while the main effect of information, $F(2, 49) = 0.45$, $p = .64$, and the faces × information interaction, $F(2,49) = 1.89$, $p = .16$, did not reach significance. This suggests that the BP was systematically lower for the angry than for the neutral faces. The emotion-related lengthening effect on the perception of time thus tended to emerge with the omnibus analysis of variance using 3 information conditions whose 2 conditions with lengthening-based instructions. However, as suggested by several researchers in statistics (Furr & Rosenthal, 2003; Judd, 2000; Rosenthal & Rosnow, 1985), in order to evaluate our theoretical predictions efficiently (a priori hypothesis), we decided to run a one-way ANOVA on PB for each information groups taken separately. The analyses revealed that the difference in the BP between the neutral and the emotional faces, $F(1,17) = 5.55$, $p = .03$, $\eta^2_P = .25$, was significant in the no-information and the true information conditions, $F(1,16) = 8.31$, $p = .01$, $\eta^2_P = .34$. Nevertheless, the differences in the BP between the neutral and the emotional faces did not reach significance between these two conditions, although the leftward shift of the bisection function seemed to be greater in the true information than in the no-information condition ($p > .05$). In addition, in the false condition, in which the participants received incorrect information about the effect of emotion on time perception, the significant difference in the BP between the neutral and the angry faces was no longer observed, $F(1,16) = 0.07$, $p = .81$.

The ANOVA on the subjective assessment of the arousal level (Self-Assessment Manikin) induced by the perception of faces confirmed a significant main effect of faces (Angry faces: $M = 5.54$, $SE = .25$; Neutral faces: $M = 2.56$, $SE = .16$, $F(1,48) = 114.87$, $p = .0001$, $\eta^2_P = .71$), whereas the effect of information and the information x faces interaction failed to reach

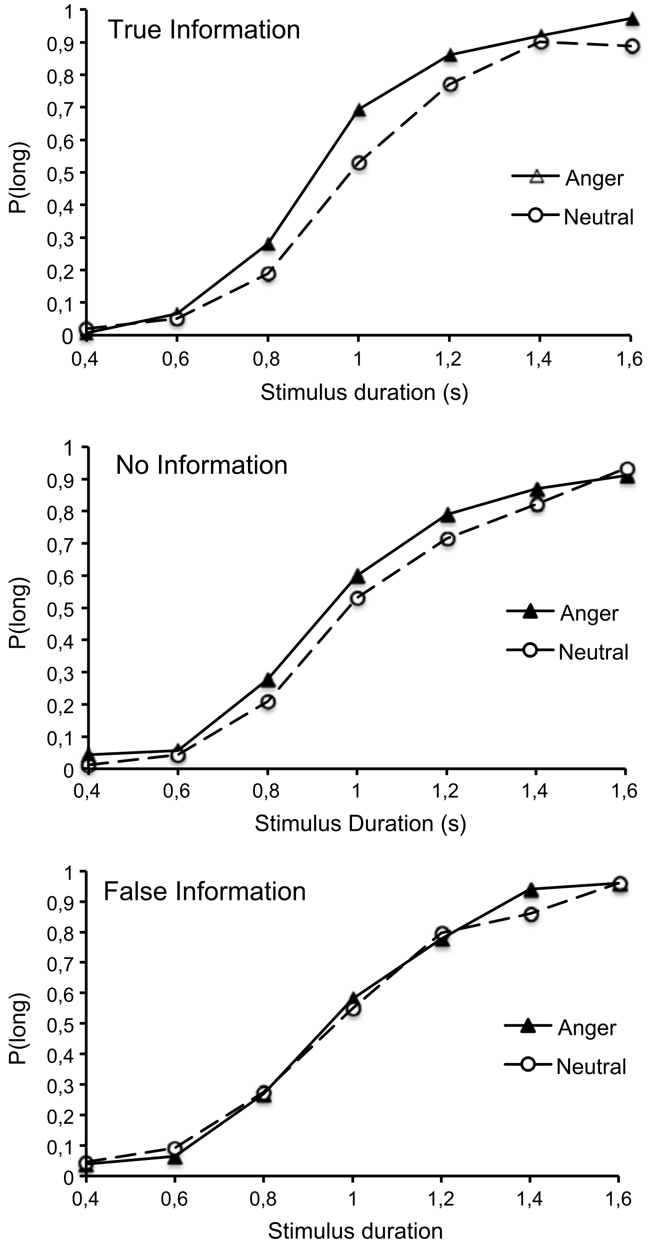

Fig. 1. Proportion of long responses (*p*(*long*)) plotted against stimulus durations (s) for the angry and the neutral facial expressions when the participants received true information, no-information or false information.

significance (all $p > .05$). Consequently, in each information condition, the angry faces were always judged to be more arousing than the neutral faces.

In summary, the results of Experiment 1 suggest that the effect of emotional faces (angry faces) on the perception of time tended to emerge in all experimental conditions. However, when the participants received information that contradicted observed behavior, the emotional effect did not reach significance. The false information thus suppressed/reduced the time distortion initially induced by the emotional stimuli. Our results also suggest that this knowledge is not in itself capable of producing a time distortion in bisection. Indeed, the incorrect information did not produce a temporal effect on time judgment in the opposite direction (shortening) to that originally observed in the no-information condition. Although the participants received information indicating that the perception of angry faces produces a shortening effect, they did not judge the period of presentation of the angry faces to be shorter than that of the neutral faces. Consequently, explicit information about the nature of the emotional effect on time perception seems to modulate the basic emotional effect on time judgment, rather than produce an effect by itself. In order to verify the role of false information in time judgments, we decided to conduct a second experiment examining the effect of different types of false information on the time judgment of faces expressing different emotions: namely anger, disgust and shame. As confirmed by Experiment 1, the facial

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Table 1
Mean and standard error of bisection points and Weber ratios for the neutral and anger faces in the groups receiving true information, no-information and false information.

	Bisection point		Weber ratio	
	M	SE	*M*	SE
True information				
Neutral	975	43.25	0.17	0.11
Anger	903	40.61	0.14	0.06
No-information				
Neutral	1014	42.03	0.17	0.12
Anger	953	39.47	0.18	0.11
False information				
Neutral	934	43.25	0.19	0.16
Anger	945	40.61	0.16	0.09

expression of anger produces a lengthening effect in the no-information context. Some studies have found that, in contrast to the expression of anger, the perception of disgusted and ashamed faces did not produce lengthening effects on the perception of time in bisection (Droit-Volet & Meck, 2007; Gil & Droit-Volet, 2011a,b). Consequently, in order to examine whether explicit information can produce a temporal effect that is not dependent on the task (emotional context), two opposing types of false information were given to the participants. For the angry and the disgusted faces judged as arousing, the participants were informed that the perception of angry/disgusted faces shortens time estimates (shortening effect), and, for the ashamed faces judged as non-arousing, that the perception of shameful faces lengthens time estimates (lengthening effect). Our hypotheses was that the false information would only have a significant effect on time judgment when the perception of emotional faces originally produced a time distortion in the no-information condition, i.e., in the case of the angry faces but not the disgusted and the ashamed faces.

3. Experiment 2

3.1. Participants

One hundred and nineteen new female students ($M = 19.77$, $SD = 1.52$) from Blaise Pascal University participated in this experiment in return for a course credit.

3.1.1. Material and procedure

The material and the procedure were the same as those used in Experiment 1, except for the emotional material to be timed which took the form of faces expressing 4 different emotions: anger, disgust, shame and a neutral emotion. The angry and disgusted faces were selected from Ekman's battery (Ekman & Friesen, 1976) and the ashamed faces from that compiled by Beaupré and Hess (2005) as also used in Gil and Droit-Volet's study (2011b). The participants were assigned to the angry ($N = 40$), the disgust ($N = 39$) or the shame ($N = 40$) group. In each group, there were two sub-groups of participants that differed as a function of the information received (false information *vs.* no-information). In the false information group, the text incorrectly informed the participants that ashamed/disgusted/angry faces cause a subjective lengthening/shortening/shortening of time, so that ashamed/disgusted/angry faces tend to be overestimated/underestimated/ underestimated compared to neutral faces. In the no-information groups, the participants did not read any text before performing the temporal bisection task.

3.2. Results

Fig. 2 shows the bisection functions for the anger, disgust and shame groups when the participants received no information or false information. Overall Analyses of Variance were performed on BP and WR with two between-subjects factor (emotional group, information group) and one within-subjects factor (emotional faces *vs.* neutral faces). The BP and WR were derived from the significant fits of individual data obtained with the pseudo-logistic function (Table 2). As in Experiment 1, the analyses on WR did not show any significant effect (all $p > .05$), suggesting that sensitivity to time remained constant in the different experimental conditions. More interestingly, the ANOVA on BP revealed a 3-way interaction between emotional group, information group and faces, $F(2,113) = 5.58$, $p = .005$, $\eta^2_P = .09$, with a significant main effect of faces, $F(1,113) = 6.55$, $p = .01$, $\eta^2_P = .06$. Subsequently, an ANOVA was run on BP for each emotional group taken separately. For the anger group, there was a significant main effect of faces, $F(1,38) = 9.98$, $p = .003$, $\eta^2_P = .21$, and a significant faces × information interaction, $F(1,38) = 12.25$, $p = .001$, $\eta^2_P = .24$, with the main effect of information being non-significant ($p > .05$). This interaction indicated that the difference in the BPs between the angry and the neutral faces was significant in the no-information group, $t(19) = 5.98$, $p = .001$, whereas it did not reach significance in the false information group, $t(19) = 0.21$, $p = .84$. Unlike the anger group, for the disgust group and the shame group there were no significant main effects of faces ($F(1,37) = .39$,

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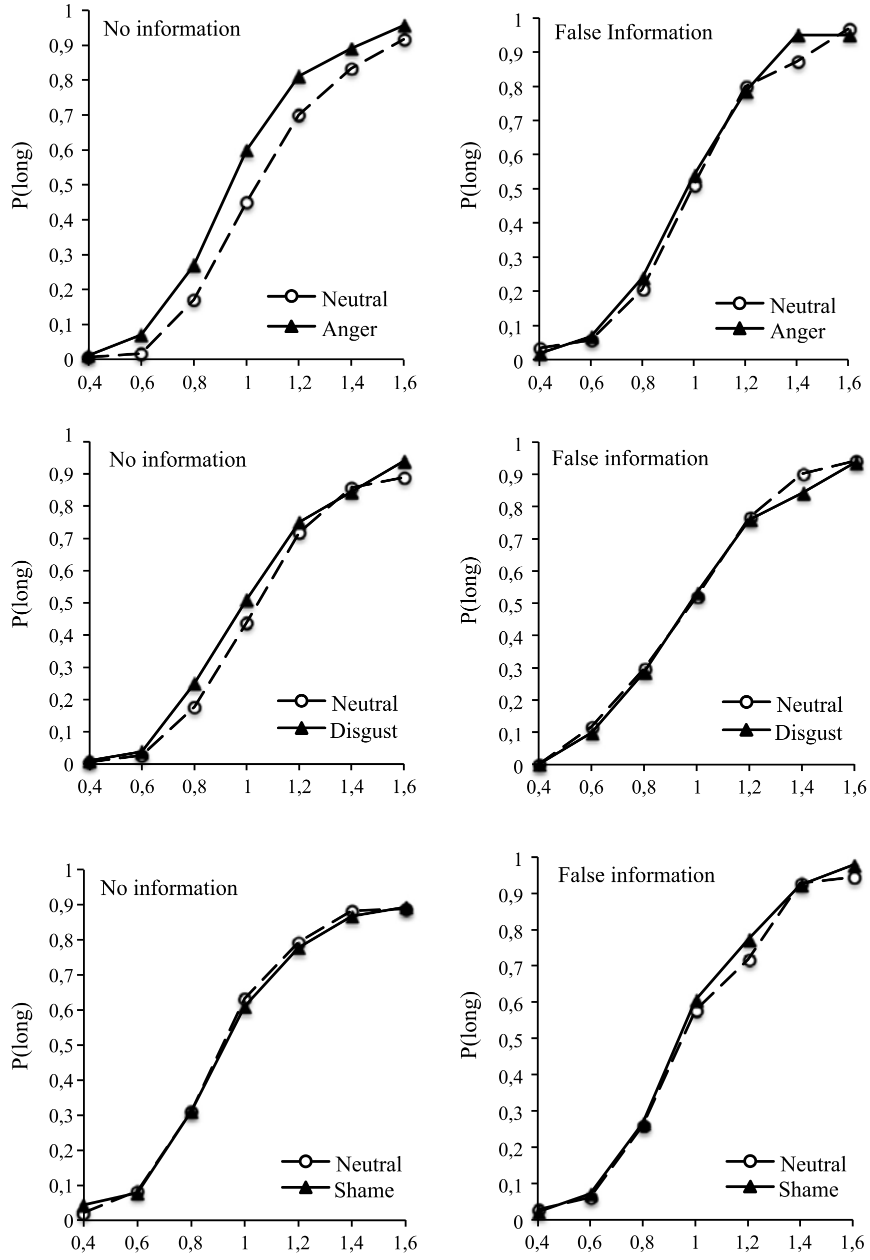

Fig. 2. Proportion of long responses ($p(long)$) plotted against stimulus durations (s) for the neutral and the emotional facial expressions (anger, disgust and shame) when the participants received no information or false information.

$F(1,38) = .64$, respectively) or information group ($F(1,37) = .99$, $F(1,38) = .25$), and no significant interaction involving these two factors ($F(1,37) = .74$, $F(1,38) = 2.87$) (all, $p > .05$).

The ANOVA on the self-assessment Manikin scores for arousal with the faces and the information as factors showed that the participants judged the disgusted faces to be more arousing than the neutral faces (5.02 *vs.* 2.95), regardless of information condition (only a significant main effect of faces, $F(1,37) = 39.19$, $p = .0001$ $\eta^2_p = .52$), whereas the ashamed faces were judged to be as low arousing as the neutral faces (3.43 *vs.* 3.23) (all effects, $p > .05$). To summarize, the results of Experiment 2 confirmed that explicit information that described an erroneous relationship between time and emotion reduced the temporal effect that was automatically produced by emotional faces in the no-information condition (anger groups), but was not powerful enough to produce either a shortening or lengthening temporal effect when no emotional effect was originally observed in the no-information condition (disgust and shame groups).

4. General discussion

The present study examined how declarative knowledge modulates the effect of emotional stimuli (facial expression) on time judgments in a bisection task. First of all, the results found in the no-information groups replicated those found in

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Table 2
Mean and standard error of bisection points and Weber ratios in the anger, the disgust and the shame condition for the neutral and emotional faces in the no-information and the false information group.

	Bisection point		Weber ratio	
	M	SE	*M*	SE
Condition: Neutral-anger				
No-information				
Neutral	1063	38.2	0.17	0.02
Anger	923	38.6	0.18	0.02
False information				
Neutral	1010	38.2	0.17	0.02
Anger	1017	38.6	0.13	0.02
Condition: Neutral-disgust				
No-information				
Neutral	1024	34.2	0.16	0.01
Disgust	985	42.8	0.17	0.02
False information				
Neutral	953	35.0	0.19	0.02
Disgust	959	43.9	0.21	0.02
Condition: Neutral-shame				
No-information				
Neutral	921	36.7	0.20	0.02
Shame	936	38.1	0.22	0.03
False information				
Neutral	974	36.7	0.16	0.02
Shame	932	38.1	0.15	0.03

numerous studies showing a lengthening of perceived durations in response to negative high-arousal emotional stimuli compared to neutral stimuli. Indeed, the psychophysical function in bisection was shifted toward the left and the BP was significantly lower for the angry faces than for the neutral faces. Even though emotional reactions are always a difficult material to work with (Fayolle & Droit-Volet, 2014), this finding indicates that the distortion of time in response to the effect of a high-arousal emotion is robust.

More interestingly, our results revealed the important role played by declarative knowledge in the effect of emotional stimuli on the judgment of time. Indeed, when the participants were told either that the perception of angry faces produces a lengthening effect (true information) or that it leads to a shortening effect (false information), the effects of corresponding facial expression on the judgment of time were amplified and reduced, respectively. Nevertheless, in our study, the down-regulation of emotional effects on time perception seemed to be more significant than their up-regulation. As expected, our results were thus entirely consistent with the appraisal theories of emotion, which hold that an individual's focus on affect and/or emotional context may change his or her expression of emotion (for a review, see Grandjean & Scherer, 2009). However, our results also demonstrated that the declarative knowledge modulated, i.e. reduced, the emotional effects on the perception of time, but did not trigger a temporal effect. Indeed, in Experiment 1, the false information about a shortening effect reduced the lengthening effect originally observed in the no-information condition, with the result that the significant temporal difference between the angry and the neutral faces was no longer observed. However, this false information did not lead to a shortening effect consistent with the description of emotion–time relationships presented in the information text seen by the participants. Similarly, in Experiment 2, the false information about a shortening effect in the case of disgusted faces and a lengthening effect in the case of ashamed faces did not result in any effect, either shortening or lengthening, on time judgments. In particular, in the no-information group, these emotional facial expressions did not spontaneously induce an emotional reaction that significantly altered the judgment of time in bisection (see also, Droit-Volet & Meck, 2007; Gil & Droit-Volet, 2011a,b). To summarize, when emotional effects automatically occurred in response to emotional stimuli (angry faces), knowledge modified the intensity of this effect on the perception of time. However, when emotional effects did not automatically occur in response to emotion stimuli, the declarative knowledge did not cause this effect to emerge. Consequently, our study demonstrates that declarative knowledge seems to regulate rather than trigger the effects of emotional stimuli on time judgment. In other words, emotional knowledge inhibits and, to a lesser extent, enhances the emotional effects on the perception of time, but is not in itself able to generate a temporal effect. Overall, our results are consistent with appraisal models of emotion that argue that although emotions are triggered by emotional stimuli, cognitive appraisal nevertheless permits a certain flexibility in emotional responses (Grandjean & Scherer, 2009). As explained by Scherer (2001), the role of conscious processes lies in the cognitive regulation of emotion.

We can thus assume that the internal clock system speeds up automatically in response to the perception of threatening stimuli (Droit-Volet et al., 2013). However, the question that can be raised now is: at what level of time processing does cognitive regulation act to modify the distortion of time triggered by emotion? Fig. 3 illustrates different hypotheses. In his attentional theory, Zakay (1992) referred to the level of relevance and importance of time in a given context. His idea is that the level of temporal relevance will increase the level of temporal awareness which should, in turn, modify the amount of

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attention devoted to time. This interpretation therefore supports the idea that temporal awareness acts as an attentional control. If this is indeed the case, we can assume that participants pay less attention to emotional stimuli that are considered as less relevant. This is the case, for example, of an angry friend whose anger has less of an effect on you when you consider him or her to be completely hysterical. The significance of his/her anger in terms of behavior is thus reduced. A first hypothesis (panel 1, Fig. 3) is therefore that participants divert attention away from the emotional stimuli and try, for example, to ignore their hysterical friend. According to the internal clock models, attention acts at an early stage of time processing via an attentional gate mechanism or an attention-controlled switch that connects the pacemaker-like system to the accumulator (Lejeune, 1998; Thomas & Weaver, 1975; Zakay & Block, 1996, 1998). Following this line of argument, Lamotte et al. (2012) explained that participants' knowledge of their subjective time distortions leads them to use attention monitoring strategies that reduce these time distortions in an experimental context. We can therefore assume that, when people allocate fewer attentional resources to emotional stimuli that are considered as less significant, the attentional gate between the pacemaker and the accumulator is less open and that the number of pulses entering the accumulator is therefore reduced.

However, the control of attention can also act at a later stage of time processing, i.e. not before but after the accumulator. The volume of pulses produced by an automatic acceleration of the internal clock rate in a threatening situation could thus automatically enter the accumulator (Droit-Volet, 2013). The second hypothesis (panel 2, Fig. 3) is therefore that the control of attention consists in inhibiting, or erasing, in memory the temporal content that automatically enters the accumulator.

The third hypothesis is that judging emotional stimuli to be irrelevant reduces the level of arousal induced by these emotional stimuli, which in turn reduces the speed of the internal clock (panel 3, Fig. 3). This approach considers that the participants themselves down-regulate the physiological reactions induced by the emotional stimuli. In a recent study, Peira, Fredrikson, and Pourtois (2014) showed that healthy participants can efficiently use detectable biofeedback (heart rate) to reduce their emotional reactions in response to visual emotional stimuli. In the domain of timing, Meissner and Wittmann (2011) measured participants' awareness of heart rate by asking them to attend to their own heartbeats and count them silently. These authors found that the more aware subjects were of their heartbeat, the more accurately they performed in a duration reproduction task. In sum, it is possible that the participants used bodily information to consciously down-regulate their emotional reaction, thus attenuating the speeding-up of the internal clock. In the theories of embodied time it has been suggested that the self-awareness of bodily information contributes to time judgment (e.g., Craig, 2009;

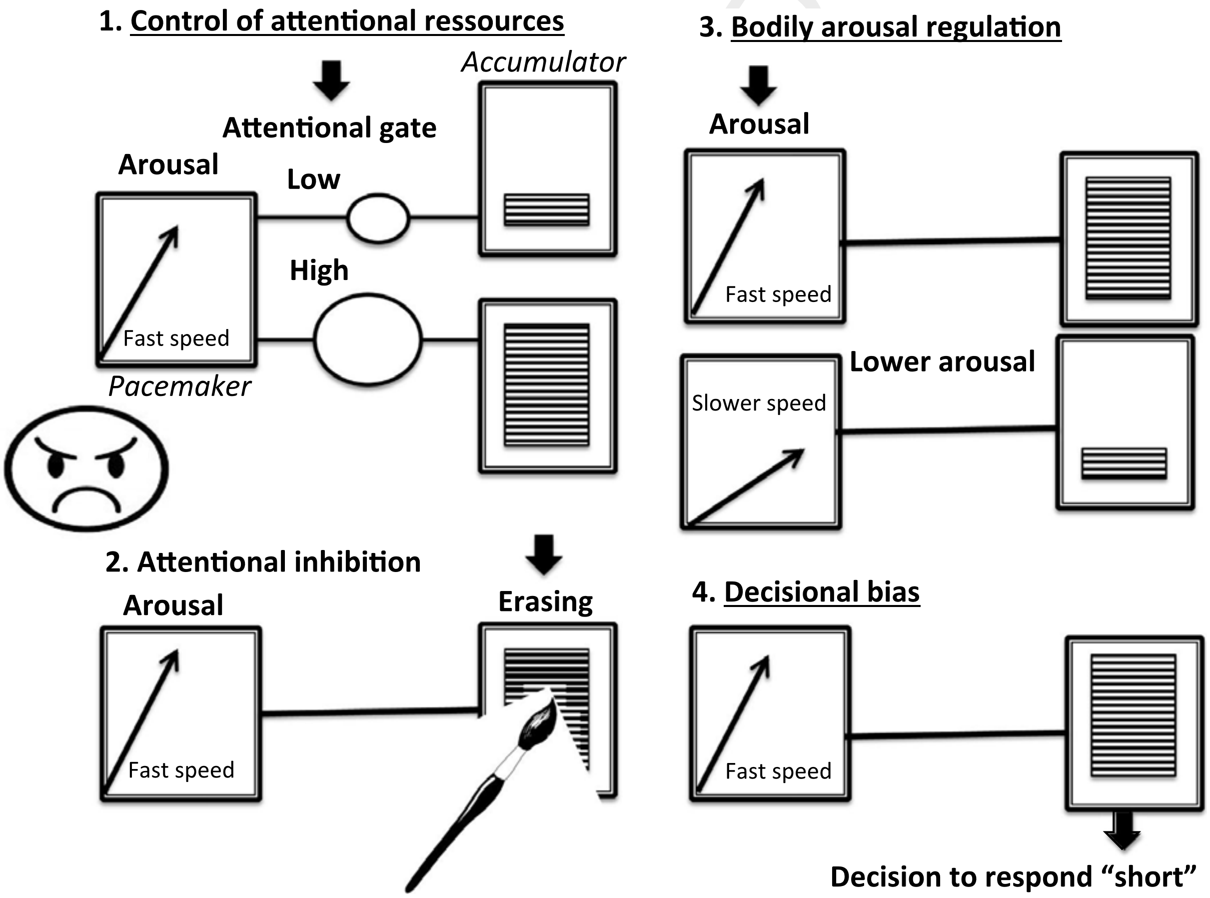

Fig. 3. Hypotheses about the level of time processing at which cognitive regulations act to modify the distortion of time triggered by emotion: (1) control of attentional resources, (2) attention inhibition, (3) bodily arousal regulation and (4) decisional bias.

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Droit-Volet, 2014; Droit-Volet & Gil, 2009; Droit-Volet et al., 2013; Wittmann, 2014). However, in our study, the scores on the self-assessment of arousal level in response to the perception of angry faces did not change with the nature (false or true) of the explicit information received.

A fourth hypothesis relates to decision-making bias. This holds that participants would respond "short" more often because they are aware of their tendency to respond long in emotional conditions. Such a tendency would mask the lengthening effect at the behavioral level. However, the modeling of individual bisection data demonstrates that changes in decisional processes only affect the proportion of responses in the middle of the bisection curve, i.e. in the case of "ambiguous" durations when the participants do not know whether the durations are more similar to the short or the long standard (Droit-Volet & Wearden, 2001; Wearden & Jones, 2013). In particular, this bias in the middle of the psychophysical functions was not observed in our false information groups.

Finally, there is a series of hypotheses concerning the mechanisms that mediate the effects of knowledge on emotion-induced time distortions that require the conduction of further experiments before they can be validated. Regardless of the mechanisms involved, the original contribution of our study is to reveal the important role of temporal awareness in determining the extent of subjective time dilation under the effect of emotion.

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An Evaluation of the Effect of Auditory Emotional Stimuli on Interval Timing

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Abstract
Emotions modulate cognitive processes, including those involved in the perception of time. A number of studies have demonstrated that the emotional modulation of interval timing can be described in terms of an attentional or an arousal-based mechanism, depending on the exact task setup. In this paper, two temporal generalization experiments with auditory emotional stimuli as distractors are presented. These experiments are modeled after the work by Lui et al. (*PLoS One*, 2011, *6*, e218292011) who, using visual distractors, provided evidence for an attentional account of emotion-regulated modulation of the perception of time. Experiment 1 replicates the findings of Lui et al., and thus generalizes their work to auditory stimuli. However, Experiment 2, in setup highly similar to Experiment 1, failed to find any effects of emotional modulation on interval timing. These results indicate that emotional effects on interval timing, although often reported, might not be as ubiquitous as earlier research has (implicitly) suggested.

Keywords
Interval timing, time perception, emotion, auditory stimuli, pacemaker–accumulator models, attention vs. arousal, temporal modulation

1. Introduction

Emotional states have a strong impact on cognitive processes and the resulting behaviors (for reviews, Dolan, 2002; Schirmer, 2014), although the exact mechanisms underlying this connection are still topics of discussion (e.g., Pessoa, 2008; Zeelenberg et al., 2006). One line of work focuses on how emotional states influence the perception of time (e.g., Droit-Volet, 2013; Droit-Volet & Meck, 2007; Fayolle et al., 2013, 2015; Gan et al., 2009; Gil & Droit-Volet, 2009; Lui et al., 2011; Meck & MacDonald, 2007; Noulhiane et al., 2007), with different research groups

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proposing different mechanisms. Interestingly, all these mechanisms have links to the influential pacemaker–accumulator framework of time perception.

The pacemaker–accumulator model of time perception, often formalized in terms of the Scalar Timing Theory (e.g., Church, 2003; Gibbon et al., 1984; see Van Rijn et al., 2014 for a recent review) is based on four different components; a pacemaker, an accumulator, a memory store and a comparator. The pacemaker emits a steady stream of pulses, and as soon as the start of a to be timed event has been perceived, the accumulator starts to accrue pulses. When the to-be-timed interval has finished, the number of accrued pulses is compared to duration representations stored in long-term memory in order to make an adequate temporal response. The Scalar Timing Theory has provided a thorough theoretical framework in terms of which many temporal phenomena can be interpreted. By embedding this theory in a general cognitive architecture (Taatgen et al., 2007; Van Rijn & Taatgen, 2008), computational models of complex cognitive tasks can now include a principled account of the temporal aspects of these tasks (e.g., Kujala & Salvucci, 2015; Moon & Anderson, 2013). Moreover, this integration allows to further constrain timing theories (Taatgen & van Rijn, 2011).

An important addition to the pacemaker–accumulator theories is the 'attentional gate' proposed by Zakay and Block (1995). This metaphorical 'gate', located between the pacemaker and the accumulator, influences the speed of accrual in the accumulator, with a partly-closed gate resulting in slowed accumulation of pulses. As it is assumed that the gate is opened as a function of the amount of attention directed to the timing task, this 'attentional gate' model can be used to describe attentional influences on time processing. Thus, when attention has to be divided between the to-be-timed stimulus and a secondary task or event, the subjective perception of time will be affected as fewer pulses accumulate per unit of objective time (but see Taatgen et al., 2007, for a paradigm in which attentional modulation does not influence the perception of time and Buhusi & Meck, 2009, for alternative views of attentional time sharing).

Based on the pacemaker–accumulator model, two explanations for emotion-induced temporal distortions have been proposed. The first explanation refers to the role of *attention* for temporal processing (e.g., Schirmer, 2011), and cites evidence that individuals more readily attend to emotional than to neutral stimuli. Moreover, this explanation holds that emotions influence the attentional gate, thereby changing the number of accumulated pulses such that subjective time becomes longer or shorter. Specifically, a stimulus will be perceived as longer if it is emotional as compared to neutral. However, a neutral stimulus that is timed on the backdrop of distractors, will be perceived as shorter if distractors are emotional as compared to neutral.

The second explanation of emotion-induced temporal distortions involves *arousal* (e.g., Droit-Volet & Meck, 2007). According to this account, increased arousal leads to an increased pacemaker rate. Compared to neutral stimuli, emotional stimuli result, by influencing the arousal level, in a greater number of accumulated pulses and are, therefore, perceived as longer. Moreover, neutral stimuli timed on the backdrop of distractors are perceived as longer if distractors are emotional as compared to neutral. In addition, based on higher arousal levels, the onset of emotional stimuli could be perceived more efficiently or faster than the onset of neutral stimuli, also resulting in an increased perceived duration.

Although there have been many studies about how emotions affect the processing of time, the findings of these studies are inconsistent, with some studies interpreted as evidence for an attentional modulation and others for an arousal modulation, or for a combination of both. For example, Lui et al. (2011) explored the role of visual emotional and neutral distractors in the timing of neutral events using a temporal generalization paradigm. Subjects were shown two neutral stimuli for which they had to indicate whether the second stimulus (S2) was presented for a longer or shorter time period than the first stimulus (S1), which had a constant duration. Emotion was manipulated by presenting a task-irrelevant picture, either emotional or neutral, in between S1 and S2. Across a number of experiments, Lui and colleagues found that, on average, S2 was perceived as shorter when preceded by an emotional as compared to a neutral distractor. In line with the attention modulation reasoning outlined above, this suggests that greater attention directed to the encoding of the emotional stimulus, presented just before the timing stimulus, comes at a cost of attention directed to the processing of time (for similar results, see this issue Lake et al., 2016).

Droit-Volet et al. (2004) provided evidence for an arousal-based modulation of the perception of time. Using a temporal bisection task with emotional faces as stimuli reflecting the durations, they found a systematic overestimation of time for the emotional faces (i.e., expressing anger, happiness or sadness) compared to the neutral faces. This effect has been replicated across many studies (e.g., this issue Droit-Volet et al., 2016; Eberhardt et al., 2016). In addition, Noulhiane et al. (2007) found evidence for an arousal modulation of time perception when stimuli were presented in the auditory domain. In their sound reproduction task, subjects were more likely to overestimate the duration of an emotional tone, as reflected in a lengthened reproduction, than a neutral tone.

Due to the high variety in experimental designs, it remains unclear whether there is one modulation that, in general, accounts for emotion-induced temporal distortion, or whether the modulation is perhaps task or domain specific. To address the issue of generalizability, the present study adapted the paradigm of Lui et al. (2011), who argued that emotional effects on time perception could be explained by an attention modulation. Instead of their visual distractor stimuli, the experiments reported here used auditory distractor stimuli. Although a large number of earlier studies have indicated that stimuli presented in the auditory domain might evoke slightly different timing processes than stimuli presented in the visual domain (e.g., Grondin, 1993; Grondin & Rousseau, 1991; Penney et al., 2000, 2014; Van Wassenhove et al., 2008), these studies generally acknowledge that the main temporal processes are in place irrespective of the modality used. Therefore, effects should be alike when participants are presented negative valence distractors in the auditory and in the visual domain. To increase the emotional response, participants were conditioned to associate a colored square with a neutral auditory stimulus, and a differently colored square with a negative auditory stimulus (see, for a similar setup, Lake et al., 2016). By presenting these cues probabilistically before the auditory distractor stimulus, we expected to increase the emotional response to the auditory distractors, as earlier work has shown that uncertainty during anticipation increases the neural responses to emotional stimuli (Sarinopoulos et al., 2010).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty naïve participants (mean age = 21.25; SD = 2.90; range 18–19; 11 male) were recruited from the student participant pool of the Department of Psychology at the University of Groningen and were offered partial course credits in exchange for participation. All participants reported having normal or corrected-to-normal sight and normal hearing. Ethics approval was obtained from the Psychology Ethics Committee of the University of Groningen.

2.1.2. Materials and Procedure

The experiment, implemented in E-Prime v2, consisted of four blocks: two practice blocks, one conditioning/sound-rating block and one experimental block. In the first two practice blocks, participants were familiarized with the temporal generalization task. This task consisted of two successively presented visual stimuli (S1 and S2), and participants were instructed to judge whether S2 was presented for a longer or shorter duration than the earlier presented S1. The stimuli were filled black circles with a diameter of nine millimeters presented against a white background in the center of a computer screen (a 22″ Illyama Vision Master Pro 513 monitor set to a resolution of 1280 × 1024, 85 Hz), which was located at an approximate distance of 60 cm from the participant. Participants responded by pressing the '*z*' key to indicate that S2 was perceived as shorter, and 'm' to indicate that S2 was perceived as longer than S1. For a schematic representation of the trial setup, see Fig. 1.

The first practice block consisted of twelve trials in which S1 was presented for 1200 ms and S2 for 800, 1000, 1400 or 1600 ms (each S2-duration was presented three times, in random order). After familiarization with the basic structure of the temporal generalization task using these durations, the second practice block commenced in which participants were presented the same S2 durations as presented during the experiment proper (i.e., 1040, 1120, 1280 or 1360 ms, with each duration presented ten times, in random order).

The purpose of the third block was to elicit an association between visual cues and the emotional valence of sounds, and to obtain ratings of the valence of these sounds. On each trial of this block, participants saw a single blue or green square of nine by nine millimeters in the center of the computer screen and heard a prerecorded sound (played over headphones at ~ 65 dB) of, respectively, a negative or neutral event. A total of eighteen different sounds were used. An initial sound set, provided by A. Schirmer (National University of Singapore), was supplemented with sounds collected from an online database (www.freesound.org). From these sounds nine were selected by the authors

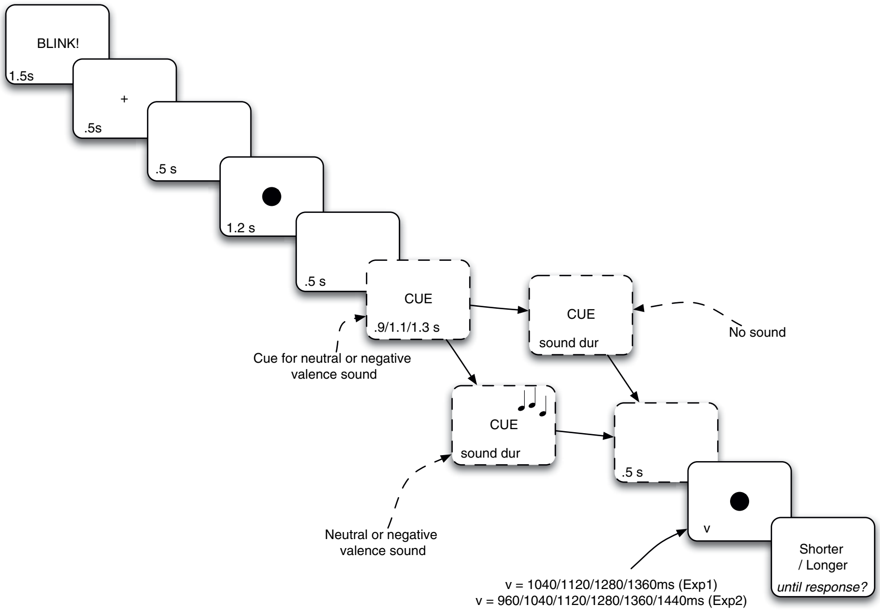

Figure 1. The trial setup of the temporal judgment task in Experiments 1 and 2. See text for further details.

as neutral and nine others as negative (see Table 1 for a complete overview). Although care was taken to select sounds of similar duration, the naturalistic nature of the stimuli hampered balancing of both groups (range neutral: 1075–1899 ms, range negative: 1758–1913 ms). Mean durations were 1628 ms and 1842 ms for neutral and negative sounds, respectively (difference marginally significant, $\Delta = 214$, $t(16) = 1.97$, $p = 0.066$).

To create an associative link between sound valence and square color, the green and the blue square preceded neutral and negative sounds, respectively. Each trial started with the presentation of one of the two squares for 500 ms. Next, a sound was played over a pair of headphones, after which the subjects were presented a continuous scale (from 0 for ‘neutral’ to 10 for ‘unpleasant’) on which they rated the emotional valence of the sound via mouse click. In total, there were 36 trials, each square–sound combination was presented and rated twice.

The experiment proper started in the fourth block, in which the temporal generalization task was combined with the presentation of the colored squares and sounds in between S1 and S2. On each trial, one of the two colored squares was presented for 900, 1100 or 1300 ms. These jittered durations were chosen to allow for the buildup of expectancy and to prevent that the presentation duration influences later temporal performance. Additionally, jittered durations increased uncertainty as sounds might occur at 900, 1100 or 1300 ms after square onset, or not at all. On half the trials, no sound was presented (the no-sound condition), on the remaining trials an associatively linked emotional sound (with-sound condition) was played to evoke an emotional response. The no-sound condition was included to leave participants uninformed about whether or not they will hear a sound, to prevent habituation, and to increase the strength of the emotion manipulation (Sarinopoulos et al., 2010).

A schematic overview of the trial set-up is presented in Fig. 1. Each trial started with a screen presenting the word 'BLINK' for 1500 ms instructing the subjects to blink their eyes now rather than during the remainder of the trial. This screen was followed by a fixation cross (500 ms), a blank screen (1000 ms), S1 (1200 ms), a second blank screen (500 ms), the colored square representing the cue (blue/green, for 900, 1100 or 1300 ms), followed by the combined presentation of the square and the sound in half of the trials, or followed by the presentation of the square for a randomly selected duration equal to that of one of the eighteen sounds. After this, a blank screen was presented for 500 ms, followed by the presentation of S2 (either 1040, 1120, 1280, or 1360 ms) and eventually a response screen with a question mark indicating that the response should be made by pressing the 'z' or 'm' key. A new trial started after a response was made.

In total there were 216 trials: Each of the cells in the 2 × 2 design consisting of cue (neutral/negative) and sound presence conditions was presented 54 times, allowing for three presentations of each of the 18 sounds in the with-sound condition. The S2 durations were pseudo-randomly distributed, resulting in 52 to 56 presentations of each S2 duration per participant. After 108 trials, a short break was introduced in which subjects were instructed to press the space-bar when they were ready to continue. The experiment lasted approximately fifty minutes and took place in the presence of the experimenter in a room where subjects were tested either individually or in pairs.

2.1.3. Method of Analysis

Data from the conditioning/sound-rating block and the experimental block were analyzed. Valence ratings collected in the conditioning/sound-rating block were evaluated by comparing the mean ratings of the sounds with a *t*-test. The temporal generalization data collected in the experimental block were analyzed using logistic mixed-effect models. The dependent variable in these models was whether the participant responded 'long' (1) or 'short' (0). Because of this coding, the estimated betas reflect the change in the proportion of 'long' responses, expressed on a logit-scale. Compared to the traditional approach of estimating parameters on a subject-by-subject basis which are then entered into an ANOVA, logistic mixed-effect models provide a more powerful analysis method. This method allows for, among other advantages, the straightforward inclusion of continuous covariates, analyzing designs with unequal number of observations per cell, for assessing the goodness of fit of a model, and to compare the goodness of fit with alternative models. We have utilized this method in earlier work (Van Rijn, 2014), and a more extensive description of the method and its application to psychophysical data can be found in a recent methods paper (Moscatelli et al., 2012).

We entered predictors representing whether the sound was present, whether a negative or neutral cue was used, and the interaction of these predictors as fixed factors in the mixed-effect model. We also entered the duration of S2 as a fixed effect, but used model comparisons to assess whether interactions between S2 duration and the other fixed effects were warranted. Similarly, we assessed whether the inclusion of trial number (i.e., 'time on task') and cue duration was warranted using model comparisons. For the fixed factors representing sound presence and valence, deviation or effects coding was used (sound: 0.5; no-sound: –0.5; neutral: –0.5; negative: 0.5), trial number was rescaled to a range from –0.5 to 0.5, the duration of the cue was expressed as the deviation in seconds from 1.1 s (i.e., –0.2, 0, 0.2), and the duration of S2 was encoded as deviation in seconds from 1.2 s (i.e., –0.16, –0.08, 0.08, 0.16). As random effects, we entered a factor representing participant to account for (intercept) effects associated with specific participants. As not all trials involved the presentation of a sound, the sounds were not entered as a random factor.

2.2. Results

The ratings obtained in the conditioning/sound-rating block indicated an appropriate operationalization. The neutral sounds were rated between 1.76 and 3.45 ($M = 2.34$, SD = 1.39; see Table 1) and the negative sounds between 6.05 and 7.88

Table 1.
Brief descriptions of the negative and neutral sounds used in Experiment 1 (and 2). Numbers in parentheses indicate the rating given to these sounds in Experiment 1. One of the Phone ringing sounds was replaced by a 'bell' sound (rated with 2.3) in Experiment 2. See text for further explanation.

Negative sounds	Neutral sounds
Chalk screeching on blackboard (7.4)	Boing, spring-like sound (2.1)
Dental drill (7.1)	Doorbell (ding dong) (2.1)
Fork scraping in bowl (7.2)	Clarinet playing (1.8)
Group of people screaming (7.9)	Horse whinny (2.4)
Squeaky screw driver (7.6)	Birds singing (2.4)
Squeaky wheel (6.1)	Phone ringing (3.0)
Scratching materials (7.6)	Babbling and running sounds of a baby (2.0)
Screeching noise of a microphone (7.0)	Samba drums and background singing (1.9)
Shrieks of a knife on a glass bottle (7.2)	Phone ringing (3.4)

($M = 7.23$, SD = 2.06). This difference was statistically significant indicating that the negative sounds were indeed perceived as more negative than the neutral sounds ($\Delta = 3.89$, $t(19) = 17.32$, $p < 0.001$).

Data of the temporal generalization study are depicted in Fig. 2, in which the four lines depict the four cells of the two (valence) by two (sound presence) design, plotted as a function of the four S2 durations. To analyze these data, we started with the simplest logistic mixed model containing the factors sound presence, valence, their interaction, and S2 duration. When we compared this model with a more complex model in which interactions between S2 duration and the other factors were entered, the simpler model prevailed ($\chi^2 = 0.852$; df = 3; $p = 0.837$). To ensure that the jittered duration associated with the cue presentation did not influence the results, we also compared a model in which the cue duration was entered as a fixed factor, but, again, the simpler model was preferred ($\chi^2 = 0.192$; df = 1; $p = 0.661$). Similarly, including trial number did not improve the fit of the model ($\chi^2 = 2.24$; df = 1; $p = 0.135$). Although the non-significant χ^2 test indicates that the inclusion of trial number is not warranted, it is relevant to note that the associated estimate is negative, which is in the same direction as the effects of valence and the interaction between valence and sound presence. In other words, habituation is unlikely to have affected those effects in qualitative terms.

The resulting model, which is the base model we started with, contains significant effects for all factors. An intercept of −0.22 ($z = -2.32$, $p = 0.020$) indicates that, at the average duration of S2, the proportion of 'long' responses significantly deviated from chance (estimated P(Long): 0.45). In other words, S2 duration was

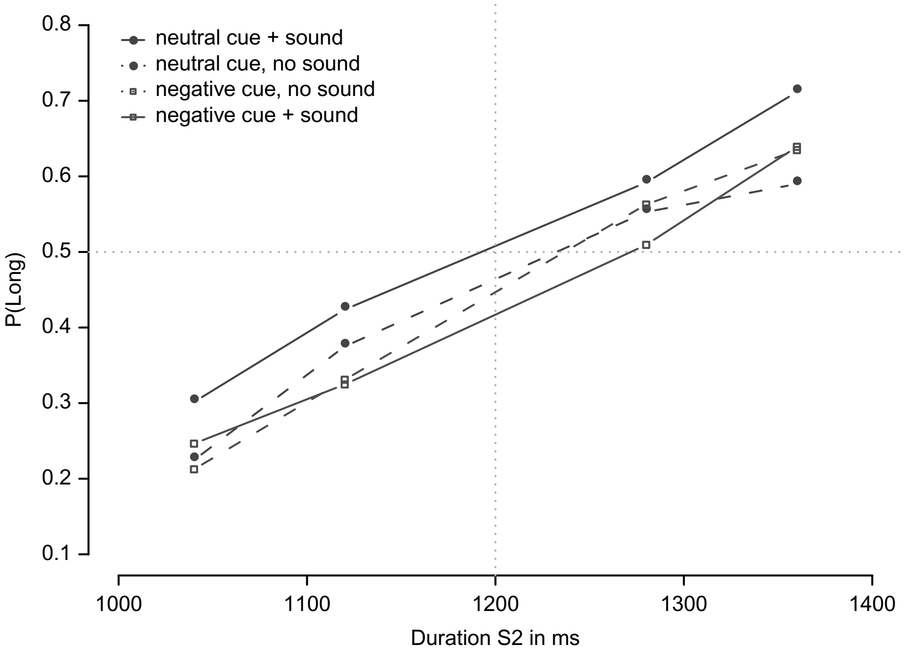

Figure 2. Proportion of 'long' responses for the four S2 durations for the two emotional valence and two sound presence conditions in Experiment 1. This figure is published in color in the online version.

underestimated. Due to the deviation coding, the interpretation of the other parameters is less straightforward. The significant main effect of valence ($\beta = -0.16$; $z = -2.46$, $p = 0.014$) indicates that, when the cue is negative, people are less likely to respond 'long'. The main effect of sound presence ($\beta = 0.15$; $z = -2.32$, $p = 0.020$) indicates that omitting the sound increases the proportion of 'long' responses. Importantly, these main effects are modulated by an interaction between sound presence and valence ($\beta = -0.39$; $z = -2.97$, $p = 0.003$). The proportion of 'long' responses for the neutral/no-sound condition and for the negative/sound condition is lower than the proportion of 'long' responses for the other two conditions. The duration of S2 had, obviously, a large effect on the proportion 'long' responses ($\beta = 5.44$; $z = 20.4$, $p < 0.001$), indicating that with longer durations the proportion of 'long' responses increased. To ensure that these effects were not driven by differences in sound durations, we compared the simplest model with a model that additionally contained a predictor encoding for the duration of the sound (deviation in seconds from the mean duration). Again, the simpler model was preferred, indicating that the added complexity was not warranted ($\chi^2 = 0.024$; df $= 1$; $p = 0.135$). Inspecting the other estimates of the more complex model also showed that all estimates where highly similar to the ones in the simpler model, suggesting that even if the more complex model were warranted, it would have led to similar conclusions. To assess whether any effects of valence can be observed when no sound was presented, we conducted a separate analysis on the no-sound trials. As might be expected on the basis of Fig. 2, the two square colors alone did not significantly influence the proportion of 'long' responses ($\beta = 0.034$; $z = 0.363$, $p = 0.717$).

2.3. Discussion

The results are in line with Lui et al.'s (2011) work with respect to the hypothesized effects in the sound condition: when a negative sound is presented, the duration is perceived as shorter resulting in fewer 'long' responses. This can be explained by a modulation of attention: a negative sound captures more attention than a neutral sound, which comes at a cost to attention allocated to time perception, hence pulses are missed and the S2-durations are perceived as shorter. Although the S2 durations were selected with the intention to observe a large number of correct responses for the more extreme durations, we failed to observe the typical sigmoid pattern. We, therefore, conducted a second study in which a shorter and a longer S2 duration were added and in which the sound durations were better controlled. Additionally, one of the two phone-ringing sounds was replaced by a bell sound, and green and red cues were used instead of green and blue cues to ensure a larger color contrast and a more naturalistic mapping.

3. Experiment 2

3.1. Methods

3.1.1. Participants

A total of 23 naïve subjects (mean age = 22.9; SD = 2.63; range: 19–30, 11 male) participated. All subjects were enrolled at the University of Groningen and received 10 Euros per hour in exchange for participation. All participants reported to have normal or corrected-to-normal sight and normal hearing. Ethics approval was obtained from the Psychology Ethics Committee of the University of Groningen.

3.1.2. Materials

With a few exceptions, the materials used in Experiment 2 were similar to those used in Experiment 1. First, as two phone ringing sounds were used in Experiment 1, one was replaced by the sound of a bell. Second, the sounds were edited to ensure more similar durations for the two conditions. Removing or adding parts to the signal resulted in a time range of 1738 to 1902 ms and 1758 to 1913 ms for the neutral and negative sounds, respectively. These differences in duration were non-significant ($M_{\text{Neutral}} = 1838.7$ and $M_{\text{Negative}} = 1842.6$; $\Delta = 3.9$, $t(16) = 0.138$, $p = 0.89$). Third, green and red squares were used to increase color contrast. The red cue indicated the negative valence condition, the green cue the neutral valence condition. Fourth, as the data collected in Experiment 1 suggested that responses to the shortest and longest S2 durations were far from asymptotic, we added two extreme durations (960 and 1440 ms).

3.1.3. Procedure

As her/his EEG was collected during this experiment, each participant was tested individually in a shielded room. However, due to technical problems the signal-to-noise ratio was too low to warrant the reporting of these data.

The practice blocks and the conditioning/sound-rating blocks were identical to those in Experiment 1, with the exception of two more extreme durations added to the second practice block. This increased the number of trials in the second practice block as all durations were again repeated ten times, in random order.

The experimental block consisting of the temporal generalization task with cues and sounds was identical to Experiment 1, except for the two additional S2 durations and the new color–cue mappings. In total there were 180 trials: 90 trials for the with- and 90 for the no-sound condition, half of which were negative and half of which were neutral. Each sound was presented 5 times. The S2 durations were pseudo-randomly distributed, resulting in 28 to 32 presentations of each S2 duration per participant. After 90 trials, participants could take a short, subject-paced break. The whole experiment took about 45 minutes.

3.1.4. Method of Analysis

The method of analysis was equivalent to that of Experiment 1.

3.2. Results

Again, the sound ratings indicated a proper operationalization. The neutral sounds were rated from 1.06 to 3.59 ($M = 2.03$, SD = 1.96) and the negative sounds from 5.56 to 8.22 ($M = 7.37$, SD = 2.02), resulting in a significant difference between the two sound conditions ($\Delta = 5.34$, $t(22) = 18.07$, $p < 0.001$).

The main data of the temporal generalization study are depicted in Fig. 3. As can be seen from this picture, the results clearly deviate from those obtained for

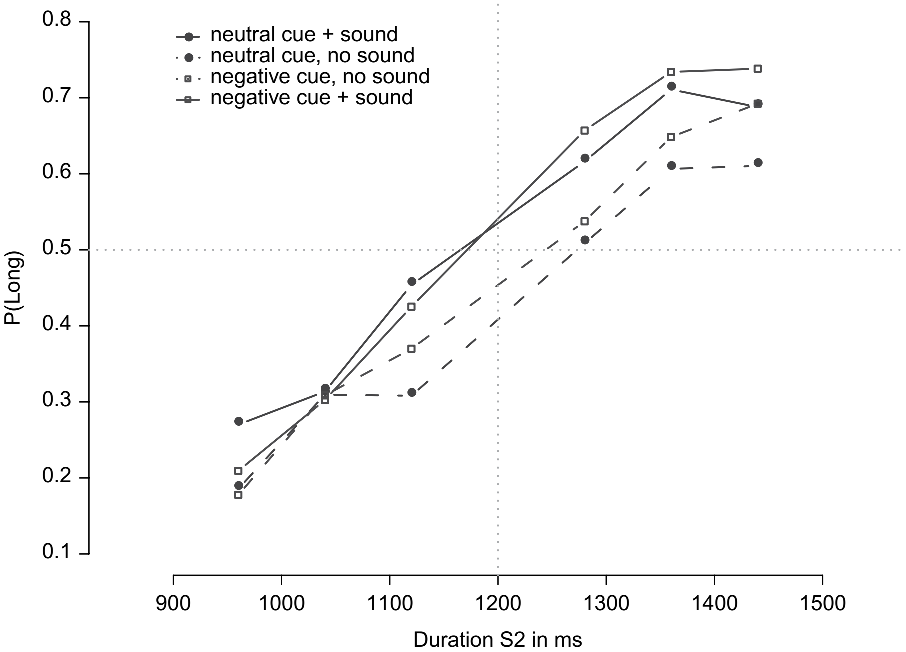

Figure 3. Proportion of 'long' responses for the six S2 durations for the two emotional valence and two sound presence conditions in Experiment 2. This figure is published in color in the online version.

Experiment 1 as there is no clear difference between the neutral and negative sound conditions.

To quantify these results, we again started with the simplest logistic mixed model containing the factors sound presence, valence, their interaction, and S2 duration. As for Experiment 1, we tested a number of more complex models. Both the more complex model that included S2 duration interacting with sound presence and valence ($\chi^2 = 5.284$; df = 3; $p = 0.152$) and the more complex model that included the cue duration ($\chi^2 = 1.315$; df = 1; $p = 0.252$) were non-preferred over the simpler model. However, the more complex model that also included trial number was preferred over the simpler model ($\chi^2 = 9.015$; df = 1; $p = 0.003$). Extending this model with sound duration was not warranted ($\chi^2 = 0.026$; df = 1; $p = 0.872$).

The preferred model consisted of a non-significant intercept ($\beta = -0.13$; $z = -1.19$, $p = 0.232$) and a highly significant effect of S2 duration ($\beta = 4.77$; $z = 22.7$, $p < 0.001$) indicating that longer S2 durations were associated with a higher proportion of 'long' responses. A significant effect of sound presence ($\beta = 0.350$; $z = 5.08$, $p < 0.001$) indicated that trials with sound were associated with higher proportions of 'long' responses than trials without sound. The effect of valence ($\beta = -0.120$; $z = 1.74$, $p = 0.082$), and the interaction between sound presence and valence ($\beta = -0.219$; $z = -1.59$, $p < 0.111$) were non-significant. The trial effect was significant ($\beta = -0.35$; $z = -3.00$, $p = 0.003$), indicating that participants started to respond short more often as the experiment progressed.

Of these results, the lack of a significant main effect of valence is most important and indicates that Experiment 2 failed to replicate Experiment 1. At the same time, the estimated beta is negative for both Experiments 1 and 2, and the effect in Experiment 2 could be interpreted as 'borderline significant'. However, Fig. 3 indicates that this interpretation is not supported by the data, as no effect can be observed in the sound condition (the solid lines). Moreover, an effect of emotional valence should be stronger in the sound conditions than in the no-sound conditions, another hypothesis which is clearly not supported by the data. Therefore, the results of Experiment 2 are at odds with the assumption that emotional auditory stimuli affect the perception of time.

4. General Discussion

Do emotional stimuli affect the subjective experience of time? The results of Experiment 1 support an affirmative answer to this question: durations in the emotional sound condition were perceived as shorter than durations in the neutral sound condition. These results are in line with the study of Lui et al. (2011), and generalize their findings from the visual domain to the auditory domain. Moreover, they are most straightforwardly explained by an attentional mechanism: a negative sound captures more attention compared to a neutral sound, which comes at the cost of attention allocated to time perception, hence pulses are missed and the S2 durations are perceived as shorter. In the no-sound condition, that is when only the cue was presented that could be used to predict the valence of the sound, no effect was observed. As we cannot quantify how well the association between cue and valence was learned, the absence of an effect might simply be due to a too weak association between the visual cue and the sound. In other words, seeing the colored square may not have evoked an emotional response. However, effects of conditioning might also be negated by color-inherent responses as in the design of Experiment 1 (and 2) the colors of the cues were not counterbalanced. Thus, if a cue signaling a negative sound caused a stretching of time, the negative sound effect would have been canceled out. As these effects cannot be quantified with the current setup, no firm conclusions should be drawn based on the absence of an effect in the no-sound condition.

To sum up, the present results can be seen as an auditory analogue of earlier work, as they support the view that hearing a negative sound results in an underestimation of time immediately after the sound was heard. In other words, perceived time is slowed down in situations preceded by an unpleasant experience (see, for example, Gan et al., 2009; Lui et al., 2011; Noulhiane et al., 2007). Although this attentional account fits the present results, it is possible that in other temporal tasks the emotional modulation is driven by changes in arousal. Moreover, as we have not explicitly measured biophysiological markers of arousal, it could be that some of the observed results are driven by an interplay between arousal and attentional processes (see also this issue Droit-Volet et al., 2016; Eberhardt et al., 2016, Schirmer et al., 2016).

Irrespective of the underlying mechanisms, an important observation is that Experiment 2 failed to replicate the findings of Experiment 1. Moreover, post-hoc explorations have failed to unravel why Experiment 2 failed to show effects: there were no participants with clearly outlying data, nor did certain sounds illicit qualitatively different responses (a conclusion also supported by the similar results for the sound ratings in Experiments 1 and 2). In Experiment 2, as in Experiment 1, the presentation of a sound between the presentation of the standard and the comparison intervals affected the subjective perception of time, an effect that can be explained in terms of an arousal-based mechanism.

A potential explanation for the lack of valence effects is that participants in Experiment 2 might have been more motivated, as EEG data were collected in addition to behavioral data. If higher levels of motivation resulted in a more focused processing of temporal information, the emotional modulation might not have been strong enough to distort the accumulation of time (Droit-Volet et al., 2016). Another potential explanation, also related to the EEG setup of Experiment 2, is that A. Schirmer (personal communication, Sept. 26, 2015) indicated that emotional effects might be more difficult to observe when participants are tested in a separate room without other participants or the experimenter present. Yet another explanation could be that in this experiment more trials were run than in earlier studies assessing the emotional effects on timing. For example, in Lui et al. (2009) AQ1 participants were presented only 64 trials. However, the lack of an effect of trial number in Experiment 1, and the relatively minor influence of the inclusion of trial number on the other parameters in Experiment 2 make this explanation less likely. A final alternative explanation might relate to the shorter time between trials AQ1 in our experiments, as in the study by Lui et al. (2009) trials were separated by about nine seconds. Although this could, of course, be a cause for the lack of effect in Experiment 2, the observation of a valence effect in Experiment 1, which has a similar setup as Experiment 2, makes this explanation questionable.

As Experiment 1 seems to be most in line with earlier (e.g., Gan et al., 2009; Lui et al., 2011; Noulhiane et al., 2007) and recent (Lake et al., 2016) results, both with similar and slightly different experimental setups (e.g., Gan et al., 2009; Lui et al., 2011; Noulhiane et al., 2007), we are tempted to place more trust in the results of Experiment 1. At the same time, Experiment 2 is an interesting wake-up call for researchers studying the emotional modulation of interval timing: rerunning a study with participants from a similar participant pool and a highly similar experimental setup made some presumably stable effects disappear. In addition, to assess how emotional stimuli influence interval timing, an important line of research should be to establish how robust these findings are by running a number of large-scale, preregistered studies (Open Science Collaboration, 2015), and to address whether there are certain interindividual differences that might explain the susceptibility to emotional influences (Schirmer et al., 2016). In addition, the differential effects of emotional stimuli suggest that running a series of preregistered, adversarial collaborations (Matzke et al., 2015) might be necessary to advance this line of research on interval timing.

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AQ1: P 13 Lui et al. (2009): This reference okay as added to the list, or was Lui et al. (2011) intended?

Pupillary Response Indexes the Metrical Hierarchy of Unattended Rhythmic Violations

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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 for beat perception. In addition, to what extent beat perception is open for learning or dependent on musicality 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 musicality, 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.

Keywords: beat perception, music cognition, attention, pupil dilation

1. Introduction

1.1. 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 human infants can utilize from about four years of age (Endedijk, Ramenzoni, Cox, Cillessen, Bekkering, & Hunnius, 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 (Ladinig, Honing, Háden, & Winkler, 2009; Geiser, Sandmann, Jäncke, & Meyer, 2010; Winkler, Háden, Ladinig, Sziller, & Honing, 2009; Bouwer, Van Zuijen, & Honing, 2014), while other studies have suggested that attention is necessary to establish a representation of the beat (Geiser, Sandmann, Jäncke, & Meyer, 2009; Chapin et al., 2010). 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 (Honing, Bouwer, & Háden, 2014; Ladinig et al., 2009; Winkler et al., 2009; Bouwer et al., 2014). 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 the these early EEG potentials reflect the magnitude of the violation (Kononowicz & Van Rijn, 2014; Näätänen et al., 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 (Ladinig et al., 2009; Winkler et al., 2009; Bouwer et al., 2014). 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 rock drum rhythm (Figure 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 (Ladinig, Honing, Háden, & Winkler, 2011). 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 focussed 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, Bouwer, & Háden, 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 behavioural, fMRI and ERP experiments, which have resulted in partly ambiguous results. While some studies show that musical training enhances beat processing (Vuust et al., 2005; Chen, Penhune, & Zatorre, 2008), 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 training influences beat perception. As the MMN amplitude might not reflect differences in beat salience (Ladinig et al., 2009; Bouwer et al., 2014), 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; Steinhauer & Zubin, 1982; Preuschoff, ‘t Hart, & Einhäuser, 2011). Second, pupil dilation has been suggested to reflect preconscious processing (Laeng, Sirois, & Gredeback, 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.

1.2. 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., Kahneman, 1973; Ahern & Beatty, 1979; Granholm, Asarnow, Sarkin, & Dykes, 1996), emotional arousal (e.g., Hess and Polt, 1960; Hamel, 1974), memory strength and encoding (e.g., Van Rijn, Dalenberg, Borst, & Sprenger, 2012; Wolff, Scholz, Akyürek & Van Rijn, 2015), language processing (e.g., Vogelzang, Van Rijn, & Hendriks, accepted pending minor revisions), and dynamical attention (e.g., 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 Zylderberg, Oliva, Sigman, 2012; Willems, Damsma, Wierda, Taatgen, & Martens, 2015; Wolff, et al, 2015). 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, ‘t Hart, and Einhäuser (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 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 behavioural 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, Dayun 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 elicit a larger phasic NA signal than frequent targets. In accordance with this result, Alexinsky, Aston-Jones, Rajkwoski, and Revay (1990) found that an increased target frequency led to a decrease in phasic LC activity.

1.3. 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 (e.g., 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-NE 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 (2014) 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 (2014) 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. The authors therefore argued that response conflict 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 show a pupillary response to visual stimuli presented in the blind visual field, and thus were not consciously seen (Weiskrantz, Cowey, and Barbur, 1999; Tamietto et al., 2009). 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 (2014) 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.

1.4. 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 musicality entails more pronounced beat perception. Participants are asked to perform a visual target detection task while a continuous stream of 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 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 musicality 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 musicality.

2. Methods

2.1. Participants

Twenty participants (10 female, mean age 20.9, range 19-26) participated in the experiment for course credits. Participants were naive to the 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.

2.2. 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 (Figure 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 sound was omitted at the most salient position (position 1) or the second most salient position (position 5), respectively.

2.3. 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 x 4 patterns) and 20 deviants (10 repetitions x 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 musicality of 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.

2.4. 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.

2.4.1. 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 analysed.

To investigate the effect of omissions, the pupil dilation in deviant patterns (D1, D2) and standard patterns (S2, S3, S4) will be compared to the dilation in base pattern S1. In order to control for the different location of the omissions within the drum pattern, S1 was time-locked and baseline corrected separately for each comparison to the time point at which the comparison pattern deviated from S1. 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. That is, 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. Similarly, as S4 patterns could not be followed by a D1 pattern by design, only 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.

2.4.2. 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 analysed with Linear Mixed Models (LMM) using the *lme4* package (version 1.1-7) in R version 3.1.2 (Bates, Maechler, & Bolker, 2012). Before analysis, the fixed factors Baseline and Trial were centred 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 was omitted whereas 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 & Rouder, 2014). We will denote the evidence for H_0 over H_1 as BF_{01}.

3. Results

3.1. Pupil Dilation Results

Figure 2 and Figure 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 to 660 ms after omission onset ($t_{\text{crit}} = 3.18$, *p*s < .027; Figure 2A). In contrast, no differences were found between D2 and S1 (t_{crit} = 3.18, *p*s > .91; Figure 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 > 0.21), 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 S1 and both D1 and D2 in the Control blocks (t_{crit} = 2.99 and 2.95 respectively, *p*s > 0.93; Figure 2C and 2D), showing that the deviating pupillary response to D1 and (if an effect 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 1. The model for the AUC of the deviants showed a significant negative effect of Trial (β = -5.25, *t* = -5.65, $p < .001$) and Baseline (β = -139.31, *t* = -35.25, $p < .001$), 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 (β = -2.55, *t* = -2.19, *p* = .029), 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 (β = 1.41, *t* = 0.90, BF_{01} = 164).

Overall, General Musical Sophistication was not a significant predictor of the AUC of the deviants (β = 0.18, *t* = 0.42), nor a predictor of the difference in AUC between D1 and D2 (β = -0.17, *t* = -0.10). Bayes factor analysis showed that a model excluding the main effect of General Musical Sophistication and its interaction with Pattern was preferred over the model including these factors with BF_{01}= 19, providing strong evidence (Jeffreys, 1961)

Table 1. Average AUC of the difference waves per pattern and condition.

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

for the view that the musical sophistication does not predict the pupillary response. Thus, more musical participants did not show a larger pupil dilation in response to deviants than less musical participants. Furthermore, musicality 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 $BF_{01} = 4405$, 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 > .12). The model without Musical Sophistication was preferred over the model including Musical Sophistication with $BF_{01} = 665$, providing, again, decisive evidence against including musical sophistication as a predictor for the pupillary response.

3.2. 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 ($t(37.9) = -0.28$, $p = 0.78$ and $t(34.4) = 0.63$, $p = 0.54$ respectively).

4. Discussion

In this study, we have investigated whether participants perceived beat and the hierarchical aspects of meter 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 (Ladinig et al., 2009; Winkler et al., 2009; Bouwer et al., 2014), 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 (Geiser et al., 2009; Chapin et al., 2010), 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 musicality, we did not find an effect of musicality on the pupillary response to omissions at the different metrical positions, nor did musicality have an effect on the difference in dilation between D1 and D2.

4.1. 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 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 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 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 should 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 musicality 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 musicality needs to be better specified. For example, Cicchini, Arrighi, Cecchetti, Giusti, and Burr (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.

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 musicality.

4.2. 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 (2014), 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 et al. (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 (NA) activity than frequent stimuli (Dayun and Yu, 2006; Alexinsky et al., 1990). In this way, the current study delivers further support for the proposed role of the LC-NA system as a signaller 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 signalling 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. However, 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 responsiveness of the pupil to the auditory information. 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.

5. 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 musicality, 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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