Mechanisms of short interval timing: How temporal structure modulates the perception of duration

by

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Abstract

Keeping track of time is a fundamental challenge the brain needs to accomplish to successfully interact with the environment. However, perceived time is not equivalent to physical time. Disentangling influencing factors and quantifying resulting distortions of time and duration perception gives important insights into underlying computational and neural mechanisms. This thesis focuses on the modulation of short interval duration estimates by the internal temporal structure of the interval. Chapter 1 introduces contemporary models, research paradigms and findings, and outlines distortions due to temporal structure as a promising research direction. The experiments described in Chapter 2, 3 and 4 use psychophysics to systematically investigate the influence of the temporal arrangement of interval fillers. It is shown that temporal regularity and predictability lead to a robust overestimation of duration. This may be explained via a logarithmic accumulation of perceived over physical time or increased neural response magnitudes toward regular stimulation due to neural entrainment. Chapter 5 reports an experiment using electroencephalography (EEG) which gives evidence for a neural response magnitude account by showing a direct relationship between the overestimation of regularity and entrainment strength. Chapter 6 summarizes the findings and puts them into a broader context of temporal and general perceptual processing.

Acknowledgments

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List of Publications and Contribution

During the course of my doctoral studies at the University of Birmingham, the following work was published or has been presented at conferences.

Published Articles

Horr, N. K., & Di Luca, M. (2015a). Taking a long look at isochrony: Perceived duration increases with temporal, but not stimulus regularity. *Attention, Perception and Psychophysics*, 77, 592–602.

Horr, N. K., & Di Luca, M. (2015b). Filling the blanks in temporal intervals: The type of filling influences perceived duration and discrimination performance. *Frontiers in Psychology*, 6, 114.

Horr, N. K., & Di Luca, M. (2015c). Timing rhythms: Perceived duration increases with a predictable temporal structure of short interval fillers. *Plos One*, 10, e0141018.

Horr, N. K., Wimber, M., & Di Luca, M. (2016). Perceived time and temporal structure: Neural entrainment to isochronous stimulation increases duration estimates. *Neuroimage*, 132, 148–156.

Conference Presentations

Horr, N. K., & Di Luca, M. (April 2014). Perception of duration with irregularly filled intervals. *International Conference on Timing and Time Perception (ICTTP 2014)*, Corfu, Greece.

Horr, N. K., & Di Luca, M. (March 2015). Taking a long look at rhythms: Distortions of perceived duration due to the temporal structure of interval filling. *57th Conference of Experimental Psychologists (TeaP 2015)*, Hildesheim, Germany.

Horr, N. K., & Di Luca, M. (July 2015). Timing Rhythms: Stimulus grouping distorts short interval duration perception. *15th Rhythm Production and Perception Workshop (RPPW 2015)*, Amsterdam, Netherlands.

Horr, N. K., & Di Luca, M. (August 2015). Mechanisms of short interval timing: The influence of interval filling on perceived duration and discrimination performance. *38th European Conference of Visual Perception (ECVP 2015)*, Liverpool, UK.

Horr, N. K., Wimber, M., & Di Luca, M. (September 2015). Perceived duration of isochronous sequences: Is there a link between neural entrainment and temporal judgments? *Entrainment of Brain Oscillations Conference*, Delmenhorst, Germany.

Contribution

I took the major part in study design, programming of experimental paradigms, data collection, analysis and manuscript writing of all the studies reported in this thesis. Coauthors listed advised and edited.

Chapter 1

Introduction and Overview

1.1 Aspects of psychological time and focus of the present thesis

The concept of psychological time does not refer to a unified system or process, but entails a multitude of mechanisms related to the perception of temporal stimulus characteristics. Besides stimulus duration these include, for example, onset, offset, temporal order and synchroneity (for a recent overview see Grondin, 2010). The brain's ability to process temporal aspects of stimuli and to keep track of time is crucial for connecting the plethora of incoming sensory information to a coherent percept, for making predictions about upcoming stimulus events that allow an efficient allocation of attentional resources, for action preparation and accurately timed execution and therefore ultimately for a successful interaction with the environment. In praxis, humans perform remarkably well when it comes to temporal judgments (e.g., Allan, 1979). However, estimates of time are prone to many illusions and distortions demonstrating that psychological time is by no means equivalent to physical time (e.g., Allan, 1979; Eagleman, 2008). Both the diversity of sensory and cognitive functions falling into the realm of time perception and the lack of a single dedicated sensory organ or brain network for temporal estimation, makes it difficult to disentangle underlying mechanisms. Therefore, despite the ubiquity of temporal processing in everyday perception and action, the question of how the brain is able to keep track of time, is still far from understood.

The present thesis focuses on duration as the temporal stimulus characteristic of interest. However, further distinctions are needed in the research field of duration perception. One important basis of distinction is according to the range of time intervals in question. Different

mechanisms of estimating duration have been suggested for intervals in the sub-second in contrast to the supra-second range. While sub-second intervals seem to be processed mainly in a sensory, that is, automatic fashion, processing of supra-second intervals is thought to be influenced by cognitive control and requires cognitive resources (e.g., Rammsayer & Lima, 1991). Findings on a neural level suggest automatic timing to be based on a network of motor areas while cognitive timing involves higher level cortical regions like the parietal and prefrontal cortex (e.g., Lewis & Miall, 2003). This speaks in favor of strongly differing temporal processing strategies for sub- and supra-second intervals. Three to seven seconds marks another cut-off point in the duration perception literature. This time span has been suggested to give rise to the subjective experience of "now", in which direct sensory information are kept and compared in working memory. Longer time spans may no longer be linked to a single experience of the present moment (e.g., Block & Gruber, 2014; Pöppel, 1997). Gruber and Block (2013), for example, showed that if a sequence of stimuli is presented with an interstimulus interval (ISI) of more than three seconds, the subjective experience of an event happening is giving way to a mere knowing that changes occurred. Also for intervals longer than a few seconds, temporal perception is far from continuous and several breaks that indicate a switch of underlying mechanisms have been found in longer interval ranges (e.g., Eisler, Eisler, & Hellström, 2008).

Beyond the interval range in question, another fundamental distinction in the field of duration perception is made between prospective in contrast to retrospective estimates. In prospective duration judgments the judging individual knows in advance that temporal perception is the focus of the given task and that he or she will be asked to make some kind of duration estimate on the stimuli or events presented. In retrospective duration judgments the individual is naive to the relevance of temporal aspects in the given task and is not aware that he or she will later have to give an estimate based on those (see e.g., Grondin, 2010). Block

and Gruber (2014, p.2) depicted this distinction as "experienced versus remembered" time. In prospective judgments (experienced time) attentional mechanisms play an important role and a lot of theoretical and empirical work has been done to disentangle their specific influence (e.g., Brown, 1997; Hicks, Miller, & Kinsbourne, 1976; Taatgen, Van Rien, & Anderson, 2007; Thomas & Weaver, 1975; Zakay & Block, 1997). Retrospective temporal judgments (remembered time) on the other hand are strongly linked to memory processes (e.g., Block, & Gruber, 2014; Zakay & Block, 2004).

For my doctoral research, I was interested in disentangling basic computational and neural mechanisms of duration perception with as little as possible influence of additional cognitive processes like executive functions or memory. The focus of this thesis is therefore on short intervals in the sub-second to second range and on prospective duration estimates. Due to its superior temporal resolution (e.g., Burr, Banks & Morrone, 2009; Vroomen & Keetels, 2010) the auditory modality is specifically suitable to study psychological time. In all of the present experiments auditory sequences are used to demarcate the intervals on which duration judgments are based. The experiments described in Chapter 2–4 use psychophysics in order to calculate participants' accuracy and duration discrimination performance with auditory sequences of varying temporal structure. The experimental tasks follow a two-interval-forced choice manner by asking participants to determine which of two presented intervals is the one longer in duration. It is discussed which kinds of models of duration perception may be in line with the observed perceptual variations due to temporal structure. The experiment reported in Chapter 5 makes use of electroencephalography (EEG) to take a closer look at the neural mechanisms that may underlie the distortions observed in Chapter 2–4. The remains of Chapter 1 will give a brief and non-exhaustive overview over core models, methodologies and experimental findings that form the theoretical background to my experimental work on perceived duration distortions due to temporal structure and underlying

computational and neural mechanisms. According to the focus of the present thesis the reviewed approaches, methods and findings are not necessarily limited to prospective short-interval timing, but all apply to it and are presented in this respect.

1.2 Contemporary models of time and duration perception

Two basic ideas of how the processing of duration and other temporal stimulus characteristics is implemented in the brain have been suggested and form two fundamental classes of models on temporal perception, the dedicated as opposed to the intrinsic models (for an overview see Ivry, & Schlerf, 2008). Dedicated models assume that there are specific brain modules, networks or mechanisms dedicated to temporal processing. Intrinsic models on the other hand propose that temporal processing and perception evolves from more general brain mechanisms, not dedicated or even specifically related to timing.

1.2.1 Dedicated models

First and still highly popular approaches to explain duration perception via a dedicated process are internal clock models (e.g., Matell & Meck, 2000; Treisman, 1963), also termed interval models (e.g., McAuley & Jones, 2003; Pashler, 2001), in which the clock is represented by an accumulator counter mechanism. Such models assume one or more accumulator counter clocks that can be – at arbitrary points – started and stopped due to stimulus input. Interval duration is then estimated in a comparison process between the count for the current interval and a reference in memory. The most prominent and most frequently investigated example of an accumulator counter model is the scalar timing theory (or scalar expectancy theory, SET). Scalar timing, which the SET was set out to account for, is the linear increase of the standard deviation of duration estimates with an increase in their mean, a phenomenon that is, at least within limited time ranges, robustly observed in the duration literature (e.g., Gallistel & Gibbon, 2000; Gibbon, 1992). Originally developed as an animal

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model of time perception (e.g., Church, Meck, & Gibbon, 1994; Gibbon, 1977; Lejeune, Ferrara, Simons, & Wearden, 1997), the SET has by now proven successful in explaining and predicting a multitude of human time perception data and in this context has been modified and developed further (e.g., see Allan, 1998 and Wearden, 2003). The SET assumes three basic cognitive components of temporal perception – an internal clock, a memory process and a comparison process. The internal clock consists of a pacemaker continuously sending pulses at a certain rate to an accumulator. The flow of pulses from pacemaker to accumulator is controlled by a switch that is opened and closed by stimuli serving as time interval markers. The pulses that reach the accumulator are transferred forward to a working memory store from where they are compared to reference memory. This memory store is continuously updated by experience with temporal information. Comparing the content of working memory and reference memory according to a specific comparison process the subject eventually comes to his or her temporal judgment. The attentional gate model (AGM, e.g., Zakay, & Block, 1997) adds onto the basic SET framework to account for findings on the influence of attention in duration perception (e.g., Brown, 1985; Brown, 1997; Burle & Casini, 2001). It assumes a gate controlled by attentional mechanisms between the pacemaker and the accumulator. For a detailed account of SET see for example Gibbon and Church (1990), for an overview over further accumulator counter models see for example Grondin (2001).

Basic accumulator counter accounts explain timing mechanisms on a computational level. It is not straight-forward to find a biologically plausible neural representation for an internal clock following the criteria outlined in these models. Several neural implementations (see Meck & Benson, 2002 for an overview) have been suggested, for example along the lines of single cells or cell assemblies that keep track of timing via ramping activation (e.g., Merchant, Harrington & Meck, 2013). However, some assumptions of accumulator counter models, like the idea of an unbounded accumulation process, have been fundamentally

questioned regarding their biological plausibility (e.g., Matell & Meck, 2000). Alternative internal clock or interval models with a stronger biological foundation have been proposed. Such models keep the general structure of a resettable internal clock, a memory and a comparison process, but differ in basic principles regarding the functioning of the internal clock mechanism – and thereby the brain's ability to keep track of time. One of the most popular examples of a biologically founded internal clock model is the striatal beat-frequency model developed by Matell and Meck (2004) on the basis of earlier accounts (Miall, 1989). The beat-frequency model suggests the internal clock to be based on a coincidence detector of oscillatory phase. With stimulus input marking the beginning of an interval, the phase of neural oscillations from different neural populations is reset, so that all of them start at the same phase. As each neural population has its own dynamics, they become out of phase again with time passing. The role of the coincidence detector is then to read out the phase distribution at the end of the interval. The phase distribution is unique at any given point in time after interval onset, that is, after phase reset, and can therefore encode interval duration. Matell and Meck (2004) propose that structural and functional characteristics of the basal ganglia, which have been associated with timing behavior in multiple studies (e.g., Harrington, Haaland, & Hermanowicz, 1998; Lejeune et al., 1997), make latter an ideal candidate to act as a coincidence detector of cortical and thalamic neural oscillations. Multiple other models have been suggested, which, similar to the beat-frequency model, assume an internal clock that tracks time via unique neural signatures varying with interval duration. For example, dynamical changes of neural firing patterns (e.g., Grossberg & Schmajuk, 1989) or stages of memory decay (e.g., Staddon & Higa, 1999) may code for duration.

Not all dedicated models assume one or more arbitrarily resettable internal clocks linked to a memory and a comparison process to be the core of temporal processing. Rather than a mechanism that explicitly tracks interval duration from a beginning to an end point, beat-

based models (e.g., Keele, Nicoletti, Ivry, & Pokorny, 1989; Pashler, 2001) propose external stimulation to produce internal beats that are continued onward and provide a reference for future events. Entrainment models (e.g., Large & Jones, 1999; McAuley & Jones, 2003; McAuley & Kid, 1998), for example, put oscillatory mechanisms at the core of temporal perception. In contrast to the beat-frequency account (Matell & Meck, 2004) they, however, do not depend on a reset of oscillations at the beginning of the estimated interval. Dynamic attending theory (e.g., Jones & Boltz, 1989; Large & Jones, 1999), suggesting attention and therefore perceptual sensitivity to fluctuate with oscillatory phases, forms the basis of entrainment models of perceived timing. The crucial characteristic of oscillations in an entrainment model is that they gradually adjust their phase so that the temporally regular peak is placed where a stimulus is expected. Temporal prediction and estimation is then enabled by comparing the peak of the oscillatory process to the actual appearance of the stimulus (in time, too early or too late). Neural entrainment, that is, phase adjustment to regular external stimulation, has indeed been found as an ubiquitous phenomenon of neural oscillations (e.g., Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; see Henry & Herrmann, 2014 for a discussion on the connection between dynamic attending theory, entrainment models of perceived timing and neural entrainment). As changes of stimulus expectation lead to changes in the internal beat, beat-based models are suitable to explain how temporal sensitivity as well as perceived timing and duration of an interval may be dependent on the temporal structure the interval is embedded in. Internal clock and beat-based models are of course not mutually exclusive. In fact, empirical results hint at differential processing of absolute (interval-based) and relative (beat-based) temporal information (e.g., Ivry, Spencer, Zelaznik, & Diedrichson, 2002; McAuley & Jones, 2003; Pashler, 2001). Using functional magnetic resonance imaging (fMRI) Teki and colleagues (Teki, Grube, Kumar, & Griffiths, 2011) observe this distinction as well on a neural level. They propose an olivocerebellar network to be active when subjects

engage in absolute duration estimates in an irregular context and a striato-thalamo-cortical network when a regular/rhythmic context allows for relative duration judgments.

One aspect that all dedicated models have in common is the idea of modularity (e.g., Ivry, & Schlerf, 2008). That is, dedicated models assume duration estimation to underlie specialized timing mechanisms localizable in specific neural regions or networks. Some brain regions have been consistently associated with temporal processing as well in animals as in humans. A plethora of experimental findings and model simulations speak for an involvement of subcortical areas primarily associated with motor functions, that is, the cerebellum (e.g., Buonomano & Mauk, 1994; Medina, Garcia, Norres, Taylor, & Mauk, 2000; Perrett, 1998) and the basal ganglia (e.g., Harrington et al., 1998; Jin, Fujii & Graybiel, 2009; Lejeune et al., 1997; Matell & Meck, 2004). The thalamus is another subcortical region that seems to play a role in time and duration perception (e.g., Komura et al., 2001; Tanaka, 2007). On top of this, processing of temporal information has been located all over the cortex (prefrontal cortex: e.g., Oshio, Chiba & Inase, 2008; motor cortex: e.g., Renoult, Roux, & Riehle, 2006; premotor cortex: e.g., Lucchetti & Bon, 2001; supplementary motor area: e.g., Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2008; posterior parietal cortex: e.g., Leon & Shadlen, 2003; early sensory processing areas: e.g., Duysens, Schaafsma, & Orban, 1996; He, Hashikawa, Ojima, Kinouchi, 1997). Beyond brain regions, also a variety of event-related neurophysiological markers have been demonstrated to be responsive to duration and other temporal stimulus characteristics in different experimental tasks (N1 and P2, e.g., Kononowicz & Van Rijn, 2014; CNV, e.g., Pfeuty, Ragot, & Pouthas, 2005; MMN: e.g., Tse & Penny, 2006; P300: e.g., Gibbons & Rammsayer, 2005). In accordance with this wide range of temporally crucial markers, no particular frequency of neural oscillations seems to stand out in terms of temporal processing, but all major frequency bands have been reported to be involved in different kinds of timing situations (see Wiener & Kanai, 2016 for an

overview). The multitude of brain regions and neurophysiological correlates associated with time and duration perception of course, by themselves, do not speak against the basic idea of dedicated networks governing different aspects of temporal perception. However, they do demonstrate the diversity of temporal processing strategies and raise the question whether it is feasible to summarize different aspects of temporal perception in the framework of a centralized timing mechanism.

1.2.2 Intrinsic models

While dedicated models have a long tradition in temporal perception research, the idea of temporal processing being incorporated in brain mechanisms, that have neither evolved for nor are specialist regarding the processing of time, is a rather recent one (e.g., Ivry and Schlerf, 2008). The basic idea behind intrinsic models is that time and duration perception naturally originate from neural dynamics and thereby form an inherent base of brain functioning rather than one or multiple specialized mechanisms. Note that the distinction between dedicated and intrinsic models is not as clear as their definition may suggest. In fact, many of the basic mechanisms reviewed in the previous section, though initially described as specialized processes to enable time and duration perception, could, at least with few alterations, be considered as inherent brain dynamics that serve other functions, but due to their basic processing characteristics show the natural ability to keep track of time.

One explicitly intrinsic proposal how non-specific brain activation might give rise to duration estimates is such estimation being based on the magnitude of neuronal activity elicited during an interval (e.g., Eagleman & Pariyadath, 2009; Lebedev, Doherty & Nicolelis, 2008; Matthews et al., 2014; Reutimann et al., 2004). If we assume that the magnitude of neural activity is, at least partly, determined by the stimulation during the interval, this account could explain a couple of behavioral findings that suggest a relationship between perceived duration and variables representing the magnitude of the stimulation like number of

stimuli presented in the interval (e.g., Buffardi, 1971), stimulus intensity (e.g., Berglund, Berglund, Ekman & Frankenhaeuser, 1969) or size and number of elements in a spatial display (e.g., Xuan, Zhang, He, & Chen, 2007). Considering the phenomenon of repetition suppression (e.g., Fahy, Riches & Brown, 1993; Rainer & Miller, 2000), that is, the decrease of neural activation toward repeated stimulation, a magnitude approach is further in line with findings that demonstrate a decrease in perceived duration due to repeated or prolonged stimulation (e.g., Efron, 1970; Pariyadath & Eagleman, 2008) and an overestimation of oddball, that is, rare, as compared to standard, that is, frequent, stimuli (e.g., Birngruber, Schröter & Ulrich, 2014; Kim & McAuley, 2013).

Alternatively, interval duration may be extracted from neural network states that systematically change over time (e.g., Buonomano, 2000; Mauk & Buonomano, 2004). As opposed to the notion of a dedicated internal clock encoding duration based on changes from the beginning of the estimated interval, such a state dependent network (SDN) would not provide a linear metric of time and would not give an absolute representation of any given interval duration. An SDN would therefore predict perceived duration to be strongly contextual. Such contextuality is well in line with experimentally observed distortions of perceived duration, for example, due to the stimulation preceding the interval (e.g., Karmakar & Buonomano, 2007).

Intrinsic estimation of duration may either be enabled by neural regions and networks sustaining their activation in absence of stimulus input or may be dependent on neural activation that arises from specific, for example sensory, processing networks (e.g., Burr, Tozzi, & Morrone, 2007). A dependency on stimulus processing networks would give a plausible explanation for perceived duration differing between different stimulus modalities (see for example Grondin, 2003 for an overview on such differences). Also the finding that changes of perceived duration due to adaptation is tuned to the retinotopic location of the

stimulus (e.g., Ayhan, Bruno, Nishida, & Johnston, 2009; Johnston, Arnold, & Nishida, 2006) speaks for multiple specific networks rather than one general activation trace encoding interval duration. If we assume temporal processing to be an intrinsic characteristic of neural circuitry, any neural network could potentially be involved in time and duration estimates and which specific regions will be found in experimental studies is simply dependent on the choice of task and stimulation during and previous to the estimated intervals (e.g., Mauk & Buonomano, 2004).

1.2.3 Summary and reflection

To the current point, none of the models proposed to explain time and duration perception on a conceptual, computational or neural level can be considered superior and hardly any two models are, in principle, mutually exclusive. All models have their specific strengths and weaknesses when it comes to explaining experimental results on different aspects of short-interval prospective duration judgments. Assuming that internal states as well as external stimulus characteristics or task requirements can change pacemaker pulse frequencies and switch latencies, many observed distortions of duration perception could be modelled successfully with the SET or related accounts (e.g., Allan, 1998; Burle & Casini, 2001; Klink, Montijn, & van Wezel, 2011; Wearden, Norton, Martin, & Oliver, 2007). However, other authors are stressing the shortcomings of this approach and point out how certain empirical findings can better be understood without the assumption of an accumulator counter (e.g., Grossberg & Schmajuk, 1989; Matell & Meck, 2004; Staddon & Higa, 1999), a resettable clock (e.g., McAuley & Jones, 2003; Schulze, 1978) or even without any dedicated timing mechanism (e.g., Karmarkar & Buonomano, 2007; Spencer, Karmarkar & Ivry, 2009). Furthermore, it is still a matter of debate as to what extent different observations on short interval duration perception can be explained in one coherent framework and where conceptual and mechanistic distinctions need to be made. A deeper understanding of the

possibly multiple mechanisms underlying duration perception and their connective elements requires further empirical research aiming at an integration and conceptual clarification of different levels and approaches to temporal processing.

1.3 Psychophysical methods to investigate duration perception

Psychophysical methods in duration perception research disentangle the relationship between perceived and physical time and quantify factors that lead to duration distortions. They thereby provide an empirical basis for developing conceptual and computational models of time and duration perception and are necessary to trace down both biologically and experimentally plausible neural mechanism. Multiple different paradigms have been applied to investigate characteristics and influencing factors of short interval duration judgments in human participants (for an overview see Grondin, 2010). According to the focus of the present thesis the following chapter will review commonly used methods concerned with prospective duration estimates, that is, in which the participant knows in advance that a judgment on duration will be required during or after stimulus presentation.

1.3.1 Experimental paradigms

The most straightforward paradigm of investigating duration perception is verbal estimation. In a verbal estimation task the participant is presented with an interval and gives his or her duration estimate via a value in a commonly used temporal unit like milliseconds or seconds (e.g., Ihle & Wilsoncroft, 1983). Vice versa, in a production task the participant may be given a duration in a common temporal unit and has to produce it, for example, via timed button pressing (e.g., Brown, 1995). The inherent problem of these methods is, however, that participants have to use an arbitrary unit as reference and it remains unclear whether distortions come from actual changes in perceived timing of the target interval or distortions in the reference itself (e.g., Zakay, 1990). One paradigm that overcomes this problem is the

method of reproduction (e.g., Schiffmann & Bobko, 1977). Here, the participant is presented with the target interval and, rather than stating its duration verbally, has to reproduce it, again, for example, via timed button pressing. Note that results from verbal estimation and production or reproduction paradigms have to be interpreted in opposite directions: While for verbal estimation duration is obviously overestimated when higher values are reported, increased duration of produced or reproduced intervals reflect the underestimation of duration (e.g., Penton-Voak, Edwards, Percival, & Wearden, 1996). This is because, if time seems to be passing quicker (overestimation of duration), the participant will feel that the interval to be produced matches the reference after a shorter physical time span than if time seems to be passing slower (underestimation of duration).

Besides methods focusing on the estimation or production of one interval, many commonly used paradigms are based on duration comparisons with two or more intervals being judged against each other (see Grondin, 2010 for an overview and classification). In single stimulus paradigms participants are first familiarized with one or more standard stimuli and then are presented one interval per trial, which they have to compare to the memorized standards. In a temporal bisection task (e.g., Allan & Gerhardt, 2001), for example, there is a long and a short standard and participants have to respond in every trial whether the target interval is closer to either one or the other. In a temporal generalization task (e.g., Wearden, 1992) only one standard is presented and participants simply have to state whether the target interval is of equal or different duration compared to this standard.

While in single stimulus paradigms the standard has to be kept in memory, duration discrimination approaches present participants with two intervals in every trial and they have to decide either whether the two are similar in duration or which of the two is the longer (or shorter) one. It is possible to always present the non-varying standard interval first and the comparison interval second. This improves participants' performance (e.g., Grondin &

McAuley, 2009; Lapid, Ulrich, & Rammsayer, 2008), however it leads to a bias due to stimulus order, the so-called time-order error, with the second stimulus being overestimated as compared to the first one (e.g., Allan, 1977; Hellström, 2003). To diminish order as a confounding factor the presentation of standard and comparison intervals as first or second can be randomized. A discrimination task with randomized interval order and two response alternatives (first interval or second interval being the longer or the shorter one) is called two-interval forced-choice task (e.g., Yeshurun, Carrasco, & Maloney, 2008). Of course, discrimination paradigms can also be implemented with more than two intervals or response alternatives per trial, though this seems rather rare in the duration perception literature. For example, Phillips and colleagues (Phillips, Gordon-Salant, Fitzgibbons, & Yeni-Komshian, 1994) presented participants with three intervals per trial and had them report which one differed from the other two in duration.

All experiments reported in the present thesis use a two-interval forced-choice task, in which participants are presented with two stimulus sequences per trial and have to decide via button pressing which of the two is longer in duration. Different types of stimulus sequences (for example, temporally regular and temporally irregular ones) are compared and their order as well as their assignment to standard (always one second) or comparison (between 500 and 1500 ms) are counterbalanced and pseudorandomized.

1.3.2 Analysis of perceived duration accuracy and precision

On the basis of data from the described duration judgment paradigms a psychometric function that relates perceived to physical duration can be created (see e.g., Klein, 2001 for a detailed explanation of psychometric functions, fitting and parameter estimation). Specifically, in a two-interval forced-choice task, as used in the present thesis, the physical duration difference between standard and comparison or different interval types would be plotted on the x-axis and the proportion of judging interval A to be longer than interval B on the y-axis. From these

response proportions two measures can be derived: The point of subjective equality (PSE) and the just noticeable difference (JND).

The PSE measures the accuracy of perceived duration, that is, to what extent duration estimates differ systematically from physical duration. In a two-interval forced choice task the PSE is the physical duration difference at which the proportion of judging interval A as longer than interval B is 50% and therewith the point on the physical duration axis at which participants are guessing because they perceive the two intervals as of equal duration. If the PSE is not significantly different from zero there is no distortion between the perceived duration of the two intervals, that is, the intervals are perceived to be equal when they are actually of equal physical duration. If the PSE is significantly higher or lower than zero this hints at an overestimation of the duration of one as compared to the other interval type.

The JND in turn is a measure of precision or, in case of a two-interval forced choice task, duration discrimination performance. The JND can be conceptualized as the variability of duration judgments, that is, the steepness of the curve or the difference in physical duration for two fixed points on the y-axis (e.g., 75% minus 50% judging one interval type as longer than the other one). Higher JND values, that is, higher variability of duration discrimination judgments and a flatter psychometric curve, indicate an overall worse performance.

There are many different approaches to calculate the PSE and JND (for an overview see Klein, 2001; Wichmann & Hill, 2001a; Wichmann & Hill, 2001b). The approach used in the present thesis is the Spearman-Kärber Method (Miller & Ulrich, 2001; Ulrich & Miller, 2004). The Spearman-Kärber Method does not make any specific assumptions regarding the form of the psychometric function, solely that it is monotonously increasing. It fits in the proportion values between every two stimulus levels, that is, physical duration differences, and adds a beginning and an end level at which the proportions of responding interval A to be longer are set to 0% and 100% respectively. The PSE and JND are then defined as the first

and second moment of the distribution underlying each participant's response proportions. With s_{1-k} being stimulus levels (physical duration difference between the two compared intervals) and p_{1-k} being response proportions for each stimulus level, PSE and JND can be calculated analytically as:

$$PSE = \sum_{i=1}^{k} \frac{(p_i - p_{i-1})}{2}(s_i - s_{i-1})$$

$$JND = \sqrt{\sum_{i=1}^{k} \frac{(p_i - p_{i-1})}{2}((s_i - s_{i-1}) - PSE)^2}$$

Accuracy (PSE) and precision (JND) of temporal estimates in different experimental conditions does not only give insights into general human time keeping abilities and limitations, but also into factors that lead to the subjective over- and underestimation of duration or changes in sensitivity. The present thesis is focused on the measurement of duration distortions and changes in discrimination performance due to the manipulation of temporal interval structure and the implications of such for computational and neural mechanisms of duration perception.

1.4 Distortions of perceived duration

Numerous findings on systematic distortions in duration estimates demonstrate that the physical and perceived passage of time are not equivalent. Rather than solely depending on physical interval duration, perceived duration is strongly influenced by the context in which the interval is presented as well as temporal and non-temporal characteristics of stimuli demarcating and filling the interval.

An impressive demonstration of the relativity of perceived duration is the so-called temporal order error leading to a bias toward perceiving the second stimulus in a two-interval comparison task as longer than the first one (see e.g., Allan, 1977; Hellström, 2003).

Furthermore duration estimates of any given interval are influenced by the duration of earlier and to a lesser degree even later presented distractor intervals (e.g., Burr, Della Rocca, & Morrone, 2013; Nakajima, Ten Hoopen, Hilkhuysen, & Sasaki, 1992). Such findings show that the estimated duration of an interval, even if making no changes to its form or presentation, is modulated solely by the context it is presented in. Subjective internal states have also been shown to modify perceived duration. For example, increasing arousal levels lead to an overestimation of respective intervals (e.g., Droit-Volet, Brunot, & Niedenthal, 2010; Penton-Voak et al., 1996).

When manipulating non-temporal characteristics of a stimulus to be judged in duration, experimental results hint at the presentation of complex spatial patterns to be perceived as longer than simpler ones (e.g., Schiffman & Bobko, 1974). Stimulus familiarity, repeated stimulation and predictability of the upcoming stimulus on the other hand decrease subjective duration judgments (e.g., Avant, Lyman, & Antes, 1975; Pariyadath, & Eagleman, 2007). Moving stimuli are perceived as longer than stationary ones and this effect increases with an increase in movement speed (e.g., Brown, 1995), but can also be modified by other movement patterns (Matthews, 2011). Besides those and many other unimodal stimulus characteristics (see, e.g., Allan, 1977; Eagleman, 2008; Grondin, 2010 for an overview), stimulus modality as well plays a remarkable role in duration perception. For example, auditory stimuli are perceived as longer than visual stimuli (e.g., Goldfarb & Goldstone, 1964; Goldstone & Lhamon, 1974) and visual stimuli are perceived as longer than tactile stimuli (e.g., Tomassini, Gori, Burr, Sandini, & Morrone, 2011).

Duration estimates may be based not only on the presentation of one stimulus display, but on intervals marked by one, two or multiple stimuli. Investigating intervals made up of multiple stimuli, the probably best-known and studied distortion is the filled duration illusion (e.g., Hasuo, Nakajima, Tomimatsu, Grondin, & Ueda, 2014; Rammsayer & Lima, 1991;

Thomas & Brown, 1974; Wearden et al., 2007): Filled intervals are perceived as longer than empty intervals. Filled intervals are intervals containing sensory input. This can be in form of a continuous stimulus lasting during the entire interval or in form of sequences of filler stimuli with the first and last one marking the beginning and the ending of the interval. Empty intervals, on the other hand, do not contain any sensory input. They are either marked solely by an onset and offset stimulus or by a gap in a continuous stimulus. Extending on the filled duration illusion, it has been shown that the more filler stimuli there are between the onset and offset of a filled interval, the longer it is perceived (e.g., Buffardi, 1971). Stimuli in the beginning of the interval have a stronger influence on this filler effect than stimuli in the end of the interval (Adams, 1977; Goldstone & Goldfarb, 1963; Schiffman, & Bobko, 1977).

Little research has been done on whether and how the temporal structure of interval fillers modulates perceived duration. This is surprising given the crucial role of temporal structure in perceptual processing (e.g., Rohenkohl, Cravo, Wyart, & Nobre, 2012). Regarding duration perception, Matthews (2013) demonstrated that temporally regular sequences are perceived longer than accelerating or decelerating ones, while the specific effect of acceleration and deceleration depends on the overall range of interval duration. Thomas and Brown (1974) and Grimm (1934) gave preliminary evidence for an overestimation of temporally regular as compared to irregular stimulation. Interestingly, results on non-temporal factors seem to suggest simple patterns and predictability of upcoming stimulus characteristics to decrease perceived duration (e.g., Pariyadath & Eagleman, 2007; Schiffmann & Bobko, 1977). Preliminary evidence on the role of temporal structure may therefore hint at a special role of temporal regularity and predictability in perceived duration – in line with its special role in other areas of sensory processing.

A main criterion when evaluating and comparing different models of perceived duration should be their capability to predict and explain empirical findings like the ones reviewed

above. Investigating and integrating distortions of perceived duration is therefore essential for the advance toward realistic models of time and duration perception. While previous research placed its emphasis on the role of context-sensitivity, non-temporal stimulus characteristics, and the amount of interval filling, the present thesis is systematically investigating how the temporal structure of interval fillers in a sequence influences this sequences' perceived duration and what implication the observed distortions have for underlying mechanisms.

1.5 Overview of the present thesis

In the present thesis, I will present my doctoral research focused on computational and neural mechanisms of short-interval duration perception as revealed by distortions of perceived duration due to the temporal structure of filler stimuli.

In Chapter 2, three psychophysical experiments investigating distortions in the perception of interval duration due to complete regularity in time (isochrony) are presented. It is shown how isochrony as compared to random jittering of stimulus arrival times (anisochrony) prolongs the perceived duration of an interval, while regularity concerning non-temporal stimulus characteristics (sound amplitude and sound frequency) does not lead to any distortions. The striking effect of isochrony can be explained in the framework of an internal clock or interval model (e.g., Matell & Meck, 2000; Treisman, 1963) when a logarithmic relationship between physical and perceived time is assumed. Alternatively, the isochrony effect may be in line with the previously proposed relationship between perceived duration and neural response magnitudes (e.g., Eagleman & Pariyadath, 2009), as neural entrainment to regular stimulation can be expected to maximize neural responses toward isochronous intervals (e.g., Schroeder & Lakatos, 2009).

In Chapter 3, two psychophysical experiments that investigate discrimination performance and perceived duration in different types of filled intervals (continuous, isochronous and anisochronous) and empty intervals (demarcated by a beginning and an end

marker) are presented. The results show continuous and isochronous intervals to be discriminated better than empty intervals, while discrimination performance for anisochronous intervals is worst. The overestimation of filled as compared to empty intervals (filled duration illusion, e.g., Thomas & Brown, 1974) is shown to be stronger for stimulus sequences, both isochronous and anisochronous, than continuous intervals. The overestimation of isochronous as compared to anisochronous intervals is replicated. Further analysis of the data demonstrates that duration estimates heavily depend on dynamics between the intervals to be compared. It is hypothesized that this may be because different cues for duration estimation are available for the different interval types and such cues may determine the specific mechanisms used for comparing the two intervals.

Chapter 4 presents two psychophysical experiments on the distinct influence of different fully predictable rhythms. A general overestimation of rhythms as compared to anisochronous sequences is observed. No significant difference between perceived duration of isochrony and rhythms can be found, but the perceived duration bias differ between different rhythm types with a tendency to overestimate isochrony. The results can be modelled using a non-linear clock model as described in Chapter 2. Similarly, as proposed in Chapter 2, the finding of temporal predictability resulting in a perceptual increase of interval duration may be explained by increased neural response magnitudes due to neural entrainment.

Chapter 5 reports an EEG experiment in which the connection between neural entrainment and duration estimates as suggested in Chapter 2 and 4 are tested. Entrainment to isochronous sequences in the stimulation frequency (4 Hz) and its second harmonic (8 Hz) is demonstrated. Most interestingly, physically identical isochronous intervals show stronger 4 Hz entrainment when perceived as longer than when perceived as shorter and this effect is correlated with participants' PSE, that is, their subjective bias toward overestimating isochronous intervals. The EEG results therefore give evidence for a connection between

neural entrainment and perceived duration. Following a neural response magnitude approach of perceived duration, neural response magnitudes are proposed as the link between entrainment and duration perception.

Chapter 6 gives a summary over the present findings on duration distortions due to temporal structure and its implications for underlying computational and neural mechanisms. The results are then discussed in a broader context of models explaining temporal as well as general perceptual processing. Finally, limitations of the approaches proposed to explain the observed effect of regularity and predictability are pointed out, open questions are raised and an outlook on how the present data can serve as a starting point for future research on the role of temporal structure in time perception is given.

Chapter 2

Taking a long look at isochrony: Perceived duration increases with temporal, but not stimulus regularity

Three experiments that investigate duration distortions due to temporal regularity (isochrony) as compared to irregularity (anisochrony) are reported. It is shown that isochronous intervals are overestimated as compared to anisochronous intervals, an effect increasing with the level of anisochrony (Experiment 1). The isochrony effect is present over a wide range of stimulation rates, as defined via the number of stimuli in each of the one second standard intervals (Experiment 2), and is genuinely based on temporal interval structure, as manipulation of the regularity of non-temporal stimulus characteristics does not lead to distortions (Experiment 3). The results are discussed in the framework of a logarithmic clock model as well as a neural response magnitude approach of perceived duration with response magnitude being modulated by entrainment.

2.1 Abstract

A commonly observed phenomenon to elucidate distortions of perceived duration is the filled-duration illusion: a temporal interval delimited by two marker signals is perceived to be shorter than the same interval with several identical filler signals. Previous investigations have focused on regularly spaced (isochronous) fillers and the influence of their temporal structure has not been considered. We find that intervals with isochronous fillers are perceived to last longer than their anisochronous counterparts. The illusion increases with the amount of deviation from isochrony and with the number of fillers. Findings also indicate that perceived duration is specifically affected by temporal irregularities, as randomization of the fillers' sound amplitude or frequency does not cause an appreciable distortion. These results can be accounted for by both pacemaker-accumulator models and entrainment models.

2.2 Introduction

Stimulus duration is not always perceived veridically, because it depends on many factors beyond physical time (see Allan, 1979 for a classic and Grondin, 2010 for a recent review). For example, non-temporal stimulus characteristics, such as familiarity (e.g., Devane, 1974; Witherspoon & Allan, 1985), complexity (e.g., Schiffman, & Bobko, 1974), sensory modality (e.g., Goldstone & Lhamon, 1974; Wearden, Todd & Jones, 2006), and context (e.g., Dyjas & Ulrich, 2014; Hellström, 2003), influence perceived interval duration. Disentangling the principles and mechanisms underlying such effects is crucial for the development of a realistic model of temporal perception.

A striking source of distortions in perceived duration is due to the filling of the interval to be judged. A long-known phenomenon, which has been replicated with several experimental variations, is the filled-duration illusion whereby filled intervals are perceived to last longer than empty intervals of the same duration. Empty intervals in this context can be intervals defined solely by a beginning and an end marker (e.g., Rammsayer & Lima, 1991), but can also be implemented as a gap in an otherwise continuous signal (e.g., Rammsayer & Leutner, 1996; Wearden et al., 2007). Filled intervals, instead, can be continuous signals (e.g., Hasuo et al., 2014; Rammsayer & Lima, 1991) or intervals consisting of a number of regularly spaced fillers (e.g., Adams, 1977; Buffardi, 1971; Thomas & Brown, 1974).

In comparison to the multitude of studies addressing the filled-duration illusion, there is surprisingly little research investigating whether and how filler characteristics and temporal structure influence duration judgments. One of the few exceptions are findings showing that perceived duration increases with the number of fillers and that fillers presented toward the beginning of the interval lead to longer perceived duration than fillers presented toward the end (e.g., Adams, 1977; Buffardi, 1971; Goldstone & Goldfarb, 1963; Schiffman & Bobko, 1977). Furthermore, Grimm (1934) asked participants to compare regularly and irregularly

spaced intervals of the same physical duration and found that regularly spaced intervals are more frequently judged as longer in a three alternative task (longer, shorter, or equal). Using a temporal reproduction task, Thomas and Brown (1974) failed to observe a significant difference in perceived duration between regular and irregular intervals, although there were more responses indicating shorter irregular stimuli. Matthews (2013) recently reported how regularly spaced fillers are perceived longer than accelerating or decelerating ones. These results suggest that the timing of the fillers can play an important role in the estimation of interval duration.

We investigated whether deviations from isochrony and filler regularity lead to distortions of perceived duration. All experiments employed a duration discrimination task in which participants judged which of two intervals appeared to last longer (two-interval forced choice, 2IFC). This allowed to increase measurement sensitivity and to diminish response biases that could have affected early results (e.g., Thomas and Brown, 1974) to quantify the magnitude of the effect. Each trial comprised two intervals: one with isochronous auditory beeps and one where the timing of beeps diverged from isochrony (the order of the two types of intervals was random and counterbalanced). Either of the two intervals varied in duration across trials; that is, we varied the time between the beginning of the first beep to the ending of the last and all of the segments accordingly. In Experiment 1, we investigated whether the amount of variation in the regularity of fillers influences duration perception. In Experiment 2, we tested the influence of filler density (the number of fillers in a fixed time) on the observed effect of temporal structure. Experiment 3 served to find out whether irregularity of non-temporal filler properties (sound amplitude or frequency) could also influence perceived duration.

2.3 General methods

2.3.1 Participants

A total of 74 students from the University of Birmingham participated in the experiments for course credits or a payment of 6 GBP/h. Participants were naive to the purpose of the investigation, reported normal auditory sensitivity, and took part in only one of the experiments. Experimental procedure and data collection followed the ethical guidelines of the Declaration of Helsinki (2012) and was approved by the Science, Technology, Engineering & Mathematics Ethical Review Committee of the University of Birmingham.

2.3.2 Experimental design

Participants reported which of two intervals appeared to last longer (2IFC, Figure 1a). One interval was regular and one was irregular (in Experiments 1 and 2 the regular interval was isochronous and the irregular interval was anisochronous; in Experiment 3a and 3b both the regular and the irregular interval were isochronous, but the fillers of the irregular interval had varying properties). One of the intervals was always 1000 ms (standard); the other one (counterbalanced between the regular and the irregular interval) could be 500, 700, 850, 1000, 1150, 1300, or 1500 ms (comparison). The order of regular and irregular as well as of standard and comparison intervals was pseudorandomized and counterbalanced. The proportions of regular intervals reported to be longer than irregular intervals were obtained at each level of duration difference between regular and irregular. The points of subjective equality (PSE) and the just noticeable differences (JND) were estimated using the Spearman-Kärber Method as the first and second moments of the distribution (Miller & Ulrich, 2001; Ulrich & Miller, 2004).

PSE values represent the physical duration difference between the regular and the irregular interval at which perceived duration is equal (in milliseconds). A positive PSE value

(A)

General Paradigm (Two-Interval Forced-Choice)

"Which of the two intervals was the longer one?"

250ms 250ms 250ms 250ms vs. 245ms 230ms 350ms 175ms

(order pseudorandomized and counterbalanced across trials)

(B)

Experiment 1: Varying anisochrony of the irregular intervals
range of temporal displacement of fillers: 0,10, 20, 30, 40 or 50%

Experiment 2: Varying number of fillers in both intervals
number of fillers: 3, 4, 6, 9, 13 or 18

Experiment 3: Varying stimulus characteristics of the irregular interval
range of sound amplitude: 80, 78-82, 76-83, 72-84, 66-85 or 42-86 dB
range of sound frequency: 1000, 820-1180, 640-1360, 460-1540, 280-1720 or 100-1900 Hz

Figure 1. Overview of the 2IFC tasks in the experiments. (A) General Paradigm: In each trial participants compare the duration between two intervals (one regular and one irregular, order pseudorandomized). (B) Experiment 1 (top): different levels of anisochrony are presented (and compared against isochrony). Experiment 2 (middle): different numbers of fillers are presented (equal for the two, one isochronous, one anisochronous, intervals to be compared). Experiment 3 (bottom): two isochronous intervals are presented, one regular, one irregular, in the irregular interval fillers vary in sound amplitude (Experiment 3a) or sound frequency (Experiment 3b).

indicates the overestimation of the irregular interval. A negative PSE value indicates its underestimation. JND values indicate the duration difference at which subjects can discriminate the duration of the two intervals (again in milliseconds). The fillers making up the intervals were 10 ms tones (1000 Hz in Experiments 1 and 2) with 1-ms onset and offset tapering. A gap of 3 seconds separated the presentation of the two intervals to be compared. An overview of the conditions tested in the 3 experiments is given in Figure 1. All experiments lasted approximately 1 hour.

2.4 Experiment 1

To investigate whether and how the temporal structure of fillers influences perceived duration, we asked participants to compare isochronous sequences of fillers to anisochronous sequences and varied the level of anisochrony in the irregular sequence (Figure 1b, top).

2.4.1 Material and methods

Twenty students (15 female, mean age = 21.0 ± 4.2) participated in the experiment. Intervals contained five fillers (10 ms, 1000 Hz, 70 dB SPL tones). Stimuli were presented via headphones. Trials consisted of one isochronous and one anisochronous interval. The anisochronous intervals were created by randomizing the time of the three middle filler signals. The time at which fillers were presented was perturbed by randomly sampling from a uniform distribution of ± 10, 20, 30, 40 or 50 % of the duration of the otherwise constant interstimulus interval (ISI). For the 1000 ms standard interval, the ISI corresponded to a jitter that could reach ± 25, 50, 75, 100, 125 ms respectively. It should be noted that randomization by 50 % of the ISI is the highest anisochrony that prevents two successive fillers to overlap. Participants performed 336 duration discrimination judgments resulting from 8 repetitions of 42 trials obtained through all combinations of comparison duration (7) and levels of anisochrony (6). The trial sequence was randomized.

2.4.2 Results and discussion

From the proportion of responses as a function of the difference in physical duration between the regular and the irregular interval (Figure 2a), we obtained PSE and JND values for each level of anisochrony (Figure 2b). Visual inspection hints at a decrease of the PSE with an increase in the level of anisochrony. Due to the frequently observed influence of stimulus order on duration judgments (e.g., Allan, 1977; Dyjas & Ulrich, 2014; Hellström, 2003) and the idea that the presentation of a regular sequence might influence duration perception of following intervals (e.g., Halpern & Darwin, 1982; McAuley & Jones, 2003), we also included the order of isochronous and anisochronous intervals into our statistical analysis by calculating PSEs separately for isochronous first and anisochronous first trials.

A two-way repeated measure ANOVA on PSE values with the factors level of anisochrony (0, 10, 20, 30, 40, or 50 %) and order of intervals (regular first or irregular first)

was conducted. The difference in duration between regular and irregular intervals increases with the level of anisochrony (Figure 2a) as revealed by the significant main effect of anisochrony on PSE values ($F_{(5,95)}$ = 9.3, $p < 0.001$, η_p^2 = 0.33). Post-hoc tests reveal a significantly longer perceived duration of the isochronous interval for conditions with anisochrony > 30 % (single sample t-test on PSE against zero asynchrony, two-tailed, significant outcomes are reported as asterisks in Figure 2b: 10 %, $t_{(19)}$ = 0.3, p = 0.76, d = 0.07; 20%, $t_{(19)}$ = −1.2, p = 0.27, d = 0.26; 30%, $t_{(19)}$ = −2.4, p = 0.026, d = 0.54; 40 %, $t_{(19)}$ = −2.7, p = 0.014, d = 0.60; 50 %, $t_{(19)}$ = −5.8, $p < 0.001$, d = 1.30). Comparing PSE values of adjacent conditions there is a close to significant decrease of PSE values between 20 and 30 %, the major significant decrease takes place between 40 and 50 % asynchrony (10 vs. 20%, $t_{(19)}$ = 1.4, p = 0.18, d = 0.31; 20 vs. 30%, $t_{(19)}$ = 1.8, p = 0.09, d = 0.40; 30 vs. 40%, $t_{(19)}$ = 0.3, p = 0.75, d = 0.07; 40 vs. 50%, $t_{(19)}$ = 3.5, p = 0.003, d = 0.78).
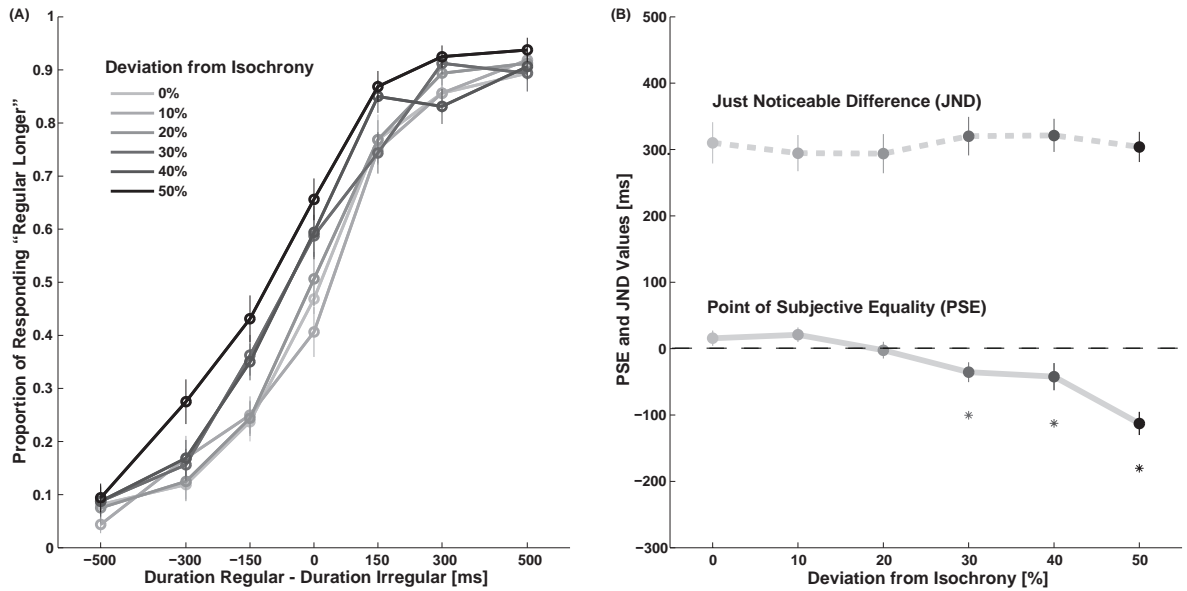
Figure 2. Results of Experiment 1. (A) Probability of the isochronous interval being reported as longer over the physical difference between isochronous and anisochronous interval duration. (B) PSE and JND values for the different levels of anisochrony. Asterisks indicate a significant difference to the zero deviation from isochrony PSE ($p < 0.05$). Error bars are S.E.M.

As shown by a main effect of interval order, irregular intervals are perceived to be shorter when they are presented first in the trial than when they are presented second with a difference of 52 ms ± 16 ms (mean ± standard error of the mean [SEM]; $F_{(1,19)} = 11.0$, $p = 0.004$, $\eta_p^2 = 0.37$). The significant effect of interval order is in accordance with the frequent observation that the first interval in a discrimination task is being perceived as shorter than the second one (e.g., Allan, 1977; Hellström, 2003). The interaction of the two factors (level of anisochrony and interval order) is not significant ($F_{(5,95)} = 1.4$, $p = 0.23$, $\eta_p^2 = 0.07$). This lack of an interaction shows that the bias toward underestimating the first interval is independent of the effect of judging isochronous intervals as longer than anisochronous intervals.

An overall reasonable performance is indicated by the mean JND value of 307 ms ± 23 ms. The order of presentation of regular and irregular intervals affects performance ($F_{(1,19)} = 15.7$, $p = 0.001$, $\eta_p^2 = 0.45$; two-way repeated measurement ANOVA of JND values with factors interval order and level of anisochrony) with performance being worse if the isochronous interval is presented first (310 ms ± 24 ms vs. 255 ms ± 26 ms). The level of anisochrony does not affect duration comparison performance ($F_{(5,95)} = 0.6$, $p = 0.60$, $\eta_p^2 = 0.03$) and neither does so in conjunction with order ($F_{(5,95)} = 1.9$, $p = 0.09$, $\eta_p^2 = 0.09$).

In sum, the results of Experiment 1 indicate that the temporal structure of fillers has a strong influence on perceived duration. Specifically, isochronous spacing of fillers leads to longer perceived duration compared with anisochronous spacing and the difference increases with the level of anisochrony. The effect could be observed independent of the temporal order of isochronous and anisochronous intervals. A question that remains open from Experiment 1 is to what extend the effect depends on the rate at which filler stimuli are presented, that is, the number of fillers in the one second standard interval.

2.5 Experiment 2

Experiment 2 investigated whether the difference in perceived duration between isochronous and anisochronous intervals is modulated by the presentation rate for filler signals (Figure 1b, middle). We tested this by increasing the number of fillers in the interval while maintaining the average duration of the intervals (1 second), thus affecting the density of the interval and the number of fillers per second.

2.5.1 Material and methods

Twenty students participated in the experiment (18 females, mean age = 19.6 ± 1.4). The fillers in the irregular interval were spaced according to the highest level of anisochrony used in Experiment 1 (in a range of 50 % of the ISI). As in Experiment 1, stimuli were presented via headphones. In every trial, two intervals with an equal number of fillers were compared. The average duration of all intervals was 1 second. There were 6 blocks where the intervals were made of 3, 4, 6, 9, 13, or 18 fillers. Each block comprised 56 trials, resulting from 8 repetitions of the 7 comparison durations. Block and trial sequence were randomized.

2.5.2 Results and discussion

Results are displayed in Figure 3, and they replicate the findings of Experiment 1. Isochronous intervals are perceived to be longer than their anisochronous counterparts. The effect is present with every number of fillers tested (3, $t_{(19)} = -4.1$, $p < 0.001$, $d = 0.91$; 4, $t_{(19)} = -2.5$, $p = 0.022$, $d = 0.56$; 6, $t_{(19)} = -2.8$, $p = 0.011$, $d = 0.63$; 9, $t_{(19)} = -5.3$, $p < 0.001$, $d = 1.19$; 13, $t_{(19)} = -5.3$, $p < 0.001$, $d = 1.19$; 18, $t_{(19)} = -4.9$, $p < 0.001$, $d = 1.10$), even though the effect measured in ms gets stronger as a function of the number of fillers. In a two-way repeated measurement ANOVA on PSE values a main effect of number of stimuli is observed ($F_{(5,95)} = 4.8$, $p < 0.001$, $\eta_p^2 = 0.20$). Post-hoc tests reveal that a significant decrease of PSE takes place between 6 and 9 filler stimuli (3 vs. 4: $t_{(19)} = -0.6$, $p = 0.54$, $d = 0.13$; 4 vs. 6: $t_{(19)}$

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= 0.3, p = 0.77, d = 0.07; 6 vs. 9: $t_{(19)}$ = 2.3, p = 0.032, d = 0.51; 9 vs. 13, $t_{(19)}$ =1.2, p = 0.23, d = 0.27; 13 vs. 18, $t_{(19)}$ = −0.2, p = 0.84, d = 0.04). Interval order is influencing the judgment in the same direction as in Experiment 1; that is, the irregular interval is perceived as shorter when it is presented first compared with when it is presented second ($F_{(1,19)}$ = 25.4, p < 0.001, η_p^2 = 0.57), and the interaction with filler number is not significant ($F_{(5,94)}$ = 1.5, p = 0.18, η_p^2 = 0.08). The overall mean JND is 386 ms ± 16 ms. No significant effects have been found on JNDs (number of fillers: $F_{(5,95)}$ = 1.7, p = 0.14, η_p^2 = 0.08; stimulus order: $F_{(1,19)}$ = 0.1, p = 0.74, η_p^2 < 0.01; interaction: $F_{(5,95)}$ = 1.4, p = 0.21, η_p^2 = 0.07).

In sum, isochronous intervals are perceived to be longer than anisochronous ones over a wide range of filler rates. The difference in perceived duration seems to be increasing with more fillers.
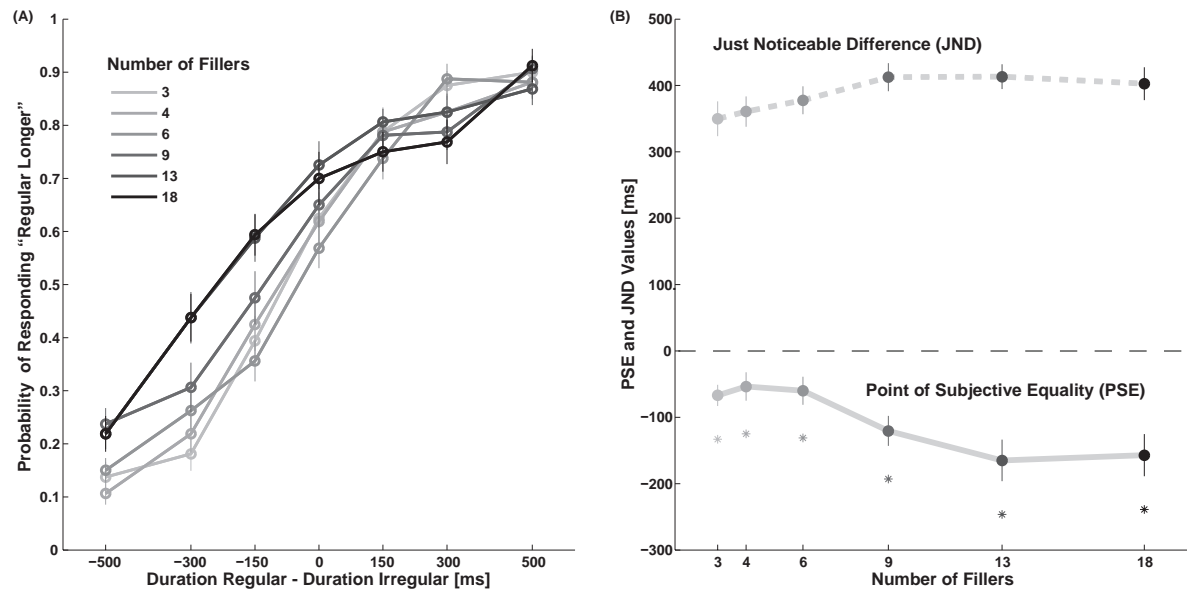
Figure 3. Results of Experiment 2. (A) Probability of the isochronous interval being reported as longer over the physical difference between isochronous and anisochronous interval duration. (B) PSE and JND values for the different numbers of fillers. Asterisks indicate a significant difference to zero (p < 0.05). Error bars are S.E.M.

2.6 Experiment 3

Experiment 3 was conducted to test whether the observed effect of temporal structure can be generalized to non-temporal irregularities in filler characteristics (Figure 1b, bottom). Therefore, the independent variable was the level of irregularity of the fillers regarding sound amplitude (Experiment 3a) or sound frequency (Experiment 3b).

2.6.1 Material and methods

Seventeen students (all female, mean age = 19.1 ± 0.8) participated in Experiment 3a and another 17 students (15 females, mean age = 19.5 ± 1.0) participated in Experiment 3b. Both intervals presented in a trial were now regularly spaced (isochronous) and contained five fillers. For the regular interval, the fillers were identical (1000 Hz, 80 dB SPL), whereas for the irregular interval they varied at random in either their acoustic amplitude (Experiment 3a) or frequency (Experiment 3b). There were six levels of amplitude and frequency variations. Amplitudes varied around 80 dB SPL in a range of either ± 0, 78.1–81.7, 75.6–82.9, 72.2–84.0, 66.4–85.1, or 41.9–86.0 dB SPL. Sound frequencies varied around 1000 Hz in a range of ± 0, ± 180, ± 360, ± 540, ± 720, or ± 900 Hz. Due to sound amplitudes up to 86 dB, stimuli were, in contrast to Experiment 1 and 2, presented via speakers. As in Experiment 1, the independent variable was varied trial-by-trial, so that there were 8 blocks of 42 trials each (7 durations of the standard stimulus times 6 ranges of variation), sequence randomized.

2.6.2 Results and discussion

Figure 4 shows the response proportions as well as PSE and JND values for Experiment 3a and 3b. As expected from visual inspection, there is no significant change in perceived duration due to increased amplitude irregularity (2-way repeated measurement ANOVA on PSE, $F_{(5, 80)} = 0.4$, $p = 0.88$, $\eta_p^2 = 0.03$) nor to sound frequency ($F_{(5, 80)} = 0.9$, $p = 0.48$, $\eta_p^2 = 0.05$). The effect of interval order as well was not significant in Experiment 3a ($F_{(1,16)} = 0.7$, p

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$= 0.40$, $\eta_p^2 = 0.04$) and there was no interaction ($F_{(5,80)} = 1.0$, $p = 0.44$, $\eta_p^2 = 0.04$). In Experiment 3b there was a significant effect of temporal order ($F_{(1,16)} = 13.7$, $p = 0.002$, $\eta_p^2 = 0.46$), indicating that again the interval is perceived to be shorter when it is presented first in the trial than when it is presented second. There was no interaction between irregularity and interval order ($F_{(5,80)} = 0.6$, $p = 0.69$, $\eta p^2 = 0.04$). The overall mean JND was 297 ms ± 19 ms in Experiment 3a and 292 ms ± 16 ms in Experiment 3b. No significant differences were found between JND values ($p > 0.1$).
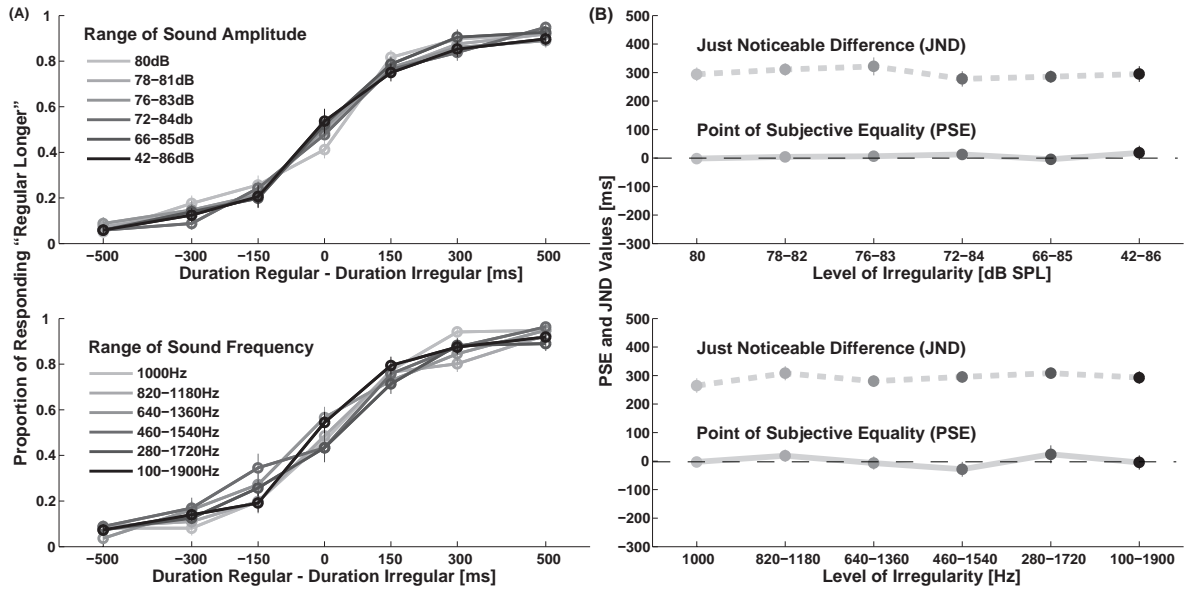
Figure 4. Results of Experiment 3. (A) Probability of the regular interval being reported as longer over the physical difference between regular and irregular interval duration for Experiment 3a (top) and Experiment 3b (bottom). (B) PSE and JND values for the different levels of irregularity, that is, the different ranges of sound amplitude (top) and sound frequency (bottom). Error bars are S.E.M.

Overall, we do not find that irregularity in the properties of isochronous fillers leads to a difference in perceived duration. Therefore, the effect of isochronous and anisochronous fillers on duration judgments seems to be specific to irregularity in time and cannot be explained via a general effect of filler predictability or novelty.

2.7 General discussion

The present experiments aimed at investigating the role of the temporal structure of interval fillers on perceived duration. Specifically, intervals with regularly spaced (isochronous) fillers were compared with intervals with irregularly spaced (anisochronous) fillers. Consistent with early reports (Grimm, 1934; Thomas & Brown, 1974), we find that isochronous intervals are perceived as being longer than their anisochronous counterparts, an effect that increases with the level of anisochrony and with the number of fillers.[1] Our results expand the findings of Thomas and Brown (1974) obtained with a reproduction task by showing that with a direct comparison between isochronous and anisochronous intervals there is a consistent difference in perceived duration; that is, the isochronous interval is perceived as being longer. Such distortions in perceived duration are not replicated with fillers that are isochronous but irregular in terms of non-temporal properties (amplitude and frequency). This demonstrates the special role of temporal structure of filler signals in the estimation of interval duration. It therefore strengthens our understanding of the filled duration illusion, indicating that what is important is not the characteristics of interval fillers, but when those fillers appear.

In addition, we should consider that the two non-temporal irregularity conditions (amplitude and frequency) might as well lead to a deviation from perceived isochrony. It has been shown that the perceptual latency of 1000 Hz sounds measured through simple reaction

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[1] To make sure that the observed difference in perceived duration is not due to the repeated presentation of multiple trials, but can already be found in a single comparison, we asked 60 participants to make a single 2IFC judgment in the manner of Experiment 1. We used the highest level of anisochrony and the number of fillers from Experiment 1 (5 signals for each interval). The order of the two one-second intervals was counterbalanced between participants. 76.7% of participants judged the isochronous interval to be longer ($\chi^2_{(1)} = 21.7$, $p < 0.001$), demonstrating that the difference in perceived duration between isochronous and anisochronous intervals is present already at individual trial level.

times varies in a range of roughly 70 ms with a change in stimulus intensity between 40 dB and 80 dB as the one used in Experiment 3a (Pfingst, Hienz, Kimm, & Miller, 1975, as in Luce 1986). For the frequency changes used in Experiment 3b, changes in perceptual latency are roughly 50 ms and have been suggested to be due to the different perceived amplitude that stimuli of a different sound frequency have (Pfingst et al. 1975). According to these values, jittering the fillers' properties should be perceptually equivalent to presenting them with an anisochrony in the middle-low range of anisochronies used in Experiment 1. The level of perceived anisochrony due to filler properties is thus insufficient to produce a significant difference in perceived duration.

Two contemporary types of models of temporal perception, interval models and entrainment models, conceive duration estimates to be based on the comparison of sensory information to a memory component. This memory component could either be a duration reference memory as proposed by interval models or the phase and period of the rhythmic context as proposed by entrainment models. In the following, we will take a closer look at the predictions of these models regarding the present data.

2.7.1 Interval models

Interval models propose a way of representing the duration of an interval via a resettable accumulator counter mechanism. The internal clock model by Treisman (1963) and the SET model (e.g., Church, Meck, & Gibbon, 1994; Gibbon, 1977; Gibbon & Church, 1990) are prominent examples of such type of models. Previous studies on distortions of perceived duration due to stimulus irregularity have found that unexpected, irregular stimuli in a sequence (oddballs) lead to an overestimation of perceived duration (e.g., Birngruber, et al., 2014; Pariyadath & Eagleman, 2007; Schindel, Rowlands, & Arnolds, 2011). This effect has been explained in the framework of interval models, suggesting that the clock mechanism is sped up by novelty, unpredictability, and irregularity in a sequence. Indeed, it has been shown

repeatedly that an increase in arousal or attention due to a stimulus leads to an overestimation of perceived duration (e.g., Burle & Casini, 2001). According to these observations, interval models should predict that (1) irregular intervals should be perceived to last longer than regular ones and (2) such effects should be independent of the type of irregularity (temporal properties or other non-temporal filler characteristics). Our results however falsify both predictions as filler anisochrony leads to a decrease (rather than an increase) in perceived duration and distortions are observed only for irregularity in time and not in other properties of the fillers.

We should consider, however, that there is a fundamental difference between the current paradigm and the ones in the literature that found an increase of perceived duration with stimulus irregularity. In our study, sequences where either completely regular or completely irregular, whereas the previous results have been obtained from a violation of expectations. For the irregular stimuli of the current experiment, no expectations about stimulus timing (Experiment 1 and 2) or stimulus characteristics (Experiment 3) could be built up. Therefore, it is not surprising that complete interval irregularity does not lead to the arousal/attention effects that have been found in previous studies as no expectations have been violated.

Interval models could in principle account for the current results without appealing to a change in the clock speed if specific characteristics of the clock could explain why isochronous sequences would lead to a higher accumulated duration estimate than anisochronous sequences. This is possible, when assuming (a) a logarithmic relationship between physical and perceived duration (i.e., a concave relationship according to Thomas and Brown's scheme, 1974), and (b) a reset of the accumulator counter mechanism at the beginning of each subinterval. The total duration estimate would then be calculated by adding up the duration of the subinterval estimates (Matthews, 2013; Thomas & Brown, 1974). The logarithmic encoding of perceived time is equivalent to a representation of the duration of the

overall interval based on the geometric — rather than arithmetic — mean of the subintervals (e.g., Allan & Gibbon, 1991; Church & Deluty, 1977). Whereas the arithmetic mean of 1 s isochronous and anisochronous intervals would be identical, the geometric mean would be larger for isochronous sequences. This could be the reason for an underestimation of interval duration that is specific to irregularity in time and thus explain the effects of regularity in Experiment 1 and 2 as well as the lack of an effect in Experiment 3.

To determine whether a logarithmic interval model predicts the observed decrease in PSE values with an increase in temporal irregularity as well as filler number, we derive its analytical expression. To obtain the PSE values for the conditions in the experiments, we need to determine the physical duration of an isochronous interval T^i that perceptually matches the duration of the anisochronous interval ($T^a = 1000$ ms), so that:

$$\psi(T^i) = \psi(T^a),$$

where ψ represents the psychometric function relating the physical stimulus to the internal representation, which we assume to be logarithmic. After applying such transformation, the contribution of each of the N subintervals (D^i_s and D^a_s) could be summed to determine the perceived duration of the overall interval at PSE:

$$\sum_{s=1}^{N} \log(D^i) = \sum_{s=1}^{N} \log(D^a_s).$$

The anisochronous interval as the standard D^a adds up to 1000 ms. The duration of the isochronous interval T^i is not fixed. The value of D^i can be obtained by $D^i = T^i/N$ and substituted in the formula above so that the left-hand side is simplified to:

$$\log \left(\frac{T^i}{N} \right) N = \sum_{s=1}^{N} \log (D_s^a) \,.$$

From this, T^i can be obtained analytically according to

$$T^i = N e^{\frac{1}{N} \sum_{s=1}^{N} D_s^a} \,.$$

The PSE is then simply PSE $= T^i$-$T^a = T^i$-1000. Figure 5 shows the outcome of simulating Experiment 1 and 2, by randomly drawing 1000 samples of an anisochronous interval for each condition and calculating the mean over the respective PSE values. It can be seen that the simulated PSEs follow a pattern similar to the average values obtained experimentally (see Figures 2 and 3). This similarity confirms that a logarithmic interval model may account for our data in both experiments.

2.7.2 Entrainment models

Entrainment models (e.g., McAuley & Jones, 2003) explain temporal perception without assuming a resettable clock. They propose perceived duration to be based on oscillatory mechanisms. The peak of the oscillation coincides with the expected time point of stimulus arrival and duration is to be determined in comparison to this point (early or late onset). Phase and period of the oscillation gradually adapt entraining to stimulus sequences. Indeed, effects of neural entrainment to rhythmic sequences have been found in multiple electrophysiological studies. For example, low-frequency oscillations in the primary auditory as well as in the primary visual cortex were observed to adapt their phase to rhythmic stimulus input (e.g., Lakatos et al., 2008; Lakatos, Chen, O'Connell, Mills, & Schroeder, 2007). Neural entrainment at higher frequency bands has been proposed to be the basis of rhythmic perception (e.g., Ding, Sperling & Srinivasan, 2006; Lakatos et al., 2005; Zanto, Snyder &
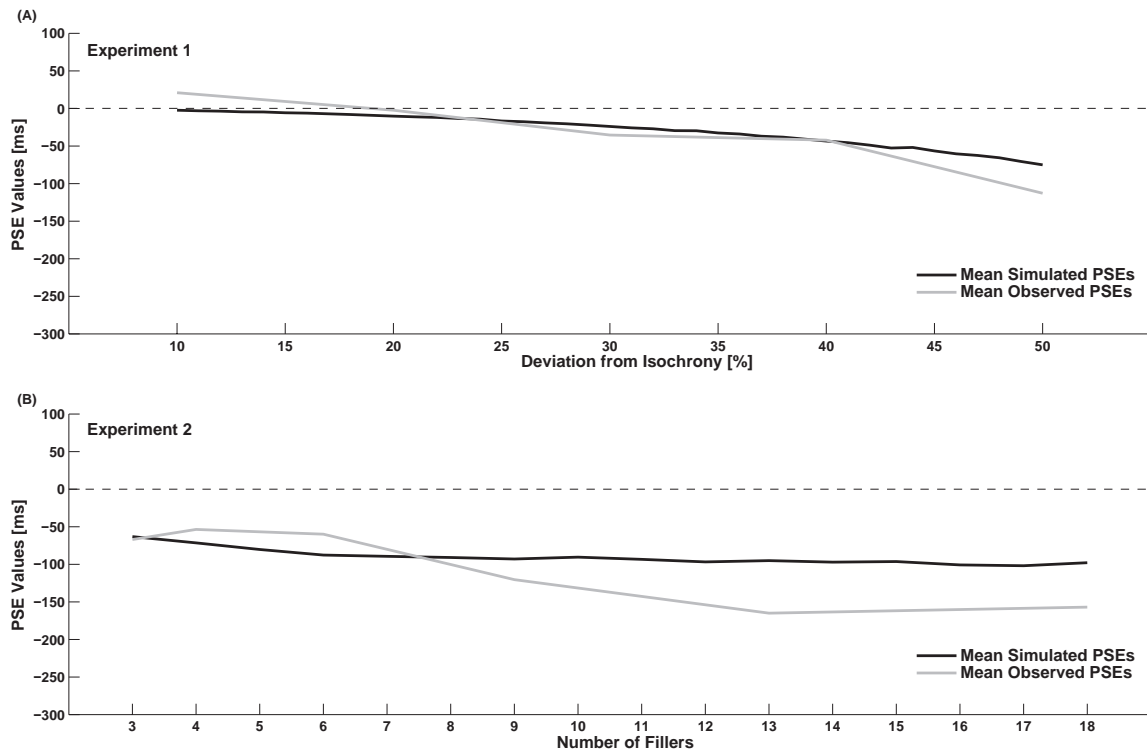
Figure 5. Comparison of the experimental and simulated PSE values (mean over 1000 repetitions for each condition) assuming a logarithmic relationship between physical and perceived time and a clock reset at the beginning of every subinterval. (A) Simulation of Experiment 1. The x-axis represents the deviation of the anisochronous interval from isochrony. (B) Simulation of Experiment 2. The x-axis represents the number of filler stimuli in both the isochronous and the anisochronous interval.

Large, 2006). The peak of the oscillation has been shown to relate to heightened attention and higher neural excitability (e.g., Sanchez-Vives & McCormick, 2000; Steriade, Nunez & Amzica, 1993). That is, the time at which an input arrives will determine whether the input is being amplified or attenuated depending on the phase of the underlying neural oscillation. In this sense, entrainment has been suggested as a mechanism of attentional selection, changing response gain and reaction times with an expected stimulus (e.g., Cravo, Rohenkohl, Wyart, & Nobre, 2013; Fries, Schröder, Roelfseman, Singer, & Engel, 2002; Lakatos et al., 2008; Schroeder & Lakatos, 2009). Following this idea, fillers of a regularly spaced interval would likely coincide with the peak of the entrained oscillatory period, that is, the point of highest neural excitability.

It has been suggested that perceived duration increases with an increase in neural response toward a stimulus (e.g., Eagleman & Pariyadath, 2009). This does not only give a framework to explain effects of arousal and attention (e.g., Burle & Casini, 2001; Thomas & Weaver, 1975), but it also can account for the filled duration illusion as filled intervals should have an increased neural response compared with empty ones (e.g. Thomas & Brown, 1974; Wearden et al., 2007) and the increase is a function of the number and duration of the fillers (e.g., Buffardi, 1971). Assuming that the neural response toward fillers is strongest at the beginning of an interval and habituates with repeated exposure (e.g., Polich, 1989) also the finding of a higher impact of stimuli in the beginning compared with the end (e.g., Adams, 1977; Buffardi, 1971) conforms to the idea of a link between perceived duration and neural response magnitude.

It is not immediately evident why isochronous intervals would elicit higher responses and an increase in perceived duration as compared to anisochronous ones, given that the total magnitude of the sensory input is identical. In the framework of neural entrainment, however, an isochronous sequence causes fillers to arrive at the peak of entrained neural oscillations, leading to amplification and thus to higher overall neural activity. On the other hand, fillers in an anisochronous sequence are unlikely to arrive at the same phase of the neural oscillation, thus causing different (and lower) levels of amplification. This leads to a lower overall neural response to the fillers in an anisochronous interval when compared to an isochronous interval. Therefore, perceived duration, if it is related to neural response magnitudes, should be longer for isochronous than for anisochronous sequences as observed in Experiment 1. The account of entrainment related to neural response magnitudes would as well predict the results of Experiment 2. Assuming predictability and thereby neural entrainment to built up with the number of isochronous stimuli (e.g., Stefanics et al., 2010), an increased number of fillers leads to an increasing average difference in the response toward isochronous in contrast to

anisochronous stimuli. This may explain our finding of an increase in the difference between perceived isochronous and anisochronous duration with an increase in the number of fillers. Finally, isochronous fillers that are irregular for non-temporal properties would entrain the neural oscillation in the same way as regular fillers do. In accordance to this prediction we find no difference in perceived duration due to non-temporal irregularity in Experiment 3.

2.8 Conclusions

Our results demonstrate longer perceived duration estimates due to regularity in time (isochrony) compared with temporal irregularly (anisochrony). Such a bias in perceived duration is not present when non-temporal properties of the fillers are made irregular. We show that the change in perceived duration as a function of anisochrony level and number of stimuli is, in principle, consistent with a logarithmic encoding of perceived duration in the framework of a resettable clock (Matthews, 2013; Thomas & Brown, 1974). Furthermore, the perceptual difference between isochronous and anisochronous intervals could be explained in the context of entrainment models, because isochronous filler stimuli coincide with higher neural excitability and lead to an increased magnitude of the overall neural response. As entrainment increases with more filler stimuli, the response gain becomes larger and the difference in perceived duration between isochronous and anisochronous sequences becomes more evident. Simulations confirm that the observed distortions of perceived interval duration due to temporal structure are in accordance with the predictions of a logarithmic interval model. In order to determine whether the predictions of the entrainment model are quantitatively consistent with our results, we would need to identify the function relating neural response magnitudes to perceived duration, which at the moment is unknown.

Chapter 3

Filling the blanks in temporal intervals: The type of filling influences perceived duration and discrimination performance

This research was published in:

Two experiments that investigate duration distortions and discrimination performance in different types of intervals are reported. The four interval types of interest are intervals consistent of one continuous stimulus (continuous intervals), intervals filled with sequences of short stimuli, isochronously spaced (isochronous intervals) or anisochronously spaced (anisochronous intervals) and intervals solely demarcated by a beginning and an end marker (empty intervals). Duration discrimination performance is best for the comparison of two continuous or isochronous intervals, followed by empty intervals and worst for the comparison of two anisochronous intervals (Experiment 1). The pattern of perceived duration distortions revealed by comparing any two differential interval types shows inconsistencies (Experiment 2). The latter can only be explained by dynamics based on the comparison process rather than the perception of individual intervals.

3.1 Abstract

In this work we investigate how judgments of perceived duration are influenced by the properties of the signals that define the intervals. Participants compared two auditory intervals that could be any combination of the following four types: intervals filled with continuous tones (*filled* intervals), intervals filled with regularly-timed short tones (*isochronous* intervals), intervals filled with irregularly-timed short tones (*anisochronous* intervals), and intervals demarcated by two short tones (*empty* intervals). Results indicate that the type of intervals to be compared affects discrimination performance and induces distortions in perceived duration. In particular, we find that duration judgments are most precise when comparing two isochronous and two continuous intervals, while the comparison of two anisochronous intervals leads to the worst performance. Moreover, we determined that the magnitude of the distortions in perceived duration (an effect akin to the filled duration illusion) is higher for tone sequences (no matter whether isochronous or anisochronous) than for continuous tones. Further analysis of how duration distortions depend on the type of filling suggests that distortions are not only due to the perceived duration of the two individual intervals, but they may also be due to the comparison of two different filling types.

3.2 Introduction

Many factors other than the physical duration of an interval influence perceived duration (see Allan, 1979 for a classic and Grondin, 2010 for a recent overview). For example, perceived duration is influenced by the filling of the interval to be judged as highlighted by the well-known filled duration illusion, whereby filled intervals are perceived as longer than their empty counterparts. This effect has been observed in a wide range of experimental conditions, with the definition of "filling" varying across studies. Several studies used continuous signals as filled intervals (e.g., Craig, 1973; Goldfarb & Goldstone, 1963; Hasuo et al., 2014; Steiner, 1968; Wearden et al., 2007) and compared those to empty intervals, which are typically consisting solely of a short beginning and end marker or a gap in a continuous signal (see Wearden et al., 2007 for a comparison of those two variations). Another type of filled interval leading to the filled duration illusion is a sequence of short filler signals that is compared to an empty interval lacking such fillers (e.g., Adams, 1977; Buffardi, 1971; Thomas & Brown, 1974). The magnitude of the overestimation for the latter type of filled intervals has been shown to increase with the number of fillers (Buffardi, 1971; Schiffman & Bobko, 1977). This overestimation has been termed "Illusion of a Divided Time Interval" by Ten Hoopen, Miyauchi, & Nakajima (2008).

Duration judgments with filled intervals are mostly investigated with regularly-timed tones, that is, isochronous rhythms. However, it has recently been reported that the temporal structure of fillers influences perceived duration. For example, Matthews (2013) showed that isochronous intervals are perceived to last longer than accelerating or decelerating ones. Horr and Di Luca (2015a) found that isochronous intervals are perceived to last longer than anisochronous ones and that this effect increases not only with the amount of anisochrony but also, like the filled duration illusion, with the number of fillers (this is in accordance with tendencies found in earlier studies, see Grimm, 1934; Thomas & Brown, 1974).

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Overall, this line of research indicates that the type *and* structure of interval filling influences perceived duration. To gain further insight into the mechanisms underlying short interval duration perception also discrimination performance has to be investigated experimentally. Rammsayer and Lima (1991) reported that filled intervals made up of a continuous signal are discriminated better than empty intervals. It remains to be determined, whether this superior discrimination of filled as compared to empty intervals is only true for one type of filled intervals, namely intervals filled with a continuous signal (e.g., a continuous sound) or can as well be generalized over intervals filled with sequences of short filler signals (e.g., short tones). It further remains to be investigated how discrimination performance differs between such continuous and short filler intervals of different temporal structure.

In the present article, we investigate how the type of interval filling affects perceived duration and discrimination performance using four types of auditory intervals: continuous, isochronous, anisochronous, and empty intervals. In Experiment 1, we investigate duration discrimination performance by having participants compare two intervals of the same type. In Experiment 2, we aim at quantifying the perceptual distortions for each interval type. To our knowledge, this is the first attempt to quantify how the type of filling influences the magnitude of the "filled duration illusion." Such discrimination is important to understand the mechanisms involved in short-interval duration perception as it constraints the type of cognitive mechanisms employed in prospective time judgments.

3.3 General methods

3.3.1 Participants

A total of 35 healthy volunteers with normal auditory sensitivity participated in the experiments for course credits or a payment of 7 GBP/h. All participants were naive to the purpose of the study, reported normal auditory sensitivity and took part in only one of the experiments. The experimental data collection and storage followed the ethical guidelines of

the Declaration of Helsinki (2012) and was approved by the Science, Technology, Engineering, and Mathematics Ethical Review Committee of the University of Birmingham.

3.3.2 Experimental design

Participants performed a two-interval forced-choice task, deciding via button pressing which of two intervals had been the one of longer duration. A trial consisted of a 1000 ms standard interval and a comparison interval of 500, 700, 850, 1000, 1150, 1300, or 1500 ms duration spaced by a random interval between 2000 and 2300 ms. The order of standard and comparison intervals was pseudorandomized and counterbalanced across trials. Experimental stimuli constituting an interval were 1000 Hz 70 dB tones with 2.5 ms ramped onset and offset. Each interval consisted either of (a) a beginning and end tone lasting for 10 ms each (empty interval), (b) five 10 ms regularly-timed filler tones (isochronous interval), (c) five 10 ms irregularly-timed filler tones (anisochronous interval) or of (d) a tone lasting for the entire interval duration (continuous interval). For the anisochronous intervals, temporal irregularity was created by randomly moving the onset of individual filler tones inside a range of plus or minus half of the interstimulus interval (i.e., 250 ms in the standard interval). Stimuli were presented via headphones. Participants' individual response proportions were assessed in relation to the physical duration difference between interval types. The point of subjective equality (PSE) and the just noticeable difference (JND) were estimated using the Spearman-Kärber-Method as the first and second moment of the data obtained from each participant (Ulrich and Miller, 2004).

3.4 Experiment 1: Duration discrimination performance

To investigate differences in duration discrimination performance across interval types, we asked participants to compare two intervals of the same type (continuous, isochronous, anisochronous and empty).

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3.4.1 Material and methods

Seventeen healthy volunteers (15 female, 21.7 ± 2.8 years) participated in Experiment 1. In each experimental trial, participants reported which of two intervals was longer. According to the different interval types, four conditions were defined: continuous, isochronous, anisochronous, and empty. Each of the four conditions was presented in a block. The sequences of blocks (conditions) were randomized for each participant. Every block contained eight repetitions of all seven possible durations of the comparison interval (Mayer, Di Luca, & Ernst, 2014). In every block the eight repetitions of each comparison duration were counterbalanced and pseudorandomized according to which interval (standard or comparison) was presented first. In total participants made 224 duration comparisons in 4 blocks of 56 trials each. The entire experiment lasted about 40 min.

3.4.2 Results

In Figure 1a response proportions and Figure 1b PSE and JND values are displayed. Each participant's average JND is lower than 600 ms, which means that all of them were reasonably capable of performing the task. As participants were comparing two identical intervals, there should be no difference between PSE values across conditions ($F_{(3, 67)} = 1.6$, $p = 0.20$, $\eta_p^2 = 0.09$). More interestingly, there is a significant difference of JND values between conditions ($F_{(3, 67)} = 15.4$, $p < 0.001$, $\eta_p^2 = 0.49$). Post-hoc tests indicate that the following differences are statistically significant: Duration discrimination is better for continuous than empty (paired sample t-test on JND, $t_{(16)} = 3.9$, $p = 0.0013$, $d = 0.95$) and anisochronous intervals ($t_{(16)} = 7.6$, $p < 0.001$, $d = 1.84$). Discrimination is better for isochronous than empty ($t_{(16)} = -2.2$, $p = 0.043$, $d = 0.53$) and anisochronous intervals ($t_{(16)} = 4.5$, $p < 0.001$, $d = 1.09$). Furthermore, discrimination is better for empty than anisochronous intervals ($t_{(16)} = 2.4$, $p = 0.030$, $d = 0.58$). There is no significant difference between continuous and isochronous intervals ($t_{(16)} = 1.7$, $p = 0.12$, $d = 0.41$). In short, continuous and isochronous intervals are

discriminated best, followed by empty intervals, while discrimination performance is worst for anisochronous intervals.
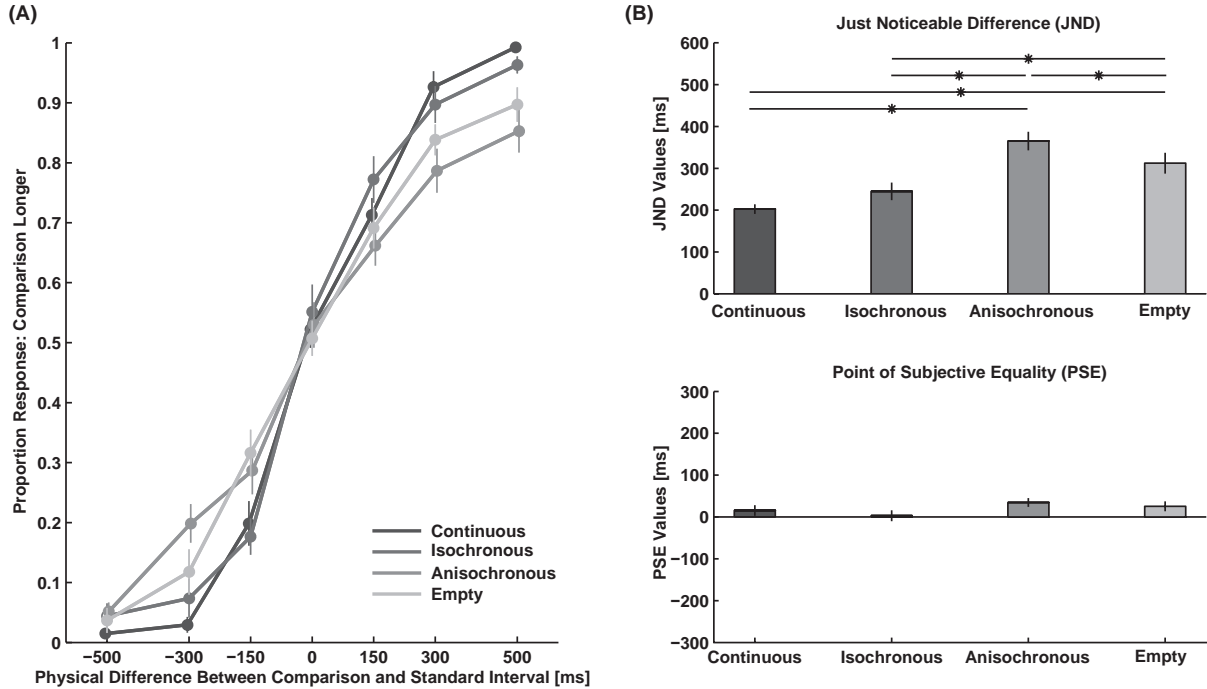
Figure 1. Results of Experiment 1. (A) Participants' responses recoded to indicate the proportion of responses where the comparison interval was judged longer than the standard interval as a function of physical duration difference. (B) Point of subjective equality (PSE) and just noticeable difference (JND) calculated from response proportions using the Spearman-Kärber method. Asterisks indicate differences in performance between intervals of different types as identified by the horizontal lines. Error bars are S.E.M.

3.5 Experiment 2: Distortions of perceived duration

To investigate whether distortions of perceived duration depend on the type of interval filling, we asked participants to compare the duration between all types of filled intervals and the empty intervals. Furthermore, we asked participants to compare the duration of different types of filled intervals.

3.5.1 Material and methods

Eighteen healthy volunteers (12 female, 22.1 ± 3.3 years) participated in Experiment 2. In

each trial, participants made their duration judgment for two intervals of different types. Six conditions were defined according to all possible combinations of the four interval types: (1) continuous vs. empty, (2) isochronous vs. empty, (3) anisochronous vs. empty, (4) continuous vs. isochronous, (5) continuous vs. anisochronous, and (6) isochronous vs. anisochronous. Each condition was presented in a separate block of trials. As in Experiment 1 sequences of blocks (conditions) and trials were fully randomized. The order of standard (1000 ms) and comparison (500 – 1500 ms) intervals was counterbalanced and the standard could be either of the two types of intervals presented in the block. Data from the combination of order and standard type is presented combined. Participants performed a total of 336 duration discrimination judgments resulting from 6 blocks of 56 trials each. The entire experiment lasted about 60 min.

3.5.2 Results

Figure 2a shows response proportions and Figure 2b shows average PSE and JND values obtained across participants. Again as in Experiment 1, average JND values for each participant are lower than 600 ms indicating a reasonable performance. The PSE values depend on the type of filling (One-Way r.m. ANOVA: $F_{(5,107)} = 23.4$, $p < 0.001$, $\eta_p^2 = 0.58$). In every condition containing empty intervals PSEs are significantly lower than zero (single sample t-test on PSE against 0, continuous/empty: $t_{(17)} = -4.0$, $p < 0.001$, $d = 0.94$; isochronous/empty: $t_{(17)} = -8.6$, $p < 0.001$, $d = 2.03$; anisochronous/empty: $t_{(17)} = -9.4$, $p < 0.001$, $d = 2.22$). This indicates the presence of the filled duration illusion, that is, the duration of empty intervals being underestimated as compared to filled intervals. Isochronous intervals are perceived as longer than anisochronous ones ($t_{(17)} = -2.5$, $p = 0.025$, $d = 0.59$), whereas the PSE does not differ from 0 when comparing continuous and isochronous ($t_{(17)} = 1.5$, $p = 0.15$, $d = 0.35$) as well as continuous and anisochronous intervals ($t_{(17)} = 1.2$, $p = 0.24$, $d = $

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0.28). The magnitude of bias (PSE value) is lower for continuous intervals than for isochronous intervals (paired sample t-test on PSE isochronous/empty vs. PSE continuous/empty: $t_{(17)} = 3.0$, $p = 0.008$, $d = 0.71$) as well as for anisochronous intervals (PSE anisochronous/empty vs. PSE continuous/empty: $t_{(17)} = 3.5$, $p = 0.003$, $d = 0.82$). There is no significant difference in bias between isochronous and anisochronous (PSE isochronous/empty vs. PSE anisochronous/empty: $t_{(17)} = 0.8$, $p = 0.43$, $d = 0.18$). No significant difference is observed in JND values across conditions (One-Way ANOVA on JND, $F_{(5, 107)} = 2.0$, $p = 0.09$, $\eta_p^2 = 0.10$), with a tendency toward better performance in conditions where one of the compared stimuli is a continuous interval. A comparison of JND values between Experiment 1 and 2 indicates higher performance when comparing intervals
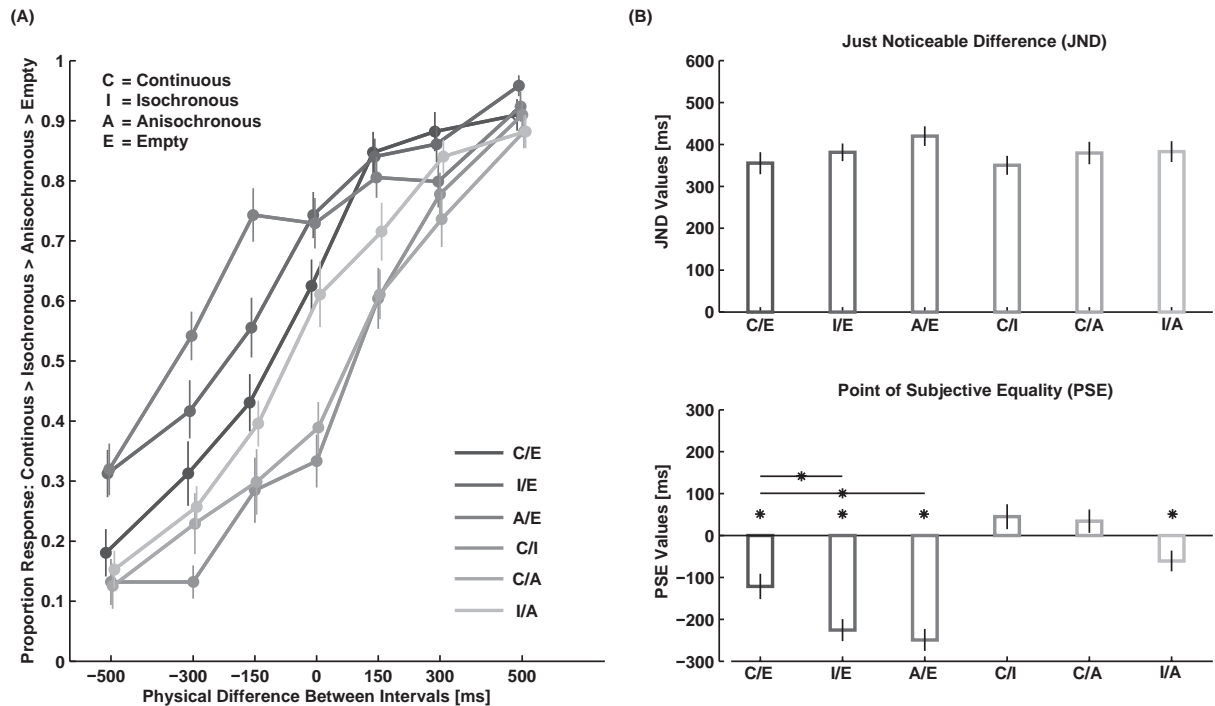
Figure 2. Results of Experiment 2. (A) Proportions of judging continuous > isochronous > anisochronous > empty as a function of the duration difference between standard and comparison. (B) Point of subjective equality (PSE) and just noticeable difference (JND) calculated from response proportions using the Spearman-Kärber method. Asterisks indicate a significant difference of the PSE from zero and between the three conditions comprising one empty interval. Error bars are S.E.M.

of the same type rather than of different types (two sample *t*-test on average JND for each participant: $t_{(33)} = 4.3$, $p < 0.001$, $d = 1.50$, 380 ± 20 ms vs. 280 ± 10 ms).

3.6 General discussion

The present article investigates discrimination performance and perceived duration of four types of auditory intervals: continuous tones, isochronous sequences of tones, anisochronous sequences of tones, and empty intervals. Such interval types have been commonly used in experiments investigating the filled duration illusion and related distortions of perceived duration (e.g., Rammsayer & Lima, 1991; Thomas & Brown, 1974; Wearden et al., 2007), but until now they have never been systematically tested against each other. We find that discrimination performance changes depending on the interval types to be compared. When comparing the same types of intervals, continuous and isochronous intervals are discriminated better than empty intervals. Discrimination performance for anisochronous intervals is worse than for all other interval types. The filled duration illusion is found to be stronger for tone sequences, both isochronous and anisochronous, than for continuous intervals. The result of the comparison of different types of filled intervals, however, indicates that there are no differences in duration judgments between continuous tones and tone sequences, and that isochronous sequences are perceived as longer than anisochronous ones.

3.6.1 Discrimination performance

Differences in duration discrimination performance between interval types demonstrate that participants make use of the structure of interval filling to arrive at their duration estimates. That is, for the different interval types they use either different sources of information or there is a common mechanism that changes in precision depending on the interval types.

Our data indicates that when comparing intervals of the same type, continuous and isochronous intervals are better discriminated than empty ones. This is in line with the idea

that higher sound energy in the interval improves discrimination performance (Carbotte & Kristofferson, 1973 , see however Abel, 1972 and Creelmann, 1962 for empirical evidence that does not support this notion). Rammsayer & Lima (1991) suggest that filled intervals are discriminated better than empty intervals because they elicit a higher neural firing rate, which is translated to a superior temporal resolution. This would predict a better discrimination performance for sound sequences than for continuous intervals because a continuous sound would be subject to habituation (e.g., Polich, 1989). In addition, Horr and Di Luca (2015a) hypothesized that due to neural entrainment (e.g., Cravo et al., 2013; Lakatos et al., 2008), stimuli in isochronous sequences should arrive at the point of highest neural responsiveness leading to a further increase in neural response in isochronous intervals when compared to continuous intervals. However, our results (Figure 1b) do not show a significant difference between continuous intervals and isochronous sequences. Also the finding of anisochronous sequences being discriminated worse than continuous tones and empty intervals is not in accordance with a neural firing rate explanation. The higher temporal resolution caused by increased neural responses can therefore only account for the decrease in performance found with empty as compared to continuous and isochronous intervals, as the lack of difference between continuous and isochronous intervals and even more so the remarkably worse performance for anisochronous as compared to all other intervals remains unexplained.

Another possibility to explain the observed pattern of discrimination performance is to appeal to the number of cues available for a single duration judgment. It has been shown that filled intervals defined by auditory and visual stimuli provide redundant cues to duration that allow a statistically optimal increase in performance (Hartcher-O'Brien, Di Luca, & Ernst, 2014). Here, we posit that in some conditions there are redundant cues related to duration also for unisensory stimuli and this could lead to better discrimination performance compared to the conditions where only one cue is available. In particular, Hartcher-O'Brien et al. (2014)

identify the filling of the interval as an important factor that can modulate the modality of integration, as empty intervals consist of two markers that only allow the identification of two time points and of the subtended empty duration between them. In contrast, continuous tones allow duration estimates by using the overall sensed energy in addition to (and independently from) the information carried by the temporal difference between beginning and ending time points. For isochronous intervals, the regular temporal structure allows to estimate duration based solely on the interval between successive tones (if the number of tones is known). Although the same cue is present with anisochronous intervals, the random timing of tones should actually be deceptive and lead to a reduced precision in duration judgments. If we interpret our data along these lines, the pattern of results suggests that the base duration judgment performance is achieved with empty intervals. In filled intervals the brain can use additional duration cues if both intervals carry such cues, that is, with trials with two intervals of the same type as in our Experiment 1. Such cues can either increase (as in the case of continuous or isochronous intervals), but also decrease discrimination performance (as with anisochronous intervals). If two intervals of different types are compared, additional cues cannot be used, leading to a worse discrimination performance over all conditions in Experiment 2 as compared to Experiment 1.

3.6.2 Distortions of perceived duration

The goal of Experiment 2 was to characterize duration distortions between the four interval types of interest. PSE data shows that the effect of the filled duration illusion (e.g., Buffardi, 1971; Hasuo et al., 2014; Steiner, 1968; Thomas & Brown, 1974; Wearden et al., 2007) is present for every type of filled interval we tested. The data however indicates that the magnitude of the filled duration illusion is higher with isochronous and anisochronous than with continuous intervals. That is, PSE values are significantly lower for the comparison between isochronous/empty and anisochronous/empty than for continuous/empty intervals.

We hypothesize that different additional duration cues present in filled intervals could be responsible for this. For example, for some comparison types participants could use neural response magnitudes, as there seems to be a positive relation between those and perceived duration (see Eagleman & Pariyadath, 2009). The difference in the results with continuous intervals and tone sequences could then be due to the comparatively lower neural response with continuous intervals due to neural adaptation (e.g., Polich, 1989). The higher peak of neural response with isochronous as compared to continuous intervals could further be due to neural entrainment, at the expected time points (Lakatos et al., 2008). Appealing to overall energy in neural responses is intriguing because it can account for the filled duration illusion, for the higher effect of tone sequences as compared to continuous tone and for the here replicated difference between isochronous and anisochronous intervals (Horr & Di Luca, 2015a). An alternative explanation for the differentiation between isochronous and anisochronous intervals taken alone could be a logarithmic relationship between physical and perceived duration of intervals between tones (see Horr & Di Luca, 2015a; Matthews, 2013; Thomas & Brown, 1974).

The attempt to account for the overall pattern of results in Experiment 2 by appealing to one of the discussed single mechanism is limited by two apparent internal inconsistencies of the data. (1) Even though the direct comparison of isochronous with anisochronous intervals leads to a significant difference in perceived duration, the magnitude of the filled duration illusion measured by comparing a filled to an empty interval is *not* different for isochronous as compared to anisochronous intervals. (2) Even though the direct comparison of tone sequences (both isochronous and anisochronous) with continuous intervals does not lead to a significant difference, the filled duration illusion (again measured by comparing a filled to an empty interval) is weaker for continuous sounds than for isochronous and anisochronous intervals.

To investigate the magnitude of inconsistencies in our data, we used the PSE values from the different comparison conditions to calculate relative duration distortions for each interval type as described in Mayer et al. (2014). Here we can express PSE values as the difference in the two physical durations $PSE_{12} = D_1 - D_2$ that leads to identical perceived durations $D'_1 = D'_2$. As perceived duration can be expressed as $D' = D + d$, where d represents the distortions in perceived duration D' from the objective duration D, we can formulate PSE as a function of perceived durations and distortions:

$$PSE_{12} = D_1 - D_2 = D_1' - \widetilde{d_1} - D_2' + \widetilde{d_2}$$

But because perceived durations D'_1 and D'_2 are identical at PSE, we can simplify the formula as the difference in duration distortion:

$$PSE_{12} = D_1 - D_2 = \widetilde{d_2} - \widetilde{d_1} \ .$$

In fact, PSE can be expressed not only relatively to the objective duration D, but also as the difference in duration distortion d from any value a as such:

$$PSE_{12} = \left(a + \widetilde{d_2}\right) - \left(a + \widetilde{d_1}\right) = \widetilde{d_2} - \widetilde{d_1} \ .$$

In the following, d_1 and d_2 will represent the relative distortion in perceived duration with respect to a, the average duration distortion in the experiment. If we want to express the six PSEs obtained in the conditions of Experiment 2, we can use the following system of equations:

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$$\begin{bmatrix} pse_{continuous/empty} \\ pse_{isochronous/empty} \\ pse_{anisochronous/empty} \\ pse_{continuous/isochronous} \\ pse_{continuous/anisochronous} \\ pse_{isochronous/anisochronous} \end{bmatrix} = \begin{bmatrix} -1 & 0 & 0 & 1 \\ 0 & -1 & 0 & 1 \\ 0 & 0 & -1 & 1 \\ -1 & 1 & 0 & 0 \\ -1 & 0 & 1 & 0 \\ 0 & -1 & 1 & 0 \end{bmatrix} \begin{bmatrix} d_{continuous} \\ d_{isochronous} \\ d_{anisochronous} \\ d_{empty} \end{bmatrix},$$

that is:

$$p = M\,d\,.$$

If d were the absolute value of distortion, such system would have infinite solutions. But here we express d relatively to the average duration distortion in the experiment a, so that a single solution to this linear system can be approximated using the Moore-Penrose pseudoinverse M^{+}:

$$d_{estimated} = M^{+}\,p\,.$$

We apply this formula to the data obtained from each participant so to calculate the mean distortion in perceived duration for the four types of intervals tested (Figure 3a). Here, $d = 0$ refers to a duration distortion equal to the average duration distortion a over all interval types tested in Experiment 1 (see Mayer et al., 2014). Empty intervals are perceived as shorter than continuous intervals (paired sample t-test on d values, $t_{(17)} = 5.2$, $p < 0.001$, $d = 1.23$), isochronous intervals ($t_{(17)} = 14.5$, $p < 0.001$, $d = 3.42$), and anisochronous intervals ($t_{(17)} = 8.4$, $p < 0.001$, $d = 1.98$). Moreover, continuous intervals are perceived as shorter than isochronous ones ($t_{(17)} = -2.5$, $p = 0.02$, $d = 0.59$). There is no difference between continuous vs. anisochronous ($t_{(17)} = -1.7$, $p = 0.10$, $d = 0.40$) nor isochronous vs. anisochronous ($t_{(17)} = 1.5$, $p = 0.15$, $d = 0.35$) intervals. PSEs can be reconstructed from calculated distortions by:

$$p_{reconstructed} = M\,d_{estimated}\,.$$

Such formula makes it possible to determine whether PSE values in the comparison task were solely dependent on the sum of single interval distortions. The comparison between observed and reconstructed PSE values is displayed in Figure 3b. Observed and reconstructed data differ significantly as indicated by the interaction term of a Two-Way r.m. ANOVA on PSE values with factors condition and empirical or reconstructed ($F_{(5,85)} = 5.3$, $p < 0.001$, $\eta_p^2 = 0.24$). The values for the continuous/empty (paired sample t-test on PSE, $t_{(17)} = 2.8$, $p = 0.013$, $d = 0.66$), anisochronous/empty ($t_{(17)} = -3.4$, $p = 0.003$, $d = 0.80$), continuous/isochronous ($t_{(17)} = -2.7$, $p = 0.016$, $d = 0.64$), and isochronous/anisochronous conditions ($t_{(17)} = -2.7$, $p = 0.015$, $d = 0.64$) differ significantly between empirical and reconstructed. Only the difference in the continuous/anisochronous ($t_{(17)} = -0.9$, $p = 0.36$, $d = 0.21$) and isochronous/empty conditions ($t_{(17)} = 0.47$, $p = 0.64$, $d = 0.11$) were not significant.

The present inconsistencies indicate that distortions in two-interval forced-choice duration judgments do not solely depend on the perceived duration of the two intervals compared, which challenges the assumption of simple difference models (see e.g., Green & Swets, 1973; Macmillan & Creelman, 2005; Thurston, 1994). Context effects regarding the sequence in which stimuli are presented (e.g., Dyjas & Ulrich, 2014; Hellström, 1985, 2003) and the distribution of durations (e.g., Brown, McCormack, Smith, & Steward, 2005; Jazayeri & Shadlen, 2010; Wearden & Ferrara, 1995; Wearden & Lejeune, 2008) have frequently been reported in the literature. To test whether our results could be accounted for by hysteresis in duration judgments, that is, if there is a distortion of perceived duration depending on the type of filling of the previous interval, we performed a 2×6 Two-Way r.m. ANOVA on PSE values with factors presentation order (which of the two intervals was presented first) and comparison type (the six comparison conditions, cf. Figure 2). In accordance with the literature (e.g., Dyjas & Ulrich, 2014; Hellström, 2003) we find a significant bias to judge the second interval as longer than the first one ($F_{(1,\ 17)} = 12.7$, $p = 0.002$, $\eta_p^2 = 0.57$) and as

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expected the factor comparison type is significant ($F_{(5, 85)} = 23.45$, $p < 0.001$, $\eta_p^2 = 0.43$).

Most importantly, there is no significant interaction between the factors order and comparison type ($F_{(5, 85)} = 1.20$, $p = 0.31$, $\eta_p^2 = 0.07$) suggesting that the inconsistencies in PSE we found cannot be accounted for by appealing to the presentation order of the intervals alone.
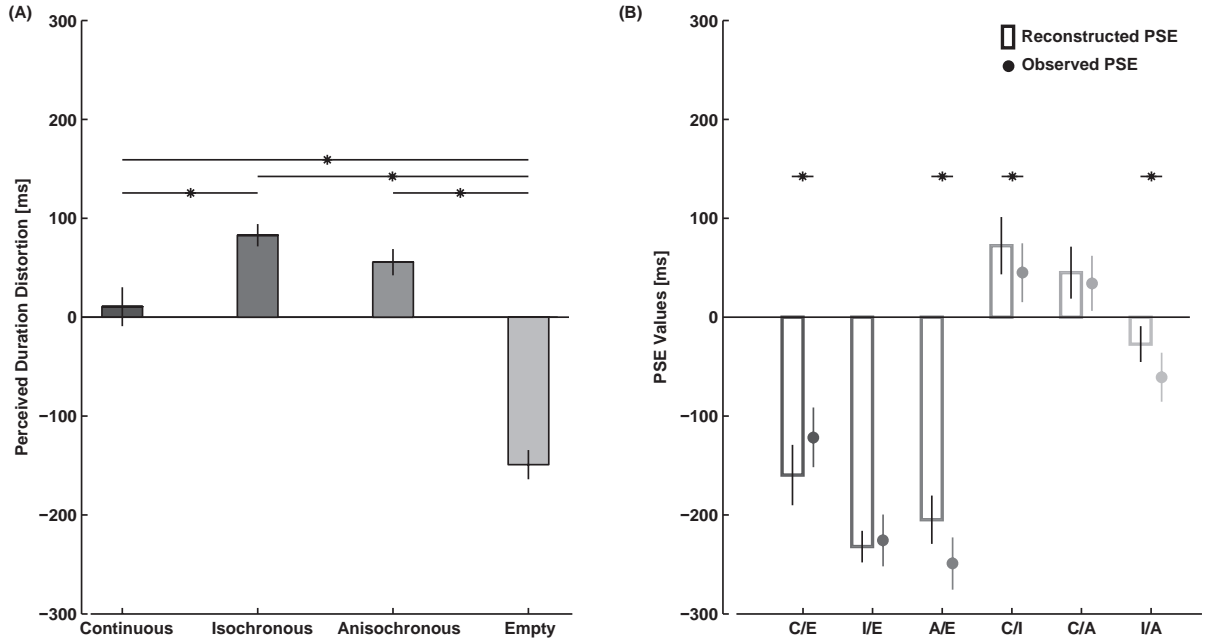
Figure 3. Analysis of perceived duration distortions obtained from empirical PSE values. (A) Perceived duration distortions relative to the mean of all intervals tested (the zero point on the vertical axis corresponds to the average distortion across the interval types tested) calculated from the empirical PSE values according to the system of equations described in the text. Asterisks represent a significant difference in distortion between two interval types as indicated by the horizontal lines. (B) Empirical PSE values compared to reconstructed PSE values from the calculated perceived duration distortions. Asterisks indicate a significant difference between the two, suggesting that factors other than duration distortion of the two intervals to be compared might have affected participant's judgments.

Though it remains unclear what are the factors inducing inconsistencies in the data across conditions, one may speculate that different mechanisms could be used to compare durations when intervals to be compared are of the same type and of different types. We have discussed

previously that duration judgments performed with the same type of intervals as in Experiment 1 could be aided by additional cues that are correlated to temporal duration (e.g., total energy and timing between successive tones). With the exception of isochronous and anisochronous intervals, the trials in Experiment 2 do not allow a direct comparison of additional cues to duration. Participants may have tried to map different cues to improve the comparison (i.e., mapping total energy in one interval to subinterval duration) thus creating response biases which lead to one type of interval to be reported longer more often than the other. Such biases would be dependent on the pair of stimuli involved in the comparison and could thus explain the inconsistencies observed in our data.

3.7 Conclusions

Our results highlight the influence of interval type on discrimination performance and perceived duration. The observed effects have several implications regarding the computational and neural mechanisms underlying duration judgments. Differences in discrimination performance can be explained by considering the presence of multiple cues for duration discrimination when comparing intervals of the same type. Also distortions in perceived duration can be accounted for by appealing to such additional cues, particularly neural response magnitude, which is higher for continuous and anisochronous stimuli compared to empty, but is even higher with isochronous stimuli due to neural entrainment. Interestingly, inconsistencies in the pattern of results indicate that duration judgments in a forced-choice comparison task are affected by factors other than distortions in perceived duration of the individual intervals. Such factors need to be taken into account to understand internal inconsistencies in duration comparisons between different interval types.

Chapter 4

Timing rhythms: Perceived duration increases with a predictable temporal structure of short interval fillers

This research was published in:

The two experiments reported investigate duration distortions due to interval fillers made up of fully predictable rhythms. An overestimation of all rhythms compared to anisochronous, that is, temporally unpredictable intervals, is observed (Experiment 1). No overall significant distortions between rhythms and isochronous intervals is found, though there is a tendency toward understimating rhythms. Duration distortions between rhythms and isochronous intervals differ between different rhythm types (Experiment 2). The data are modelled in a logarithmic accumulator counter framework. Also implications for a neural response magnitude approach of perceived duration are discussed.

4.1 Abstract

Variations in the temporal structure of an interval can lead to remarkable differences in perceived duration. For example, it has previously been shown that isochronous intervals, that is, intervals filled with temporally regular stimuli, are perceived to last longer than intervals left empty or filled with randomly timed stimuli. Characterizing the extent of such distortions is crucial to understanding how duration perception works. One account to explain effects of temporal structure is a non-linear accumulator counter mechanism reset at the beginning of every subinterval. An alternative explanation based on entrainment to regular stimulation posits that the neural response to each filler stimulus in an isochronous sequence is amplified and a higher neural response may lead to an overestimation of duration. If entrainment is the key that generates response amplification and the distortions in perceived duration, then any form of predictability in the temporal structure of interval fillers should lead to the perception of an interval that lasts longer than a randomly filled one. The present experiments confirm that intervals filled with fully predictable rhythmically grouped stimuli lead to longer perceived duration than anisochronous intervals. No general over- or underestimation is registered for rhythmically grouped compared to isochronous intervals. However, we find that the number of stimuli in each group composing the rhythm also influences perceived duration. Implications of these findings for a non-linear clock model as well as a neural response magnitude account of perceived duration are discussed.

4.2 Introduction

Perceived duration of an interval is influenced by interval filling. A well-known and consistent effect demonstrating this influence is the filled-duration illusion (e.g., Adams, 1977; Buffardi, 1971; Thomas & Brown, 1974; Wearden et al., 2007): Intervals demarcated by a beginning and an end marker are perceived to last longer if they contain a number of short filler stimuli (filled intervals) rather than if there is no stimulation between the two markers (empty intervals). Recently it has been shown that not only the number and duration of interval fillers make a difference in perceived duration (Buffardi, 1971; Schiffmann & Bobko, 1977), but also their temporal structure plays a role (Horr & Di Luca, 2015a, b; Matthews, 2013). Here, we intend to further explore the role of temporal structure on perceived duration.

Effects of temporal structure on perceived duration could be explained in the framework of an accumulator counter mechanism by hypothesizing a non-linear accumulator that is resetting at the onset of every stimulus delimiting a subinterval (Buffardi, 1971; Matthews, 2013). The overall duration is then the sum of each accumulated subinterval. Such a clock model with a logarithmic accumulator adheres to the empirical finding of a decrease in perceived duration with higher filler anisochrony, i.e. randomness (Horr & Di Luca, 2015a), as whatever is added to the physical duration of one subinterval will be perceptually less than the same physical duration being subtracted from the other subintervals. The logarithmic clock model also predicts the finding that a higher number of filler stimuli increases the perceived duration difference between temporally regular compared to temporally irregular intervals (see Horr & Di Luca, 2015a for a mathematical model).

An alternative explanation for distortions due to temporal structure is based on the relation between perceived duration and neural response magnitude. It has been proposed (Eagleman & Pariyadath, 2009; Matthews et al., 2014) that a higher neural response to a

stimulus leads to a longer perceived duration, for example due to a stronger representation in memory (memory trace). Recent studies have provided experimental evidence that neural response magnitude can account for perceived duration, both with monkey single cell recording techniques (Mayo & Sommer, 2013; Sadeghi & Pariyadath, Eagleman, & Cook, 2011) and with human magnetoencephalography methodologies (Kononowicz & Van Rijn, 2014; Noguchi & Kakigi, 2006). In this context, the increase in perceived duration with more filler stimuli can be straightforwardly explained by a higher cumulative neural response (Buffardi, 1971; Schiffmann & Bobko, 1977). On the other hand, changes in perceived duration due only to differences in temporal structure require further consideration. An interesting phenomenon that stems from temporal regularity is the entrainment of neural activity (e.g., Ding et al., 2006; Lakatos et al., 2008; Lakatos et al., 2007; Zanto et al., 2006). Exposure to isochronous stimulation leads to modification of the phase of neural oscillations so that the isochronous stimuli arrive at the peak of neural oscillations. It has further been shown that stimulus processing is modulated by the phase of neural oscillations, that is, the point in time at which a stimulus arrives determines whether the elicited signal is amplified or attenuated (e.g., Sanchez-Vives & McCormick, 2000; Steriade et al., 1993). Consistent with this idea, Lakatos and colleagues (Lakatos et al., 2008) suggested that neural entrainment guides attentional selection, so that response gain is higher for stimuli arriving in phase with the neural oscillation. Isochronous intervals would therefore elicit higher neural responses than equivalent anisochronous intervals because each stimulus would arrive at the point of highest response amplification. For anisochronous sequences, instead, each stimulus would arrive at a random phase of the oscillation, so that there is equal probability of amplification and attenuation, that evens out overall modulation due to oscillatory phase. Linking this back to a response magnitude account of perceived duration, an overestimation of isochronous as compared to random stimulation due to entrainment is what would be expected.

In the present line of experiments, we test whether and how rhythmic spacing of the stimuli filling an interval influence perceived duration. Investigating such changes in perceived duration allows us to better understand the role of temporal structure on perceived duration and to explore to what extent it is in line with the two accounts of duration distortion (non-linear clock and entrainment). The predictions of a non-linear clock model can be calculated for stimuli of any kind of structure, including the rhythmic ones we use here. The reason for using a rhythmic structure is that the timing of each filler stimulus is fully predictable just after listening to the first rhythmic group. In such a case, neural entrainment should happen in a similar way as for isochronous stimulation and rhythmic, just like isochronous intervals, should be perceived as longer than random intervals. We further explore whether there is a difference in perceived duration between isochrony and different types of rhythms.

A two-interval forced-choice task was used to compare the perceived duration of different rhythmic against random or isochronous intervals. In every trial, participants reported which of two intervals was the longer one. To exclude possible response biases the order of the two compared interval types as well as their duration (standard 1000 ms or comparison of several durations up to $\pm$ 500 ms) was counterbalanced and randomized. In Experiment 1 we presented participants with one rhythmic and one random interval. According to the non-linear clock model account, which predicts decreased duration with increased randomness in the interval, as well as the neural magnitude account, proposing increased duration due to entrainment, we hypothesized that predictable rhythmic intervals will be perceived to last longer than their random counterparts. In Experiment 2 the same rhythmic intervals were compared against isochronous sequences to determine whether duration estimates differed due to rhythm type despite complete predictability of stimulus timing for both intervals.

4.3 Experiment 1

To test the hypothesis that predictability in a stimulus sequence generally leads to an overestimation of perceived duration and to what extent this effect may be related to the rhythmic structure of the interval, we asked participants to compare intervals of different rhythm types to randomly timed intervals.

4.3.1 Material and methods

Twenty-four volunteers (15 female, 20.5 ± 2.7 years) that reported having normal hearing participated in the experiment for course credits or a payment of 7 GBP/h. Written consent was obtained from each participant. Experimental data collection and storage followed the ethical guidelines of the Declaration of Helsinki (2012) and was approved by the Science, Technology, Engineering & Mathematics Ethical Review Committee of the University of Birmingham.

Participants performed duration judgments on auditory intervals filled with a varying number of 1000 Hz tones at 70 dB SPL which lasted 10 ms with 1 ms on and off ramp. Stimuli were presented via headphones. In every trial, two intervals (one rhythmic and one randomly timed) with the same number of stimuli were presented in succession. Random intervals were created by randomly moving the onset of individual filler tones (except the beginning and end tone) in an originally isochronous sequence within a range of half of the isochronous interstimulus interval. For rhythmic intervals, groups of tones were presented with a fixed interstimulus interval and the tone between every two groups was omitted. In the following we will refer to the rhythms according to the number of stimuli in each of the rhythmic groups (i.e., a rhythm with n stimuli in each group is called group-of-n rhythm). Four rhythm conditions were defined according to the number of stimuli within a group, that is, group-of-2, group-of-3, group-of-4 and group-of-5 rhythms. To determine whether there is an influence not only of the number of stimuli within a group, but also of the number of

groups per sequence, group-of-2 rhythms could consist of three, four or five groups per interval. For the other three types of rhythms there were three groups per interval.

Duration judgments were obtained in a two-interval forced-choice task. In every trial, participants pressed a button corresponding to which of two intervals appeared to last longer, the left button for the first one or the right button for the second one. One of the two intervals was always rhythmic, the other one random. One interval was always 1000 ms long, while the other interval had a duration of 500 ms, 700 ms, 850 ms, 1000 ms, 1150 ms, 1300 ms or 1500 ms. Varying durations of an interval solely changed the frequency of filler tones, while the number of fillers as well as their relative temporal relationships stayed intact. The different rhythmic patterns were presented blocked with the sequence of blocks randomized between participants. Figure 1 schematically displays the task and the temporal structure of intervals compared.

In total, participants made 336 duration discrimination judgments in 6 blocks of 56 trials each. The order of presentation of the rhythmic and random interval as well as the order of the 1000 ms interval and the variable duration interval was pseudorandomized and counterbalanced within each block. That is, in a quarter of the trials each the rhythmic interval was (a) 1000 ms long and preceded by a varying random interval, (b) 1000 ms long and followed by a varying random interval, (c) varying in duration and preceded by a 1000 ms random interval and (d) varying in duration and followed by a 1000 ms random interval. The sequence of trials was differently randomized for each participant. The experimental session lasted about 1 hour.

Participants' individual response proportions were assessed in relation to the physical duration difference between the rhythmic and the random interval. With 56 trials per block and 7 possible durations compared to 1000 ms, there were 8 repetitions at every duration

TASK: Which of the two intervals is longer in duration?
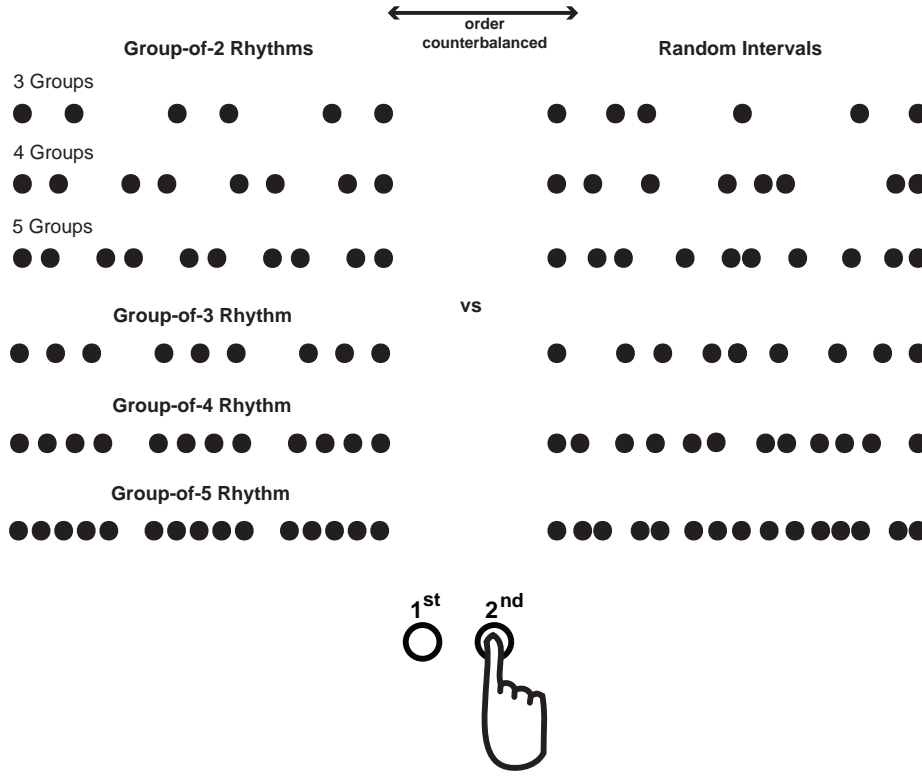
Figure 1. Experimental Task in Experiment 1. Intervals compared in Experiment 1 displayed for two intervals of equal duration. Each rhythmic interval was compared to a random interval. The number of tones was always equal for the two intervals compared and their order was counterbalanced.

difference. The point of subjective equality (PSE) and the just noticeable difference (JND) were estimated using the Spearman-Kärber-Method as the first and second moment of the distribution underlying the raw data obtained from each participant (Miller & Ulrich, 2001; Ulrich & Miller, 2004). With p_i being response proportions and s_i being the 7 duration differences between the rhythmic and the random interval presented at each trial, we define $s_0 = -1350$ ms and $s_8 = 1350$ ms and we assume $p_0 = 0$ and $p_8 = 1$. PSE and JND can then be derived analytically as such:

$$PSE = \sum_{i=1}^{8} \frac{(p_i - p_{i-1})}{2}(s_i - s_{i-1}) \ ; \ JND = \sqrt{\sum_{i=1}^{8} \frac{(p_i - p_{i-1})}{2}((s_i - s_{i-1}) - PSE)^2}$$

4.3.2 Results and discussion

Response Proportions, PSE and JND values separated by rhythm condition are shown in Figure 2. As there is no significant difference between the PSE and JND for the three group-of-2 rhythms with different number of groups (one-way r.m. ANOVA on PSE: $F_{(2,46)} = 0.37$, $p = 0.69$, $\eta_p^2 = 0.02$; on JND $F(2,46) = 0.57$, $p = 0.56$, $\eta_p^2 = 0.02$), the results for the group-of-2 rhythms are presented together. The PSE averaged across the four rhythmic conditions is significantly lower than zero (-60 ± 18 ms, t-test against 0, two-tailed: $t_{(23)} = -3.1$, $p = 0.006$, $d = 0.62$), indicating that rhythmic intervals are perceived as longer than anisochronous intervals. The duration required for an anisochronous stimulus to match a rhythmic one does not differ for rhythms composed of groups of different number (one-way r.m. ANOVA on PSE, $F_{(3,69)} = 0.24$, $p = 0.87$, $\eta_p^2 = 0.01$). The overall JND indicates that people were able to discriminate within the given range of 500 ms duration difference (378 ± 18 ms). JND does
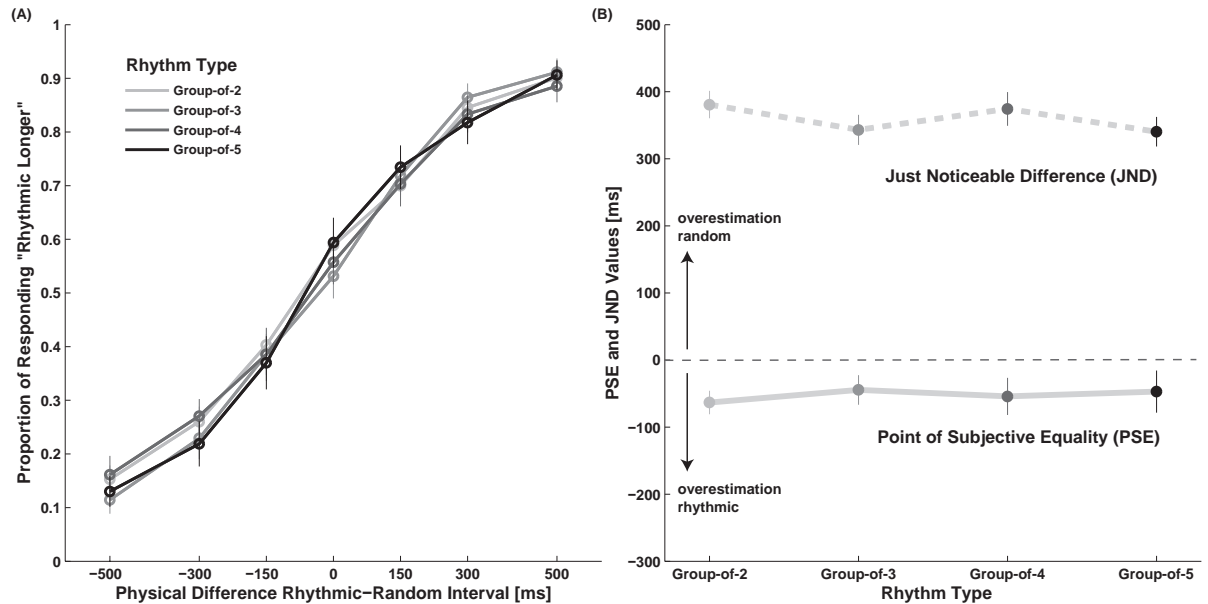
Figure 2. Results of Experiment 1. (A) Proportions of responses indicating the rhythmic interval to be longer than the random interval as a function of physical duration difference. (B) Point of subjective equality (PSE) and just noticeable difference (JND) calculated from response proportions with the Spearman-Kärber method. Error bars are S.E.M.

not significantly vary across conditions (one-way r.m. ANOVA on JND, $F_{(3,69)} = 1.93$, $p = 0.13$, $\eta_p^2 = 0.08$). Overall, the data highlights a general underestimation of the duration of random intervals compared to rhythmic intervals.

4.4 Experiment 2

To test whether the change of perceived duration due to rhythmic structure as compared to random filling is solely due to the predictability of stimulus timing, we asked participants to compare the duration of intervals composed of two fully predictable sequences of stimuli, one rhythmic and one isochronous.

4.4.1 Material and methods

Twenty-four new volunteers (12 female, 21.3 ± 2.4 years) participated in Experiment 2. Experimental procedure and ethical guidelines were similar as in Experiment 1. Experiment 2 differed from Experiment 1 only in the replacement of random intervals by isochronous intervals. That is, in every trial one rhythmic interval was compared to one isochronous interval. Again the experiment consisted of 6 blocks defined by the six rhythmic patterns. Task and interval structures are displayed in Figure 3. Participants made 336 duration discrimination judgments, with 56 trials per block, that is, 56 trials comparing a specific type of rhythm to an isochronous interval with the same number of stimuli.

4.4.2 Results and discussion

Figure 4 shows response proportions, PSE, and JND values. As in Experiment 1, the three group-of-2 patterns did not differ in terms of PSE or JND and were grouped together (one-way r.m. ANOVA on PSE: $F_{(2,46)} = 0.11$, $p = 0.90$, $\eta_p^2 = 0.08$; on JND: $F_{(2,46)} = 2.07$, $p = 0.14$, $\eta_p^2 = 0.08$). The PSE averaged across the four rhythmic conditions shows a tendency of rhythmic intervals to be perceived as shorter than isochronous intervals, however this

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**TASK: Which of the two intervals is longer in duration?**
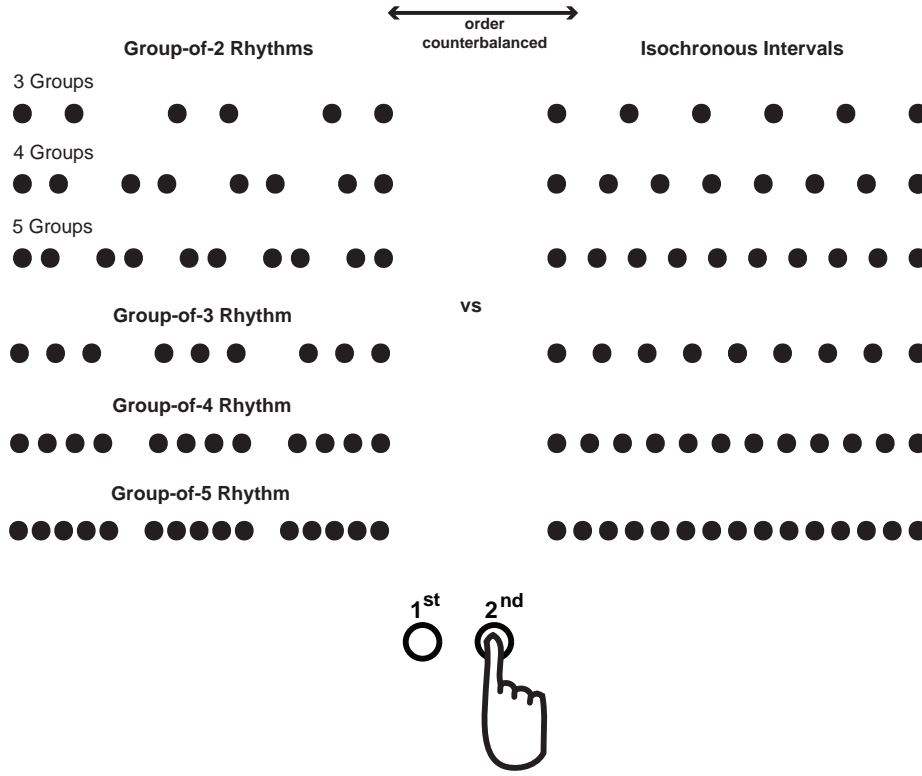
Figure 3. Experimental Task in Experiment 2. Intervals compared in Experiment 2 displayed for two intervals of equal duration. Each rhythmic interval was compared to an isochronous interval. The number of tones was always equal for the two intervals compared and their order was counterbalanced.

underestimation is not statistically significant (33 ± 20 ms, t-test against 0, two-tailed: $t_{(23)} = 1.9$, $p = 0.07$, $d = 0.39$). The duration required for an isochronous interval to perceptually match a rhythmic interval changes depending on the rhythm condition (one-way r.m. ANOVA on PSE: $F_{(3,69)} = 3.3$, $p = 0.027$, $\eta_p^2 = 0.13$). The main effect of rhythm condition on PSE seems to be carried by the difference between group-of-2 rhythms and rhythms with more than two stimuli per group (paired sample t-test on PSE, two-tailed, between group-of-2 and: group-of-3, $t_{(23)} = 2.51$, $p = 0.02$, $d = 0.51$; group-of-4 $t_{(23)} = 2.56$, $p = 0.018$, $d = 0.52$; group-of-5 $t_{(23)} = 2.38$, $p = 0.026$, $d = 0.48$). The average JND is similar to the one obtained in Experiment 1 (330 ± 20 ms) and does not significantly vary across conditions (one-way r.m. ANOVA: $F_{(3,69)} = 2.00$, $p = 0.074$, $\eta_p^2 = 0.10$). In sum, we do not observe a statistically

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significant difference in perceived duration between isochronous and fully predictable rhythmic intervals as a whole, but we register a change in perceived duration depending on the number of stimuli in the groups of the rhythmic interval.
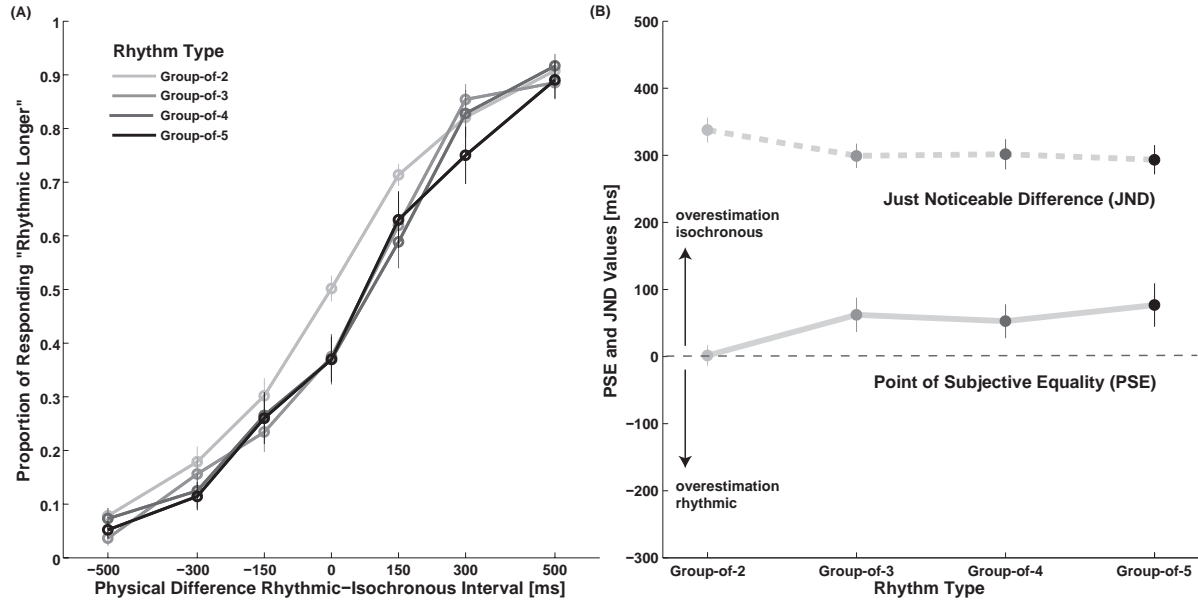
Figure 4. Results of Experiment 2. (A) Proportions of responses indicating the rhythmic interval to be longer than the isochronous interval as a function of physical duration difference. (B) Point of subjective equality (PSE) and just noticeable difference (JND) calculated from response proportions with the Spearman-Kärber method. Error bars are S.E.M.

4.5 General discussion

The present line of experiments were set out to investigate how the rhythmic structure of interval fillers influences perceived duration. More specifically, we tested whether the observed overestimation of isochronous as compared to random intervals (Horr & Di Luca, 2015a,b) can be due to the predictable temporal pattern of isochronous intervals. We further explored whether different temporal patterns, even if fully predictable, lead to differential distortions of perceived duration. In Experiment 1 we found that rhythmic intervals are perceived to last longer than random intervals. Experiment 2 did not reveal a general

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difference in perceived duration between isochronous and rhythmic intervals.

The overestimation of isochronous compared to random intervals can be accounted for by both a non-linear clock model with a logarithmic accumulator reset at the beginning of every subinterval and by a neural response magnitude account assuming that filler stimuli which arrive at a predictable point in time lead to increased responses due to entrainment (Horr & Di Luca, 2015a). The predictions of the two models for rhythmic intervals, instead, are not immediately evident. In the following we will take a closer look at those and discuss to what extent these two models fit the present data.

4.5.1 Non-linear clock model

It has been shown that a logarithmic accumulation of perceived duration in an interval clock framework could explain the overestimation of perceived duration due to isochrony (Thomas & Brown, 1974). Furthermore, such a non-linear accumulation would predict the observed increase of this effect with increasing anisochrony and with increasing sequence length (Horr & Di Luca, 2015a). Would a non-linear clock model also predict an overestimation of rhythmic sequences as compared to anisochrony? What would it say about the comparison of isochrony and rhythms?

To simulate PSE values from the non-linear clock model, the physical duration T^1 that is needed for an interval to be perceived of equal duration as another interval T^2 can be expressed by

$$\psi(T^1) = \psi(T^2)$$

Where ψ represents the psychometric function that relates physical to perceived duration. The non-linear clock model assumes that: (1) the clock is reset at every filler tone demarcating the beginning of a new subinterval (Narkiewicz, Lambrechts, Eichelbaum & Yarrow, 2015), (2) the complete interval duration is obtained by summing up the perceived durations of the

subintervals D, that is, $\psi(T) = \sum_{s=1}^{N} \psi'(D_s)$, and (3) the relationship between the physical and the perceived duration of the subintervals is logarithmic (Matthews, 2013; Thomas & Brown, 1974), $\psi'(D) = \log(D)$. This leads to:

$$\sum_{s=1}^{N} \log(D_s^1) = \sum_{s=1}^{N} \log(D_s^2)$$

which by applying the sum rule of the logarithm simplifies to:

$$\prod_{s=1}^{N} D_s^1 = \prod_{s=1}^{N} D_s^2.$$

The PSE value is obtained by setting either $\sum_{s=1}^{N} D_s^1 = 1s$ and thus $\sum_{s=1}^{N} D_s^2 = \text{PSE}$ or vice versa. Figure 5 shows the PSE values obtained for the different rhythms. In Experiment 1 we simulated the anisochronous intervals by drawing the mean over 1000 random samples. In Experiment 2 sampling is not necessary as the timing of the filler stimuli is completely determined. In general, the simulated PSE values from Experiment 1 and 2 indicate an underestimation of random and an overestimation of isochronous intervals as compared to rhythmic intervals. They further show a general tendency of a decrease in perceived duration with rhythmic groups containing more stimuli. The results of the simulation have a pattern similar to the observed data. There is no significant difference between observed and simulated PSE values between any of the groups in Experiment 1 (t-tests against simulated value, $p > 0.6$) and Experiment 2 (t-test against simulated value for group-of-2, $t_{(23)} = 1.9$, $p = 0.07$, $d = 0.39$, all others $p > 0.5$). The model prediction of an overestimation of perceived duration for rhythmic intervals as compared to anisochronous intervals is in line with the results of Experiment 1. However, the predicted overestimation of duration for isochronous over rhythmic intervals is not statistically confirmed by the results of Experiment 2. Experiment 1 shows no differential distortions between rhythmic conditions, whereas the

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results of Experiment 2 are in line with the predictions that rhythms composed of groups with fewer stimuli should be perceived to last longer.
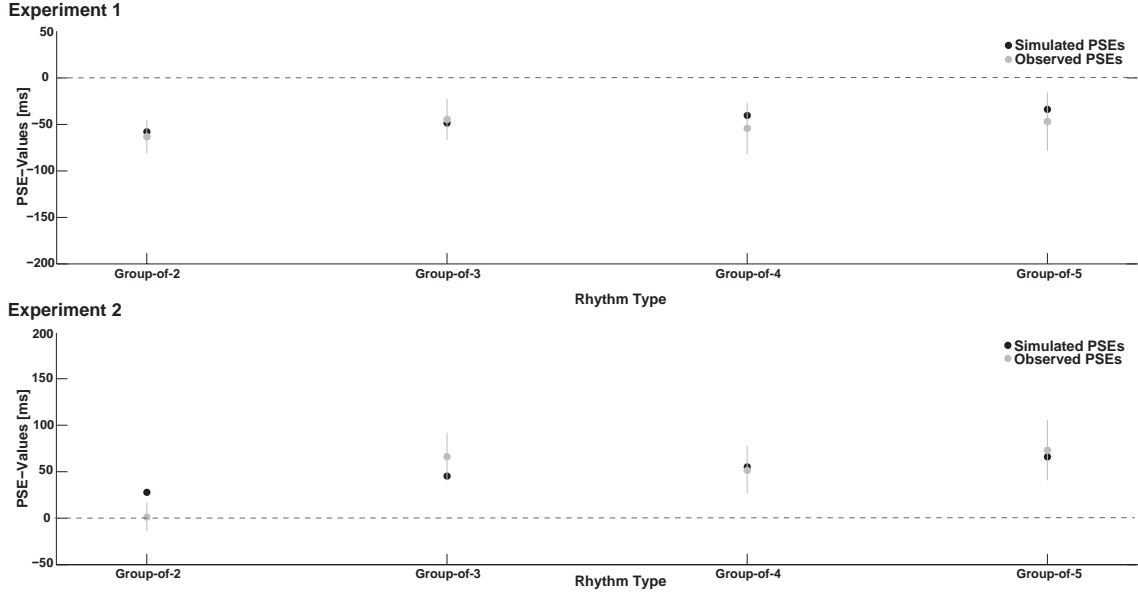
Figure 5. Simulation of PSE values according to a non-linear clock model. Observed and simulated PSE values. In Experiment 1 simulated PSE values are the mean over 1000 repetitions. In Experiment 2 there is only one simulated PSE value due to the deterministic temporal distribution. The x-axes represent the different comparison conditions as they were in the experiment. Error bars for observed PSE values are S.E.M.

4.5.2 Entrainment/Neural response magnitude model

The overestimation of rhythmic intervals as compared to random ones observed in Experiment 1 is predicted from a model where the increase of neural response magnitudes due to entrainment translates to an increase in perceived duration (Horr & Di Luca, 2015a; for effect of entrainment: Ding et al., 2006; Lakatos et al., 2008; Lakatos et al., 2007; Zanto et al., 2006). If we assume that any fully predictable rhythm would generate a similar amount of entrainment, then we should not expect differences in perceived duration between isochronous and rhythmic intervals and all rhythmic groupings should be perceived as having similar duration. The results of Experiment 1 do not highlight a change in perceived duration

as a function of group size. Moreover, the results of Experiment 2 show no significant difference in perceived duration of rhythmic and isochronous stimuli, but they highlight an unexplained change in perceived duration as a function of the number of stimuli composing the rhythmic groups. This difference makes it worth thinking about whether and how a model based on entrainment plus neural response magnitude could explain differences between different rhythmic groupings.

A possibly crucial difference between grouping conditions may lie in the number of stimuli that it takes to be able to make predictions on the arrival of a future stimulus. In an isochronous sequence, the inter-stimulus-interval (ISI) between only two stimuli is sufficient to predict the arrival of every other stimulus in the sequence. To make the same prediction in a rhythmic interval, there are several pieces of information required, that is, (a) the ISI between two stimuli, (b) the number of stimuli in a group, and (c) the ISI between two groups of stimuli. Therefore, the observer will necessarily have to wait for the onset of the first stimulus in the second group of stimuli to be able to predict the timing of all of the following stimuli. To sum up, in order to accurately predict all following stimuli, it takes two stimuli in the isochronous sequence, three stimuli in a group-of-2, four stimuli in a group-of-3, five stimuli in a group-of-4 and six stimuli in a group-of-5 rhythm. As prediction is delayed, entrainment and thus amplification of neural response in rhythmic intervals may start later, consequently decreasing the overall neural response magnitude and leading to a shorter perceived duration. The predictions of this account would also be qualitatively in line with the predictions of a non-linear clock model, namely, a linear decrease of perceived duration with increased number of stimuli per group. Future studies with a wide range of stimuli per group and a direct comparison between different rhythm types are necessary to test whether such predictions hold. An alternative approach to explain distortions between different rhythmic intervals in the entrainment/neural response magnitude framework may be chunking

mechanisms that gear phase locking toward the rhythmic groups rather than the individual tones (Janata & Grafton, 2003; Merzenich, Schreiner, Jenkins & Wang, 1993).

4.6 Conclusions

Previous research has shown that isochronous intervals are overestimated as compared to anisochronous intervals (Horr & Di Luca, 2015a). The present experiments demonstrate that fully predictable rhythmic structures influence perceived duration in the same way as isochrony. This type of temporal distortion suggests that a temporal structure that allows the prediction of stimulus timing increases the perceived duration of intervals.

Both non-linear clock models and the proposal of a connection between perceived duration and entrainment strength due to neural response magnitudes could explain the observed overestimation of isochronous as well as rhythmic intervals compared to random interval filler spacing. The interval clock model predicts a decrease of perceived duration with rhythms composed of more stimuli. The predictions of the magnitude model depend on whether we assume equal or different entrainment strengths for different rhythmic structures. Further research is needed to put additional constraints on a model explaining perceived duration distortions due to temporal structure. Such research should use broader ranges of grouping numbers and directly compare different interval types to determine whether the overestimation of predictable intervals is equivalent for all rhythms including isochrony and, if not, to disentangle general patterns of distortions between such interval types.

Chapter 5

Perceived time and temporal structure: Neural entrainment to isochronous stimulation increases duration estimates

This research was published in:

An EEG experiment is reported that tests the hypothesis of a relationship between neural entrainment and the overestimation of isochronous intervals. Entrainment is measured as a prolonged increase in phase consistency over trials. Isochronous intervals show clear entrainment in the stimulation frequency (4 Hz) and its second harmonic (8 Hz). When using entrainment channels to test the difference between physically identical intervals perceived as longer and those perceived as shorter, an increase of entrainment strength for intervals perceived as longer is found. The latter effect is specific to isochronous intervals in the 4 Hz frequency band and is positively correlated with participants' individual tendency to overestimate isochrony. The relationship between duration estimates and entrainment is interpreted in a neural response magnitude framework of perceived duration, though limitations and alternative explanations are discussed.

5.1 Abstract

Distortions of perceived duration can give crucial insights into the mechanisms that underlie the processing and representation of stimulus timing. One factor that affects duration estimates is the temporal structure of stimuli that fill an interval. For example, regular filling (isochronous interval) leads to an overestimation of perceived duration as compared to irregular filling (anisochronous interval). Here, we use EEG to investigate the neural basis of this subjective lengthening of perceived duration with isochrony. In a two-interval forced choice task, participants judged which of two intervals lasts longer – one always being isochronous, the other one anisochronous. Response proportions confirm the subjective overestimation of isochronous intervals. At the neural level, isochronous sequences are associated with enhanced pairwise phase consistency (PPC) at the stimulation frequency, reflecting the brain's entrainment to the regular stimulation. The PPC over the entrainment channels is further enhanced for isochronous intervals that are reported to be longer, and the magnitude of this PCC effect correlates with the amount of perceptual bias. Neural entrainment has been proposed as a mechanism of attentional selection, enabling increased neural responsiveness toward stimuli that arrive at an expected point in time. The present results support the proposed relationship between neural response magnitudes and temporal estimates: An increase in neural responsiveness leads to a more pronounced representation of the individual stimuli filling the interval and in turn to a subjective increase in duration.

5.2 Introduction

An interesting distortion in the subjective estimate of duration for intervals in the millisecond-to-second range is the filled duration illusion: intervals that are filled with either a sequence of short stimuli (e.g., Adams, 1977; Buffardi, 1971; Horr and Di Luca, 2015b; Thomas & Brown, 1974) or with one continuous stimulus (e.g., Hasuo et al., 2014; Horr & Di Luca, 2015b; Rammsayer & Lima, 1991) are perceived to last longer than empty intervals that only consist of a beginning and an end marker. Filled duration and related illusions are good examples of how distortions of perceived duration can foster the formulation of hypotheses regarding the conceptual and neural mechanisms underlying the brains' ability to estimate interval duration. There are several possible explanations for the filled duration illusion. Most straightforwardly, the illusion is in line with a neural magnitude approach of perceived duration. The fundamental assumption of a magnitude approach is that the degree of neural activity concurrent with the stimulation during an interval is directly related to the interval's perceived duration (e.g., Eagleman & Pariyadath, 2009; Matthews et al., 2014). This approach is not only able to explain how higher magnitude, e.g., higher stimulus intensity (e.g., Berglund et al., 1969), bigger stimulus size (e.g., Xuan et al., 2007), and higher number of stimuli in the interval (e.g., Buffardi, 1971), leads to increases in perceived duration. It also explains a decrease in perceived duration with stimulus repetitions or extended presentation (e.g., Birngruber et al., 2014; Chen and Yeh, 2009; Efron, 1970; Kim and McAuley, 2013; Pariyadath and Eagleman, 2008; Tse, Intriligator, Rivest, & Cavanagh, 2004). This is because repeated stimulation leads to a more efficient neural representation of the stimulus (e.g., Grill-Spector et al., 2006; Wiggs & Martin, 1998) and therefore repetition suppression, that is, decreased neural activation concurrent with repeated stimulation (e.g., Fahy et al., 1993; Rainer and Miller, 2000).

Horr and Di Luca (2015a, 2015c) recently showed that not only the amount of filling in

an interval, but also the temporal structure of fillers can influence perceived duration: For example, regularly spaced (isochronous or rhythmic) tone sequences cause intervals to be perceived as longer compared to those with a random (anisochronous) filler spacing. A tendency that isochronously filled intervals are overestimated as compared to anisochronously filled intervals has also been reported by Grimm (1934) and Thomas and Brown (1974). Consistent with these findings, a recent study by Matthews (2013) showed that isochronously filled intervals are perceived as longer than intervals filled with accelerating or decelerating sequences. Horr and Di Luca (2015a) further demonstrated that the bias toward overestimating isochronous intervals increases with the number of stimuli per interval. They also showed that the isochrony bias is specific to regularity in time, as no distortions in duration are induced when varying regularity in non-temporal filler characteristics (e.g., sound intensity or pitch), as long as the average characteristics of sounds in irregular sequences are the same as for regular ones.

Although not as immediately obvious as for the filled duration illusion, the overestimation of isochronous stimulation may as well be in line with a neural magnitude approach of perceived duration. To understand why, we have to take a closer look at the phenomenon of neural entrainment: Neural oscillations are assumed to adapt to the rhythm of regular stimulation, so that the expected arrival time of each stimulus consistently coincides with a specific phase of the entrained oscillation (e.g., Ding et al., 2006; Lakatos et al., 2008; Lakatos et al., 2007). The phase of neural oscillations has further been shown to modulate neural excitability (e.g., Canolty and Knight, 2010; Schroeder and Lakatos, 2009). Entrainment has been suggested to amplify the response to stimuli of interest which arrive at an expected time (and therefore during "high-excitability phases" of the oscillation) while attenuating all other stimulation (e.g., Cravo et al., 2013; Ng, Schroeder & Kayser, 2012; Schroeder et al., 2008; Schroeder and Lakatos, 2009). Assuming that perceived duration

increases with the neural response during the timed interval, isochronous intervals would then be overestimated because the neural response elicited by an isochronous sequence is higher than the response elicited by an anisochronous sequence. A higher neural response toward isochronous stimulation can be assumed because each stimulus in an isochronous sequence arrives at the point of maximal neural responsiveness, whereas in an anisochronous sequence the stimuli arrive at random points in the pattern of periodic excitability.

If the proposed entrainment mechanism is responsible for the overestimation of duration with isochronous intervals, we should be able to directly relate the amount of neural entrainment to the magnitude of overestimation in perceived duration. To test this hypothesis, we used EEG to record neural responses during a simple two-interval forced choice task in which each trial consisted of a pair of one isochronous and one anisochronous interval. We performed three tests of our specific entrainment hypothesis, using pairwise phase consistency (PPC, Vinck, Van Wingerden, Womelsdorf, Fries, & Pennartz, 2010) as a measure of the degree to which the phase of the EEG consistently entrained to the regular external stimulation. First, we compared PPC between the isochronous versus the anisochronous sequences to demonstrate entrainment toward the frequency at which isochronous stimuli were presented (4 Hz). Second, we compared PPC between physically identical intervals to determine whether entrainment is higher during the presentation of intervals which subjectively appear to last longer. Third, we correlated the PPC effect of perceived duration with participants' general tendency to overestimate isochrony.

5.3 Methods

5.3.1 Participants

Thirty students (25 females, 20.2 ± 3.2 years) from the University of Birmingham participated in the experiment for course credits or a payment of 6 GBP/h. Two participants were excluded due to their performance in the behavioral task (JND > 0.6). Another four participants had to

be excluded because too few trials (< 20) were left in at least one response condition after EEG artifact rejection. Data of 24 participants (21 females, 20.5 ± 3.5 years) were used for the analysis. As reported in the results section, behavioral data of participants excluded due to insufficient EEG trial numbers had a pattern in line with the overall behavioral findings. All participants were naive to the purpose of the experiment and reported normal auditory sensitivity. The experimental procedure and data collection followed the guidelines of the Declaration of Helsinki (2012), and the protocol was approved by the Science, Technology, Engineering and Mathematics Ethical Review Committee of the University of Birmingham.

5.3.2 Experimental design and task

Participants were presented with two intervals per trial and had to decide which of the two was longer in duration (two-interval forced choice, 2IFC, Figure 1a). Each interval consisted of five 1000 Hz 60 dB SPL tones of 10 ms duration with a 1 ms onset and offset tapering. Because the first sound marked the beginning of the interval and the last sound marked its end, a stimulus was presented on average every 250 ms, leading to an average stimulation frequency of 4 Hz. One of the two intervals to be compared within a trial was always isochronous, that is, the filler tones were equally spaced, while the other one was anisochronous, that is, had a random spacing of the filler tones. Anisochrony was created by randomly moving the onset of the filler tones in a range extending ± half the interstimulus interval in the isochronous sequence. The order of the isochronous and the anisochronous interval was pseudorandomized and counterbalanced between trials and trial types (see below). There was a random gap of 1.5 to 2 s between intervals.

In total, participants performed 272 duration comparisons arranged in four blocks of 68 trials each, randomized in sequence. In half of the trials, the isochronous and anisochronous intervals had an equal duration of 1000 ms. Only these trials were used for EEG analysis to exclude the influence of physical differences in interval durations and thus compare brain

activation solely based on (1) temporal structures and (2) perceived duration. In the other half of the trials, the standard interval (either isochronous or anisochronous) was 1000 ms long, while the comparison interval lasted for 500, 700, 850, 1150, 1300, or 1500 ms (500 and 1500 ms 28 trials each, all others 20 trials each). Although EEG recordings from trials with varying interval durations were not analysed, these conditions were necessary to give participants a feasible task and assess their response proportions dependent on physical duration differences. Values for the points of subjective equality (PSE) and the just noticeable differences (JND) were estimated as the first and second moment of each participants' individual data obtained with the Spearman–Kärber method (Miller and Ulrich, 2001; Ulrich & Miller, 2004). This was crucial to ensure that participants (1) were sufficiently able to perform the task (JND < 0.6) and (2) showed the previously observed bias (Horr & Di Luca, 2015a) toward judging isochronous intervals as longer than anisochronous intervals (PSE < 0).

5.3.3 Procedure and EEG recording

Participants were seated 60 cm away from a switched-off computer screen whose center was marked with a fixation point. Auditory stimuli were presented via one speaker positioned 20 cm underneath the fixation point. Responses were given with the right hand using the "left" and "right" buttons of a computer keyboard. Participants could begin each block by pressing the space button and every trial in a block would start randomly between 1200 and 1700 ms after they gave a response. Participants were instructed to avoid eye and muscle movements during the presentation of the auditory sequences. They were told to take a break for as long as they wanted between blocks and, if necessary, to take a short break between two trials by delaying their response. The experiment lasted between 30 and 40 min. 1.5 h were reserved to give participants detailed instructions on the task and recording procedure as well as to mount the EEG cap and electrodes.

EEG was recorded using an ActiveOne Biosemi System (BioSemi, Amsterdam, The

Netherlands) with an EEG cap of 128 Ag/AgCl electrodes, including the standard locations of the extended international 10/5 system. Electrode offsets were kept below 50 mV. The signal was digitized at a rate of 2048 Hz and offline down-sampled to 500 Hz. Electrodes were re-referenced offline to the average over all non-rejected channels.

5.3.4 EEG analysis

Data were analyzed using Matlab 8.1.0.604 (The MathWorks, Natick, Massachusetts) and the Matlab-based software package Fieldtrip (Oostenveld, Fries, Maris, & Schoeffelen, 2011). The EEG signal was filtered between 1 and 30 Hz and down-sampled to 500 Hz. As explained above, only trials with two intervals of the same physical duration (1 s) were used for EEG analysis. From each trial two epochs were defined: the 1 s isochronous interval and the 1 s anisochronous interval. Each epoch contained the 1 s interval, plus pre- and poststimulus periods of 1500 ms (to allow for onset and offset effects of the filter for later time-frequency transformation). Noisy epochs and channels were rejected according to inspection of the raw data as well as semi-automatic visual inspection of outlier trials and channels. In order to compare between participants, rejected channels were interpolated by the average of their neighboring channels weighted by distance. No more than five channels had to be replaced for any participant. Eye artifacts were removed with principal component analysis using a logistic infomax ICA algorithm (Makeig, Bell, Jung, & Sejnowski, 1996).

Epochs were divided according to the following conditions: (1) temporal structure (i.e., isochronous or anisochronous) and (2) response (i.e., intervals perceived as longer or shorter). Participants for whom less than 20 trials per any condition remained after artifact rejection were excluded from further analysis. All four participants excluded for this reasons had too few trials in the isochronous perceived as shorter and anisochronous perceived as longer condition. For the remaining participants, the mean number of isochronous perceived as longer (= anichronous perceived as shorter) trials was 73.75 ± 18.8, and the mean number of

isochronous perceived as shorter (= anisochronous perceived as longer) trials was 42.04 ±
13.85.

We used the measure of pairwise phase consistency (PPC, Vinck et al., 2010) in order to
test for neural entrainment. The PPC is the average of the circular correlation between the
phases of neural oscillations in each possible pairing of trials from a condition. The time-
frequency representation of the data and the phase angles to compute the PPC were obtained
in a frequency range from 2 Hz to 20 Hz using complex Morlet wavelet convolution with 5
wavelet cycles to achieve a balanced frequency- and time-resolution (Cohen, 2014, pp. 170f).
On the basis of the respective phase angles, one PPC value can be calculated for each channel
at each frequency and each point in time. With N being the number of trials per condition and
φ and ω being the paired phase angles, the PPC is computed as:

$$PPC = \frac{2}{N(N-1)} \sum_{j=1}^{N-1} \sum_{k=j+1}^{N} \cos(\varphi_j)\cos(\omega_k) + \sin(\varphi_j)\sin(\omega_k)$$

External sensory stimulation typically leads to an increase of phase consistency between
trials around stimulus onset (e.g., Brandt, 1997; Jansen, Aggarwal, Hedge, & Boutros, 2003).
This increase may be due to phase reset of ongoing oscillations (e.g., Klimesch, Sauseng,
Hanslmar, Gruber, & Freunberger, 2007; Makeig et al., 2002), a neural population response
leading to additive power (e.g., Jervis, Nichols, Johnson, Allen, & Hudson, 1983; Schroeder
et al., 1995) or a combination of both (Min et al., 2007). While the phase consistency to a
single stimulus rapidly decreases after stimulus onset as oscillations between trials quickly
become out of phase, entrainment leads to a prolonged increase of phase coherence. This
prolonged increase has been argued to reflect oscillations in the stimulus frequency being
aligned to the regular stimulation (e.g., Schroeder et al., 2008).

The PPC was chosen over other measures of intertrial phase consistency since its

magnitude is not affected by the number of trials per condition (Vinck et al., 2010). While other measures of intertrial phase consistency overestimate the population statistics with finite sample sizes, that is, are biased toward higher values for lower trial numbers, the PPC is independent of such bias. A bias-free measure was crucial in the present experiment, as participants' behavioral tendency toward judging isochronous intervals as longer in duration led to grossly unequal trial numbers for the two response options and equating trial numbers would have led to a substantial loss of statistical power. We present the results of the following analyses performed on the PPC data. (1) The PPC was compared between isochronous and anisochronous intervals using a cluster-based permutation test (Maris & Oostenveld, 2007) over all channels, frequencies, and time points. This allowed us to identify channels, frequencies and time points showing significant entrainment. (2) Intervals judged as longer and intervals judged as shorter (despite the same physical duration) were compared for channels and frequencies of interest as identified from the previous analysis. The two response options (longer or shorter) were compared separately for isochronous and anisochronous intervals using a running t-test with a moving 50 ms time window for the mean over the entrainment frequencies and channels (e.g., Schneider, Debener, Oostenveld, & Engel, 2008). (3) Participants' individual PPC difference between isochronous intervals judged as longer and as shorter was correlated with their PSE, that is, the overall behavioral tendency of judging isochronous intervals to last longer.

5.4 Results

5.4.1 Behavioral results

Participants' response proportions as a function of the physical duration difference between intervals is shown in Figure 1b. The mean JND is 370 ms ± 20 ms, indicating a reasonable performance since the longest duration difference presented (500 ms) is reliably distinguished. Data of two participants is excluded due to a JND higher than 600 ms.

(A)

10 ms, 1000 Hz

vs

1st 2nd

(B)

PSE = -87 ms ±19
JND = 372 ms ±20

Proportion of Responding "Isochronous Longer"

Physical Duration Difference Isochronous - Anisochronous Interval [ms]
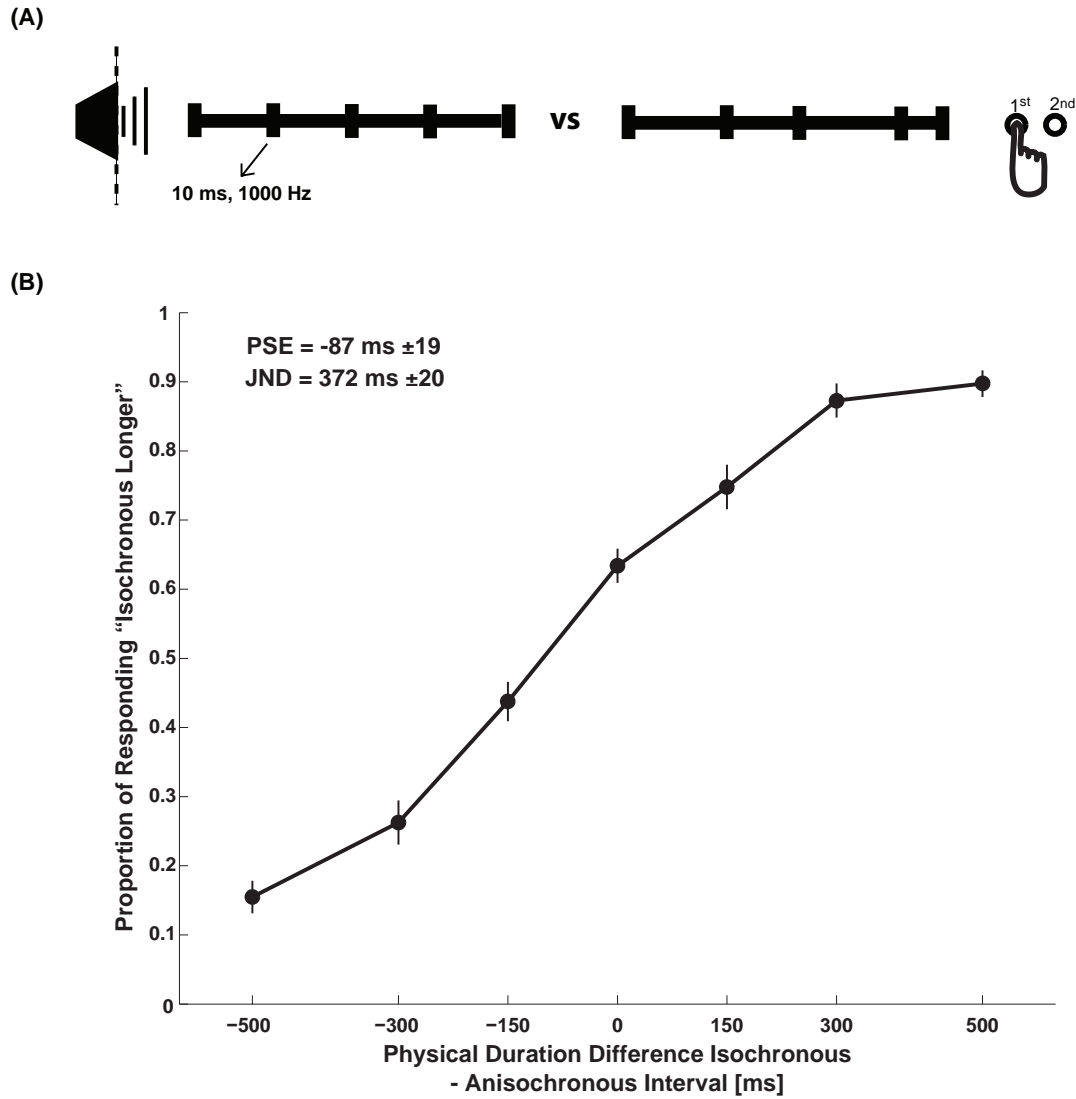
Figure 1. Paradigm and behavioral results. (A) In a two-interval forced choice manner participants had to decide which of two intervals, one isochronous and one anisochronous, was longer in duration. The sequence of intervals was counterbalanced. (B) Response proportions are plotted as a function of the physical duration difference between the isochronous and anisochronous interval. Point of subjective equality (PSE) and just noticeable difference (JND) values were calculated as the first and second moment of the distribution using the Spearman–Kärber method.

The mean PSE is −87 ms ± 19 ms, indicating a significant overestimation in the duration of the isochronous interval (single sample t-test on PSE against 0: $t_{(23)} = -4.5$, $p < 0.001$, $d = 0.93$). Note that participants excluded from analysis due to insufficient trial numbers after artifact rejection had PSEs of −11 ms, −200 ms, −155 ms and −86 ms, respectively, with a

JND less than 600 ms, so each of them showed at least a slight bias toward judging isochronous intervals as longer, and excluding them did not change the conclusions from behavioral results. The overall overestimation of isochronous intervals is further confirmed by looking only at those trials in which the isochronous and anisochronous interval are of the same physical duration. For such trials, participants judged the isochronous interval as longer in 63.4% ± 2.4% of cases (single sample t-test on proportions against 50%: $t_{(23)} = 5.4$, $p < 0.001$, $d = 1.10$).

5.4.2 EEG results

In order to ensure that entrainment of neural oscillations toward regular auditory sequences is present in the EEG data, and to determine the channels and frequencies showing significant entrainment for our next analysis steps, we first examined the difference in PPC between isochronous and anisochronous intervals (see Figure 2a for PPC overview over all channels; see Figure S1a for the same contrast with a more commonly used measure of intertrial phase coherence, ITPC, that averages over all phase angle vectors within each condition). We compared isochronous and anisochronous intervals across the whole time span of interest from 250 ms (defining the average onset time of the second stimulus, and thus the earliest time at which entrainment can be expected) to 1000 ms, and frequencies from 2 to 20 Hz. As expected, the PPC for isochronous intervals is significantly increased around 4 Hz (3.5–4.5 Hz), that is, the stimulation frequency. This effect present over 14 out of 128 channels. Furthermore, a significant PPC increase for isochronous intervals is found around 8 Hz (7.5–8.5 Hz) over 86 out of 128 channels (permutation-based statistics, cluster-corrected, $p < 0.05$, see Figure 2b, c for topographies). The latter finding may be explained by the fact that 8 Hz is the second harmonic to the stimulation frequency. Entrainment to harmonic frequencies has been observed in previous research (e.g., Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Wimber, Maaß, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012). Using the mean over all

entrainment channels at a given frequency, a running average t-test ($p < 0.05$, with 50 ms sliding time windows) revealed that the PPC is significantly higher for isochronous as compared to anisochronous intervals from 450 to 750 ms at 3.5 to 4.5 Hz, and from 150 to 750 ms at 7.5 to 8.5 Hz (see Figure 3a, d). Together, the contrast between isochronous and anisochronous intervals therefore produced the expected results in terms of entrainment toward isochronous auditory stimulation.

Next, we tested for an actual relation between entrainment and perceived duration, as determined by separating intervals according to participants' subjective perception. Specifically, we divided isochronous and anisochronous intervals according to whether they were perceived as longer or shorter than their respective counterpart in a given trial. Note that the two groups of trials compared here (perceived as longer and perceived as shorter) are physically completely identical, and only differ in terms of participants' subjective estimates. When taking the mean over all significant entrainment channels, as displayed in Figure 2b and c, we find a significantly higher PPC at the entrainment frequency (3.5–4.5 Hz) for isochronous intervals perceived as longer compared to isochronous intervals perceived as shorter. The effect is present between 550 and 700 ms after onset of the regular stimulation (running average t-test, $p < 0.05$ at every 50 ms time bin, mean over 3.5 to 4.5 Hz; see Figure 3b; see Figure S1b for the 3.5 to 4.5 Hz analysis of isochronous sequences using ITCP). This enhanced PPC with isochronous stimuli perceived to last longer hints at an increased entrainment as compared to isochronous intervals perceived as shorter. No significant effect between subjective judgments was found when comparing the same channels and intervals at the harmonic frequency (7.5–8.5 Hz, see Figure 3e). With irregular intervals no differences were found either at 3.5 to 4.5 Hz or at 7.5 to 8.5 Hz (see Figure 3c, f; see Figure S1c for the 3.5 to 4.5 Hz analysis of anisochronous sequences using ITCP).
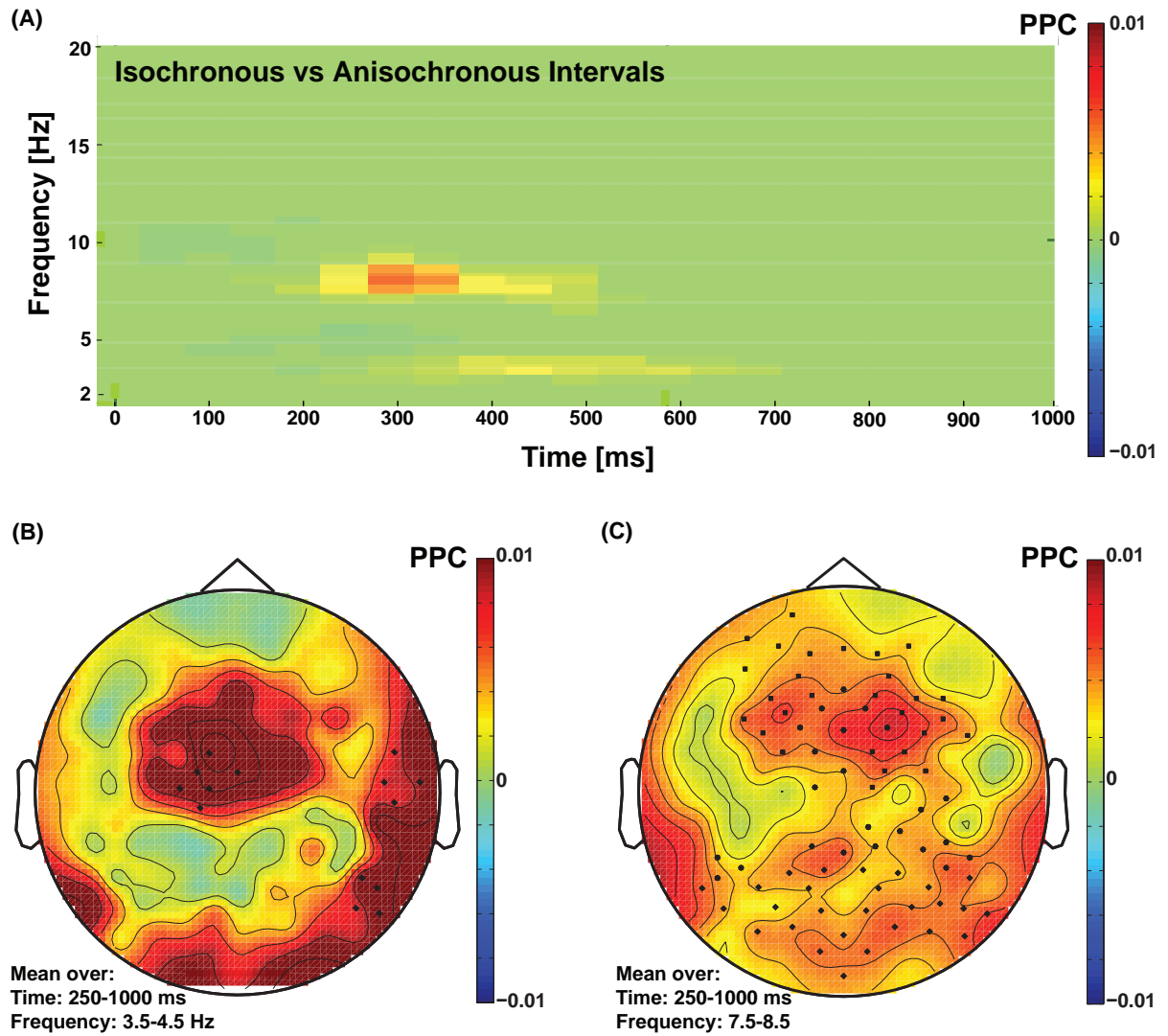
Figure 2. Pairwise phase consistency (PPC) for isochronous and anisochronous intervals of the same duration. (A) Average PPC difference between isochronous and anisochronous intervals over all channels, masked so that only significantly different activation is shown (p < 0.05, permutation-based statistics, cluster-corrected). (B, C) Topographical plots of PPC distributions for the difference between isochronous and anisochronous intervals, between 250 and 1000 ms. Significant entrainment channels are marked with dots, (B) mean over 3.5–4.5 Hz, (C) mean over 7.5–8.5 Hz.

Given the well-known relationship between attention and perceived duration (see e.g., Grondin, 2010 for a review) and the finding that intertrial phase consistency has also been shown to be increased when voluntarily attending a stimulus sequence (Kashiwase, Matsumiya, Kuriki, & Shioiri, 2012; Kim et al., 2007), an additional analysis of frequency
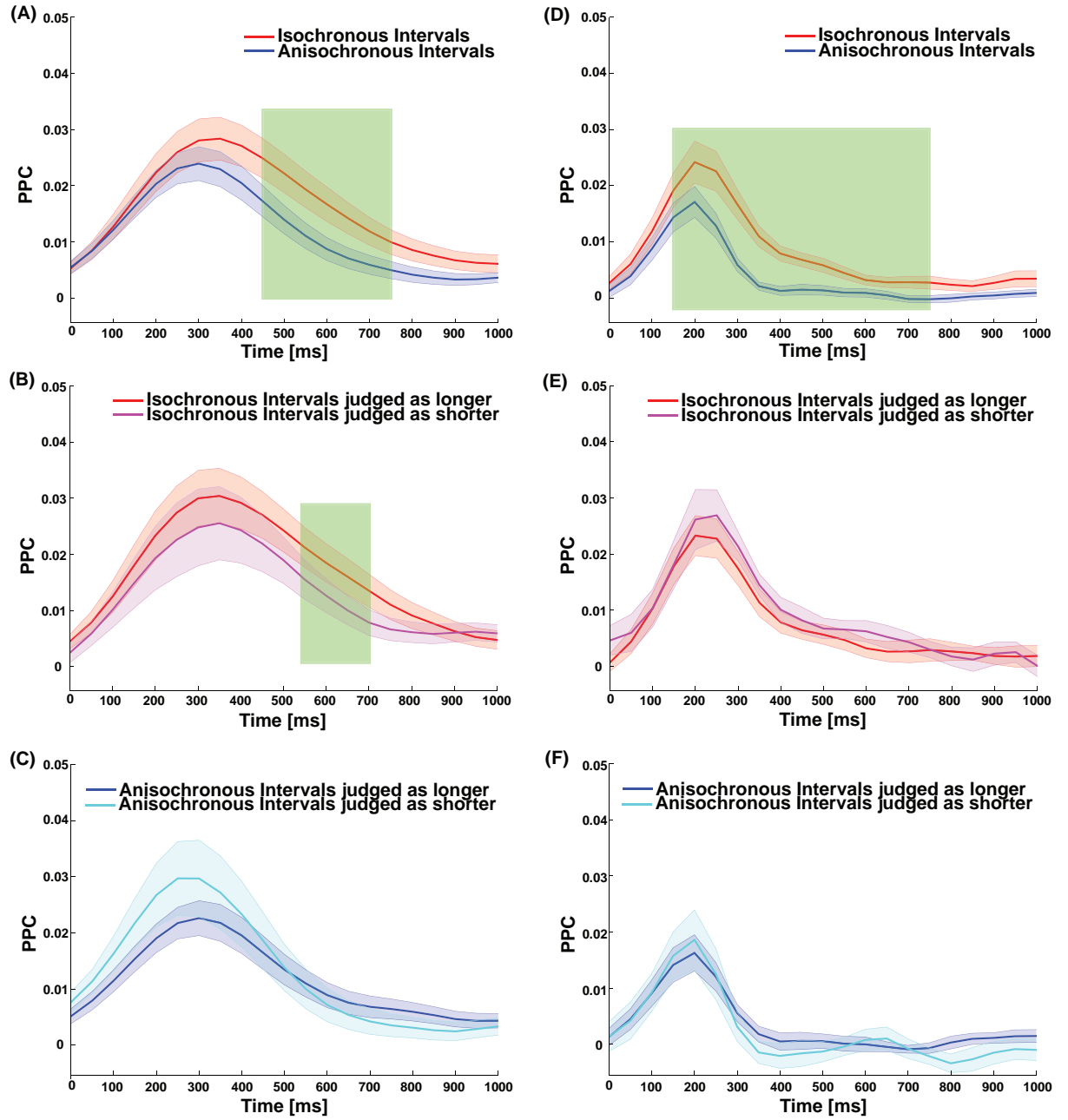
Figure. 3. Time course of PPC between 0 and 1000 ms, mean over all entrainment channels from the isochronous versus anisochronous contrast (see Figure 2b and c) and the entrainment frequency (A–C) 3.5–4.5 Hz and (D–F) 7.5–8.5 Hz. (A and D) Isochronous and anisochronous intervals. (B and E) Isochronous intervals judged as longer and isochronous intervals judged as shorter than their anisochronous counterpart. (C and F) Anisochronous intervals judged as longer and anisochronous intervals judged as shorter than their isochronous counterpart. Green segments represent a significant difference between the two conditions compared using a running average t-test (p < 0.05 at each 50 ms time bin).

power, pre- and poststimulation, specifically focusing on alpha power, was carried out to address the possible concern that the observed PPC effect was based on random attentional fluctuations. This analysis is displayed in Figure S2. Alpha power has been suggested as a neural index of top-down attention (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Van Diepen, Cohen, Denis, & Mahazeri, 2013). An increase in poststimulus alpha power (8 to 12 Hz) was found in the mean over entrainment channels (displayed in Figure 2b and c) for anisochronous intervals judged as longer compared to shorter between 350 and 500 ms (see Figure S2c). However, the contrasts with a differentiation in PPC, that is, the comparison between isochronous and anisochronous intervals (see Figure S2a) as well as isochronous intervals judged as longer and shorter (see Figure S2b), showed no significant difference in alpha power. Given there was a non-significant tendency of decreased prestimulus alpha power for isochronous intervals judged as longer compared to shorter, we checked for a correlation of the mean over alpha power (8 to 12 Hz) over the entrainment channels (displayed in Figure 2b and c) between 800 and 200 ms before stimulus onset and the PPC effect in the time span of entrainment to isochronous stimulation from 450 to 750 ms. No significant correlation was found ($r_{(22)} = -0.12$, $p = 0.56$).

Finally, we specifically tested whether the PPC difference dependent on participant's subjective report of stimulus duration is related to the general overestimation of isochronous sequences. To do so, we correlated participants' individual PSE values with the mean PPC difference between isochronous intervals perceived as longer and isochronous intervals perceived as shorter, over frequency-specific entrainment channels (displayed in Figure 2b and c), and averaged across the time span of entrainment to isochronous stimulation. At the entrainment frequency (3.5–4.5 Hz, significant time span: 400–750 ms), there is a significant negative correlation between PSE and subjective PPC differentiation ($r_{(22)} = -0.65$, $p < 0.001$; see Figure 4a). At the second harmonic (7.5–8.5 Hz, significant time span: 150–750 ms) there

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is no correlation of the subjective PPC differentiation with the overall perceived duration bias ($r_{(22)} = 0.12$, $p = 0.59$; see Figure 4b), in accordance with the general lack of a subjective duration specific PPC effect at 7.5 to 8.5 Hz. Also the difference in prestimulus alpha power (8 to 12 Hz, 200 to 800 ms before stimulus onset) between isochronous intervals perceived as longer and isochronous intervals perceived as shorter, was not correlated with PSE ($r_{(22)} = 0.19$, $p = 0.36$).
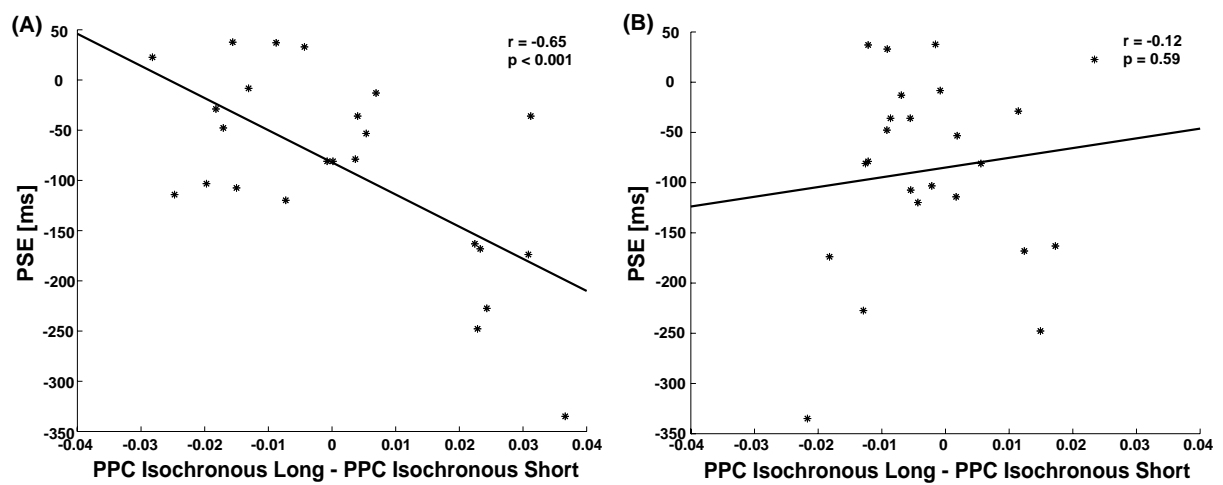
Figure 4. Correlation between the PPC effect and the behavioral overestimation of the isochronous interval. The x-axis plots the difference between the mean PPC of isochronous intervals judged as longer versus shorter for (A) 3.5–4.5 Hz and 450–750 ms (time span of significant 3.5–4.5 Hz entrainment effect), averaged over the 3.5–4.5 Hz entrainment channels (see Figure 2b), and (B) 7.5–8.5 Hz and 150–750 ms (time span of significant 7.5–8.5 Hz entrainment effect), averaged over the 7.5–8.5 Hz entrainment channels (see Figure 2c). The y-axis represents the subject-by-subject PSE value in ms.

5.5 Discussion

In the present experiment, we investigated the neural mechanisms underlying the overestimation of isochronous (temporally regular) as compared to anisochronous (temporally irregular) auditory sequences. More specifically, we tested whether neural entrainment toward stimuli that appear at regular points in time may mediate duration distortions driven by

isochrony. This hypothesis arises from the proposal that perceived duration is linked to the magnitude of neural responses concurrent with the stimulation in the relevant interval (e.g., Eagleman & Pariyadath, 2009; Matthews et al., 2014). Neural entrainment has been shown to cause increased neural responsiveness toward temporally expected compared with unexpected stimuli and has been suggested as one possible neural mechanism by which temporal attention enhances stimulus processing (e.g., Lakatos et al., 2008). Based on these observations, we hypothesized that due to entrainment, higher average neural responses to stimuli presented in an isochronous than an anisochronous sequence would form the neural basis of behavioral distortions in perceived duration. The present results show an increase in pairwise phase consistency (PPC) for isochronous as compared to anisochronous sequences around the entrainment frequency (4 Hz) and its second harmonic (8 Hz). This finding of increased oscillatory phase coherence in response to regular auditory stimulation strongly suggests that neural responses entrain toward the isochronous stimulation. Most interestingly, we found that over EEG channels showing general entrainment (in either frequency), the PPC at 3.5–4.5 Hz shows a significant increase between 500 and 750 ms for isochronous intervals that are perceived as longer compared to those that are perceived as shorter than their anisochronous counterparts. Note that latter effect can only be driven by perceptual differences, as there are no physical differences between the two intervals presented. An even stronger link to behavior is suggested by the finding that the same PPC effect between isochronous intervals perceived as longer versus shorter is negatively related with a participant's point of subjective equality. That is, participants who show a larger average PPC difference between the isochronous intervals that are over- versus those that are underestimated also tend to show a larger overall bias toward overestimating isochronous (compared to anisochronous) intervals. These findings support the idea that neural entrainment, resulting in enhanced neural responsiveness, underlies our behavioral illusion of perceptually overestimating isochrony.

A correlation between neural response magnitudes and perceived duration has been suggested on the basis of previous research on a behavioral as well as neural level. A plethora of behavioral findings demonstrates that the magnitude of stimulation occurring during a given interval influences its estimated duration. Such an increase of perceived duration with the magnitude of stimulation is shown in the filled duration illusion (e.g., Adams, 1977; Hasuo et al., 2014; Thomas and Brown, 1974) as well as the increase of perceived duration with an increased number of fillers in the sequence (Buffardi, 1971). Furthermore, perceived duration increases with stimulus intensity, size and number of stimuli (e.g., Berglund et al., 1969; Xuan et al., 2007) as well as with stimulus complexity (Roelofs and Zeeman, 1951; Schiffman & Bobko, 1974). Another commonly observed distortion of perceived duration is the oddball effect with deviant stimuli being perceived as longer than repeated ones (e.g., Birngruber et al., 2014; Chen & Yeh, 2009; Kim & McAuley, 2013; Tse et al., 2004). Within a neural magnitude framework, the latter finding can be explained via a habituation of neural responses toward repeated stimulation, that is, repetition suppression (e.g., Fahy et al., 1993; Rainer & Miller, 2000), or vice versa increased attention and therefore increased neural responses to novel stimuli (e.g., Linden et al., 1999; Ranganath and Rainer, 2003). Finally, an increase of perceived duration with moving as compared to stationary stimuli has been reported (Brown, 1995) that may be explained via recruitment of additional neural networks, and therefore higher activation when perceiving motion (Dupont et al., 1994).

Behavioral findings indicating overestimation of duration for stimuli that lead to increased neural responses can only provide limited evidence toward the actual neural mechanisms underlying this perceptual bias. To confirm a neural relationship, neurophysiological studies are needed. Sadeghi et al. (2011) conducted an experimental task with moving dot stimuli. They showed that the stimuli moving in an unexpected direction (oddballs), which were overestimated in duration by human participants, elicited higher firing

rates and response durations in neural recordings from middle temporal and visual cortex of awake monkeys. More direct evidence comes from Mayo and Sommer (2013) showing that neurons in the frontal eye field of monkeys, who were trained to classify an interval as longer or shorter than a reference stimulus, have higher firing rates during intervals judged as "long" as compared to those judged as "short." Furthermore, Kononowicz and Van Rijn (2014) demonstrated that the amplitude of event-related-potentials (N1-P2 amplitude) in humans is a valid indicator for the subjective difference between target and reference stimuli and, unlike latency, amplitude difference correlates with perceived duration difference between the two stimuli. All these studies support the idea that neural response magnitudes are to some degree involved in the process leading to the estimate of duration with short intervals.

At a first glance, the overestimation of isochronous as compared to anisochronous stimulus sequences observed in the present and previous studies (Horr & Di Luca, 2015a) seems to be in conflict with magnitude-related overestimation due to, for example, novelty and complexity. If an entrained stimulus is temporally expected, why would it cause a bias similar to unexpected, deviant oddball stimuli? To answer this question, note that in traditional oddball paradigms, the deviant is embedded in a regular stimulation of repeated stimuli. The differentiation between predictability of stimulus characteristics and predictability of stimulus arrival in time is demonstrated by McAuley and Fromboluti (2014), showing that oddballs presented earlier than expected are actually underestimated in perceived duration, while overestimation is strongest for late oddballs. This influence of arrival time is diminished in an anisochronous stimulation sequence. Such results suggest that predictability in time should be investigated separately from effects of stimulus expectation, novelty and habituation. Neural entrainment has been proposed as a mechanism underlying attentional selection by modulating neural oscillations in relevant cortical assemblies to be in phase with regular stimulus presentation, and therefore enabling the
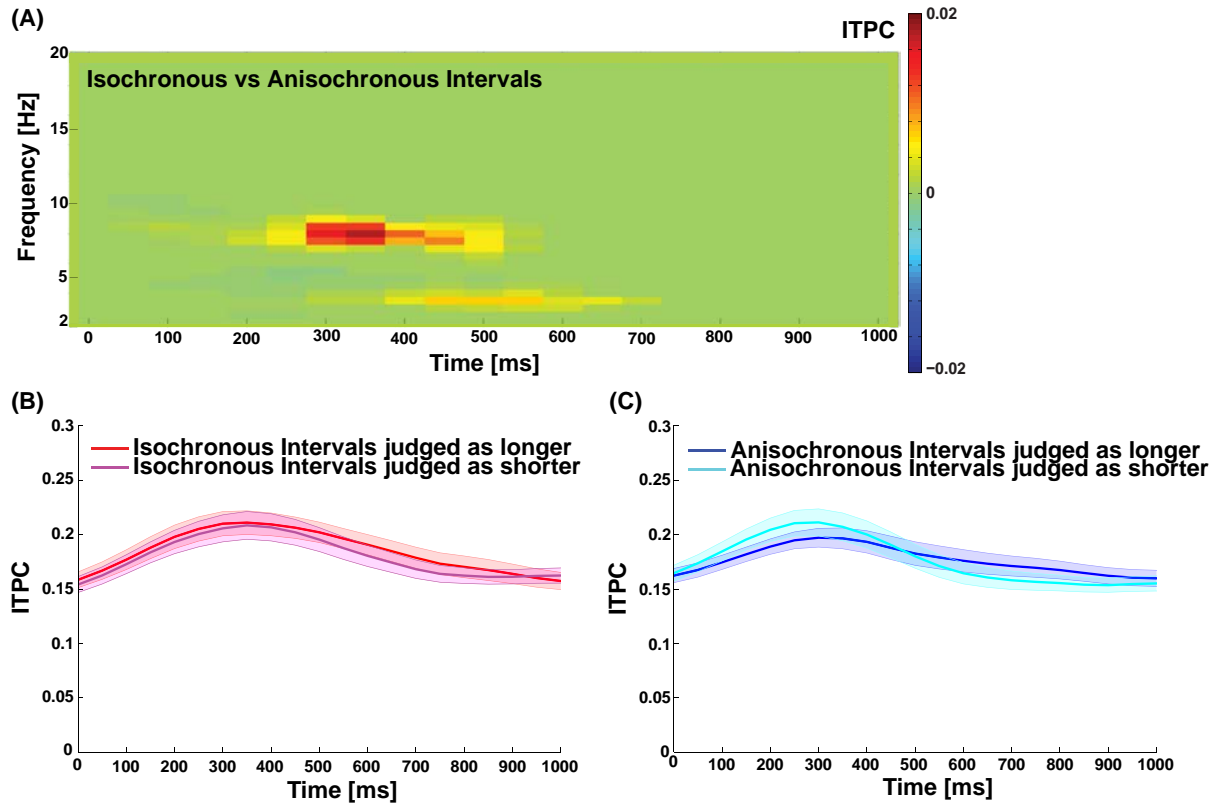
Figure S1. (A) Average intertrial phase coherence (ITPC) difference for isochronous and anisochronous intervals over all channels, masked so that only significantly different activation is shown ($p < 0.05$, permutation-based statics, cluster-corrected). (B and C) Time course of ITPC between 0 and 1000 ms, mean over all entrainment channels from the isochronous versus anisochronous contrast and the entrainment frequency 3.5–4.5 Hz for (B) isochronous intervals and (C) anisochronous intervals judged as longer and shorter. ITCP is computed as the lengths of the over trials averaged phase angle vectors (Tallon-Baundry et al., 1996). Phase angles, as for the PPC, were obtained using complex Morlet wavelet convolution with 5 wavelet cycles. Comparison with Figure 2A and Figure 3C and E shows that PPC and traditional ITPC measure similarly disentangle entrainment in the stimulation frequency and its second harmonic and show similar tendencies regarding the differentiation according to perceived duration.

highest neural responsiveness and behavioral accuracy at those points in time where the stimulus is expected (e.g., Cravo et al., 2013; Lakatos et al., 2008; Schroeder and Lakatos, 2009). This involvement, in turn, links back to the connection between neural response magnitudes and perceived duration of stimuli in an isochronous sequence.
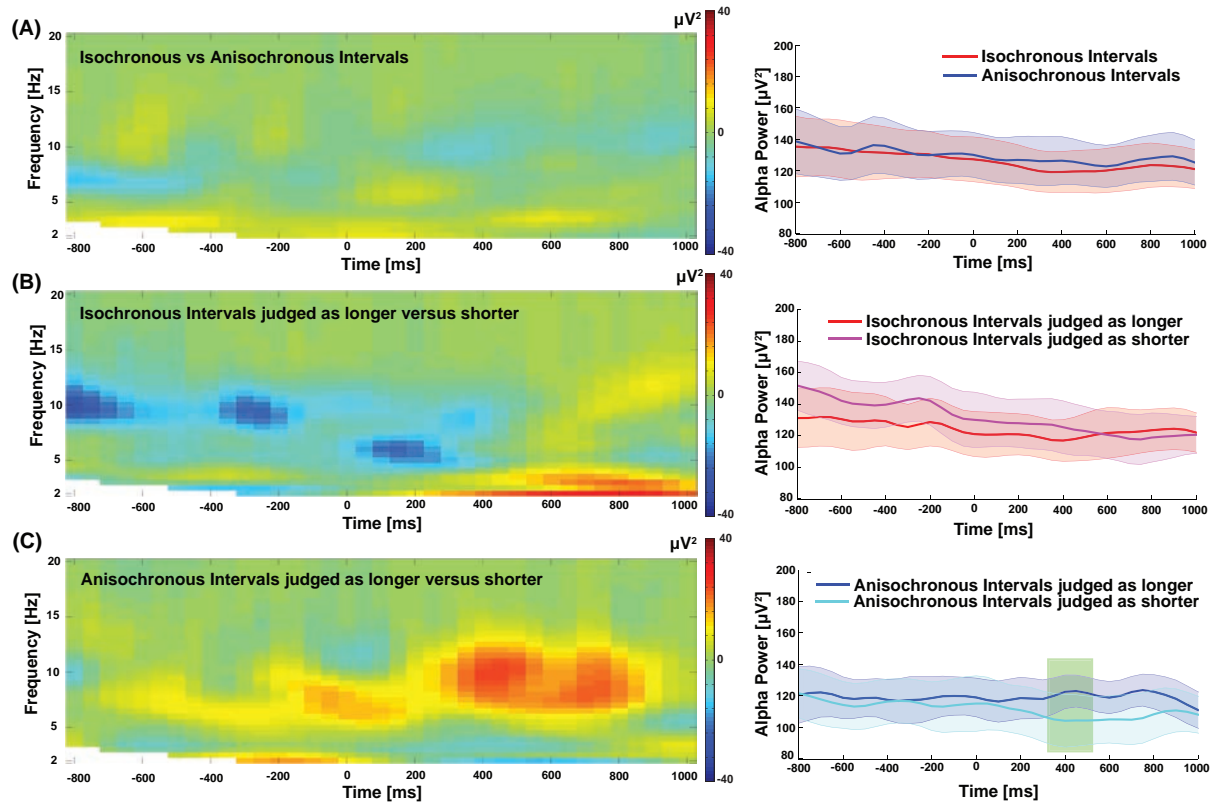
Figure 2S. Frequency power for the mean over entrainment channels (3.5 to 4.5 Hz and 7.5 to 8.5 Hz) in (A) isochronous versus anisochronous intervals, (B) isochronous intervals judged as longer versus shorter, and (C) anisochronous intervals judged as longer versus shorter. The time-frequency representation was obtained using a complex Morlet wavelet convolution with 5 wavelet cycles. No baseline correction was applied. The plots on the left (in A–C) show the difference between the two intervals compared. No masks are applied. A permutation-based test shows no significant clusters for any of the contrasts. The plots on the right (in A–C) show mean alpha power (8–12 Hz) for the respective conditions. Green segments mark a significant differences between the two conditions ($p < 0.05$ at each 50 ms time bin).

The present study is, to our knowledge, the first to demonstrate a direct link between the strength of neural entrainment toward regular stimulation and the perceived duration of entrained intervals. It should be noted that the critical comparison in this work is based on completely identical stimulus sequences, so that the increase in PPC for isochronous sequences judged as longer relative to those judged as shorter is genuinely related to perceived rather than physical duration. In line with the suggested role of neural entrainment

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in improved processing of temporally predictable stimuli, as well as previous experimental findings supporting a relationship between neural response magnitudes and perceived duration, we interpret the present results within a neural response magnitude framework: Neural entrainment in regular sequences leads to an increased neural response toward each individual stimulus in the sequence, and therefore to higher average neural responses in isochronous intervals, which in turn increases duration estimates.

An alternative explanation for the connection between PPC and duration judgments may be along the lines of attentional mechanisms. As noted above, entrainment itself can be considered a mechanism of attentional selection (e.g., Lakatos et al., 2008), attentional markers like the P3b are influenced by regular stimulation (Schmidt-Kassow et al., 2009), and attention, in turn, is related to perceived duration (e.g., Grondin, 2010). In this respect, the idea that attention (as interconnected with entrainment and respective changes in neural response magnitudes) is related to the overestimation of isochrony is well in line with our interpretation of the data in a neural response magnitude framework of perceived duration. To minimize the possible concern that the PPC difference between intervals perceived as longer and intervals perceived as shorter is due to random fluctuations in attention (e.g., Kashiwase et al., 2012; Kim et al., 2007), we checked for differences in pre- and poststimulus alpha power over entrainment channels. Phases of low alpha power have been related to states of high responsiveness toward external stimulation while high alpha power is associated with low excitability phases (e.g., Hanslmayr et al., 2011; Klimesch et al., 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). As shown in Figure S2, for anisochronous intervals, an increase in alpha power over entrainment channels during intervals perceived as longer was found between 350 and 500 ms. This finding is surprising, as one would assume decreased alpha power being related to a state of higher attention toward external stimulation (e.g., Hanslmayr et al., 2011) and thereby longer perceived duration. Independent of how the

difference in anisochronous intervals can be interpreted, the PPC effect for isochronous intervals perceived as longer versus those perceived as shorter is not paralleled by a significant difference in alpha power. There is a non-significant tendency of decreased prestimulus alpha power for isochronous intervals perceived as longer; however, this tendency is not correlated with either the subject-wise PPC effect for isochronous intervals nor the subject-wise PSE. The present analysis of alpha power therefore makes an interpretation of the PPC effect solely based on random attentional fluctuations unlikely. Although beyond the scope of the present article, the observed poststimulus alpha effect in anisochronous sequences and the non-significant prestimulus tendency for isochronous sequences may speak toward a role of attentional states in the current task and could be an interesting subject for future exploration.

Going back to the initial interpretation of the PPC increase being related to an increase in neural response magnitude and therefore increased perceived duration, it must be kept in mind that the present work does not provide a direct measure of neuronal firing. It can therefore only hint at neural response magnitude being the modulating factor that leads to an influence of entrainment on temporal estimates. Future research should aim at clarifying the proposed relationship between neural response magnitudes, entrainment, and perceived duration, for example, by investigating the interaction between entrained (and non-entrained) stimulus presentation and other ways of modifying neural response magnitudes (e.g., stimulus intensity) regarding their effect on perceived duration. Future experiments should also attempt to establish a trial-to-trial relationship between entrainment and perceived duration, for which the present study did not have sufficient power, and take a closer look at how inter-individual differences in entrainment strength predict different perceived duration distortions. Furthermore, clarification is needed regarding entrained channels and frequency bands that are crucially influencing duration estimates. In the present data, when comparing isochronous

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versus anisochronous sequences, we found the expected increase of PPC around the stimulation frequency, 4 Hz, but even more channels showed an increase around the harmonic frequency, 8 Hz (see Figure 2B). An increase in the PPC, but no changes in power, around 8 Hz for isochronous as compared to anisochronous intervals, hints at the 8 Hz PPC effect also reflecting stimulus-driven entrainment rather than, for example, resonance with participants' intrinsic alpha rhythm. However, the difference in PPC between isochronous intervals judged as longer and those judged as shorter was present only at 3.5 to 4.5 Hz, but not 7.5 to 8.5 Hz, suggesting that entrainment at the fundamental frequency but not the second harmonic drives the behavioral overestimation of isochrony. Similarly, the correlation of the PPC difference due to perceived duration with the amount of behavioral overestimation of isochronous sequences was only present at 3.5 to 4.5 Hz over 3.5 to 4.5 Hz entrainment channels. The absence of a similar relationship between 7.5 and 8.5 Hz phase consistency and perceived duration may hint at a different functional role of the PPC increase in the harmonic frequency of isochronous stimulation (see, e.g., Campbell and Maffei, 1970; Di Russo et al., 2001; Kim et al., 2007 for a functional differentiation between fundamental and harmonic frequency in visual stimulation) and may put into question whether the latter is genuinely related to entrainment, or a different physiological mechanism. Future studies varying the stimulation frequency and testing whether entrained channels as well as the link with perceived duration differ between different frequency bands, and potentially interact with an individual's dominant theta and alpha frequencies, may be able to shed further light on this issue.

In sum, the present experiment is the first to show a direct link between neural entrainment and duration judgments. It thereby demonstrates that the overestimation of isochronous as compared to anisochronous auditory stimulation (Grimm, 1934; Horr & Di Luca, 2015a; Thomas & Brown, 1974) may be explained based on neural response magnitudes. We believe that the present approach is a good starting point for future research

investigating how, and to which extent, the link between entrainment strength, neural response magnitude, and duration perception may explain different experimental findings regarding the influence of interval structure and temporal predictability on perceived duration.

Chapter 6

General Discussion and Outlook

6.1 Summary of research agenda and main findings

6.1.1 Background and rationale

The present thesis is a contribution to research aimed at understanding computational and neural dynamics of time and duration perception. It takes the approach of disentangling and quantifying factors that modulate duration estimates. Those are then used to draw conclusions regarding underlying mechanisms. Experimental findings on distortions of perceived duration give valuable insights into temporal processing in different contexts and form the empirical basis for formulating realistic models. The most prominent accumulator counter model, scalar timing theory (e.g., Allan, 1998), for example, was set out to explain scalar timing, that is, the increase of variance in duration estimates with an increase in the mean. Beat-based models (e.g., McAuley & Jones, 2003), to give another example, were constructed and adapted to explain the observed context-dependency of perceived duration. Considering the multitude of models that attempt to explain time and duration perception on a conceptual, computational and neurobiological level, it is crucial to formulate clear criteria for evaluation. One main criterion of a good model must be its ability to explain and integrate old and new experimental findings on the relationship between physical and perceived time and the interaction of duration estimates with factors other than physical duration (e.g., Addyman, French & Thomas, 2016; Müller & Nobre, 2014). Research on perceived duration distortions therefore sets the cornerstones of what any model needs to incorporate and explain.

Multiple studies have investigated the influence of different stimulus characteristics that distort the estimated duration of a stimulus (e.g., Allan, 1979; Eagleman, 2008). Other lines of research are concerned with the estimation of intervals filled with multiple stimuli (e.g.,

Adams, 1977; Buffardi, 1971; Thomas & Brown, 1974; Wearden et al., 2007). The latter have mainly focused on the amount or density of the filling. A couple of findings, however, hint at the temporal structure of interval fillers as a crucial source of perceived duration distortions. Adams (1977) found that stimuli clustered at the beginning of an interval lead to stronger overestimation of this interval than stimuli clustered at the end. Thomas and Brown (1974), in line with Grimm (1934), found a non-significant tendency of a regular (isochronous) filler spacing leading to an overestimation of perceived interval duration. Matthews (2013) showed that isochronous sequences are perceived as longer than accelerating or decelerating ones. Furthermore, multiple findings demonstrate that the temporal structure an interval is embedded in influences perceived duration (e.g., Geiser & Gabrieli, 2013; Halpern & Darwin, 1982). Similarly, duration estimates are modulated by repetition, expectation and predictability of stimulus characteristics (e.g., Birngruber et al., 2014; Matthews, 2011; Pariyadath & Eagleman, 2007; Tse et al., 2004). The present thesis was set out to systematically investigate how the temporal structure of a stimulus sequence influences perceived duration of the full sequence and to disentangle the role of temporal predictability in time and duration perception.

Research on temporal structure and its role in duration perception is of high theoretical interest. First of all, it can give insights into how duration estimates are sampled in relation to physical time (see e.g., Matthews, 2013; Thomas & Brown, 1974 for discussion of this on the basis of their findings). Furthermore, it sheds light on how mechanisms of duration perception fit into the general framework of active perceptual processing (e.g., Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010), that is, perceptual processing being modulated by information other than immediate stimulus input. For example, it has been shown that events arriving at an expected point in time in a predictable temporal structure are reacted to quicker and processed with higher sensitivity (e.g., Correa & Nobre, 2008; Rohenkohl et al., 2012)

than unpredicted events. Such selective perception is highly adaptive as it maximizes processing efficiency toward frequently occurring regular patterns in the environment (e.g., Schroeder & Lakatos, 2009). Given this special role of regularity in perception and its intrinsic connection to temporal estimation, investigating how regular and predictable as compared to random temporal structures modulate perceived duration, provides insights into mechanisms of duration perception in relation to general principles of perceptual processing.

6.1.2 Chapter 2: Overestimation of isochrony

The experiments described in Chapter 2 investigated the influence of isochrony, that is, complete temporal regularity, as compared to a randomly jittered spacing of interval filler stimuli. In a two-interval forced-choice paradigm participants had to decide which of two intervals marked by tone sequences is longer in duration. The filler tones in one interval were regular, while regularity was varied in the other interval.

For the first experiment in Chapter 2 each trial consisted of two intervals with five 1000 Hz 10 ms filler tones each. One interval was always completely isochronous. In the other interval, the anisochronous one, the range of random jitter was varied. This served to systematically investigate how distortions of temporal stimulus regularity would influence duration estimates. Isochronous intervals were found to be significantly overestimated as compared to anisochronous intervals from a jitter range of 30% of the isochronous interstimulus interval onward. The overestimation of isochrony differed significantly between different levels of anisochrony. It was specifically strong for a 50% jitter, that is, the highest possible jitter range before adjacent fillers would start overlapping.

In the second experiment the overestimation of isochrony as compared to anisochrony was replicated with different numbers of filler tones in the intervals, that is, different stimulation frequencies. In every trial one isochronous interval consisting of a varying number of fillers was compared to a 50% jittered anisochronous interval with the same

number of fillers. Results showed an overestimation of isochrony for each of the tested stimulation frequencies. Furthermore, the size of the isochrony effect depended on filler number. Higher filler numbers tended to lead to a stronger overestimation.

The third experiment was designed to ensure that the observed isochrony effect is actually based on temporal structure of interval fillings rather than regularity in general. Here, two fully isochronous intervals with five filler tones were compared in every trial. One interval always consisted of 5 identical fillers, in the other interval the fillers varied in non-temporal filler characteristics, that is, sound amplitude or sound frequency. No distortions of perceived duration between isochronous intervals differing in the regularity of their non-temporal filler characteristics were found. From this, it was concluded that the observed overestimation of isochrony is truly temporal in nature.

In sum, the experiments in Chapter 2 show that (1) perceived duration is overestimated for isochronous as compared to anisochronous intervals, (2) this isochrony effect increases with an increase in anisochrony and the number of stimuli per interval and (3) the overestimation of isochrony is genuinely based on temporal regularity of interval structure rather than filler regularity in general. The observed bias due to isochrony as well as its increase with stimulus number can be modelled in the framework of a resettable clock that accumulates time in a logarithmic manner (see also Thomas & Brown, 1974). Alternatively, the effect of isochrony may be explained on the basis of a neural magnitude approach of perceived duration (e.g., Eagleman & Pariyadath, 2009). As demonstrated by previous research (e.g., Schroeder & Lakatos, 2009) neural oscillations entrain to regular stimulation and this entrainment places each stimulus in a temporally regular sequence at the point of highest neural responsiveness. This leads to neural response magnitudes toward isochronous intervals to be higher than toward anisochronous intervals. Such increase in neural response magnitudes may explain the overestimation of perceived duration due to isochrony.

6.1.3 Chapter 3: Duration perception with different interval types

The experiments reported in Chapter 2 indicate that the filled duration illusion (e.g., Thomas & Brown, 1974; Wearden et al., 2007) is only a starting point in investigating the distortions of perceived duration due to interval filling, as not only the amount of filling but also temporal structure plays an important role. In Chapter 3, two experiments are reported that investigated this role further by quantifying duration discrimination performance and duration distortions with four different types of intervals: continuous, isochronous, anisochronous and empty. Continuous intervals were marked by one prolonged tone. Isochronous and anisochronous intervals consisted of respectively spaced sequences of short tones. Empty intervals were simply made up of a beginning and an end marker.

The first experiment in Chapter 3 measured duration discrimination performance with the described interval types. In every trial participants were presented with two intervals of the same type and again had to tell in a two-interval forced choice manner which of the two was longer in duration. Significant differences in discrimination performance between different interval types were found. Continuously and isochronously filled intervals were discriminated best, followed by empty intervals. Anisochronous intervals were discriminated worst.

In a second experiment perceived duration distortions between any two of the four interval types were investigated. The filled duration illusion, that is, the overestimation of filled as compared to empty intervals, was present for all filled interval types, however it was stronger for intervals filled with multiple filler stimuli, both isochronously and anisochronously spaced, than for intervals filled with a continuous stimulus. Interestingly, no difference in distortions between isochronous versus empty and anisochronous versus empty intervals could be found, even if the direct overestimation of isochronous as compared to anisochronous intervals was replicated. Furthermore, no distortions were found between isochronous and continuous as well as anisochronous and continuous intervals, even if these

interval types differed in the strength of the filled duration illusion they elicited.

Taken together, the experiments of Chapter 3 demonstrated, (1) that different types of interval filling lead to differences in both discrimination performance and perceived duration and (2) that perceived duration distortions in two-interval forced choice paradigms are not solely dependent on the individual intervals, but are also influenced by the comparison process in question. On the basis of latter observation, it was proposed that different cues for duration estimation are available in different interval types and the strategy used to compare two intervals may be determined according to the cues shared by both of them.

6.1.4 Chapter 4: Overestimation of predictable rhythms

The overestimation of isochronous as compared to anisochronous intervals reported both in Chapter 2 and Chapter 3 motivates a further exploration of the role of temporal regularity and predictability in duration perception. To this aim, the experiments reported in Chapter 4 used simple rhythmic stimuli based on group-of-n rhythms. A group-of-n rhythm is here defined as a subsequence of n stimuli followed by one stimulus omission. Importantly, as soon as the first subsequence including omission has been perceived the arrival of every following stimulus is fully predictable.

In a first experiment, the rhythmic intervals were compared to completely anisochronous and therefore unpredictable sequences matching in stimulus number. Taken together, rhythmic intervals were perceived as longer than anisochronous intervals. No significant difference in duration distortions was found between different types of rhythms, that is, rhythms with different numbers of stimuli per group.

A second experiment compared the rhythmic intervals to isochronous intervals, again matching their total number of stimuli. Taken together, no significant distortion of perceived duration between rhythms and isochrony were found. However, there was a tendency toward overestimating isochronous as compared to rhythmic intervals. Interestingly, this tendency

differed significantly according to the number of stimuli per group with two-group rhythms being perceived closest in duration to isochrony.

In sum, the experiments reported in Chapter 4 suggest (1) a general overestimation of temporally predictable as compared to non-predictable intervals and (2) an influence of temporal structure on perceived duration even when controlling for predictability. The logarithmic accumulator model as introduced in Chapter 2 captures the observed distortions due to rhythmic structure, at least to some extent. Further exploration is necessary to determine whether differences between rhythm types fully follow its pattern. Furthermore, the overestimation of temporally predictable and therefore entrainable stimulus sequences is in line with the proposed relationship between perceived duration, neural entrainment and response magnitudes. However, a neural response magnitude approach would require additional assumptions to explain perceived duration distortions due to different rhythm types, that is, different kinds of predictable sequences.

6.1.5 Chapter 5: Entrainment as the neural basis of the isochrony effect

The proposed explanation of the isochrony effect on the basis of neural entrainment in a neural response magnitude framework provides a clear experimental hypothesis: If the overestimation of isochronous and other predictable intervals is related to increased neural responses to entrained stimulus sequences, then entrainment strength should predict the perceived duration of physically identical intervals. This hypothesis was tested in the EEG experiment reported in Chapter 5.

The same two-interval forced choice paradigm as described in Chapter 2–4 was used for the EEG experiment. Every trial required a duration comparison between one fully isochronous and one fully anisochronous interval both consisting of five short filler tones. The overestimation of isochrony as compared to anisochrony could be replicated. Other than in the experiments of Chapter 2–4, here, half of the trials contained two intervals with exactly the

same physical duration. Only these trials were used for the EEG analysis. Pairwise phase consistency (Vinck et al., 2010), which indicates the consistency of the phase of neural oscillations between trials, was used as a measure of entrainment strength. Entrainment of isochronous as compared to anisochronous intervals was shown in the stimulation frequency and its second harmonic. Most interestingly, stronger entrainment in the stimulation frequency was found for isochronous intervals perceived as longer as compared to physically identical isochronous intervals perceived as shorter than their anisochronous counterparts. The increase in entrainment for intervals perceived as longer was correlated with participants' subjective tendency to overestimate isochrony.

In conclusion, the experiment in Chapter 5 hints at a direct connection between perceived duration and entrainment strength. This may be in line with a neural response magnitude approach of perceived duration. Additional research will be necessary to clarify whether the mediating variable between perceived duration and entrainment is actually a measure of neural response magnitudes and specify this relationship regarding different oscillatory frequencies and neural regions. Despite several open questions, the findings from Chapter 5 provide a simple neural model, which may serve as a starting point to further investigate the neural basis of perceived duration distortions due to their temporal structure. Future research in this direction should, for example, investigate when and to what extend the relationship between perceived duration and entrainment strength holds for interval types of different structure. This may shed light on the necessity to differentiate between different mechanisms of duration perception based on varying temporal and non-temporal cues given in the estimated intervals.

6.2 Impact in a broader research context

An overview over the most influential contemporary models of time and duration perception was given in the introduction of the present thesis. Different approaches are superior in

explaining different kinds of experimental findings on duration perception and its distortions, while, at the current point, no unified model is able to account for all of them. The experiments presented in Chapter 2–5 open up a new research avenue by taking a closer look into a previously neglected source of distortions: The influence of temporal structure on perceived duration. The following paragraph will discuss how the reported findings fit into the multitude of approaches to explain time and duration perception and thereby outline implications for mechanisms underlying temporal judgments as well as their connection to general neural dynamics of perceptual processing.

6.2.1 Relationship between physical and perceived duration

One fundamental question in duration perception research concerns the mathematical relationship between physical and perceived time (e.g., Müller & Nobre, 2014; Wearden & Jones, 2007). This question has been extensively discussed in an internal clock framework (e.g., Simen, Rivest, Ludvig, Balci, & Killeen, 2013; Van Rijn & Taatgen, 2008). The original accumulator counter model by Treismann (1963) and the basic scalar expectancy (SET) model (e.g., Gibbon, 1977) propose linear accumulators, that is, an average accumulation rate constant over the estimated interval. A linear accumulator can account for changes of perceived duration due to changes in stimulus characteristics, distractor context and subjective arousal (e.g., Burle & Casini, 2001; Klink et al., 2011; Penton-Voak et al., 1996), if we assume such changes to modify pulse rate between intervals of different conditions. Scalar expectancy, the increase of estimation variance with estimated mean, may result from a noisy linear accumulation process, which, in the SET is proposed to follow a Poisson distribution, combined with variance in the memory and decision process (e.g., Gibbon, 1992).

Other models, however, propose a clock which provides a non-linear mapping of perceived in relation to physical time (e.g., Brown, Neath & Chater, 2007; Staddon & Higa, 1999; Wackermann & Ehm, 2006). Non-linear models give the most intuitive explanations for

some experimental findings. For example, the mapping between verbal estimation or production and physical interval duration can in many experiments best be described by a power function with an exponent less than one, that is, a negatively accelerating function (see Eisler, 1976 for an overview over earlier studies). Similarly, temporal bisection tasks, in which each interval has to be assigned to either a long or a short standard, typically show that the bisection point, the point at which participants are guessing, is closer to the geometric rather than the arithmetic mean between the two standards (e.g., Allan & Gibbon, 1991). Note, however, that none of these findings seem to provide conclusive evidence for a non-linear relationship between physical and perceived time and they may still be explainable via a linear clock process (e.g., Simen et al., 2013; Wearden & Jones, 2007).

Interestingly, a linear accumulation of perceived over physical time, without any additional assumptions, would predict no distortions according to the temporal structure of interval duration. Assuming an accumulator that resets at the beginning of every subinterval and a summation of the count of all subintervals to judge the full interval duration (e.g., Matthews, 2013; Thomas & Brown, 1974), a linear accumulation with all subintervals weighted equally would lead to equal estimates, no matter how the subintervals are divided. Even if subintervals at different positions are weighted differently this could not explain a general overestimation of isochrony, independent of the temporal distribution in the anisochronous interval. The results presented in Chapter 2–4 therefore speak for a non-linear accumulation of perceived over physical duration.

Distortions of perceived duration due to controlled variation in temporal structure are well-suited to model the non-linear relationship between perceived and physical duration. Many findings of the present thesis, the overestimation of isochrony, the overestimation of predictable rhythms and the increase of the isochrony effect with the number of interval fillers, can be accounted for by a logarithmic accumulator, that is, a decrease in accumulation

rate over physical interval duration. With additional assumptions, there may be ways to explain the observed influence of temporal structure on perceived duration without ruling out a linear relationship. However, a logarithmic mapping of physical and perceived time seems to provide the simplest explanation of the present data in an internal clock framework. It remains to be investigated whether perceived duration of more complex rhythms can still be explained by a simple logarithmic model. Due to its flexibility and straightforward mathematical representation, the variation of temporal structure provides a good experimental starting point for further exploration of the relationship between physical and perceived time.

6.2.2 Neural response magnitude approach of duration perception

Most models of time and duration perception have been formulated to explain specific experimental findings. In order to approach or at least to investigate the possibility of a unified theory of temporal processing, aspects of these models that can account for a multitude of phenomena in time and duration perception need to be identified. The relationship between perceptual as well as neural magnitude and perceived duration is in line with remarkably many and diverse distortions of duration perception (e.g., Eagleman & Pariyadath, 2009; Matthews et al., 2014). Investigating the influence of non-temporal stimulus characteristics, stimuli of higher magnitude, for example, light intensity, size, and number of stimuli in space or time (e.g., Berglund et al., 1969; Buffardi, 1971; Xuan et al., 2007) have been found to increase perceived duration. These findings on stimulus magnitude are accompanied by studies showing an increase in perceived duration with stimuli that can be assumed to elicit higher neural responses, like overestimation due to complexity (e.g., Schiffmann & Bobko, 1974), movement (e.g., Brown, 1995), lack of familiarity (e.g., Avant, Lyman, & Antes, 1975), novelty as compared to repetition (e.g., Birngruber et al. , 2014) and unpredictability of stimulus characteristics (Pariyadath & Eagleman, 2007, see however Matthews, 2014; Matthews & Gheorghiu, 2016). Studies on a neural level indicate a

correlation between perceived duration and single cell firing rates in monkeys (Mayo & Sommer, 2013) as well as human ERP amplitudes (Kononowicz & Van Rijn, 2014). This converging evidence makes neural response magnitudes an interesting candidate for at least one of possibly many neural signatures involved in tracking the passage of time.

On the first glance, the overestimation of perceived duration due to isochrony and predictable rhythms, as reported in Chapter 2–4, seems to speak against a neural magnitude approach. Why would a repeatedly presented and fully predictable stimulus sequence lead to higher neural responses than a continuously changing and unpredictable sequence? To answer this question, first of all, we must differentiate temporal predictability from predictability of stimulus characteristics. Regarding predictability of stimulus characteristics, an unpredictable stimulus leads to higher neural responses (e.g., Doherty, Mesulam, & Nobre, 2005; Grill-Spector, Henson & Martin, 2006; Grotheer & Kovács, 2015) and longer perceived duration (e.g., Pariyadath & Eagleman, 2007) than a predicted stimulus. Temporal predictability, however, changes neural processing in a more complex fashion (e.g., Correa & Nobre, 2008) and leads to lower reaction times and higher stimulus sensitivity for stimuli arriving at predicted time points (e.g., Rohenkohl et al., 2012). Furthermore, the attenuating effect of stimulus predictability as well on neural responses (Schwartze, Rothermich, Schmidt-Kassow, & Kotz, 2011; see also Schwartze, Farrugia & Kotz, 2013) as on perceived duration (McAuley & Frombolutti, 2014; Meyerhoff, Huff & Vanes, 2015) is reduced when the stimulus does not arrive at a predicted point in time. Differences in neural dynamics underlying the processing of predictable stimulus onset time and predictable stimulus characteristics are therefore well in line with the seemingly contradictory duration underestimation of stimuli with predicted stimulus characteristics and overestimation of temporally predictable sequences.

The proposal of a connection between neural response magnitudes and perceived

duration may provide an explanation for the overestimation of rhythm-based temporal predictability, if we consider the special dynamics regular stimulation elicits in perceptual and neural processing: Neural oscillations entrain their phase to regular stimulus sequences (e.g., Ding et al., 2006; Lakatos et al., 2007; Lakatos et al., 2008). Due to this entrainment each stimulus presented at an expected point in time will arrive at the phase of highest neural responsiveness (e.g., Schroeder & Lakatos, 2009). Temporally regular stimulation therefore maximizes neural response magnitudes as compared to anisochronous, that is, random sequences, for which each stimulus arrives at an arbitrary phase. Following a neural response magnitude approach of perceived duration this would lead to the observed overestimation of isochronous and predictable rhythmic sequences.

In line with the proposed relationship between neural response magnitudes, entrainment and perceived duration the findings in Chapter 5 demonstrated a direct link between entrainment and duration estimates. Isochronous stimuli perceived as longer showed a stronger average entrainment strength than physically identical stimuli perceived as shorter. This effect was correlated with the subject-wise overestimation of isochrony. The reported EEG study therefore provides additional evidence for a neural response magnitude approach of perceived duration and opens up a new avenue to study this approach on the basis of neural responses to identical stimuli rather than responses to differential stimulus characteristics.

6.2.3 Mechanisms of perceptual processing

The traditional view on perceptual processing considers the brain as a passive receptor of stimulus input and conceptualizes perception as a one-directional bottom-up transfer of information from lower to higher level sensory areas. However, contemporary research acknowledges the importance of active perceptual mechanisms, that is, the top-down influence of prior experience, expectation and attention on the way a stimulus is processed (e.g., Desimone & Duncan, 1995; Moran & Desimone, 1985; Shomstein & Yantis, 2004).

Temporal regularity, that is, rhythmically occurring stimulation, is a fundamental aspect in our natural environment (e.g., Herbst & Landau, 2016; Schroeder et al., 2010). In a framework of active perception it therefore seems highly adaptive for the brain to make use of environmental regularity in order to predict and efficiently react to temporally predictable stimulus input. The crucial influence of temporal regularity on perceptual processing is demonstrated by research showing that task-relevant stimuli which arrive at an expected point in a rhythmic sequence decrease reaction times and enhance task performance compared to stimuli that arrive unexpectedly (e.g., Ellis & Jones, 2010; Jones, Moynihan, Mackenzie, & Puente, 2002; Rohenkohl et al., 2012). Neural entrainment, that is, the adaptation of oscillatory phase to regular stimulation, provides a plausible mechanistic explanation for increased processing efficiency toward regular stimulation. The phase of neural oscillations has been shown to modulate perceptual processing with an advantage for stimuli presented in an optimal phase rather than a suboptimal phase (e.g., Busch, Dubois, & Van Rullen, 2009; Ng et al., 2012; Romei et al., 2008; Van Dijk, Schoeffelen, Oostenveld, & Jensen, 2008). Neural entrainment ensures that stimuli in a regular sequence appear at an optimal phase. The additional finding that entrainment is biased toward task-relevant stimulus sequences (e.g., Besle et al., 2011; Lakatos et al., 2008; Lakatos et al., 2013; O'Connel, Barczak, Schroeder, & Lakatos, 2014) leads to the proposal of entrainment to be a fundamental mechanism of attentional selection (see e.g., Calderone, Lakatos, Butler, & Castellanos, 2014 for a review), which allows us to focus on essential input with, at least partially, predictable timing, while ignoring irrelevant background information.

Considering the ubiquity of temporal information in environmental stimuli and the involvement of temporal processing in almost any perceptual and cognitive task, it is not surprising that perceived duration is influenced by mechanisms that are fundamental to overall perceptual processing. This is in line with the basic idea of intrinsic models (e.g., Ivry

& Schlerf, 2008; Karmakar & Buonomano, 2007), according to which temporal perception is considered to be naturally evolving from neural dynamics. If an aspect of the environment modulates general stimulus processing, it should then also influence duration perception. Considering recent research that demonstrates the importance of temporal regularity in perception and its neural underpinnings (see e.g., Herbst & Landau, 2016), the parallel investigation of temporal structure in the realm of time and duration estimates is promising. Not only can such research give insights into how neural phenomena that were found to be modulated by temporal regularity, influence duration estimates, it may also reveal fundamental connections between temporal and non-temporal stimulus processing. Investigating the relationship between temporal processing and basic perceptual mechanisms is crucial to disentangle how the perception of time is embedded in overall neural dynamics and which, if any, additional processes may be necessary in order for the brain to be able to keep track and make use of temporal information. The findings reported in the present thesis propose that the modulation of perceptual processing due to neural entrainment may as well influence perceived duration and suggests neural response magnitudes as a possible link. This provides an example of how our knowledge on basic perceptual mechanisms may provide insights into neural correlates of time perception and how investigating temporal structure can provide a good starting point to take a closer look at the connection between temporal and more general stimulus processing.

6.3 Conclusions, limitations and future directions

The present thesis investigated the role of temporal structure in duration perception. A consistent overestimation of temporally regular, predictable, as compared to irregular, unpredictable, intervals was demonstrated. On a computational level these findings speak for a logarithmic relationship between physical and perceived time, assuming that the accumulation of subjective time is reset by each filler stimulus and the final estimate is

reached by adding up the count for the resulting subintervals. On a neural level, temporally regular stimulation allows for entrainment, that is, phase adjustment of neural oscillations, and thereby increases processing efficiency toward temporally expected stimuli. A relationship between perceived duration and entrainment strength, as indicated by the overestimation of regularity reported in Chapter 2–4 and confirmed by the EEG study reported in Chapter 5, is therefore in line with a neural response magnitude approach of perceived duration. The previous paragraph discussed the implications of the present findings for research on time and duration perception. This paragraph will outline limitations, open questions and future research directions.

One limitation of both the proposed logarithmic accumulator and the response magnitude approach became transparent in the experiments reported in Chapter 3. Both approaches explain the overestimation of temporal regularity based on three implicit assumptions: (1) The brain individually estimates the duration of each interval to be judged, (2) the same mechanism is used for the estimation of both intervals and (3) the interval with the higher resulting estimate is finally deemed the longer one. While these assumptions seemed unproblematic when simply comparing temporally regular and irregular intervals, Chapter 3 demonstrated that the dynamics of over- and underestimation become more complex as soon as further interval types are added. In line with previous studies, mostly focusing on order effects (e.g., Dyjas & Ulrich, 2014; Hellström, 2003), the second experiment in Chapter 3 showed the crucial role of the comparison process in participants' duration judgments. Rather than effects of order and relationship between intervals, here, inconsistencies in the comparisons between different interval types are noted and prevent the establishment of a clear hierarchy of perceived duration among the investigated interval types. For example, while the overestimation of filled as compared to empty intervals was stronger for stimulus sequences, isochronous or anisochronous, than for continuous intervals, no difference was

found between isochronous and continuous intervals. Anisochronous intervals were underestimated as compared to isochronous intervals, but not to continuous intervals, even if the latter where perceived equal when compared to isochronous intervals. It was suggested, that different interval types may provide different cues that can be used to judge duration and may therefore gauge different mechanisms. Further research is needed to disentangle the role of the comparison process and whether and how different principles hold when comparing different interval types. For example, systematically varying filler stimulus spacing, that is, temporal structure, as well as the duration of filler stimuli could explore the limits at which the isochrony or regularity effect breaks down and gives way to alternative mechanisms that may be more suitable to explain duration distortions with intervals consisting of a continuous stimulus.

The long standing discussion whether the relationship between perceived and physical time may be linear, has been reviewed in the previous paragraph and the experiments in Chapter 2–4 provide an example of how temporal structure can be used to test this relationship. Certainly, models based on a linear accumulator could be adjusted to explain influences of perceived duration due to temporal structure in general and the observed overestimation of temporal regularity in particular. However, a logarithmic accumulator seems to provide the most parsimonious explanation for the overestimation of regularity. As shown in Chapter 2 and 4, in a logarithmic model only two very basic assumptions are required to naturally prolong the perceived duration of regularity: (1) The accumulation of perceived duration is reset with every filler stimulus (e.g., Taatgen & Van Rijn, 2011) and (2) in a sum-of-segments manner (e.g., Mathews et al., 2013; Thomas & Brown, 1974) the resulting subintervals are added up to arrive at an estimate for the full interval duration. Further research will be necessary to clarify to what extend this simple model holds for perceived duration in more complex rhythmic structures. Determining whether and which

additional assumptions are needed to model perceived duration patterns based on a wider range of rhythmic conditions can then conclude to what extend an explanation along the lines of a logarithmic relationship between physical and perceived duration remains the most parsimonious to explain distortions due to temporal structure.

A multitude of observed distortions in duration perception, as reviewed in Chapter 5 and Chapter 6.2, strengthen the notion of a relationship between perceived duration and neural response magnitudes (see Eagleman & Pariyadath, 2009 and Matthews et al., 2014 for an overview). However, there are also experimental findings which speak against this approach or at least reveal duration distortions that cannot be explained in the framework of response magnitudes. For example, Herbst and colleagues (Herbst, Chaumon, Penney, & Busch 2014; Herbst, Javadi, Van der Meer, & Busch, 2013) showed that the overestimation of a flickering stimulus decreases rather than increases with flicker rate and is not related to alpha power nor CNV amplitude during stimulation. From this, the authors conclude that the flicker illusion is rather driven by subjective saliency of temporal changes than neural responses to the stimulation. In order to clarify to what extend this proposal is actually at odds with a neural magnitude approach, it would be necessary to take a closer look into the representation of subjective saliency at a neural level. Certainly, such contradictory findings show that, in order to arrive at a neurobiologically plausible and unambiguously testable model, the term "neural response magnitude" needs further clarification. Multiple different aspects of the neural response can be investigated in relation to perceived duration (e.g., single cell recordings: spike rate of specific cell types, postsynaptic or presynaptic activation, excitatory or inhibitory activation, Eagleman & Pariyadath, 2009; cortical surface recordings: neural population activity, Coon et al., 2016; EEG recordings: evoked potentials and evoked oscillatory power in certain frequencies, Herbst et al., 2013, 2014; Wiener & Kanai, 2016). Besides the neural measure of interest, the brain regions and networks, in which magnitude increases can be

expected, also need to be determined (e.g., early sensory processing or higher cortical areas, Matthews et al., 2014; bottom-up or top-down processing, Matthews & Gheorghiu, 2016). The present formulation of a neural response magnitudes approach therefore only provides a starting point to explore neural dynamics that may be related to such a magnitude proposal and further research is needed to turn this approach into a plausible mechanistic model of the neural representation of duration.

Based on findings showing that entrainment leads to an increase in neural responsiveness toward stimuli in a regular sequence (e.g., Schroeder & Lakatos, 2009), a neural magnitude approach of perceived duration is proposed to be in line with the in Chapter 2–4 reported overestimation of temporal regularity. The relationship between perceived duration and entrainment strength, as presented in Chapter 5, adds additional evidence to this proposal. Several neural dynamics have been suggested to contribute to changes of neural responsiveness due to entrainment. For example, entrainable low frequency phases have been shown to be coupled with the power of higher frequencies (e.g., Lakatos et al., 2005) and the synchronization of oscillatory frequencies was proposed to be related to changes in single cell firing rates and shifting of activation states in local neuronal essembles (e.g., Fries et al., 2002; Lakatos et al., 2005; Wolmensdorf, Fries, Mitra & Desimone, 2006). The observed relationship between neural entrainment and perceived duration makes such neural dynamics linked to entrainment interesting candidates for a clearer specification of a neural response magnitude account. However, we need to keep in mind that no direct measure of neural response magnitudes was obtained in the experiment reported in Chapter 5. Future research will have to determine, whether it is indeed neural response magnitudes or another aspect of entrainment that causes its relationship to perceived duration. In other words, future research will have to clarify whether the findings of both neural response magnitudes and entrainment increasing perceived duration are inherently linked or, in fact, independent of each other.

Such questions could, for example, be approached by exploring under which conditions entrainment and duration estimates vary together when investigating different frequencies, rhythmic structures, stimulus modalities and brain areas or networks. Furthermore, different techniques and neural measures need to be applied in order to determine whether there is a direct connection between those indicators of neural response magnitude that are modulated in entrainment and those that increase perceived duration.

In the present thesis the logarithmic and neural response magnitude model were discussed independently as two alternative possible explanations for the overestimation of temporal regularity. One may ask, of course, to what extend those two models are compatible. That is, do these models propose fundamentally different and mutually exclusive mechanisms? Or do they only seem to be incompatible because they are based on two different levels of explanation? While the neural response magnitude approach refers directly to neural processes, even if the latter need further clarification, the proposed logarithmic clock model is purely computational and there is no straightforward biological substrate for the logarithmic accumulator process. In principle, neural response magnitudes would be thinkable as a metric of accumulation. A couple of oscillatory processes leading to a non-linear accumulation of time have been suggested in previous literature (e.g., Church & Broadbent, 1990; Treisman, Cook, Naish, & MacCrone, 1994). In terms of neural entrainment intrinsic logarithmic relationships between different frequencies have been proposed (e.g., Penttonen & Buzsaki, 2003). Those may, for example via phase-amplitude coupling between low and high frequencies, be crucial for modulations of neural response magnitudes due to entrainment. While the logarithmic accumulator and neural response magnitude model can, at the present point, only be considered as two models explaining the observed results on different levels – future research may be able to determine to what extend they are compatible or could even be integrated.

In conclusion, the experiments reported in the present thesis provide a starting point for a promising approach aiding to disentangle the computational and neural mechanisms of time and duration perception – the investigation of temporal structure. Temporal structure can be flexibly and easily manipulated. Perceived duration distortions according to such manipulations provide direct implications regarding the sampling of temporal intervals, which can give crucial insights into the relationship between physical and perceived time. Furthermore, temporal structure and regularity are fundamental aspects of our environment and shape perceptual processing. Manipulating temporal structure can therefore provide novel perspectives regarding the neural substrates of perceived duration. For example, neural dynamics like oscillatory frequencies that are naturally influenced by temporal regularity may be worth taking a closer look at in the framework of duration perception. In the long run, disentangling the relationship and shared mechanism that underlie temporal and non-temporal perceptual processing will be necessary for a more complete understanding of the computational and neural dynamics underlying the brain's ability to keep track of time. Investigating the role of temporal structure, regularity and predictability may be one of multiple promising research agendas in this endeavour.

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